Vertebrate Paleobiology and Paleoanthropology Series

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John G. Fleagle
Richard E. Leakey
Editors

The Paleobiology of *Australopithecus*

Springer

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Vertebrate Paleobiology and Paleoanthropology Series

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The Paleobiology of *Australopithecus*

Contributions from the Fourth Stony Brook
Human Evolution Symposium and Workshop,
Diversity in Australopithecus: Tracking the First Bipeds
September 25–28, 2007

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For Charles Abram Lockwood and Elizabeth Hunt Harmon, young researchers whose creativity, resourcefulness, energy, and ideas remain with us through their work.

Charlie at breakfast at the Ledi-Geraru field camp, and showing his strength (with pumice). Photos by Kaye Reed.

E (as we called her) driving a field vehicle while surveying near the Omo, and smiling—although she had stepped in mud in her only shoes. Photos by Michelle Drapeau.

Preface

Australopithecus holds a special place in the study of human evolution. From the initial description of the genus by Dart in 1925 through the present, there has been ongoing discussion and debate about whether this genus is best viewed as an ape with some human features or an old, somewhat primitive version of modern humans. How much like modern humans was *Australopithecus* in its locomotion, its social behavior, and its life history? As the hominid fossil record has expanded, indeed exploded, over the nearly nine decades since *Australopithecus* was first described, it has become the most speciose genus of human ancestors with no consensus regarding how many species should actually be recognized. Similarly, there is ongoing debate about the distinctions, boundaries, and phylogenetic relationships between *Australopithecus* and related genera, including *Homo*, *Paranthropus*, and *Kenyanthropus*. What kinds of biogeographical scenarios can best explain the evolution of *Australopithecus*?

In order to address these and other issues regarding the biology of *Australopithecus*, we organized the Fourth Stony Brook Human Evolution Workshop in 2007 with the title of "*Diversity in Australopithecus: Tracking the Earliest Bipeds*". A group of scholars and students from all over the world assembled in Stony Brook New York between September 25 and September 29, 2007 for five days of presentations, discussions, and collegiality in an informal setting. This volume is derived from that workshop.

The workshop was sponsored by Stony Brook University and the Turkana Basin Institute, and was generously hosted by the President of Stony Brook, Dr. Shirley Strum Kenny in her home at Sunwood. The workshop and associated symposium were only possible through the efforts and contributions of many people and institutions, including the Provost of Stony Brook University, the LSB Leakey Foundation, Jim and Marilyn Simons, Mrs. Kay Harrigan Woods, Mrs. Mary Armour, Elizabeth Wilson, and Lawrence Martin. In addition to the contributors to this volume, numerous other people attended all or part of the workshop and contributed to the discussions (Fig. 1), including Meave Leakey, Terry Harrison, Bill Kimbel, Gary Schwartz, Fredrick Manthi, Francis Kirera, Jack Stern, Bill Jungers, Randall Susman, James Rossie, Kathryn Twiss, Lawrence Martin, Aryeh Grossman, Chris Gilbert, Ian Wallace, Jessica Lodwick.

The chapters in this monograph were formally peer-reviewed and we thank those reviewers for their time and effort in making this volume better. We thank Eric Delson, senior co-editor of the *Vertebrate Paleobiology and Paleoanthropology* Series, for his patience, guidance, good humor, and more patience in helping to publish this volume. Christopher J. Campisano, David A. Feary, and William H. Kimbel were of great support to Kaye Reed during the editorial work on this volume. In addition, we thank Andrea Baden and Ian Wallace for providing editorial and bibliographic assistance.

Fig. 1 Workshop participants. *Back row*, *left to right*: William Kimbel, Ron Clarke, Frank Brown, Richard Leakey, Matt Sponheimer, David Strait, Adam Gordon, Charlie Lockwood, John Shea; *Middle row*, *left to right*: Susan Larson, Terry Harrison, Carol Ward, John Fleagle, Andy Herries, Zeray Alemseged, Fred Grine, Gary Schwartz. *Front row*, *left to right*: Meave Leakey, Elizabeth Harmon, Kay Behrensmeyer, Fredrick Manthi, Kaye Reed, Francis Kirera, Robert Foley

Kaye E. Reed
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Chapter 1
Introduction: Issues in the Life and Times of *Australopithecus*

Kaye E. Reed

Abstract *Australopithecus* species have been a topic of debate in paleoanthropology since the original description by Dart in 1925. The Stony Brook University/Turkana Basin Institute sponsored workshop on this subject occurred in September 2007. Participants designated various *Australopithecus* species as knowns, others as known unknowns (i.e., those for which there was limited fossil material), and "biological realities?" such as *Australopithecus bahrelghazali*. The chapters in this volume address many questions that arose from these discussions—especially those regarding the paleobiology of the genus: phylogenetic validity, dating problems, biogeography, diet and especially fallback foods, sexual dimorphism, use of stone tools, and reconciling pattern and process in a fossil record of unequal scales.

Keywords Biogeography • Fallback foods • Microwear • Phylogeny • Paleobiology

Raymond Dart described the first *Australopithecus* fossil from Taung, South Africa in 1925. Since that time, numerous species attributed to that genus have been recovered, deriving from southern, eastern, and north central Africa. These species have created excitement in the general public, as they know that one of these species was likely ancestral to our own genus *Homo*. Paleoanthropologists respond in the same manner, although there is much more scientific insight into what each species may mean in the evolutionary history of the genus, and indeed, "discussion" as to whether various specimens belong in the genus or not. To address some of these issues regarding specimens and various contextual and behavioral evidence of the genus, contributors to this volume attended a workshop in the fall of 2007, sponsored by the Turkana Basin Institute and Stony Brook University and entitled *Diversity in Australopithecus: Tracking the First Bipeds*. Various questions were asked in the public lecture session on the opening day of the workshop, and potential answers and problems were discussed in subsequent days. Contributors were asked to provide rough drafts of manuscripts on particular topics before the workshop, and then, based on extensive conversations at the workshop, they were asked to revise their manuscripts for this volume.

There were lively discussions, as no one actually presented a paper except at the public session, but all present were asked to discuss the various questions. Ron Clarke told everyone that at Wenner-Gren workshops, formerly held in the Burg Wartenstein castle in Austria, there were often suggestions to "get out the swords." That set the tone for our discussions, with contributors often beginning a contra argument with, "Bring out the swords!" At the time, there was no extensive knowledge of *Ardipithecus ramidus* (White et al. 2009), nor were there any recovered specimens of *Australopithecus sediba* (Berger et al. 2011), but many of the authors here have added references to those taxa to their manuscripts, and the discoverers of *A. sediba* provided a chapter.

The questions that the participants of the workshop asked fell into four major groups: phylogeny, dating, paleobiology (including diet, fallback foods, sexual dimorphism, use of stone tools, and biogeography), and reconciling pattern and process in a fossil record of unequal scales. Phylogenetic questions ranged from how many species might be found at the sites of Sterkfontein and Makapansgat to what can phylogeny tell us about fallback foods? Dating questions and current problems involved emphatic statements regarding what was seen as a mistake, trying to date South African sites using only East African fauna, that is, other methods should be used and developed to help clarify the sequence of events in South Africa. Another focus was to urge understanding the tectonic patterns and their influence in the East African fossil record. Paleoecological and paleobiological questions were numerous, although many participants were interested in fallback foods and their

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importance to the genus, and how fallback foods may have been utilized in different regions. It was also noted that there was a strong provinciality in the populations of various species, which breaks down in the Pleistocene with other hominin taxa—what might this mean paleoecologically and biogeographically? Several people wondered if *Australopithecus* actually used stone tools—note that this was long before the discovery of putative cut marked bones at Dikika (McPherron et al. 2010). Many participants would still wonder where the stone tools are if there are cut marks. Scale was another issue—species or paleodemes; time-averaging and understanding sexual dimorphism; time-averaging within depositional environments—are we always looking at the dry season, for example? How can we map life history patterns onto the different species of *Australopithecus*? What can better knowledge of the postcranial skeleton—from juveniles and different *Australopithecus* species—tell us about diversity in function, sexual dimorphism, and foraging strategies? Biogeographical questions included whether the capability for dispersals of *Australopithecus* can be determined; what is the influence of large rivers within basins for limiting dispersals; and why have no Plio-Pleistocene hominins been recovered from Angola, North Africa or Uganda? And finally, how can we understand selection processes from patterns that are at a much greater scale than these processes likely occur?

The participants also made lists of knowns, known unknowns, and biological realities (the latter followed by a question mark). The list of known taxa included *Australopithecus afarensis*, *Australopithecus africanus*, and *Australopithecus anamensis* to which one could add the species classified by many as *Paranthropus*: *Paranthropus robustus* and *Paranthropus boisei*; known unknowns were those in which only one or very few specimens are known: *Paranthropus aethiopicus*, *Australopithecus garhi*, and *Kenyanthropus platyops*. Finally, there were questions regarding the biological reality of *Australopithecus bahrelghazali*, a second species of *Australopithecus* at Sterkfontein, and, indeed, what exactly was the species at Makapansgat—is it actually *A. africanus*? Obviously, none of the participants was aware of *A. sediba* in the fall of 2007, but we asked for a contribution from its discoverers to add to the depth of the volume. This new species may belong in the category of known unknowns for some researchers, but that is for another discussion and another workshop. The organizers of the workshop limited the discussions to the *Australopithecus* species mentioned above and decided that *Paranthropus* and *Kenyanthropus* would be the subjects of other workshops.

The name of this volume does not match the name of the workshop, because as the discussion progressed and the papers were submitted, it seemed that the incorporation of the diversity of *Australopithecus* species was in reference to their overall paleobiology. Part 1 of this volume, the context of *Australopithecus* evolution, sets up the geological and paleoecological context within which all of the *Australopithecus* species, as well as some of the other genera, occur. From these papers we learn that the genus ranges over about 2.3 million years, with the oldest species recovered in East Africa and the youngest species recovered in South Africa (Malapa). The Taung child, once thought to be among the youngest of representatives, is now in the middle of the *A. africanus* species range—with *A. sediba* now the youngest. The *Australopithecus* specimens from Sterkfontein and Malapa postdate the enigmatic specimen of *A. garhi* from the Middle Awash of Ethiopia, as well as specimens of *P. aethiopicus*. The dispersal and speciation of various species across the landscape is thus bracketed within dates that are not intuitive, and create more questions and some answers about the biogeographical patterns that we see in this genus. Within Part 1 the information we know about the paleoecology of each *Australopithecus* site is discussed, and the authors elucidate what is known about each species' habitat. In general, *Australopithecus* species appear to be habitat generalists, which simply provokes further questions about fallback foods, disparate diets among species, and apparent lack of continuous dispersal across the landscape.

Part 2 of the volume covers site distribution and issues regarding the phylogeny within the genus as well as its origination. These authors also pose more questions regarding the earliest members of the genus, such as understanding the variation and biogeographic distribution of *A. anamensis* in light of the newer recoveries in northern Ethiopia; understanding the temporal range of *A. afarensis* because there is a widespread unconformity in the northern Awash basin that likely eliminates much of the data necessary to understand its LAD there; and understanding the phylogenetic connections to possible descendants such as *Homo* and *Paranthropus*. Later members of the genus also supply controversy of a sort, for example, the longevity of what is known as the *A. africanus* lineage and the variation among specimens begs the question as to how many species of *Australopithecus* are represented by the individuals currently assigned to that taxon in South Africa. There appear to be as many phylogenetic solutions to this question as there are researchers, and there are key specimens that are involved in this debate with StW 53 being among the most controversial. Finally, the newest member of the genus, *A. sediba*, is also discussed with regard to its relationship to other *Australopithecus* and to *Homo*.

Part 3 examines various biogeographical perspectives and evolutionary models and how they can be used to examine evidence regarding ancestor–descendant relationships. This section addresses questions of scale and processes in considering the adaptive radiation of the genus—and arrives at an interesting conclusion that

Australopithecus evolution falls short of a true adaptive radiation, and is better explained by other evolutionary models. None of the authors in this section questioned the hypothesis of an anagenetic lineage from *A. anamensis* to *A. afarensis* (Kimbel et al. 2006), although there are researchers who do not accept that view. Lockwood (2013) asks what is the evidence for a member of the *A. anamensis–A. afarensis* lineage as an origin for the *A. africanus* like hominins in South Africa? Can one explain the many cranial features present in both *A. africanus* and *Homo* through a biogeographical model of ancestor–descendant relationships? There are hints of answers to these questions in these chapters, and Foley (2013), Lockwood (2013), and Strait (2013) all mention the provinciality of these early species. If we agree that evolution occurs in small, isolated populations, then some of the biogeographical patterning that we see is necessary and, indeed, we expect to recover new members of the genus through time in some of these insulated regions, e.g., northern Ethiopia (*A. garhi*) and southern Africa (*A. sediba*), and possibly another species now included in *A. africanus.*

Part 4 considers aspects of the paleobiology of the genus. These topics include diet (as informed by microwear and isotopic data), locomotor adaptational and ontogenetic differences, as well as sexual dimorphism. These chapters explore the myriad of questions that were proposed—but still leave questions: Why is the microwear of *Australopithecus* so different among species recovered from East and South Africa? What do the differences in isotopes among species actually mean? That is, even if a taxon is mixed C3 or all C4, what does that suggest about the actual food items ingested? Newer studies in microwear (Grine et al. 2013) suggest that the purported *A. anamensis–A. africanus* lineage varied little in the overall food properties that were consumed and that hard-object feeding was not involved. These authors imply that their diet may have included some type of vegetation, but we are still not sure of the actual food items utilized. There are differing opinions as to the details of locomotion of some of the *Australopithecus* species. Although everyone agrees the species were bipedal, not all agree on whether their forelimbs were used for climbing, as some contend that the relevant features are just primitive retentions. Were there different modes of locomotion among species? While discovered after the workshop, *A. sediba* at least has some different, and interesting, skeletal morphology suggesting more differences in bauplan than previously expected.

Tragically, two of the young researchers who attended the workshop and provided initial manuscripts have been lost to the field of paleoanthropology since those fall 2007 discussions. Charlie Lockwood died in the summer of 2008 and Elizabeth Harmon in the spring of 2009. For me, editing this volume was intertwined with their lives and deaths, and having their papers, rough or not, included here was extremely important. Elizabeth's paper had been submitted and reviewed before her death, and Will Harcourt-Smith incorporated the reviewers' comments into her manuscript. Charlie's paper had not been submitted in final form, but the latest version was recovered from his computer. David Strait and John Fleagle kindly revised his manuscript, as we felt Charlie's scientific viewpoint was important to incorporate here.

It has taken a long time for this book to see the light of day, but the research described and the analyses discussed are as important today as they were in September of 2007. All of the authors provide some tentative answers to the questions posed at the workshop, and many suggest new research that should likely be done to answer some of the questions posed. But what is research that does not lead to further questions about a field? It is likely time for another workshop and further discussion on the genus *Australopithecus*, given all of the unique discoveries in the past 5 years.

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Part I
Geological and Paleontological Context

The chapters in this section provide the background for later parts of the volume by placing *Australopithecus* fossils in a broader temporal and deposition framework. In "Age Ranges of *Australopithecus* Species, Kenya, Ethiopia, and Tanzania" Francis Brown, Ian McDougall, and Patrick Gathogo review and summarize all of the geological information about the age of *Australopithecus* fossils from Eastern Africa and also the specimen of *Australopithecus bahrelghazali* from Chad. They provide charts showing correlations between geological formations and individual sites that have yielded fossils of *Australopithecus* and related taxa, as well as comparing the ranges of the different species of *Australopithecus*. The genus *Australopithecus* is found in East Africa in deposits ranging in age from 4.2 Ma to less than 2.5 Ma. *Australopithecus anamensis* has been described from sites ranging from 4.2 Ma to just under 3.80 Ma. *Australopithecus afarensis* has a well-documented range from over 3.6 Ma to just less than 3.0 Ma. However, several associated teeth from the site of Fejej in southernmost Ethiopia, dated ca. 4.2–4.0 Ma, have been attributed to that species, and some authors have suggested that *A. anamensis* and *A. afarensis* are chronospecies of a single lineage. *A. bahrelghazali* from Chad has an estimated date, based on faunal correlations of between 3.4 and 3.0 Ma. *Australopithecus garhi* is known from a single site in Ethiopia and has a well-constrained age of just slightly less than 2.5 Ma. Fossils attributed to *Kenyanthropus platyops* from northern Kenya range in age from 3.6 to 3.25 Ma.

In "A Multi-Disciplinary Perspective on the Age of *Australopithecus* in Southern Africa", Andy Herries and colleagues review and summarize the ages of *Australopithecus* species from Southern Africa and compare them with the ages of other species from Eastern Africa. They base their results on a combination of paleomagnetic correlation, electron spin resonance (ESR), and uranium lead (U-Pb) analyses as well as biochronological and stratigraphic data. They find that the oldest fossils attributed to *Australopithecus africanus* are from the Makapansgat Limeworks site dated to between 3.0 and 2.6 Ma. The type specimen of *A. africanus* from Taung is most likely in the same age range as the Makapansgat fossils. *Australopithecus* fossils from the rich but complex site of Sterkfontein are dated to between 2.6 and 2.0 Ma. However the number of contemporaneous species is a subject of debate. *Australopithecus* fossils from Gladysvale are dated to between 2.4 and 1.9 Ma. *Australopithecus sediba* from Malapa is well-dated at 2.05–1.98 Ma. Thus, *Australopithecus* fossils from Southern Africa are generally much younger than *Australopithecus* in East Africa and are contemporaneous with *Homo* and *Paranthropus*.

In “Reconstructing the Habitats of *Australopithecus*: Paleoenvironments, Site Taphonomy, and Faunas”, Kay Behrensmeyer and Kaye Reed review what can be reconstructed regarding the paleoecology of each of the species of *Australopithecus* in the context of a broader consideration of the many factors involved in deducing ecological information from the geological and paleontological records. They find that as a genus, *Australopithecus* likely occupied a wide range of habitats, and that there is evidence that the species *A. afarensis* occupied multiple habitats. However, they also note that different types of information sometimes yield conflicting evidence about the paleoecology of *Australopithecus* species.

The Editors

Chapter 2

Age Ranges of *Australopithecus* Species, Kenya, Ethiopia, and Tanzania

Francis H. Brown, Ian McDougall, and Patrick N. Gathogo

Abstract *Australopithecus anamensis, Australopithecus afarensis, Australopithecus bahrelghazali, Australopithecus garhi,* and *Kenyanthropus platyops* have all been described from eastern Africa and Chad. Principal results presented are the age of specimens assigned to these taxa that derive from sedimentary formations of the Omo Group in the Omo-Turkana Basin of Kenya and Ethiopia. Also included are ages of relevant fossils from various sites in sediments of similar age preserved in the Ethiopian Rift Valley (e.g., Hadar, Asa Issie, Aramis, Maka, Bouri), and at Laetoli in Tanzania. All ^{40}Ar/^{39}Ar ages were recalculated to a common age for the Fish Canyon sanidine fluence monitor (FCs) to eliminate small differences in age caused by different choices for this value. The value chosen for the age of the Fish Canyon sanidine monitor (28.10 Ma) is that of Spell and McDougall (2003). The overall effect is to increase ages computed using 27.84 Ma for the age of the monitor by 0.93 %, and to increase ages computed using 28.02 Ma for the age of FCs by 0.29 %. An age of 4.000 Ma using the 27.84 Ma age for FCs is thus increased to 4.037 Ma; whereas the same age computed using 28.02 Ma is increased to 4.011 Ma. Thus the differences in the stated ages are on the order of 0.02 Ma–up to about twice the length of a precessional orbital cycle. Excellent age information is available on most specimens principally due to the efforts of Paul Renne and coworkers at the Berkeley Geochronology Center (BGC), and Ian McDougall and coworkers at the Research School of Earth Sciences, Australian National University; some other information (e.g., Walter and Aronson 1993) is also useful, but less extensive than the results obtained by the workers mentioned above.

Keywords Hominin evolution • Geology • Tephrostratigraphy • Radiometric dating • Turkana Basin • Omo Group

Introduction

The principal formations of interest are those of the Omo Group in the Omo-Turkana Basin of northern Kenya and southern Ethiopia, the Sagantole, Hadar, and Bouri formations of northeast Ethiopia, and the Laetoli Formation of northern Tanzania (Fig. 2.1). At other localities, such as that at Bahr al Ghazal (KT-12), Chad, australopith fossils are dated by faunal comparison and ^{10}Be/^{9}Be determinations; in some cases it is not evident what area or thickness of strata is included in the fauna being compared.

For the present chapter, we use ages for magnetostratigraphic boundaries given in Table 2.1. These generally follow Gradstein et al. (2004) and Horng et al. (2002), with those of Kidane et al. (2007) used for the Reunion I and Reunion II subchrons. Although stated without error estimates, in many instances errors of up to 0.03 Ma are associated with each of these ages. Further, we use ages given in Table 2.2 for dated volcanic materials in the Omo-Turkana Basin, and ages listed in Table 2.3 are for dated volcanic materials at sites in Ethiopia and Tanzania, recomputed where necessary, so that the Fish Canyon Tuff sanidine reference age is identical to that used for ages in the Omo-Turkana Basin (i.e., 28.10 Ma).

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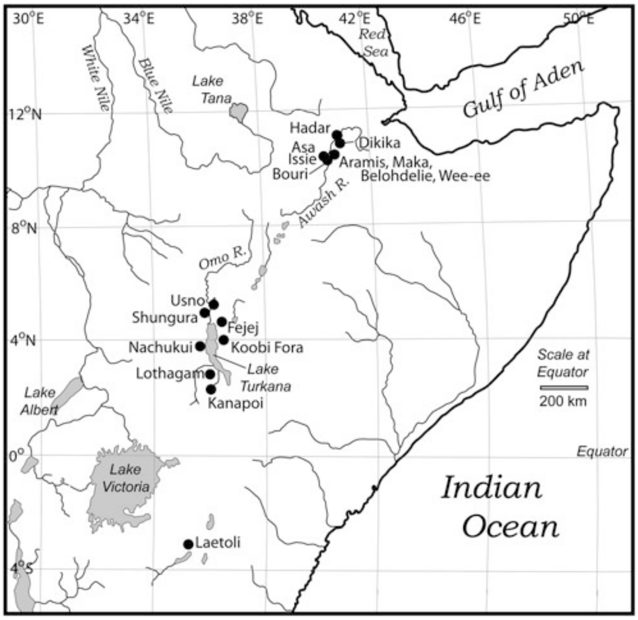


Fig. 2.1 Map of eastern Africa showing locations of most of the fossil sites mentioned in the text. Locations are generalized because some formations (e.g., Koobi Fora Formation; Shungura Formation) extend over large areas

Table 2.1 Ages of magnetostratigraphic and stratigraphic boundaries

Designation	Age (Ma)	Alternate name[a]
C1n	0.000–0.781	Brunhes
C1r	0.781–2.581	Matuyama
C1r.1n	0.988–1.072	*Jaramillo Normal*
C1r.2n	1.173–1.185	*Cobb Mt. Normal*
C2n	1.778–1.945	*Olduvai Normal*
C2r.1n	2.06–2.08[b]	*Reunion II Normal*
C2r.2n	2.15–2.20[b]	*Reunion I Normal*
C2An.1n and C2An.3n	2.581–3.596	Gauss
C2An.1r	3.032–3.116	*Kaena Reversed*
C2An.2n	3.116–3.207	
C2An.2r	3.207–3.33	*Mammoth Reversed*
C2An.3n	3.33–3.596	
C3r	3.596–6.033	Gilbert
C3n.1n	4.187–4.3	*Cochiti Normal*
C3n.2n	4.493–4.631	*Nunivak Normal*
C3n.3n	4.799–4.896	*Sidufjall Normal*
C3n.4n	4.997–5.235	*Thvera Normal*

Sources Gradstein et al. (2004) and Horng et al. (2002)

[a] Subchrons in italics

[b] Age estimates based on Kidane et al. (2007)

Table 2.2 ^{40}Ar/^{39}Ar ages of dated units in the Omo-Turkana Basin

Unit	Age and standard deviation (Ma)	
Silbo	0.751 ± 0.022	Anorthoclase[a]
U. Nariokotome	1.230 ± 0.020	Anorthoclase[a]
M. Nariokotome	1.277 ± 0.032	Anorthoclase[a]
L. Nariokotome	1.298 ± 0.025	Anorthoclase[a]
Gele	1.326 ± 0.019	Anorthoclase[a]
Chari	1.383 ± 0.028	Anorthoclase[a]
Ebei	1.475 ± 0.029	Anorthoclase[a]
Karari Blue	1.479 ± 0.016	Anorthoclase[a]
Koobi Fora	1.485 ± 0.014	Anorthoclase[a]
Lower Koobi Fora	1.476 ± 0.013	Anorthoclase[a]
Morte	1.510 ± 0.016	Anorthoclase[a]
Lower Ileret	1.527 ± 0.014	Anorthoclase[a]
Morutot	1.607 ± 0.019	Anorthoclase[a]
Malbe	1.843 ± 0.023	Anorthoclase[a]
KBS	1.869 ± 0.021	Anorthoclase[a]
Kangaki	2.063 ± 0.032	Anorthoclase[b]
G-3	2.188 ± 0.036	Anorthoclase[b]
Kalochoro	2.331 ± 0.015	Anorthoclase[b]
Tuff F	2.324 ± 0.020	Anorthoclase[b]
Tuff D-3-2	2.443 ± 0.048	Anorthoclase[b]
Lokalalei	2.526 ± 0.025	Anorthoclase[b]
Burgi	2.622 ± 0.027	Anorthoclase[b]
B-10	2.965 ± 0.014	Anorthoclase[b]
Ninikaa	3.066 ± 0.017	Anorthoclase[b]
Toroto	3.308 ± 0.022	Anorthoclase[b]
Tulu Bor	3.438 ± 0.023	Anorthoclase[b]
Lokochot	3.596 ± 0.045	Anorthoclase[b]
Moiti	3.970 ± 0.032	Anorthoclase[b]
Topernawi	3.987 ± 0.025	Anorthoclase[b]
Kanapoi Tuff	4.108 ± 0.029	Anorthoclase[b]
Upper pumiceous siltstone, Kanapoi	4.147 ± 0.019	Anorthoclase[b]
Lower pumiceous siltstone, Kanapoi	4.195 ± 0.033	Anorthoclase[b]
Pumice clasts, Apak Mb., Lothagam	4.244 ± 0.042	Anorthoclase[b]
Lothagam Basalt	4.23 ± 0.03	Whole rock[c]

All ages calculated relative to a reference age of 28.10 Ma for the Fish Canyon Tuff sanidine fluence monitor. All results on anorthoclase are arithmetic mean ages with uncertainties the standard deviation of the population. Most pooled ages are based on multiple single crystal total fusion measurements

[a] McDougall and Brown (2006)

[b] McDougall and Brown (2008)

[c] McDougall and Feibel (1999, 2003)

Table 2.3 K/Ar and ^{40}Ar/^{39}Ar ages of dated units at Ethiopian sites other than Omo, and at Laetoli standardized to a value of 28.10 Ma for the Fish Canyon sanidine fluence monitor

Unit	Age and standard deviation (Ma)	
Sagantole, Hadar, and Bouri formations		
Maoleem vitric tuff (MOVT)	2.519 ± 0.008	Sanidine[a]
Bouroukie tuff 3 (BKT-3)	2.35 ± 0.07	Alkali feldspar[b]
Bouroukie tuff 2 (BKT-2U)	2.978 ± 0.038	Alkali feldspar[c]
Bouroukie tuff 2 (BKT-2L)	2.971 ± 0.017	Alkali feldspar[c]
Kada hadar tuff (KHT)	3.205 ± 0.012	Alkali feldspar[d]
Triple Tuff (TT-4)	3.250 ± 0.010	Alkali feldspar[d]
Kadada moumou basalt (KMB)	3.311 ± 0.040	Whole rock[e]
Sidi hakoma tuff (SHT)	3.430 ± 0.030	Anorthoclase[f]
Wargolo tuff (VT-3)	3.783 ± 0.023	Alkali feldspar[g]
Cindery tuff (CT)	3.883 ± 0.083	Plagioclase[h]
Moiti tuff (VT-1)	3.925 ± 0.030	Sanidine[h]
Unnamed tuff, Sagantole Fm. (94–55 °C)	4.052 ± 0.060	Sanidine[g]
Unnamed basaltic tuff (MA02-13)	4.128 ± 0.074	Basaltic glass[i]
Marker tuff sibabi	4.303 ± 0.019	Alkali feldspar[h]
Kullunta basaltic tuff (KUBT)	4.329 ± 0.055	Basaltic glass[g]
Igida tuff complex (IGTC)	4.344 ± 0.011	Plagioclase[g]
Gaala tuff complex (GATC)	4.430 ± 0.031	Mainly sanidine[g]
Daam aatu basaltic tuff (DABT)	4.429 ± 0.053	Volcanic glass[g]
Unnamed tuff, Sagantole Fm. 94–58	4.605 ± 0.121	Plagioclase[g]
Abeesa tuff (ABCT)	4.863 ± 0.073	Plagioclase[g]
Unnamed tuff, Sagantole Fm. 94–32	4.895 ± 0.083	Plagioclase[g]
Gawto basalt	5.234 ± 0.083	Whole rock[g]
Upper unit Laetolil beds		
Yellow marker tuff	3.614 ± 0.018	Alkali feldspar[j]
Tuff 8	3.46 ± 0.12	Biotite[k]
Tuff 8	3.618 ± 0.018	Alkali feldspar[j]
Between tuffs 7 & 8 (MM25)	3.49 ± 0.11	Biotite[k]
Between tuffs 7 & 8 (75-7-7E)	3.56 ± 0.02	Biotite[k]
Tuff 7A	3.65 ± 0.02	Biotite[j]
Tuff 7	3.56 ± 0.19	Biotite[k]
Tuff 6	3.77 ± 0.05	Biotite[j]
Tuff 5	3.61 ± 0.19	Biotite[j]
Tuff between 4 & 5	3.78 ± 0.11	Biotite[j]
Tuff 4	3.80 ± 0.04	Alkali feldspar[j]
Tuff 4	3.85 ± 0.02	Biotite[j]
Tuff 3	3.71 ± 0.04	Biotite[j]
Tuff 2	3.78 ± 0.04	Alkali feldspar[j]
Tuff 2	3.85 ± 0.03	Biotite[j]
Tuff 1	3.74 ± 0.02	Biotite[j]
Base of upper unit, Laetolil beds	3.76 ± 0.03	Biotite[k]
Lower unit Laetolil beds		
Uppermost lower Laetolil beds	3.84 ± 0.02	Alkali feldspar[j]

Most results on alkali feldspar are based upon single crystal total fusion measurements, whereas most whole rock or glass measurements are from step heating experiments. In most cases the age and uncertainty are based upon a weighted mean calculation

[a] de Heinzelin et al. 1999

[b] Kimbel et al. 1996

[c] Dimaggio et al. 2008

[d] Walter 1994

[e] Renne et al. 1993

[f] Walter and Aronson 1993

[g] Renne et al. 1999

[h] White et al. 1993

[i] White et al. 2006

[j] Deino 2011; preferred ages

[k] Drake and Curtis 1987

Pliocene Formations of the Omo-Turkana Basin (the Omo Group)

Hominin taxa described from sedimentary deposits of the Omo Group in northern Kenya and southern Ethiopia include *Australopithecus anamensis*, *Australopithecus afarensis*, *Paranthropus aethiopicus*, *Paranthropus boisei*, and *Kenyanthropus platyops*. The Omo Group was defined originally by de Heinzelin (1983) as a general term to include tilted and faulted sedimentary strata of Pliocene and Pleistocene age in the Lower Omo Valley. Within the Omo Group, de Heinzelin (1983) included the Mursi, Nkalabong, Usno, and Shungura formations, and also what he termed the Loruth Kaado and Naiyena Epul beds, which are now included within the Nachukui Formation. By extension, the Koobi Fora Formation (Brown and Feibel 1986), and the Nachukui Formation (Harris et al. 1988a, b) are now included in the Omo Group. These formations consist dominantly of sands, silts and clays, deposited in fluvial, deltaic and lacustrine, environments. The Omo River, which drains the Ethiopian highlands, transported much of the sediment to the basin but there are also important contributions from lateral streams along the basin margin in many places. Two lacustrine intervals are especially prominent, one between ~4.3 and 4 Ma, and a second between ~2.0 and 1.6 Ma. Two of the formations of interest are located in the Lower Omo Valley of Ethiopia—the Shungura and Usno formations. Chronological control on formations of the Omo Group derives principally from ^{40}Ar/^{39}Ar ages measured at the Australian National University, Canberra. Directly measured ages are now available for 33 individual volcanic ash layers (Table 2.2). Because of the reasonably closely spaced direct age measurements, additional control can be added by knowing the levels of transition from normal to reversed paleomagnetic polarity and assigning the transitions to previously established chrons and subchrons of the Geomagnetic Polarity Time Scale.

Shungura Formation

The 766 m thick Shungura Formation is beautifully documented by de Heinzelin and coworkers (see de Heinzelin and Haesaerts 1983a, b). It crops out in a long (~65 km), narrow (1–9 km), north–south trending belt west of the Omo River in southern Ethiopia, and it is faulted, with most blocks having been dropped down on the east and strata dip ~10°W. de Heinzelin and Haesaerts (1983a) divided the formation into a Basal Member, followed upward by members A to L (omitting I). The base of the formation is taken as the lowest strata exposed below Tuff A; nowhere is the contact with underlying rocks exposed. A silicic tuff lies at the base of each member except for the Basal Member, which is defined as those strata which lie beneath Tuff A. Tuff A lies at the base of Member A. de Heinzelin and Haesaerts (1983a) divided each member into submembers on the basis of fining upward sequences and/or erosional surfaces, and labeled them numerically from the base upward within each member (e.g., D-3); some submembers are divided internally, and these too are numbered from the base upward within each submember (e.g., D-3-2). Tuffs not used to define members are designated by the submember or unit in which they occur (i.e., D-3-2). Fossils are abundant from Member A to Member L, and have provided an important set of fossil mammals useful for biochronology in East Africa. Below submember G-14, the formation consists principally of fluvial sediments arranged in fining upward cycles, commonly with a paleosol at the top of each. Many fossils derive from sandstones at the base of each fining upward sequence, but others come from less energetic conditions representing ancient floodplains. Chronological control is provided by direct determinations on materials from the Shungura Formation, and also by tephrostratigraphic correlations to dated units in other formations of the Omo Group. For example, Tuff C-4 of the Shungura Formation correlates with the Ingumwai Tuff of the Koobi Fora Formation, and lies below the Burgi Tuff which has been dated at 2.62 Ma. Hence C4 is somewhat older than 2.62 Ma. Other correlations provide still additional information.

Usno Formation

de Heinzelin and Haesaerts (1983b) described the 172 m thick Usno Formation that is exposed ~20 km northeast of the Shungura Formation in several small (named) patches. Fossils come principally from two of these exposures—White Sands and Brown Sands—at stratigraphic levels near the middle of the formation above tuffs U-10 and U-11, which correlate with tuffs B-α and B-β. Like the Shungura Formation, the fossils derive from fluvial deposits.

Koobi Fora Formation

Bowen and Vondra (1973; see also Bowen 1974) first provided a stratigraphy of Pliocene and Pleistocene deposits in the Koobi Fora region east of Lake Turkana. Brown and Feibel (1986) revised the stratigraphy, and defined all Pliocene and Early Pleistocene strata as part of the 525 m thick Koobi Fora Formation. The latter authors divided the

Koobi Fora Formation into eight members based on chemically distinct tephra marker horizons. From bottom to top the member names are: Lonyumun, Moiti, Lokochot, Tulu Bor, Burgi, KBS, Okote, and Chari. A major discontinuity occurs within the Burgi Member, which has a duration of ~0.5 Ma. This separates the informal lower Burgi Member (which extends upward to Lokalalei Tuff; 2.52 ± 0.03 Ma), from the informal upper Burgi Member (for which deposition begins approximately 2 Ma ago; McDougall and Brown 2008). Part of the interval missing in the Koobi Fora region is preserved in exposures of the Koobi Fora Formation at Loiyangalani (Gathogo et al. 2008), where deposits include the Kokiselei Tuff, and the depositional break occurs after eruption of flows of the Lenderit Basalt (2.02 ± 0.02 to 2.51 ± 0.03 Ma). The Koobi Fora Formation records a variety of fluvial, lacustrine, and deltaic environments, but fossils of *Australopithecus* sp. are principally known from fluvial channel deposits (see Coffing et al. 1994).

Kanapoi Formation and Nachukui Formation

These units lie disconformably above Miocene volcanic rocks. In other locations in the Omo-Turkana Basin deposition of Omo Group sediments began shortly before or after eruption of basalts of the Gombe Group (Watkins 1983; Haileab et al. 2004).

The Kanapoi Formation, located southwest of Lake Turkana in the Kerio River Valley is 37.3 m thick in its type section (Feibel 2003a). It records both lacustrine deposition and deltaic deposition by a river entering the basin from the south or southwest. Specimens recovered from this locality led Leakey et al. (1995) to propose a new species of hominin—*A. anamensis*.

At Lothagam, also located southwest of Lake Turkana ~65 km north of Kanapoi, the 37–113 m thick Apak Member of the Nachukui Formation disconformably lies above fluvial strata of the Nawata Formation (7.4 ± 0.1 to 6.5 ± 0.1 Ma; McDougall and Feibel 1999; Feibel 2003b), and below the 59 m thick Muruongori Member. The 94 m thick Kaiyumung Member lies above the Muruongori Member (McDougall and Feibel 1999). The Apak Member records rapid deposition by a meandering river on a floodplain, perhaps related to that at Kanapoi (Feibel 2003b). It is succeeded by lacustrine strata of the Muruongori Member, and then a return to fluvial conditions recorded in the Kaiyumung Member. Despite considerable effort, hominin fossils from Lothagam remain scant. A mandible recovered in 1967 is said to be from the Apak Member, and Leakey and Walker (2003) assigned four dental specimens from the Kaiyumung Member to *Australopithecus* cf. *A. afarensis*.

Where exposed west of Lake Turkana between ~3.75 and 4.25°N latitude (i.e., between the towns of Kataboi and Lowarengak), the Nachukui Formation has an aggregate thickness of 730 m (Harris et al. 1988a, b). The formation in this region is divided into the Lonyumun (4.2–4 Ma), Kataboi (3.9–3.4 Ma), Lomekwi (3.4–2.5 Ma), Lokalalei (2.5–2.3 Ma), Kalochoro (2.3–1.9 Ma), Kaitio (1.9–1.6 Ma), Natoo (1.6–1.3 Ma), and Nariokotome (1.3–0.6 Ma) members. Remains of *Australopithecus* sp. are known from the Lomekwi Member, and those of *Kenyanthropus* are known from the Kataboi Member. Facies variations occur over short lateral distances in some parts of the Nachukui Formation, and it records lacustrine, fluvial, and alluvial fan environments as described in previous publications (e.g., Harris et al. 1988a, b). Remains of *Australopithecus* sp. were recovered from alluvial plain environments, and those of *Kenyanthropus* were recovered from lacustrine margin deposits.

Pliocene Formations in Ethiopia Outside the Omo-Turkana Basin

Along the Awash River in Ethiopia several paleontological sites have yielded specimens ascribed to *Australopithecus*. Geological units include the Sagantole Formation, the Hadar Formation, and the Bouri Formation.

Sagantole Formation

With important fossils, a thickness over 200 m, and a quasi-continuous temporal record extending over ~1.5 Ma, the Sagantole Formation has received special attention. A complete section shown in Fig. 2.2 demonstrates that sedimentary units extending back well over 5 Ma in age exist in the region. Renne et al. (1999) have reviewed the geology, dating, and magnetostratigraphy of this unit, which is very well controlled, and later White et al. (2006) added still more temporal information. The Sagantole Formation has been divided into seven members (Renne et al. 1999). From the base upward these are the Kuseralee, Gawto, Haradaso, Aramis, Beidareem, Adgantole, and Belohdelie members. The Kuseralee Member consists of gypsiferous siltstones and claystones with interbedded bentonite layers and sandstones. A sandstone with a rich vertebrate fauna is succeeded by the lowermost flow of the Gawto Member. Basaltic lava flows and an agglomerate make up the Gawto Member. Fine-grained strata of the overlying Haradaso Member are succeeded by thick, cross-bedded sandstones,

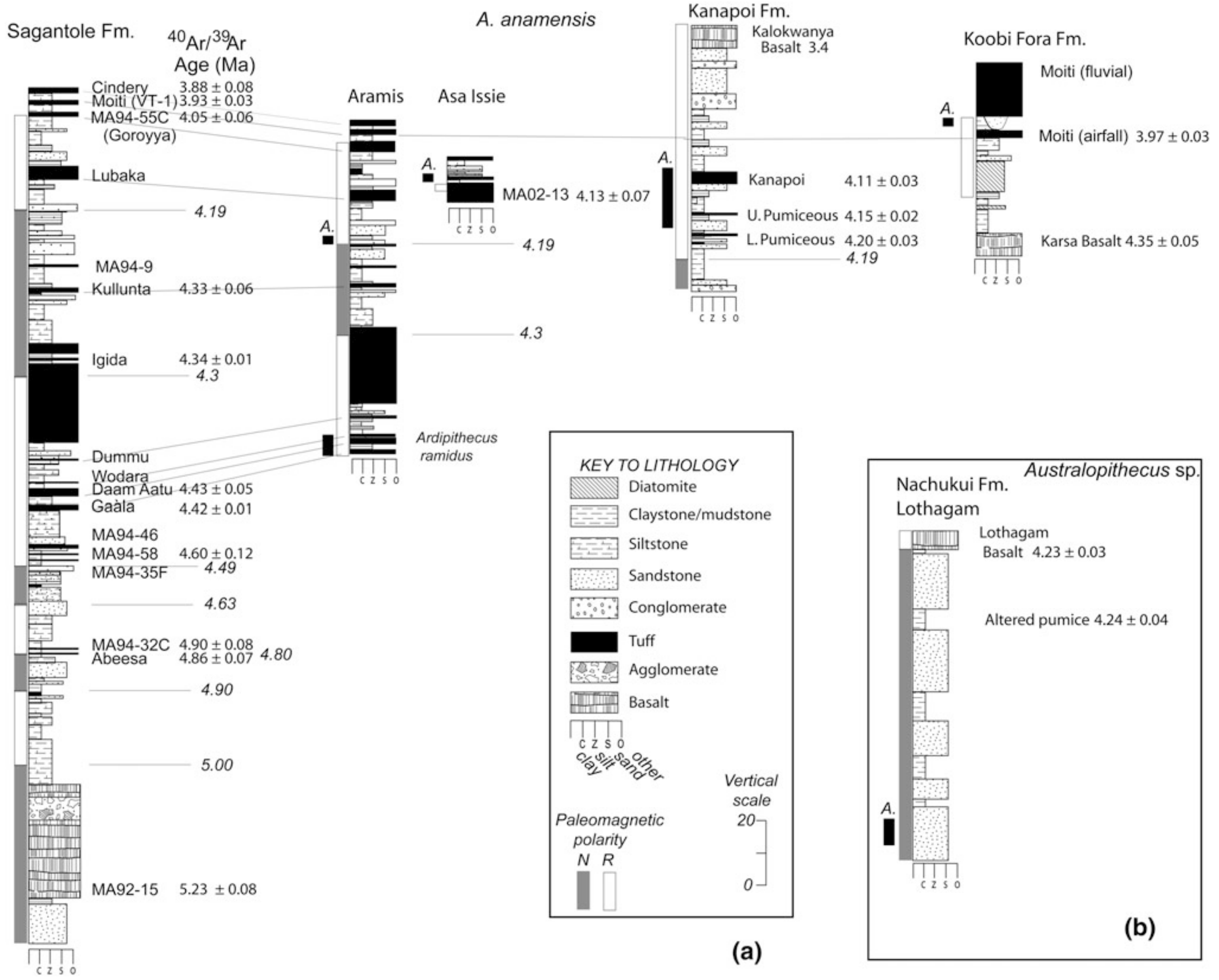


Fig. 2.2 **a** Schematic stratigraphic columns for localities from which fossils ascribed to *Australopithecus anamensis* have been recovered. The column for the Sagantole Fm. is after Renne et al. (1999); those for Aramis and Asa Issie are after White et al. (2006); that for the Kanapoi Fm. is after Leakey et al. (1998) and Feibel (2003a); and that for Koobi Fora is after Coffing et al. (1994). To the left of each stratigraphic column is a column showing paleomagnetic polarity (if known). Left of that is a *small solid bar* capped with "*A*." showing the known range of fossils in each section. Dated units are identified by name, or if a name is lacking, by sample number; ^{40}Ar/^{39}Ar ages shown with error are recalculated to an age of 28.10 Ma for the Fish Canyon sanidine fluence standard (FCs) so that ages on all columns are comparable. Ages assigned from paleomagnetic transition boundaries are shown without error and italicized. **b** Position of the Lothagam mandible (KNM-LT 329), and the dated tuff at Lothagam using information from McDougall and Feibel (2003)

and conglomerate lenses near the top. Vertebrate fossils are abundant in the silty sandstones and coarser sandstones. The Haradaso Member contains at least seven tephras (mainly altered), including the Abeesa Tuff. At the base of the Aramis Member is the Gàala Tuff Complex, which is overlain by silt, clay, and sand with calcareous layers some of which contain vertebrate fossils and fossilized seeds and dung. A coarse-grained cross-bedded sandstone at the top of the Aramis Member contains vertebrate fossils, but the member also includes gastropod-bearing limestones. Most of the Aramis Member probably records fluvial sedimentation with shallow lacustrine environments represented near the top. The Beidareem Member consists of altered basaltic tephra and locally 2–4 m of silts and silty clays between the basaltic tuffs enclose the Igida Crystal Tuff. Some 80 m of strata comprise the Adgantole Member, which is dominated by silt, clay, and sand, but also has coarse sandstone and conglomerate near the top. It contains several tuffs (e.g., Kullunta Basaltic Tuff, Lubaka Vitric Tuff, Goroyya Tuff Complex). The Goroyya Tuff Complex crops out ∼3 m below Tuff VT-1 (=Moiti Tuff) which defines the base of the Belohdelie Member. The Moiti Tuff was defined in the Omo-Turkana Basin (Cerling and Brown 1982; Haileab and Brown 1992). Extending upward to the base of the Cindery Tuff, the Belohdelie Member consists of clay, silt, and fine sand with a few thin, coarser-sand horizons, several laterally extensive vitric tephra, and a gastropod-bearing limestone beneath the Cindery Tuff. Deposition in a fluctuating shallow- to deep-lacustrine system, including swamp and lake-margin facies is suggested for this member (Renne et al. 1999). White et al. (2006) report on specimens of *A. anamensis* from this formation at Aramis, and also at Asa Issie.

Hadar Formation

The Hadar Formation, a minimum of 280 m thick, is exposed along the Awash River adjacent to the eastern escarpment of the Ethiopian Plateau (Johanson et al. 1982). The principal area (~10 km^2) from which fossils of *Australopithecus* were collected is located north of the Awash River. The strata are essentially flat lying, and have been divided into four members, the Basal, Sidi Hakoma, Denen Dora, and Kada Hadar members from the base upwards. The sedimentary strata are generally similar to those of the Sagantole Formation, but lack basaltic tephra that are so prominent in the former. Like the Sagantole Formation, the Hadar Formation contains several vitric tuffs (e.g., the Sidi Hakoma Tuff (SHT), the Kada Hadar Tuff (KHT), the Triple Tuff (TT), the Bouroukie Tuffs (BKT), etc.), which have provided material for ^{40}Ar/^{39}Ar dating. Lacustrine, lake margin, fluvial and flood plain environments are well represented, and described elsewhere (e.g., Taieb et al. 1972, 1976; Johanson et al. 1982). Near the base of the formation is the Sidi Hakoma Tuff, which correlates with the β-Tulu Bor Tuff of the Omo-Turkana Basin (Brown 1982; Walter and Aronson 1993). The site is justly famous for the discovery of many fossils now ascribed to *A. afarensis* (e.g., Taieb et al. 1976; Johanson et al. 1978; Johanson and White 1980). At Dikika, the Hadar Formation has a maximum thickness of ~160 m, and many of the units defined at Hadar itself are still recognizable (SHT, KHT, TT-4, etc.; see Wynn et al. 2006). Below the Sidi Hakoma Tuff, lacustrine clays resting on older basalts give way to shoreline facies with gastropod bearing sandstones. These are transitional to delta plain facies that contain the splendid juvenile skeleton attributed to *A. afarensis* described by Alemseged et al. (2005, 2006). Still higher in the section, lacustrine deposition resumes, and is then once again replaced by predominantly fluvially deposited strata in the upper part of the formation. In addition to the juvenile hominin, a partial mandible with associated dentition has been recovered from the area which is also attributed to *A. afarensis* (Alemseged et al. 2005).

Bouri Formation

de Heinzelin et al. (1999) named the Bouri Formation for its location on the Bouri Horst, and divided it into three members (the Hata, Daka, and Herto members) with a combined thickness of 80 m. Of interest here is the Hata Member, which is 40 m thick in its type locality. The lower part of this member is made up of silty claystones, tuffs, and mudstone, with sandstones and mudstones in the upper part. These units are interpreted as having been deposited in fluvial settings close to a shallow fluctuating lake (de Heinzelin et al. 1999). Three tuffs were recognized—the Maoleem Vitric Tuff (MOVT), a yellow-green zeolitized unit, a diatomaceous tuff 14 m higher in the section, and a bentonitic tuff with accretionary lapilli 4 m above that. This is the site from which Asfaw et al. (1999) described the new taxon *Australopithecus garhi*.

Laetolil Beds

Hay (1987) described a representative section of the Laetolil Beds exposed in northern Tanzania, and divided it into a lower unit (64 m), and an upper unit (59 m). His lower unit consists principally of aeolian tuff interbedded with air-fall and water-worked tuffs, and in some sections also contains conglomerates and a mudflow. His upper unit consists largely of aeolian tuff, but also contains air-fall tuffs and several horizons of angular rock fragments, or xenoliths. As subaerial deposits, probably on a grassland savanna, the Laetolil Beds differ sharply from other units discussed previously. K/Ar age measurements along with one ^{40}Ar/^{39}Ar age determination, principally on biotite from airfall tuffs within the sequence are the basis for the chronology of these beds (Drake and Curtis, 1987). More recent detailed 40Ar/39Ar age measurements on biotite and alkali feldspar by Deino (2011) are now the basis for the age assignments. Hominin fossils derive from the upper unit of the Laetolil Beds from levels 7 m below Tuff 3 to 9 m above Tuff 8 (Leakey, 1987).

Temporal Distribution of *Australopithecus* Species

Australopithecus anamensis

Chronologic information on this taxon is summarized in Fig. 2.2, where all columns are drawn, insofar as possible, to a standard format for ease in comparison. The position of *Ardipithecus ramidus* is also shown on this figure where it is apparent that this taxon predates the earliest occurrences of *A. anamensis* by at least 100 ka.

Representative fossils of *A. anamensis* at Kanapoi, southwest of Lake Turkana, come principally from a lower channel sandstone and overbank mudstone complex, and a distributary channel associated with the Kanapoi Tuff (4.108 ± 0.029 Ma; McDougall and Brown 2008). Altered pumiceous clasts occur in two siltstones in the lower levels of the Kanapoi sequence, and alkali feldspar crystals from them yielded ages of 4.195 ± 0.033 and 4.147 ± 0.019 Ma (Leakey et al. 1995, 1998; McDougall and Brown 2008). The oldest dated level (4.195 ± 0.033 Ma) is below the lowest *A. anamensis* specimen yet recovered. Most hominins from Kanapoi occur in strata between the lowest dated level and the Kanapoi Tuff. Fossils of *A. anamensis* have also been recovered from the Koobi Fora Formation in paleontological collecting Area 261 of the Allia Bay region. In the latter locality the specimens lie ~5 m below the Moiti Tuff (Coffing et al. 1994), within the Lonyumun Member as currently defined. However, an airfall equivalent of the Moiti Tuff lies lower in the section in Area 260 (Brown unpublished) to which the age of 3.970 ± 0.032 Ma should most likely be attributed.

Australopithecus anamensis is also known from Aramis and Asa Issie, Ethiopia, probably from the Adgantole Member of the Sagantole Formation. A single specimen from Aramis, Ethiopia, from near the base of paleomagnetic chron C2Ar (4.18 Ma) is attributed to *A. anamensis* (White et al. 2006). At Asa Issie specimens of *A. anamensis* derive from strata above a basaltic tephra layer for which the weighted mean of two plateau ages is 4.128 ± 0.074 Ma (recomputed from 4.116 ± 0.074 in White et al. 2006). These strata are of reversed paleomagnetic polarity, and assigned to chron C2Ar (4.19–3.61 Ma). The younger age limit is more difficult to assess, but White et al. (2006) suggest that the fossils lie below a vitric tuff (VT-3) correlated with the Wargolo Tuff of the Omo-Turkana Basin by Haileab and Brown (1992). White et al. (1993) reported an average age of 3.78 ± 0.02 Ma for this unit. deMenocal and Brown (1999) estimated the age of the Wargolo Tuff at 3.80 ± 0.01 Ma from its correlate in ODP Site 721. Thus, all known specimens attributed to *A. anamensis* lie between 3.8 and 4.2 Ma.

Australopithecus afarensis

Figure 2.3 shows the stratigraphic distribution of this taxon in its principal occurrences: the Hadar region and Laetoli. Some specimens from Koobi Fora, Lothagam and Fejej have also been attributed to *A. afarensis*.

Specimens attributed to *A. afarensis* at Hadar are found in the Sidi Hakoma and Denen Dora members of the Hadar Formation, bounded by the Sidi Hakoma Tuff below, and by BKT-2 above. *Australopithecus* specimens come from a variety of depositional settings; the most famous (A.L. 288-1; "Lucy") derives from a channel fill of a small stream. Site A.L. 333, which has yielded remains of at least 13 individuals, may have been preserved in overbank sediments related to an adjacent channel fill. Hominin fossils have been retrieved from floodplain, delta plain and delta-margin facies in addition to shallow lacustrine deposits in the Sidi Hakoma Member. In the Denen Dora Member, which has shallow lacustrine deposits in the lower part transitional to swamp and floodplain deposits above, hominins have been recovered not only from the sandy units, but also from finer grained deposits. Chronological control is provided not only by K/Ar and ^{40}Ar/^{39}Ar dates on intercalated volcanic ash layers, but also by paleomagnetic polarity transitions representing the Mammoth and Kaena subchrons.

K/Ar data reported by Drake and Curtis (1987) establish the general age for the Laetolil Beds, the source of the holotype of *A. afarensis* (L.H. 4; Johanson et al. 1978) but the data set is not as robust as it might be, and additional work would be of interest. In particular, errors on the age determinations are larger than those obtained for materials of comparable age in the Kenyan and Ethiopian materials, partly because biotite normally contains a much smaller fraction of radiogenic argon than feldspars.Recently, Deino (2011) provided new ^{40}Ar/^{39}Ar ages on the entire succession at Laetoli that are in general agreement with the earlier results of Drake and Curtis (1987), Harrison and Msuya (2005), and Manega (1993). Deino's preferred ages are shown on the column in Fig. 2.3, and document convincingly that the fossils from the Upper Laetolil Beds lie between 3.63 and 3.8 Ma in age.

Perhaps the best known specimen from Lothagam is a mandible (KNM-LT 329) recovered by Bryan Patterson from the lowest part of the Apak Member of the Nachukui Formation in 1967. It derives from the lowest 3 m of this member, so we only know that it is >4.22 ± 0.03 Ma in age. Leakey and Walker (2003) note that it has affinities to both *A. ramidus* and *A. afarensis*, but attribute the specimen to Hominidae indeterminate. Four dental specimens from the Kaiyumung Member of the Nachukui Formation at Lothagam were assigned to *Australopithecus* cf. *A. afarensis* by Leakey and Walker (2003). On the basis of the known paleomagnetic record, the base of the Kaiyumung Member must be ~3.5 Ma (scaling linearly between 3.58 and 3.33 Ma), but probably greater than 3.11 Ma, as only one reversed magnetozone has been reported (Powers 1980; see also McDougall and Feibel 2003). Details of the stratigraphic placement of the specimens within this

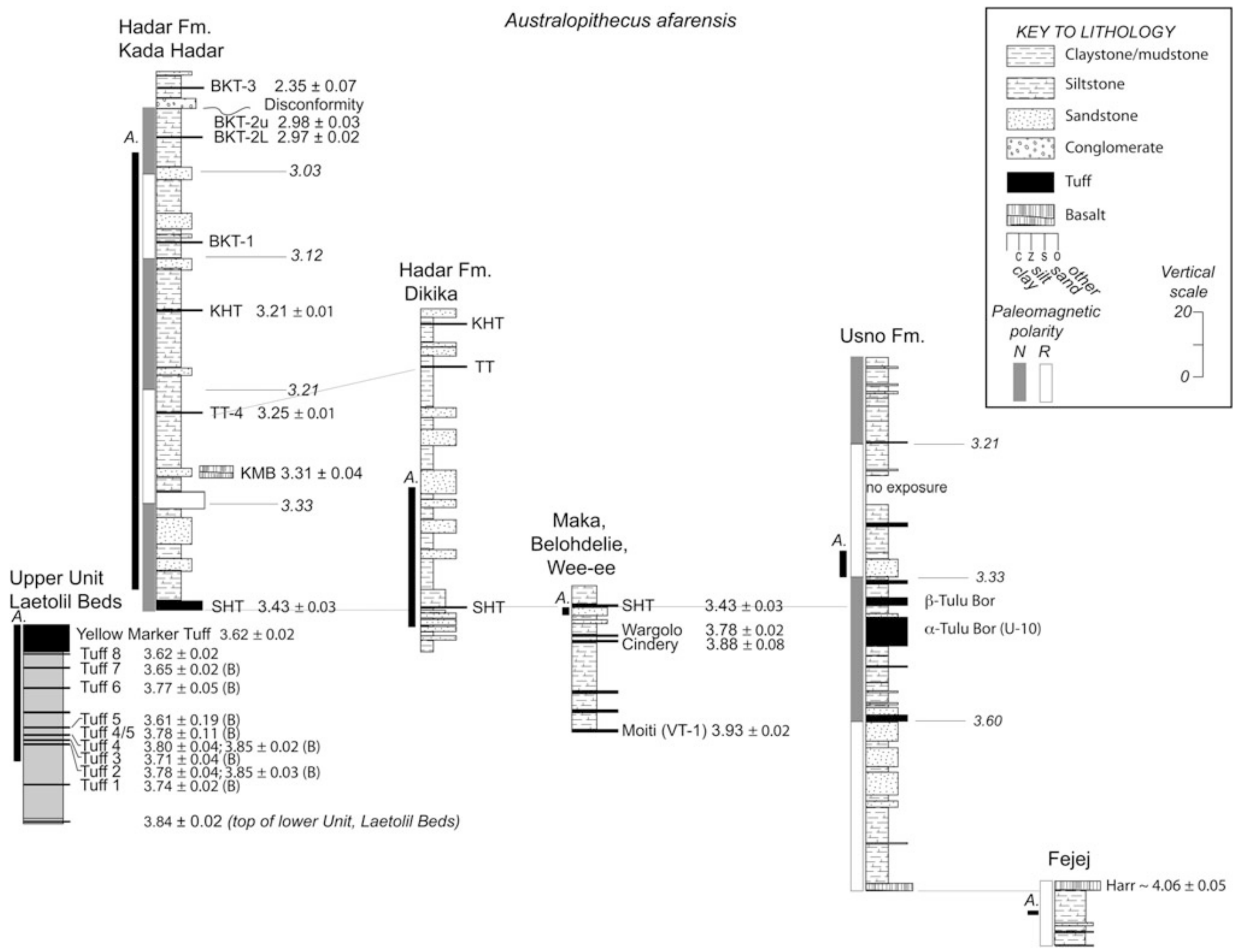
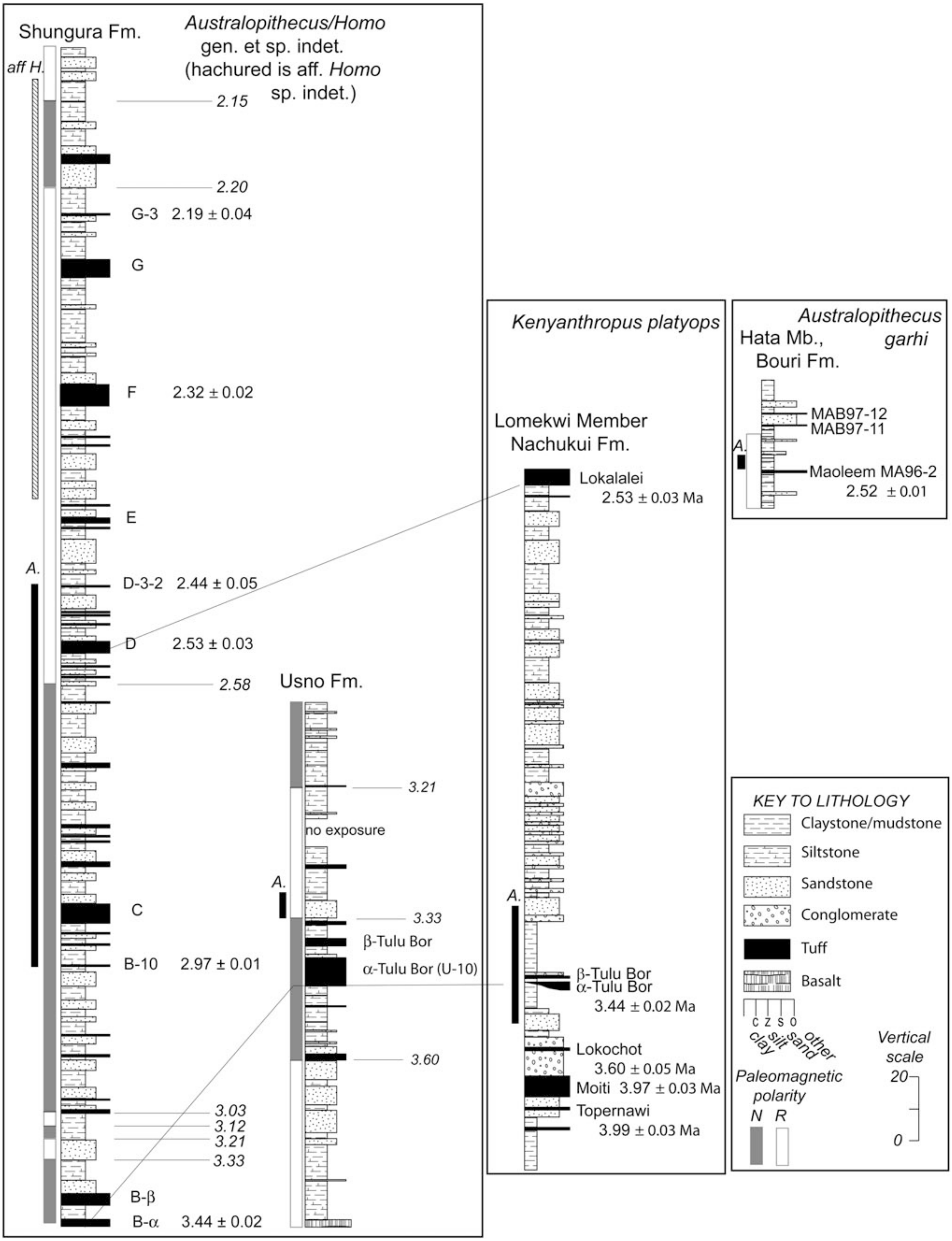


Fig. 2.3 Schematic stratigraphic columns for localities from which fossils ascribed to *Australopithecus afarensis* have been recovered. The column for the Laetolil Beds is after Hay (1987); that for Hadar is after Bonnefille et al. (2004); that for Dikika is after Wynn et al. (2006); that for Maka/Belohdelie/Wee-ee is after White et al. (1993); that for the Usno Formation is after de Heinzelin and Haesaerts (1983b); that for Fejej is after Kappelman et al. (1996). To the left of each stratigraphic column is a column showing paleomagnetic polarity (if known). Left of that is a *small solid bar* capped with "*A.*" showing the known range of fossils in each section. Dated units are identified by name, or if a name is lacking, by sample number; ^{40}Ar/^{39}Ar ages shown with error are recalculated to an age of 28.10 Ma for the Fish Canyon sanidine fluence standard (FCs) so that ages on all columns are comparable. Ages assigned from paleomagnetic transition boundaries are shown without error and italicized

member are lacking, so the specimens can only be said to lie between 3.11 and 3.5 Ma.

At Fejej, Ethiopia (Asfaw et al. 1991), there is evidence for the existence of a species of Australopithecus older than 4.0 Ma, but probably not more than 4.2 Ma, based on fossil material from a 25 m section below the Harr Basalt (Fleagle et al. 1991; Kappelman et al. 1996). On the basis of worn and fragmentary teeth they ascribed these specimens to *A. afarensis* following comparison with similar teeth from Hadar. The age of these specimens is nearly 400 ka older than *A. afarensis* at Laetoli. Provided the taxonomic attribution is correct (see Alemseged 2013)—and we stress that this determination should be based on morphology, not age—it would appear that *A. afarensis* overlaps temporally with *A. anamensis*. Thus, the temporal range of *A. afarensis*, insofar as it is currently known is from ~4.1 Ma at Fejej, to ~2.9 Ma at Hadar. On the other hand, Kimbel et al. (2006), and also White et al. (2006), argue for a linear progression from *A. anamensis* to *A. afarensis*. If the former view is correct, it would suggest that the two taxa were not a strictly anagenetic lineage, but overlapped for an extended time (see Kimbel et al. 2006). Therefore it is of the highest importance that the taxonomic identity of the specimens from Fejej be confirmed.


Shungura Fm.
Australopithecus/Homo gen. et sp. indet. (hachured is aff. Homo sp. indet.)
aff H.
2.15
2.20
G-3 2.19 ± 0.04
G
F 2.32 ± 0.02
E
A.
D-3-2 2.44 ± 0.05
D 2.53 ± 0.03
2.58
C
B-10 2.97 ± 0.01
3.03
3.12
3.21
3.33
B-β
B-α 3.44 ± 0.02
Usno Fm.
3.21
no exposure
A.
3.33
β-Tulu Bor
α-Tulu Bor (U-10)
3.60
Kenyanthropus platyops
Lomekwi Member
Nachukui Fm.
Lokalalei
2.53 ± 0.03 Ma
A.
β-Tulu Bor
α-Tulu Bor
3.44 ± 0.02 Ma
Lokochot
3.60 ± 0.05 Ma
Moiti 3.97 ± 0.03 Ma
Topernawi
3.99 ± 0.03 Ma
Australopithecus garhi
Hata Mb.,
Bouri Fm.
MAB97-12
MAB97-11
A.
Maoleem MA96-2
2.52 ± 0.01
KEY TO LITHOLOGY
Claystone/mudstone
Siltstone
Sandstone
Conglomerate
Tuff
Basalt
C Z S O
clay silt sand other
Paleomagnetic polarity
N R
Vertical scale
20
0

◀ **Fig. 2.4** Schematic stratigraphic columns for localities from which fossils ascribed to *Australopithecus/Homo* gen. et sp. indet., *Kenyanthropus platyops*, and *A. garhi* have been recovered. The column for the Shungura Formation (partial) is after de Heinzelin and Haesaerts (1983a); that for the Lomekwi Member of the Nachukui Formation is after Leakey et al. (2001) with additions from Harris et al. (1988b); that for the Hata Member of the Bouri Fm. is after de Heinzelin et al. (1999). To the left of each stratigraphic column is a column showing paleomagnetic polarity (if known). Left of that is a *small solid bar* capped with "*A*." showing the known range of fossils in each section. Dated units are identified by name, or if a name is lacking, by sample number; ^{40}Ar/^{39}Ar ages shown with error are recalculated to an age of 28.10 Ma for the Fish Canyon sanidine fluence monitor (FCs) so that ages on all columns are comparable. Ages assigned from paleomagnetic transition boundaries are shown without error and italicized

One specimen from Area 117 at Koobi Fora (KNM-ER 2602) is attributed to *A. afarensis* (Kimbel 1988). As Leakey et al. (1978) describe the specimen as lying just above 117/TIII (the Tulu Bor Tuff) it is thus <3.438 ± 0.023 Ma. No firm minimum age can be placed on this specimen, but it is likely that it lies below the Ninikaa Tuff (3.066 ± 0.017 Ma) exposed ~7 km to the southeast.

Australopithecus bahrelghazali

Brunet et al. (1995) reported an australopith mandible similar in morphology to *A. afarensis* from site KT-12, near Koro Toro in northern Chad. They state that the fauna from KT-12 "shows closest resemblances to collections from Hadar, Ethiopia with an approximate age of 3.0–3.4 Ma." Brunet et al. (1996) later assigned the specimen to a new species, *A. bahrelghazali*. The age estimate seems reasonable, and is consistent with placement of the specimen above a green pelite on which Lebatard et al. (2008) obtained a cosmogenic ^{10}Be/^{9}Be age of 3.58 ± 0.27 Ma.

Australopithecus garhi

This taxon was described by Asfaw et al. (1999) on the basis of remains from the Hata Member of the Bouri Formation in the Awash Valley, Ethiopia, lying just above the Maoleem Vitric Tuff (MOVT), with the geology described in an accompanying paper by de Heinzelin et al. (1999). The age of the MOVT is very well constrained at 2.52 ± 0.01 Ma, and strata below and above the MOVT are of reversed paleomagnetic polarity. This polarity agrees with the age determinations and places specimen BOU-VP-112 in the lowest part of the Matuyama Reversed Chron (2.58–2.20 Ma). The age suggested by de Heinzelin et al. (1999; 2.45–2.50 Ma) is well supported by the primary information. Cut marks on contemporary bone suggest that stone tools were in use by this or another creature from this time period.

Kenyanthropus platyops

Specimens collected at LO-6, from the Kataboi Member of the Nachukui Formation in the northern part of the Lomekwi drainage west of Lake Turkana are the only records of this taxon. The holotype is securely bracketed between the Tulu Bor Tuff (3.438 ± 0.023 Ma) and the Lokochot Tuff (3.596 ± 0.045 Ma), and has a probable age of 3.50 ± 0.05 Ma. The paratype lies 17 m above the Tulu Bor Tuff, and scaling on the basis of stratigraphic thickness between the Tulu Bor Tuff and the Lokalalei Tuff, has a probable age of 3.3 ± 0.1 Ma (Leakey et al. 2001). Currently there is no additional age control within the section at Lomekwi between the Tulu Bor Tuff and the Lokalalei Tuff, nor have materials been found that would be of use either for direct age measurement or correlation. Paleomagnetic stratigraphy through this section would be of considerable use in refining the age of the paratype.

Australopithecus/Homo gen. et sp. indet

Suwa et al. (1996) examined 48 mandibular postcanine teeth from members B through G of the Shungura Formation and divided them into robust and non-robust types. They consider the robust specimens from "from Members C through F (~2.9–2.3 Ma) to represent *A. aethiopicus*." Sometime during lower Member G (~2.3–2.0 Ma), the derived morphology of *A. boisei* appears. Of course, neither *A. aethiopicus* nor *A. boisei* are even considered to belong to genus *Australopithecus* by many workers, instead being assigned to *Paranthropus*. By contrast, the early non-robust types from the Shungura Formation were considered to be indeterminate to genus or species, but Suwa et al. (1996) consider the non-robust types collected from stratigraphic levels above the base of Member E (~2.4 Ma) as "aff. *Homo* sp. indet." This may be the material from the Shungura Formation that White (2002) attributed to *A. garhi*. These are included in Fig. 2.4 for the benefit of those workers who may have interest in their age. Grine et al. (2006) consider specimens from the Usno Formation (fossiliferous units are within the Mammoth event; thus

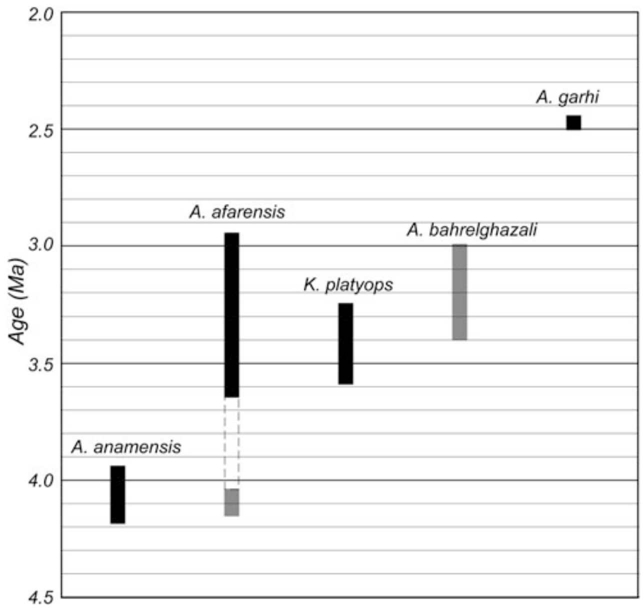


Fig. 2.5 Temporal distribution of *Australopithecus* species. The bar for *A. bahrelghazali* is shown in *gray*; it is based on biochronology and a ^{10}Be/^{9}Be age determination. The bottom part of the bar for *A. afarensis* is shown with a *dashed line* for the time interval where no specimens are known, with the record for Fejej filled in *gray* to emphasize the importance of confirming the taxonomic attribution of those specimens

3.207–3.33 Ma in age) and Member B (3.438 ± 0.023 to ~2.9 Ma) of the Shungura Formation as part of the paradigm of *Praeanthropus afarensis*, although one anonymous reviewer is "very skeptical" of these assignments. For this reason we have placed the Usno Formation sections on both Figs. 2.2 and 2.3.

Summary

Of the taxa considered here, *A. anamensis* is known to lie between 3.8 and 4.2 Ma, *A. afarensis* existed from arguably as old as ~4.1 but definitely as old as 3.65–2.97 Ma. Whether the two species were in fact coeval critically depends upon the assignment of the Fejej teeth to *A. afarensis*. *Kenyanthropus platyops*, too, overlaps temporally with part of this time, as does *A. bahrelghazali*, which appears to be reasonably placed in the range of 3.0–3.5 Ma. Finally, an age for *A. garhi* of 2.45–2.50 Ma is quite well supported. The age range for the latter taxon is perhaps artificially restricted because it is known from only a single site. This information is summarized in Fig. 2.5.

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Chapter 3
A Multi-Disciplinary Perspective on the Age of *Australopithecus* in Southern Africa

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Abstract This paper presents a review of, and new data concerning, the age of *Australopithecus* in southern Africa. Current dating suggests that Makapansgat Limeworks is the oldest hominin deposit in southern Africa, with *Australopithecus africanus* dating to between 3.0 and 2.6 Ma. The Taung Child *A. africanus* fossil from Taung is most likely penecontemporary with the Makapansgat material between 3.0 and 2.6 Ma. *A. africanus* from Sterkfontein Member 4 is estimated to date to between 2.6 and 2.0 Ma, with the Sts 5 specimen dating to around 2.0 Ma. The *A. africanus* deposits from Gladysvale are most likely contemporaneous with the Sterkfontein group with an age between 2.4 and 2.0 Ma. The potential second species of *Australopithecus*, StW 573 from the Silberberg Grotto at Sterkfontein, is most likely dated to between 2.6 and 2.2 Ma. As such, StW 573 is contemporary with *A. africanus* fossils from Member 4 and suggest that two contemporary *Australopithecus* species occurred at Sterkfontein between ~2.6 and 2.0 Ma. Based on the presence of *Equus* the *A. africanus* fossils from Jacovec Cavern also likely date to <2.4 Ma. The new *Australopithecus sediba*-bearing deposits of Malapa date to 1.98 Ma and suggests that three different species of *Australopithecus* occur in South Africa between 2.3 and 1.9 Ma. Given these dates, *A. africanus* represents the oldest southern African hominin species being found in two temporally distinct groups of sites, Makapansgat/Taung and Sterkfontein/Gladysvale, and *A. sediba* is the youngest species at ~1.98 Ma. However, if StW 53 is also *Australopithecus,* as some have suggested, then this genus survives to younger than 1.8 Ma in South Africa. *Australopithecus* thus lasted for a significant period of time in southern Africa after the genus is last seen in eastern Africa (*Australopithecus garhi* at ~2.5 Ma). This new dating indicates that the South African *Australopithecus* fossils are younger than previously suggested and are contemporary with the earliest suggested representatives of *Homo* (~2.3 Ma) and *Paranthropus* (2.7–2.5 Ma) in eastern Africa.

Keywords *Australopithecus africanus* • *Australopithecus sediba* • Sterkfontein • Makapansgat • Gladysvale • Taung • Magnetostratigraphy • Electron spin resonance • Uranium-lead dating

Introduction

Remains attributed to the genus *Australopithecus* have been recovered from nine deposits at five sites in South Africa (Fig. 3.1): (1) Member 3 (MAK/M3) and Member 4 (MAK/M4) of the western (Main Quarry) sequence of the Makapansgat Limeworks; (2) Sterkfontein Member 4 (STER/M4), the Silberberg Grotto (STER/SB) and the Jakovec Cavern (STER/JV); (3) the Gladysvale Breccia Dumps (GVBD); (4) the Taung Dart Deposits (TAUNG/DD); and (5) Malapa Facies D and perhaps also Facies E (only the fossils from Facies D have so far been classified as *Australopithecus*). Taung represents the most westerly deposit and Makapansgat the most northern and eastern with the

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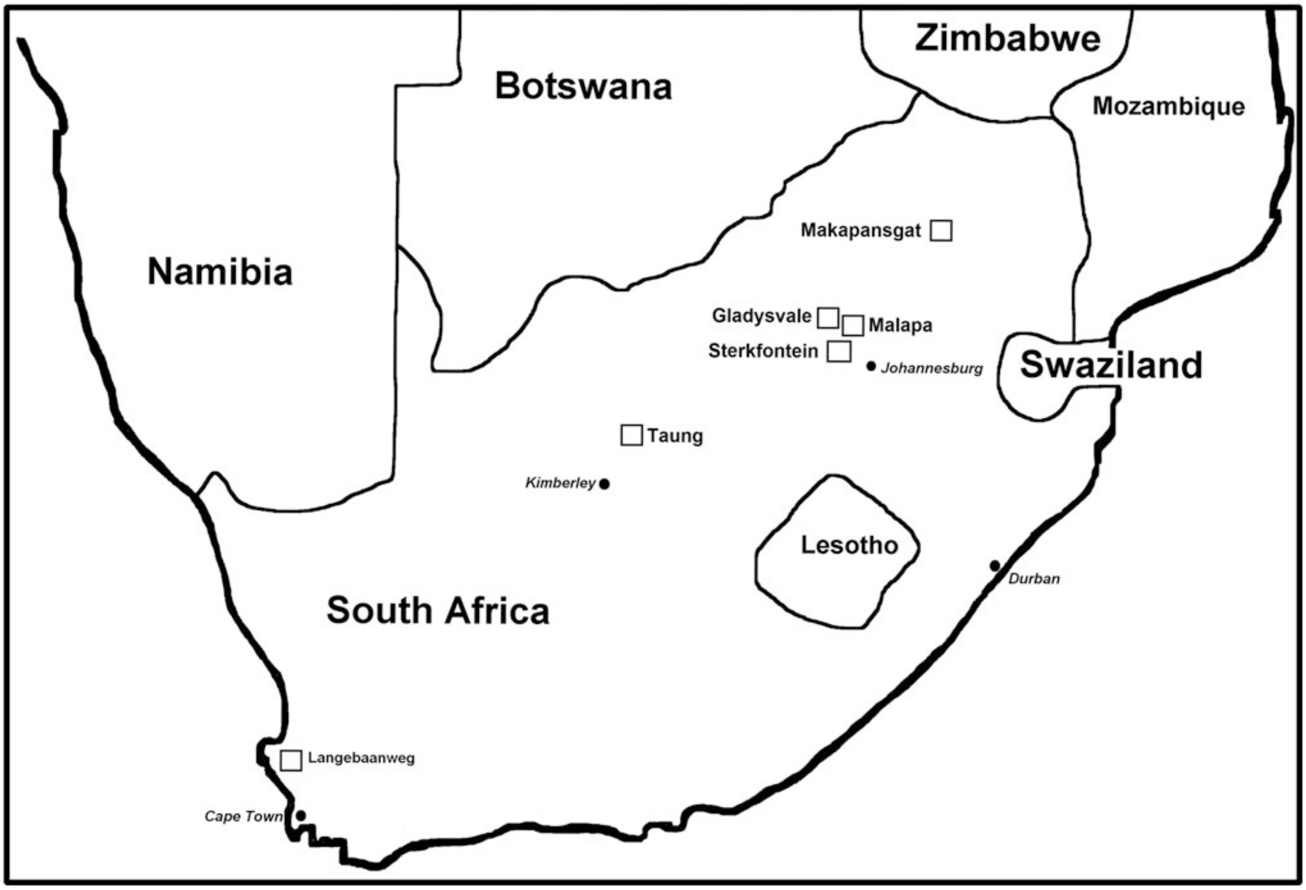

Fig. 3.1 Location of the South African hominin-bearing sites referred to in the text (after Herries et al. 2006). *Australopithecus* has been recovered from Makapansgat, Sterkfontein, Gladysvale, Malapa, and Taung

majority coming from the Cradle of Humankind World Heritage Site karst deposits between Johannesburg and Pretoria (Fig. 3.1). The majority of these fossils have been assigned to *Australopithecus africanus*, although some (Kimbel and White 1988; Clarke 1994, 1998; Schwartz 1997; Lockwood and Tobias 2002; Partridge et al. 2003; Clarke 2013) consider specimens from STER/M2 (StW 573; "littlefoot"), as well as some specimens from MAK/M3 and STER/M4, as potential members of a second, as yet undefined *Australopithecus* species. Clarke (2008) suggests that two different species exist at both Sterkfontein and Makapansgat, while others (Crawford et al. 2004) lean towards the idea that the Makapansgat and Sterkfontein fossils represent different species. Recently, Berger et al. (2010) defined a new species *Australopithecus sediba* from Malapa. How the *A. sediba* fossils may relate to the as yet undefined "second species" remains to be seen. If different from the StW 573 *Australopithecus* fossil and the bulk of the *A. africanus* fossils then three different species of *Australopithecus* may be represented in southern Africa (not including those defined by some researchers as *Paranthropus*).

All of the specimens have come from ancient, relict cave fills (paleocave deposits) and a number of fundamental problems have hampered their age assessment (Table 3.1). This chronological uncertainty has made their phylogeny difficult to assess. The last decade or so has seen the extension of the conventional age range of several dating techniques that can be applied to caves. Recent research has applied these methods to several paleocave sites in southern Africa and has shown that these methods are capable of producing internally consistent ages that are broadly similar to independent faunal estimates. Detailed results of paleomagnetic, electron spin resonance (ESR)[1] and uranium-lead (U-Pb) analysis are provided in Curnoe (1999), Herries (2003), Walker (2005), Walker et al. (2006), Pickering (2009), Dirks et al. (2010), Pickering et al. (2010, 2011a), Pickering and Kramers (2010), and Herries and Shaw (2011). This paper provides an overview of these data

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[1] All ESR age estimates in this analysis are based on a linear uranium uptake model. Further analysis is needed, particularly (TIMS) U-series analysis combined US/ESR age estimates, to confirm these ESR age estimates (as per Curnoe et al. 2001).

Table 3.1 Problems in reconstructing the depositional history and age of the southern African hominin sites

Biochronology

- Assumption of synchrony in evolutionary events among eastern and southern African species
- The vast majority of biochronological studies have been undertaken on ex situ material from miners' dumps with unknown provenance
- Due to the calcified nature of many of the cave deposits, excavations have been concentrated on decalcified material and makondos where mixing of different aged deposits is likely

Palaeomagnetism

- Poor understanding of the magnetic mineralogy of the deposits and acquisition of remanence, and suitability of deposits to paleomagnetic analysis. Work by Jones et al. (1986) showed that many samples gave random directions of magnetization at some sites. This is due to the fact the deposits are formed by collapse and so the magnetic minerals lie in randomized directions. While this is true for breccias, stable polarities can still occur in speleothem and fluvial deposits
- Inability to measure weak remanence when the first work was done in the 1970s
- Complex cave stratigraphies and short disconnected sequences

Cave formation

- Assumption of layer-cake stratigraphy in all the cave sytems deposits
- Poor understanding of the often short and unconnected stratigraphic sequences within the caves and over-interpretation of ambiguous stratigraphic relationships
- The use of a member system that has been used to classify sedimentological types of deposits rather than sequential sequences (which is the basis of a member system)
- Poor understanding of cave formation and development. The same model of cave formation and life history is used for every cave from low to high topography karst. There is evidence for the extensive re-use of palaeokarstic conduits over vast periods of time

Radiometric dating

- Lack of dating techniques that cover the Plio-Pleistocene boundary
- Lack of material applicable to radiometric dating

coupled with up-to-date biochronological and stratigraphic studies where possible. This study places an emphasis on the radiometric dates (where they occur), biochronological analysis of in situ recovered fauna, and paleomagnetic polarity records of deposits with exposed stratigraphic linkage. The overall aim is to produce a new chronology for the sites independent of faunal comparisons with eastern Africa.

The Sites

Sterkfontein

Sterkfontein Caves is one of the most complex fossil sites in the world with deposition occurring at the site throughout the entire Quaternary (last 2.6 Myr) and perhaps longer. It is also one of the richest and longest excavated hominin sites with a history of excavation spanning over 60 years. This has caused immense confusion with regards to the age and the stratigraphy of the deposits, as well as the provenience of some of the fossils. Herries and Shaw (2011) undertook Palaeomagnetic analysis at Sterkfontein using the flowstone proportion of these deposits (as per Partridge et al. 1999). This was done due to suggested problems associated with the palaeomagnetic analysis of certain clastic deposits at Sterkfontein (Jones et al. 1986), mainly related to brecciation and remanence acquisition of collapse deposits (see Table 3.1). Herries and Shaw (2011) have since done further work on the deposit including some limited work on the clastic deposits. Prior faunal studies have suggested an age estimate of >2.6 Ma for STER/M4 (Vrba 1982, 1988) and based in part on the assumption that STER/M4 faunas accumulated before a period of major global cooling at around this time (see Kuman and Clarke 2000; Vrba 2000). However, all speleothem deposits from STER/M4 record reversed directions of polarity (Figs. 3.2, 3.3, 3.4). Moreover, fine grained siltstone deposits from the edge of the sample blocks show consistent magnetic polarity to both the speleothem samples and to each other, suggesting that the clastics and speleothem were deposited at a similar period (Herries and Shaw 2011). The period between 3.03 and 2.58 Ma had a normal magnetic polarity and so STER/M4 must date to >3.03 or <2.58 Ma (Figs. 3.2, 3.3, 3.4). Few faunal estimates suggest a date of >3.0 Ma for STER/M4; however, some have suggested a date of <2.6 Ma (Delson 1988; Vrba 1995; Berger et al. 2002). Delson (1988) has suggested that the presence of *Papio izodi* and *Papio hamadryas robinsoni* indicate a date of around 2.5 Ma. The occurrence of a juvenile *Metridiochoerus shawi* mandible (sensu Cooke 2005; White et al. 2006) in the deposits suggests an age less than 2.85 Ma, while the occurrence of *Equus* implies a date <2.4 Ma (2.41–2.30 Ma; FAD of Equus in Member F of the

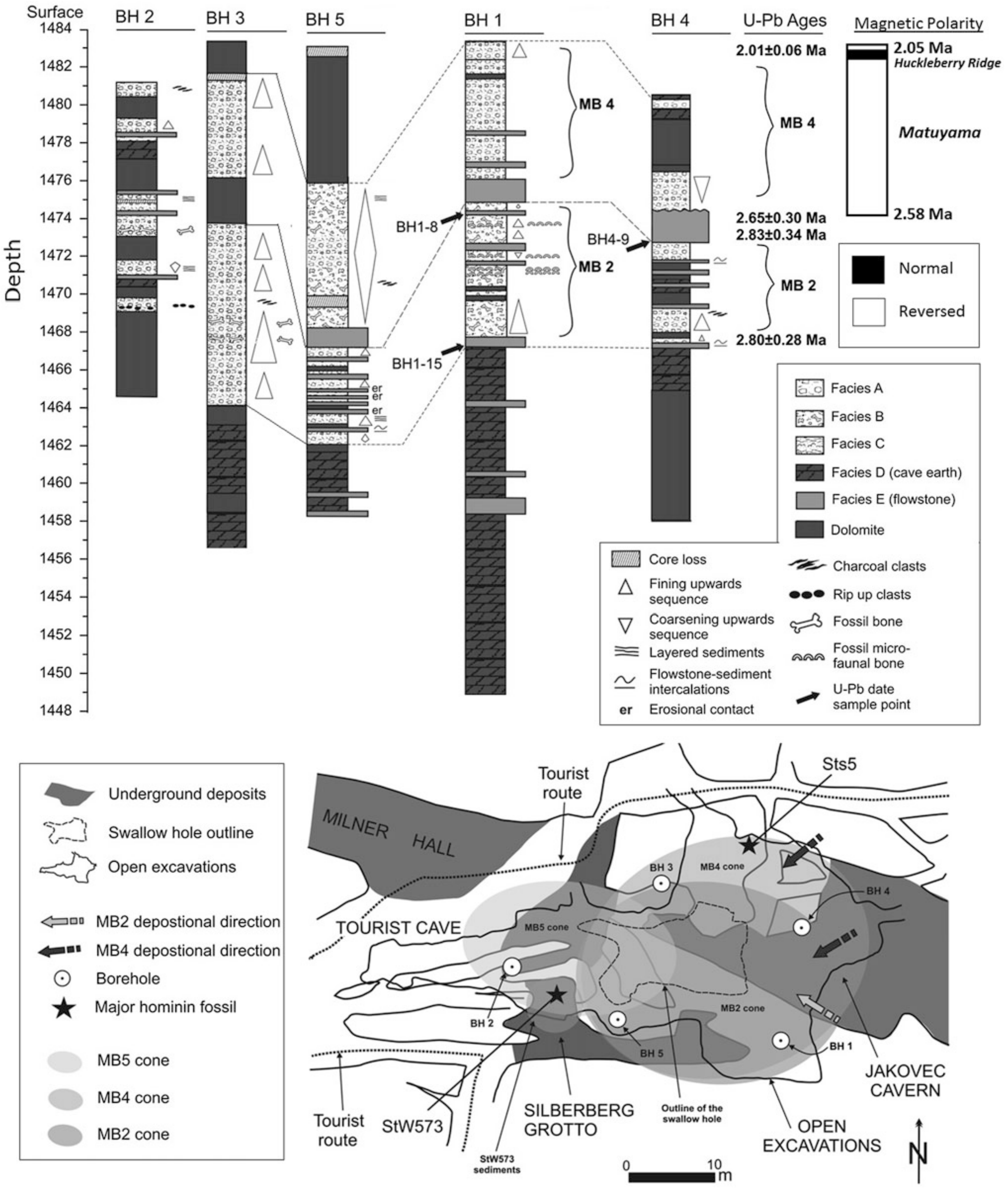

Fig. 3.2 Proposed revised stratigraphy of Sterkfontein based on Pickering and Kramers (2010). The relationship of these bore cores to the StW 573 infill in the Silberberg Grotto remains questionable

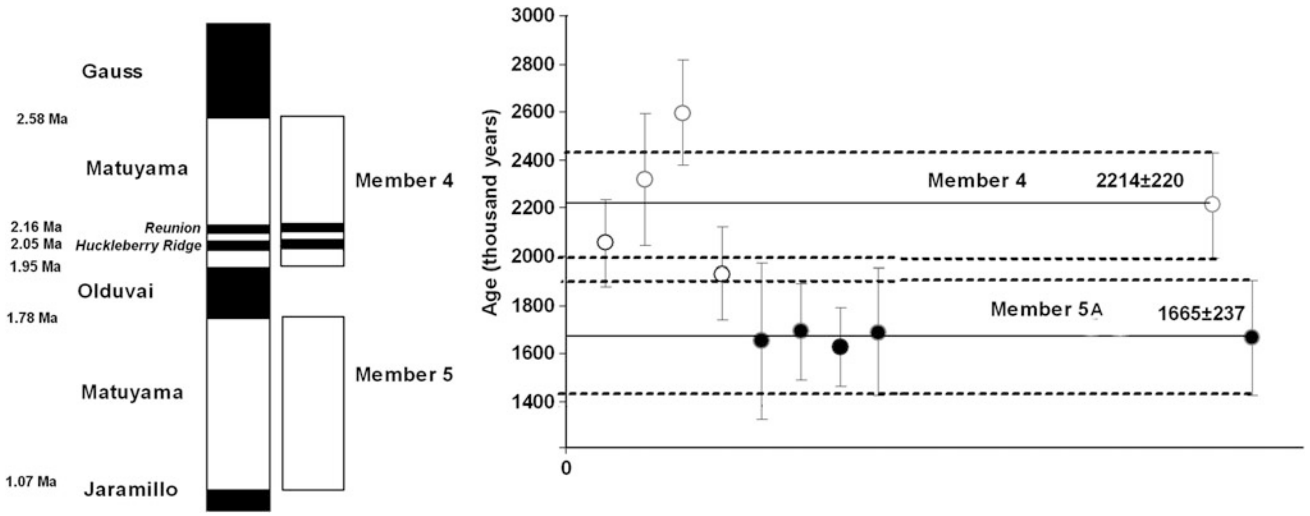

Fig. 3.3 ESR dates of Curnoe (1999) for Sterkfontein correlated against the magnetostratigraphy of Herries (2003). The ages shown are the mean for all the samples from STER/M4 and STER/M5A (after Herries et al. 2009)

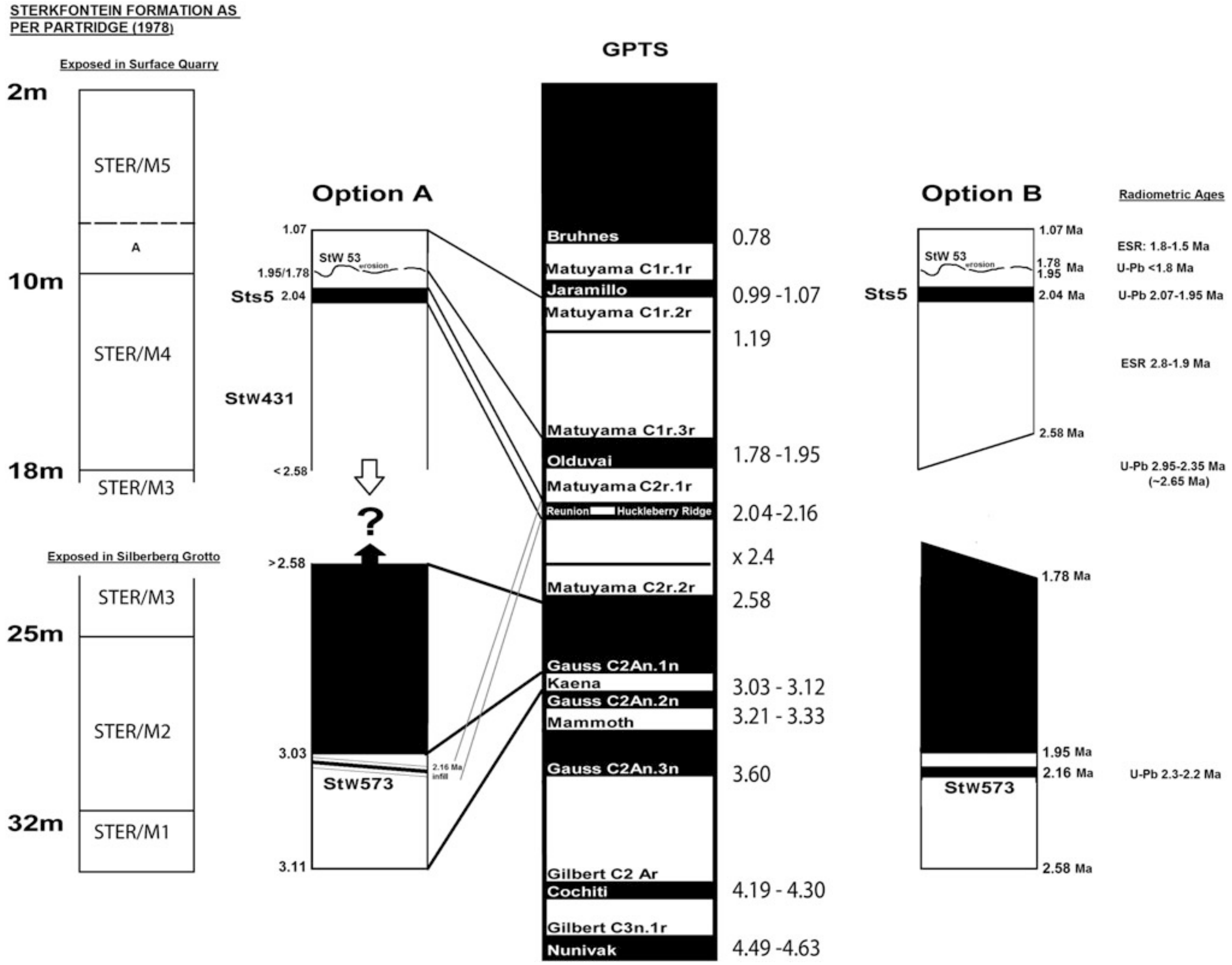

Fig. 3.4 Magnetostratigraphy of Sterkfontein based on data of Herries and Shaw (2011). Option A based on the lithostratigraphy of Partridge (1978). Option B based on correlation with uranium-lead dates of Walker (2005), Walker et al. (2006), and Pickering and Kramers (2010)

Shungura Formation; Brown et al. 1985; Geraads et al. 2004). Overall, these faunal estimates support the placement of this period of reversed polarity in the beginning of the Matuyama Chron between 2.58 and 1.95 Ma.

The occurrence of *Equus* and *P.h. robinsoni* [identified by Clarke (2002a, b) as possibly representing *Parapapio broomi*] in STER/M4 has been suggested to be due to the intermixing of younger teeth into the deposit, perhaps from STER/M5 (Vrba 1982; Clarke 2002a, b). Such an interpretation seems to be supported by the wide range of ESR dates from the STER/M4 deposits published by Blackwell (1994) and Schwarcz et al. (1994). Schwarcz et al. (1994) obtained an average age of 2.1 ± 0.5 Ma (2.6–1.6 Ma), with major peaks in the bimodal distribution at 1.72 ± 0.31 Ma (2.03–1.41 Ma) and 2.37 ± 0.29 Ma (2.66–2.08 Ma). Additional ESR analysis by Curnoe (1999) gave ages of 1.23 ± 0.16, 1.93 ± 0.19, 2.06 ± 0.18, 2.32 ± 0.28, 2.60 ± 0.22, and 3.09 ± 0.27 Ma for samples from STER/M4 (Fig. 3.3). This provided a mean weighted estimate of between 2.80 and 1.88 Ma, slightly broader than the older distribution of Schwarcz et al. (1994; 2.66–2.08 Ma). The broader age range is partly a product of a single tooth from the Type Site that suggests that some of the deposits there must be 2.8 Ma or older. This is the area first described as having Member 3 deposits exposed on the surface by Partridge (1978). This is slightly at odds with the reversed polarity for the Member 4 deposits and may simply be an issue of sampling different areas of the Member 4 deposit. Some support for an older deposit in the area of Member 4 is shown by ages of ~2.8 Ma by Pickering and Kramers (2010) for a deposit underneath Member 4, that they term Member 2, but traditionally would have been described as Member 3 by Partridge (1978, 2000).

Another tooth thought to have derived from STER/M4 gave an age of 1.16 ± 0.12 Ma (1.28–1.04 Ma). The teeth from the earlier ESR studies of STER/M4 come from excavated museum collections and so some anthropogenic mixing during earlier excavations, when the stratigraphic sequence was less well defined is likely. Moreover, the STER/M4 faunal assemblage represents the sampling of ex situ breccia blocks and various in situ excavations over 75 years (Reynolds and Kibii 2011). The teeth with younger ages (<2.0 Ma) are consistent with ESR sampled teeth securely derived from STER/M5 (Herries et al. 2009; Herries and Shaw 2011) and the exact relationship of STER/M4 and STER/M5 is hard to define in some areas. The young tooth from the Curnoe (1999) study comes from in situ excavations and apparently suggests that geological mixing of the fossils has occurred due to erosion of underlying deposits (STER/M4) before and during subsequent deposition of STER/M5. This may have caused intrusive pockets of breccia that may have included younger teeth, particularly within makondoes (solutional tubes around tree roots). Moreover, the standard practice of excavating un-calcified deposits will further exacerbate the problem, especially if from close association with makondo in-fills. Such mixing processes are shown by the study of Lincoln Cave at Sterkfontein where Acheulean style stone tools occur within the Middle Stone Age deposits (Reynolds et al. 2007).

If all the mixing noted in three separate ESR studies is due to geological processes, then this has major implications for the study of all the fossils from these deposits, including the hominins. However, the younger in situ tooth from the Curnoe (1999) study comes from an area close to the interface between STER/M4 and STER/M5 and as such it seems more likely that the tooth simply derives from within STER/M5 in an area close to the contact (Herries and Shaw 2011). The age of the tooth (1.23 ± 0.16 Ma) is consistent with other teeth from this level within the STER/M5 deposits (Herries et al. 2009; Herries and Shaw 2011), as is the 1.16 ± 0.12 Ma age from the earlier study. This suggests that some mixing has occurred although the exact reason, be it geological or due to excavation practices, is difficult to access. Kuman and Clarke (2000) suggest that such mixing is the reason for the handful of *Equus* fossils that occur within STER/M4 both due to the processes of blasting during earlier excavations and natural mixing. While the younger ages now suggested for STER/M4 do not necessarily rule out the occurrence of *Equus*, whose first appearance date (FAD) in Africa is <2.4 Ma, the only way to definitively solve the issue of intermixing of *Equus* teeth would be to directly date these fossils. *Equus* certainly occurs at Malapa soon after 2 Ma (Dirks et al. 2010; Pickering et al. 2011a) and has also been defined in Jackovec Cavern at Sterkfontein (Reynolds and Kibii 2011).

A younger date for STER/M4 is further supported by the occurrence of one or perhaps two very short normal polarity episodes in a flowstone deposit capping the majority of STER/M4, except the area containing the Sts 5 ("Mrs. Ples") specimen, which formed at roughly the same time. These short polarity periods are suggested to represent one or both of the documented events or excursions in the magnetic field between 2.58 and 1.95 Ma. The best documented and longest is the Réunion event that occurs at ~2.16 Ma and the shorter Huckleberry Ridge event at ~2.04 Ma (Carlut et al. 1999; Kidane et al. 2007). A third is the pre-Olduvai event at ~1.98 Ma (Roberts 2006; Pickering et al. 2011a, b). The age of these excursions remains imprecise due to their documentation in different recording mediums from sea cores to sedimentary sequences and lava flows, each dated via different methods with different accuracies. Their documentation in speleothem in South Africa provides the possibility to directly date the excursions using U-Pb and help refine their ages. At Malapa a reversal in speleothem has been dated to 2.026 ± 0.021 Ma (2.05–2.01 Ma) and is interpreted as representing the Huckleberry Ridge event at ∼2.04 Ma. The reversals in the Sterkfontein flowstone are suggested to represent two of these events between ∼2.16 and 1.98 Ma.

Recent U-Pb dating of this flowstone has provided an age of 2.01 ± 0.05 Ma (2.05–1.96 Ma; Pickering and Kramers 2010), which correlates with the Huckleberry Ridge at ∼2.04 Ma. Because the flowstone formed at the same time as the Sts 5 *A. africanus* fossil was deposited, an age of ∼2.04 Ma is suggested for this fossil. U-Pb dating of a basal flowstone deposit from a core into the STER/M4 deposits gave an age of 2.65 ± 0.30 Ma (2.95–2.35 Ma) and further confirms that the deposit is not older than 3.0 Ma. Taken together (Table 3.2) the U-Pb ages (2.95–1.95 Ma), ESR ages (2.80–1.88 Ma), the palaeomagnetism (<2.58–2.05 Ma) and the fauna (<2.85 to <2.36 Ma) all indicate a "best fit age" of between 2.6 and 2.0 Ma for the majority of the STER/M4 deposit from which the *A. africanus* remains have been excavated (Figs. 3.2, 3.4), with Sts 5 dating to ∼2.04 Ma. There is a further suggestion that an older fossil-bearing deposit dated to at least 2.8 Ma occurs below the main Member 4 breccia deposits. These data would also appear to suggest that STER/M4 formed over a very long time period of time covering 400–800 kyr or more. This is further indicated by the spread of ESR ages for the STER/M4 deposit compared to the very refined ages of STER/M5a, from which the StW 53 fossil was recovered (see below).

Kuman and Clarke (2000; Clarke 2008, see also Clarke 2013) believe that STER/M5A of Partridge (1978, 2000)—referred to by them as the "StW 53 infill"—is also part of STER/M4. They suggest that StW 53 is an *Australopithecus* rather than *Homo*, as most often classified (Curnoe and Tobias 2006; Smith and Grine 2008; Curnoe 2010). ESR dates for STER/M5A (Fig. 3.3; Herries et al. 2009; Herries and Shaw 2011) clearly indicate that this deposit is distinct in age from STER/M4. When combined with the palaeomagentic data it provides an age estimate of between 1.8 and 1.5 Ma (Herries and Shaw 2011). Considering the reliable age correlation between ESR, U-Pb and palaeomagnetism for STER/M4 there is little reason to discount using a linear up-take model for ESR ages from STER/M5. Confusion over the reliability of ESR age estimates (see Gilbert and Grine 2010, for an example) from this deposit have persisted due to the inclusion of a tooth from decalcified deposits in the study of Curnoe (1999), which gave a much younger age than teeth from in situ breccia. Teeth from decalcified deposits are going to have an extremely complex uranium uptake and decay history and this is suggested to be the reason for the discrepancy in ages of this one sample. All other teeth from the deposit give consistent ages. An age of <1.8 Ma is also suggested for STER/M5 based on U-Pb dating of a flowstone that formed before the deposition of STER/M5 at 1.812 ± 0.064 Ma (1.88–1.77 Ma; Pickering and Kramers 2010).

Table 3.2 Combined age estimates for the South African *Australopithecus* fossils

Sterkfontein Member 4 (Sts 5)	2.6–2.0 Ma ∼2.04 Ma
Palaeomagnetism	2.58–1.95 Ma
U-Pb	2.95–1.96 Ma
ESR	2.82–1.88 Ma
Fauna	<2.85 to <2.36 Ma
Sterkfontein SB (StW 573)	2.6–1.8 Ma (2.6–2.2 Ma)
Palaeomagnetism	2.58–1.78 Ma
U-Pb	2.44–2.06 Ma
Makapansgat Limeworks (Member 3)	2.9–2.6 Ma
Palaeomagnetism	3.03–2.58 Ma
Fauna	2.85–2.50 Ma
Gladysvale	2.4–2.0 Ma
ESR	2.53–2.01 Ma
Fauna	<2.36 to <1.89 Ma
Malapa D/E	∼1.98 Ma
Palaeomagnetism	1.95–1.78 Ma or ∼1.98 Ma
U-Pb	2.05–1.91 Ma
Fauna	2.36– ∼1.5 Ma
Taung	3.0–2.6 Ma
Fauna	2.6–2.4 Ma
Palaeomagnetism	3.03–2.58 Ma

As such, STER/M5A should either not be considered as part of the STER/M4 deposit as suggested by Kuman and Clarke (2000; Clarke 2008, see also Clarke 2013) or it should be expressly noted that it extends the younger age of the STER/M4 deposit to at least 1.8 Ma, if not younger. A safer suggestion may be to classify this deposit (StW 53 infill) as its own separate entity, intermediate in age (1.8–1.5 Ma), between STER/M4 (2.6–2.0 Ma) and STER/M5 (1.6–1.1 Ma; Herries and Shaw 2011). The older ∼2.8 Ma deposit below STER/M4 should perhaps then also be classified as another separate entity. Partridge (1978, 2000) would consider this Member 3, while Pickering and Kramers (2010) refer to it as Member 2. There is a potential tisue with both of these suggestions. Both Members 2 and 3 were originally classified by Partridge (1978) based on exposures in the Silberberg Grotto. As will be discussed below, there is no clear evidence of the association of the deposits in the cores and surface exposures and those exposed in the Silberberg Grotto and so a new neutral name should probably be adopted.

Until the 1990s, STER/M4 and STER/M5 were the only well-described fossil assemblages from Sterkfontein. Controlled excavations in the Silberberg Grotto deposits (STER/SB) have only recently been undertaken with the discovery of the nearly complete StW 573 hominin (Clarke 1999; Pickering et al. 2004) and collection of other hominin material from the Jakovec Cavern (Partridge et al. 2003). A number of incompatible age estimates have recently been proposed for the StW 573 infill (STER/SB: formerly referred to as Member 2; Clarke and Tobias 1995; McKee 1996; Tobias and Clarke 1996; Clarke 1998, 2002a, b; Partridge et al. 1999, 2003; Kuman and Clarke 2000; Berger et al. 2002; Walker et al. 2006). Biochronological age estimates have varied from 3.5 to 3.0 Ma (Clarke and Tobias 1995; Partridge et al. 2003) to an estimate of <3.0 Ma by Berger et al. (2002), who also suggested that the deposits might date to sometime between 1.95 and 1.07 Ma. A pre-3.0 Ma age for STER/SB has been suggested on the basis of the occurrence of a specimen of *Chasmaporthetes* (Turner 1997; Partridge et al. 2003) with a primitive dental morphology similar to that of *Chasmaporthetes australis* from Langebaanweg, which has been estimated to date to ~5.0 Ma (see Hendey 1981; Franceschini and Compton 2004; Roberts 2006). In contrast, McKee (1996) notes that species from the Silberberg also occur in STER/M4, but not MAK/M3, making it unlikely that Silberberg is as old as MAK/M3 (3.03–2.58 Ma; Herries 2003; and see below). Recently, Pickering et al. (2004) noted that ex situ fauna previously attributed to STER/SB might have inadvertently included materials from another deposit and they provided a much more limited faunal list, most of which is found in STER/M4 (Kibii 2004, Reynolds and Kibii 2011) or younger deposits.

Previous palaeomagnetic analysis suggested an age between <4.18 and >2.58 Ma for STER/SB (Partridge et al. 1999, 2000). The palaeomagnetic sequence starts with a long period of reversed polarity at its base that was originally estimated to date to the end of the Gilbert reversed polarity chron between 4.19 and 3.60 Ma (Fig. 3.4). The hominin fossil StW 573 was suggested to lie in calcified deposits between a speleothem with a normal polarity and a block sample with reversed, intermediate and normal polarities. Stratigraphically above this, a reversed polarity block sample occurs and then a long period of normal polarity in what Partridge et al. (1999) term as the base of STER/M3. This sequence was correlated to the Gauss normal polarity period with the reversed periods representing the Kaena (3.12–3.03 Ma) and Mammoth (3.33–3.21 Ma) events. The StW 573 skeleton was thus dated to between 3.60 and 3.21 Ma, with an estimated age of ~3.3 Ma based on depositional rates (Partridge et al. 1999). However, this was based on: (1) the original faunal age assessment of >3.0 Ma; (2) the depth of STER/SB below STER/M4; and (3) the assumption of a complete vertical column of deposits with a "layer-cake"-like stratigraphy.

As stated above, the first assumption is unreliable. The third assumption is highly unlikely for a laterally constrained, complex, ancient, and still active karstic system like Sterkfontein. As there are no visible stratigraphic sections that can be used to link the various "members", the interpretation of the stratigraphy has relied on borecores. The member system that is most often utilised in South Africa (Partridge 1978, 1979, 2000; Brain 1993) has a tendency to record types of stratigraphic deposit (i.e., calcified red silts, pink block breccia, etc.) rather than a defined series of stratigraphically linked deposits that formed sequentially (which is the geological basis of a member system). In other studied systems, the different sedimentological deposits (or members) are now interpreted to have formed at the same time, with certain deposits forming throughout almost the entire life history of the cave (Latham et al. 1999, 2002, 2003; see below). The same paleokarstic conduits have been reused numerous times over the last few million years and cavities tend to form at various levels at the same or different time periods and can even form within earlier deposits (as at Gladysvale; see below). This is highlighted by the fact that modern deposits are being deposited below STER/M4 and at a similar level to STER/SB (Herries, personal observation). Moreover, recent studies of Lincoln Cave by Reynolds et al. (2007) show that Middle Pleistocene aged cave deposits occur at the same elevation as STER/M4 and potentially include reworked early Acheulean material from STER/M5.

Recently, Pickering and Kramers (2010; Fig. 3.2) suggested through a re-analysis of the borecores that deposits referred to as STER/M3 likely represent the lateral extensions of STER/M4. The exact three dimensional relationships of the STER/SB deposits to STER/M4 remain unresolved but Pickering and Kramers (2010) suggest a complex superposition of talus cones of different ages (Fig. 3.2). Given these complications it seems that a renaming of the various Sterkfontein deposits may be needed to avoid future confusion.

Determination of the age of STER/SB was further complicated by cosmogenic isotope ages of around 4.2–3.8 Ma (Partridge et al. 2003; Muzikar and Granger 2006), which would be very unlikely given the original palaeomagnetic data and expected depositional rates. Moreover, the depositional history and geomorphology of the deposits is complex, which can have a significant effect on the age calculation if reburial has occurred or two different aged sources of quartz have been mixed. It seems likely that mixing of quartz grains of different ages has occurred and that the cosmogenic burial ages are an overestimation. Similar, ~4 Ma cosmogneic nuclide burial ages were also derived for the Jakovec Cavern fossil deposits (STER/JC), which are, like Silberberg, deep within the Sterkfontein system. While there are no comparative radiometric or palaeomagnetic ages for these deposits, there are a number of things that suggest that the Jakovec Cavern deposits are not 4 Ma. Firstly, Clarke (2008) suggests that the hominin remains from STER/JC represent *A. africanus*.

If 4 Ma, then this would make the fossils at least 1 Myr older than the oldest known fossil of this species and contemporary with *Ardipithecus* or *A. anamensis* in East Africa, something that seems unlikely given *A. africanus'* more derived characteristics. Second, Reynolds and Kibii (2011) note *Equus* as occurring in the STER/JC deposits, which again suggests they must be younger than 2.4 Ma, despite their depth in the system. As Partridge et al. (2003) envisage the STER/JC material likely infilled from a separate entrance to that which deposited STER/M4. However, it seems the infilling was contemporary with STER/M4.

Further complications came with U-Pb ages for flowstones associated with the StW 573 fossil of between 2.33 and 2.06 Ma (Walker et al. 2006; Pickering and Kramers 2010; Pickering et al. 2010), which is more consistent with the ages for STER/JC as suggested by Reynold and Kibii (2011) data. Clarke (2007), Pickering and Kramers (2010) and Herries and Shaw (2011) all agree that these U-Pb dated flowstones formed after the StW 573 fossil was deposited and so only provide a minimum age for the fossil. The fact that one of these flowstones cuts through the middle of the fossil confirms Clarke's (2007) interpretation for the upper one of these flowstones. However, the stratigraphic relationship of the other flowstones in the sequence is less certain and not all of them appear to have formed after the fossil was deposited. This is partly confirmed by the fact that the speleothem from the base of the sequence all record a consistent reversed polarity and all those from the top of the sequence record a normal polarity. Therefore, they cannot have formed at the same time. Moreover, sediment samples also indicate a reversed polarity suggesting penecontemporaneous deposition with at least some of the flowstones.

Herries and Shaw (2011) note that the original magnetostratigraphy of Partridge et al. (1999) is invalid as the normal polarity recorded in the lower flowstone is a more recent overprint from the mining process, something not seen in other samples. This work also indicates that the normal polarity period in the upper flowstone is very short and may only represent an excursion or short event rather than representing a long period of deposition as suggested by the Partridge et al. (1999) scenarios or the scenarios of Berger et al. (2002). As such, the sequence changes from a long period of reversed polarity at the base that contains the StW 573 fossil to a long period of normal polarity at the top of the sequence. Just before the reversal from reversed to normal polarity a short normal polarity episode occurs. The short normal polarity identified in the flowstone that caps the StW 573 fossil correlates well with either the Réunion or Huckleberry Ridge events at 2.16 or 2.04 Ma, respectively. Recent dating by Pickering et al. (2010) of deposits similar to those sampled by Walker et al. (2006) gave an age of 2.45–2.25 Ma (2.35 ± 0.10 Ma) and further suggests that the normal polarity reversal sampled in the capping flowstone is the older Réunion event at ~2.16 Ma and helps corroborate the age of the flowstone, if not its association to the fossil.

Given these changes to the magnetostratigraphy of the STER/SB deposits, none of the previous palaeomagnetic interpretations are valid. If, as Partridge (2000) envisaged (Fig. 3.4, Option A), the STER/SB deposits lie directly below STER/M4, then the normal polarity identified in the top of STER/SB (i.e., Member 3) would date to between 3.03 and 2.58 Ma. The underlying reversed polarity deposits could then date to between 3.11 and 3.03 Ma, making StW 573 slightly older than 3 Ma (3.1–3.0 Ma). Some potential support for this is the identification of a ~2.8 Ma deposit below STER/M4 in the surface borecores by Pickering and Kramers (2010). However, this scenario seems unlikely given the length of time that the basal reversed polarity period appears to cover based on expected depositional rates. Moreover, the association of the surface deposits with those in STER/SB remains unclear.

Two speleothem samples from the base of the Silberberg Grotto also record a reversed polarity and extend the length of the basal reversed polarity as described by Partridge et al. (1999). Given this, the reversed polarity in the base of STER/SB likely represents a longer period of time than envisaged by Partridge et al. (1999), Berger et al. (2002) or the above scenario (Fig. 3.4, Option A).

A much more likely scenario (Fig. 3.4, Option B) is that the long reversed polarity period in the base of the sequence dates to between 2.58 and 1.95 Ma, making it contemporaneous with STER/M4 as also suggested by the U-Pb ages of Pickering and Kramers (2010) and Pickering et al. (2010). The normal polarity identified in the flowstone that caps the StW 573 fossil would then represent the Réunion event at 2.16 and make StW 573 date to between 2.58 and 2.16 Ma, requiring a drastic reassessment of the depositional history of this obviously complex site. In this scenario the deep cave deposits (both STER/SB and STER/JC) mirror those outcropping on the surface and must either represent material winnowed from these deposits into deeper repositories or contemporary deposits deposited in a lower disconnected chamber and filled from a separate shaft. This is the exact scenario envisaged by Partridge (1978) in his original description of the STER/SB deposits and makes sense based on the actual occurrence of a complete skeleton like StW 573, which must have fallen in down a deep vertical shaft, directly from the surface. If this is correct then all the *Australopithecus* specimens from the site (STER/M4, STER/JC and STER/SB) date to between 2.6 and 2.0 Ma. If prior assertions by Clarke (2008) and Partridge et al. (2003) are correct, and StW 573 and Sts 5 are confirmed as separate species, then it suggests that two species were indeed present at Sterkfontein at the same time period 2.6 and 2.0 Ma. Only more detailed analysis of the various deposits will confirm which stratigraphic scenario is correct and what exactly Member 3 is as an entity or even if the various deposits classified as Member 3 are even the same thing.

Makapansgat

The Makapansgat Limeworks is the most northerly of the south African australopith-bearing sites being located close to the town of Mokopane (formerly Potgietersrus; Fig. 3.1). The Limeworks is only one of a series of fossil-bearing sites at Makapansgat, including the ~0.99 Ma Buffalo Cave (Herries et al. 2006) and the later *Homo*-bearing Cave of Hearths (Latham and Herries 2004, 2009; Herries and Latham 2009). The Limeworks represents a complex series of paleo-sedimentary deposits that were once part of a large cave system (Fig. 3.5; Latham et al. 1999; Latham and Herries 2004). No reliable absolute ages have been provided for the site (Blackwell et al. 2001; Walker 2005). Palaeomagnetic analysis was originally undertaken by McFadden et al. (1979) who concluded that the *A. africanus* deposits were probably older than 3.03 Ma (adjusted date as per Ogg and Smith 2004). Partridge et al. (2000) suggested that the deposits most likely date to between 3.21 and 3.12 Ma based on the palaeomagnetic analysis of borecores from the Central Debris Pile (CDP; Partridge 2000; formerly known as Member 4b; Partridge 1978) and the Archway. However, a number of fundamental problems exist with these earlier studies. Firstly, no direct palaeomagnetic analysis was done on the *A. africanus*-bearing grey bone breccia deposits of the Classic Section and known as Member 3 (MAK/M3) (Partridge 1978, 2000). Secondly, a number of studies (Maguire 1985; Latham et al. 2002, 2003) have shown that there are problems with the composite sequence and member system on which the original magnetostratigraphy was based. It has now been demonstrated that the Member 4 (Partridge 2000) and CDP (i.e., Member 4b; Partridge 1979) deposits were laid down synchronously in the central part of the cave when Members 2 and 3 were laid down in the Classic Section (Latham et al. 1999, 2003). The magnetostratigraphy of Partridge et al. (2000) further complicated the issue by comparing sediments of a similar sedimentological character in the east of the site with the western deposits and so defined them as the same member. This is despite the lack of stratigraphic linkage and their substantial horizontal separation as a result of the deposition of the CDP and a large arc of speleothem between the east and west repositories (Fig. 3.5). Moreover, the polarity of these borecores was determined on the basis of just their inclination (vertical field element) due to loss of horizontal orientation during drilling. Moreover, drilling has been shown to alter the inclination of borecore specimens at Makapansgat (Herries 2003). As such, all borecore magnetic data should be discounted.

The fauna from Makapansgat has come from a variety of in situ and ex situ sources and so likely represents a mixed assemblage from different areas of the site. Ex situ material from Member 2 (MAK/M2) is perhaps the least reliable as it has a siltstone matrix and this occurs at various deposits throughout the east and west of the site (Fig. 3.5). Moreover, there has been little mining of the siltstone deposits of the Main Quarry area but extensive mining of deposits in the exit quarry above Horse Mandible Cave, where in situ fossils can still be seen. Such deposits have no relationship to the hominin fossil deposits. The most secure material is that from the stratigraphically confined MAK/M3 deposit. Although some of the fauna recovered from MAK/M3 and MAK/M4 occur at Early to Middle Pliocene fossil sites, the majority of the species recovered from these deposits are most common at sites contemporaneous with Omo Shungura members B and C (3.36 ± 0.04 and 2.52 ± 0.05 Ma; Feibel et al. 1989). A suggested maximum date for MAK/M3 and MAK/M4 of between 3.36 and 2.52 Ma are consistent with previous biostratigraphic date estimates of ~3.0 Ma for MAK/M3 (Vrba 1982), 3.0–2.5 Ma (Delson 1988), 2.9–2.7 Ma for MAK/M3, 2.7–2.5 Ma for MAK/M4 (Vrba 1995), and 3.3–3.1 Ma for MAK/M3 (Reed 1996). Many of the FADs for the fauna contained within the hominin breccia fall within the range of 3.0–2.0 Ma (Vrba 2000). Taken together the various faunal studies suggest a best estimate age of between 3.1 and 2.5 Ma, and perhaps closer to 2.7 Ma. Recent comparison of the metridiochoerine suid remains from MAK/M3 to early remains from the Usno Formation suggests a range for the deposits between 2.85 and 2.58 Ma (White et al. 2006).

Palaeomagnetic analysis undertaken by Herries (2003; see also Hopley et al. 2007a; Fig. 3.6) shows that the siltstone deposits in the Main Quarry area [referred to as Member 2 west (MAK/M2w)], which lie directly beneath the *A. africanus* MAK/M3 deposits, record a normal magnetic polarity. This is consistent with the work of McFadden et al. (1979). MAK/M3 itself, as well as two phases (vuggy and chocolate) of capping speleothem, also records a normal polarity, with no stratigraphic breaks evident. The uppermost layers of the chocolate speleothem record a reversal, from normal to reversed polarity, prior to reaching a solid dolomite roof.

Based on the entire range of faunal age estimates the MAK/M3 and MAK/M2w deposits most likely date to the Gauss C2An.1n sub-chron between 3.03 and 2.58 Ma or the Gauss C2An.2n sub-chorn between 3.21 and 3.12 Ma, and therefore either represent a depositional period of 450 or 90 kyr. Some authors (Cadman and Rayner 1989; Latham et al. 2007) have suggested a relatively short period

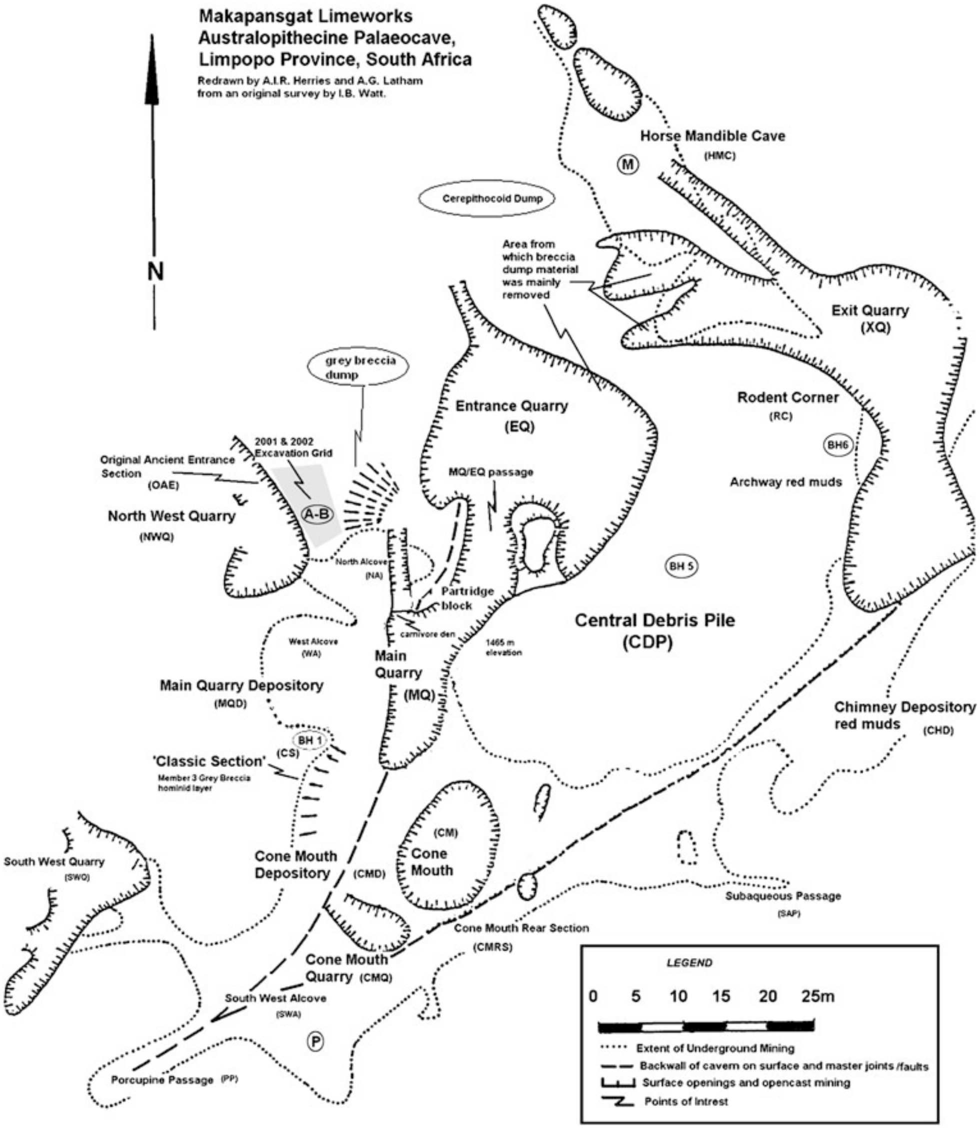

Fig. 3.5 Survey of the Makapansgat Limeworks indicating the main localities and features of the western deposits (Main Quarry, Cone Mouth, North West Quarry) and eastern deposits (Exit Quarry, Chimney Depository, Rodent Corner)

of accumulation (~100 and 14 kyr, respectively) for the MAK/M2w siltstone deposits based on a suggested annual accumulation of sediments. However, the normal polarity period is also covered by the accumulation of significant depth and two distinct phases of capping speleothem deposit and the MAK/M3 bone breccia, which would have taken significant time to form. Moreover, the bone breccia deposits were infilled from the direction of the Collapsed Cone, rather than the Main Quarry as with the underlying MAK/M2w. At this period red silt deposits (MAK/M2w) had completely sealed the former entrance to the Main Quarry area and speleothem columns had begun to grow in the cavity above the silt deposits. It is unknown whether a small hiatus could have occurred at this time between the end of deposition of the siltstone and formation of the first speleothem deposits. This makes the interpretation of depositional rates more difficult.

Direct associations can be made to a variety of deposits that occur stratigraphically below MAK/M3 and MAK/M2w in the North West Quarry. These deposits were noted by Wells and Cooke (1956) but were incorporated into larger stratigraphic entities in later stratigraphic nomenclatures (Brain 1958; Partridge 1978, 2000). These deposits consist of inter-layered speleothem and clastic deposits representing one of the original entrances to the ancient cave [Member X (MAK/MX); Latham et al. 2007] and have been informally referred to as the Original Ancient Entrance deposits (OAE; Latham et al. 1999, 2002, 2003, 2007). These deposits have been partially mined and represent a compressed record of sedimentation and precipitation. Early work by McFadden et al. (1979) indicated a series of intermediate polarities in this area of the cave. Recent work suggests that the deposits appear to record a series of alternating polarities and Herries (2003; Hopley et al. 2007a; Herries et al. 2010) suggested that they were most likely deposited during the Gauss normal polarity epoch covered by the Kaena and Mammoth events between 3.60 and 3.03 Ma (Fig. 3.6). Speleothem below this level records a long period of reversed polarity dating to between 4.19 and 3.6 Ma, with a short normal polarity period estimated to be the Cochiti event at 4.30–4.19 Ma (Herries 2003; Hopley et al. 2007a). However, analysis of the OAE clastic deposits, particularly MAK/MX, was complicated by their magnetic instability and viscosity that makes the determination of primary remanence difficult due to a strong overprinting remanence. Due to the possibility of natural overprinting in samples of such mineralogy the normal polarity samples are much less certain than reversed polarity samples. The magnetostratigraphy of this area is also complicated by the potential for stratigraphic breaks to have occurred and due to the compressed complicated stratigraphy in this area of the deposits. Work to clarify the geological and palaeomagnetic succession in this area is ongoing.

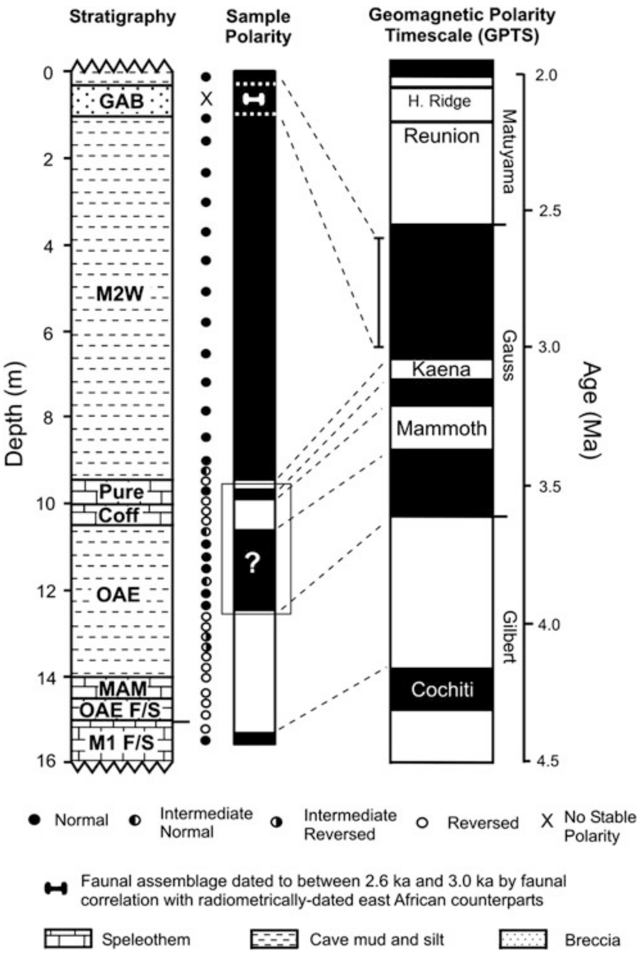

Fig. 3.6 Magnetostratigraphy of the Makapansgat Limeworks western (Main Quarry) deposits based on composite stratigraphy of Latham et al. (1999, 2002, 2003), Herries (2003), and data of Herries (2003; modified from Hopley et al. 2007a). The *question mark* signifies the area of weak, low coercivity samples and complex stratigraphy where the sequence of reversals is less certain and work is ongoing

These initial data, the mixed polarity of underlying deposits, the fact that many of the FADs for species from this deposit fall between 3.0 and 2.0 Ma and the recent assessment of *M. shawi* remains to between 2.85 and 2.58 Ma strongly suggest the placement of all the *A. africanus*-bearing deposits in the Gauss C2An.1n sub-chron between 3.03 and 2.58 Ma (Table 3.2; Fig. 3.6). Given the dates for *M. shawi* and the formation of slowly deposited multiple phases of speleothems over the fossil deposits and within the same polarity chron, a date of between 2.85 and 2.58 Ma is suggested for the Member 3 *A. africanus*-bearing deposits. However, the appearance of the species in eastern Africa is abrupt and this may suggest that, like other mammal species, it originated in southern Africa and migrated to East Africa (Pickford 2004). If this were conclusively demonstrated then its use as a biochronological marker would be less reliable and an upper age limit of 3.0 Ma should be used for the age of STER/M3 based on the magnetostratigraphy.

Australopithecus africanus fossils (MLD37/38) were additionally recovered from the Cercopithecoidea dump by Kitching (Dart 1959). This dump was located between the two main quarry mouths and is embedded in pink breccia similar to that found at the base of and as the matrix of the CDP. Partridge (2000) defines a pink siltstone deposit as a separate layer (Member 4; Member 4a of Partridge 1979) beneath the block breccia of the CDP, which has a pink siltstone matrix. In 1963, a block (the Partridge Block) was removed from the interface between the Entrance and Main Quarry area where MAK/M4 (Partridge 2000) is best exposed. The block contained baboon fossils and a femur of *A. africanus* (MLD36; Reed et al. 1993). It has generally been considered that MLD37/38 may have come from the same area as there is a similarity between the fossils and matrix. However, it is entirely possible that it comes from another area of the CDP or Member 4. While MAK/M4 near the Partridge block is suggested to date to around 2.58 Ma (Warr and Latham 2007) the CDP likely contains deposits covering the entire depositional history of the site (Latham et al. 1999); although paleomagnetism by McFAdden et al. (1979) recorded normal polarity directions from those deposits in the Main Quarry that would suggest this area is also contemporary with STER/M3. The occurrence of the MLD 37/38 fossil in STER/M4 suggests *A. africanus* may have occurred at Makapansgat until at least 2.6 Ma and its quite possible the MAK/M3 fossils are also not much older than this.

Gladysvale

Gladysvale is located on the John Nash Nature Reserve in the northern portion of the Cradle of Humankind World Heritage Site. It is a formerly mined paleocave site with extensive fossiliferous deposits within the three main internal chambers [Gladysvale Internal Deposits (GVID); Pickering et al. 2007], as well as among extensively exposed in situ calcified and decalcified sediments from sections of the karstic system that have become de-roofed due to erosion [Gladysvale External Deposits (GVED); Lacruz et al. 2002]. The stratigraphy at the site is complicated by the formation of a more recent cave system within the fossil-bearing paleocave deposits (Pickering et al. 2007; Herries and Shaw 2011). Such re-use of paleokarstic conduits is a feature of many of the southern African sites to some degree and its importance in understanding the various fossil fills at the sites has been generally overlooked or greatly simplified. Similar processes are seen at other caves in the world such as Jenolan and Naracoorte Caves in Australia (Herries and Pickering, personal observations). Here the effects are more obvious with the limestone having been tilted vertically before the secondary phase of karstification took place.

Faunal materials initially collected from ex situ GVBD include specimens attributed to *A. africanus* and a number of cercopithecoids (Berger and Tobias 1994; Plug and Keyser 1994; Lacruz et al. 2002). Again the faunal age estimates are unreliable due to their recovery from ex situ breccia blocks and the unknown provenience of the *A. africanus* fossils but they are assumed to have come from the GVID. Two species of *Equus* (*Equus burchelli* and *Equus capensis*) are present in the deposits, but can only suggest a date of less than 2.4 Ma; (Geraads et al. 2004). A range of ESR dates have been provided on the GVID with median age estimates ranging from 0.56 ± 0.78 to 2.18 ± 0.17 Ma and a maximum age of 2.34 ± 0.19 Ma for a single sample (Curnoe 1999). Given this clustering and the potentially associated fauna, the *A. africanus* fossil probably dates to a period between 2.4 and 2.0 Ma. This suggests the fossils are most likely contemporaneous with STER/M4 and STER/M2 (Table 3.2).

Taung

Taung is the most westerly of the southern African australopith-bearing sites being located along the eastern end of the Ghaap Plateau escarpment. The Buxton-Norlim site, as it is otherwise known, is a series of tufa flows of vastly different ages that were mined for lime in the early Twentieth Century. Caves formed in the tufa have yielded fossils covering at least the span of the Quaternary (last 2.6 Myr). The Taung hominin deposits represent some of the oldest, and the Equus Cave hominin-bearing hyena den deposits represent some of the youngest at <17 ka (Johnson et al. 1997). Other fossil sites are known to occur along the escarpment at Ulco and Boetsap (Curnoe et al. 2006). Although the Buxton-Norlim mine yielded the *A. africanus* holotype (Dart 1925), subsequent mining destroyed the fossil site and so it has received limited attention when compared to the other australopith-bearing sites in southern Africa. Exploration of the remaining karstic deposits by Peabody (1954) based on interviews with lime miners suggested that the *A. africanus* specimen derived from close to two witness section pinnacles referred to as the Dart and Hrdlička pinnacles (TAUNG/DD and TAUNG/HD).

Geochronological and geochemical dating (Vogel and Partridge 1984) was undertaken and suggested a ~942 ka age for the Thabaseek tufa suggesting the skull should be younger than this. However, these results have since been refuted (e.g., Butzer 1974) and the open system nature of the tufa suggests this should be seen as a minimum age estimate (Tobias et al. 1993). Palaeomagnetic analysis has also been attempted on borecores taken through the deposits (Partridge et al. 2000). As with all work done on such cores the process of coring in the Earth's magnetic field causes the formation of a rotational remanence as well as issues related to a loss of orientation if the core snaps during drilling (Herries 2003; Herries and Shaw 2011).

This may explain the random directions from the earlier study. Recent paleomagnetic analysis indiates that deposits from TAUNG/DD primarily record a normal polarity direction, while those from TAUNG/HD primarily record a reversed polarity direction.

McKee (1993a, b) divided the fossils recovered from the Taung site into those from the TAUNG/HD, including most of the identified fauna, and the TAUNG/DD, which he suggested included the *A. africanus* holotype. McKee (1993a) has suggested that as the tufa grew from west to east that the deposits close to the Dart Pinnacle are older than those of the Hrdliĉka Pinnacle. However, Gordon (1925) has stated that the infill containing the skull was part of an extensive maze cave extending ~100 m in a north–south direction and laterally to the eastern margin of the Thabaseek tufa. Gordon (1925) suggests that remnants of cave fill within this system were preserved in both the western Dart and eastern Hrdliĉka pinnacles. The excavations and borecore work by Partridge (Tobias et al. 1993) indicate that two main phases of infill occur across the Dart and Hrdliĉka pinnacles. The first is a pale reddish brown to pink clay and siltstone and the second is a yellowish-red sand and siltstone deposit (Tobias et al. 1993). Tobias et al. (1993) suggested, based on a comparison of sedimentology of sediments at the site and the matrix of the Taung Child skull itself that it actually came from the Hrdliĉka Pinnacle deposits, the opposite view of McKee (1993a, b). However, given that both the pink and red deposits occur in both pinnacles it is not a question of which pinnacle they come from, but which deposit. Both McKee (1993a, b) and Tobias et al. (1993) suggest the Taung Child came from the older pink deposits.

According to McKee (1993a, b) only seven species can be confidently associated with the Taung holotype and that most of the fossils come from the younger red sediment. Two of these are bovid species that are apparently novel to Taung (*Cephalophus parvus, Palaeotragiscus longiceps*) and have since gone missing from museum collections and cannot be evaluated (Cooke 1990). McKee (1993a, b) has noted that the two micromammalian species (*Gypsorhynchus darti* and *Gypsorhynchus minor*) in the TAUNG/DD are similar to those recovered only thus far from Makapansgat, and the extinct cercopithecoid *P. broomi* is also only found at MAK/M3 and STER/M4. He therefore suggested an age of 2.6–2.4 Ma. Preliminary paleomagnetic analysis by AIRH indicates that these pink deposits have a normal magnetic polarity that, taken with faunal age estimates from the younger red deposits, would suggest an age of 3.03-2.58 Ma for the Taung Child (Table 3.2).

Malapa

Malapa is the most recently discovered australopith-bearing site in South Africa (Berger et al. 2010) and is located near the site of Gladysvale in the northern portion of the Cradle of Humankind World Heritage Site (Fig. 3.1). The site has so far yielded two partial *Australopithecus* skeletons from re-fitted blocks of lime miners' rubble. Berger et al. (2010) assign the partial skeletons of a juvenile male and an adult female to a new species, *A. sediba*. While the fossils so far described have mainly come from ex situ blocks, their provenience is certain as the remainder of the australopith skeletons are still located in the exposed section of the paleocavity. The area excavated by the lime miners is also very small and has caused minimal disturbance to the deposits as a whole. These fossils are encased in water-laid, clastic sediments that were deposited along the lower parts of what is now a deeply eroded cave system (Dirks et al. 2010). A thick flowstone deposit, the top of which becomes interstratified with clastic deposits, divides the sediments at the site. Below the flowstone lie two deposits, Facies A and Facies B (MAL/FA-FB). Above the flowstone lie three deposits, facies C–E (MAL/FC-FE), which contain the *A. sediba* fossils that have been recovered so far (Dirks et al. 2010). These hominin-bearing deposits are then capped by another flowstone (Pickering et al. 2011a, b).

Fauna at the site includes a species of *Equus* from MAL/FD with an FAD of 2.4 Ma (Brown et al. 1985), and a species of felid (*Dinofelis barlowi*) from MAL/FE with an LAD of around 1.6–1.4 Ma (Dirks et al. 2010; Pickering et al. 2011a, b). Therefore the fauna suggests the hominins of MAL/FD and MAL/FE were deposited between 2.4 and 1.4 Ma. Double blind U-Pb dating of the deposits gives an age of 2.03 ± 0.02 Ma for the lower flowstone dividing the underlying MAL/FA-FB and the overlying hominin bearing MAL/FC-FE (Dirks et al. 2010). As such the *A. sediba* fossils cannot be older than 2.05 Ma. Palaeomagnetic analysis of the flowstone helps confirm the U-Pb ages with a short geomagnetic polarity event that most likely represents the Huckleberry Ridge event at 2.06 ± 0.04 Ma (Dirks et al. 2010). Speleothem with both or either of the Réunion and Huckleberry Ridge events now appears to occur at Malapa and within STER/M4 and STER/M2. This suggests that thick flowstone deposition was widespread in the Gauteng dolomite paleocaves around 2.2–2.0 Ma and may therefore serve as a potential marker horizon between the various deposits and caves. The very top of the Malapa flowstone has a reversed palaeomagnetic signature and suggests deposition before 1.95 Ma. The *A. sediba*-bearing sediments above the flowstone records both intermediate and normal magnetic polarities and originally suggested it was formed at the beginning of the Olduvai Subchron between 1.95 and 1.78 Ma, although likely closer to 1.95 Ma. Recent excavations at the site have identified an upper capping flowstone that was subsequently dated to 2.05 ± 0.14 Ma and indicates that it cannot be less than 1.91 Ma (Pickering et al. 2011a). This flowstone also records a reversed polarity and suggests along with the U-Pb age that it must be older than 1.95 Ma. This was at odds with the interpretation of the *A. sediba* sediments below it being dated to the Olduvai Subchron after 1.95 Ma. The only alternative during this time period is the "validated" (Roberts 2006), but due to its short duration of ~3 kyr, not often preserved Pre-Olduvai event at ~1.98 Ma. This would suggest that all the *A. sediba*-bearing sediments date to a ~3 kyr period centred on 1.98 Ma (Pickering et al. 2011a). The demagnetisation spectra of the Malapa samples (Dirks et al. 2010; Pickering et al. 2011a) clearly show the removal of any more recent overprinting of the magnetic remanence and the preservation of a stable underlying remanence. Work at other sites (Herries and Shaw 2011) clearly indicates that the South African hominin-bearing sites are capable of preserving these short geomagnetic field events but this is the first time such an event has been documented during a phase of clastic sedimentation rather than speleothem formation.

Discussion and Conclusions

This review suggests that MAK/M3 and MAK/M4 represent the oldest australopith-bearing deposits in South Africa dating to the Piacenzian stage (3.6–2.6 Ma) of the Pliocene between 3.03 and 2.58 Ma. The Taung Child *Australopithcus* fossil may also be contemporary at 3.0–2.6 Ma but its age is currently more difficult to assess with certainty. As such, Makapansgat and Taung are perhaps the only Pliocene (>2.6 Ma) hominin sites in southern Africa. *Australopithecus* seemingly first occurs in southern Africa well over a million years later than in eastern Africa, although the lack of fossil sites dated between Langebaanweg at ~5.0 Ma (Roberts 2006) and MAK/M3 (<3.0 Ma) make this currently impossible to assess. It is perhaps more likely an artifact of geology and survival of fossils than a true reflection of biogeography as only a few fossil-bearing cave deposits have yet been discovered older than 3.0 Ma. These include the Original Ancient Entrance (OAE) deposits (~4.0–3.3 Ma) and perhaps Rodent Corner at Makapansgat (Herries 2003; Hopley et al. 2006, 2007a), Bolt's Farm (Gommery et al. 2008) near Sterkfontein, and the new site of Hoogland near Pretoria (Adams et al. 2010).

The magnetostratigraphy of the australopith-bearing deposits at Makapansgat indicate that they cannot be the same age as australopith-bearing deposits at Sterkfontein, which are of a different polarity (Fig. 3.7). The geomagnetic polarity events and U-Pb dates indicate that the STER/SB and STER/M4 australopith-bearing deposits are younger, dating to the Gelasian stage (2.6–1.8 Ma) of the Pleistocene between 2.6 and 2.0 Ma. The STER/JC *A. africanus* fossils are also younger than 2.4 Ma based on the presence of *Equus.* This is a view supported by most faunal comparisons (Pocock 1987; McKee 1995; McKee et al. 1995; Vrba 1995, 2000). The younger age of Sterkfontein compared to Makapansgat may cause temporal variation in the two assemblages of *Australopithecus* that could explain some anatomical differences that have led some researchers to suggest that the Makapansgat *Australopithecus* fossils are a different species to those at Sterkfontein, where a number of fossils are suggested to have more *Homo*-like traits (e.g., Sts 19; Kimbel and White 1988; Kimbel and Rak 1993; Ahern 1998). Interestingly, more *Homo*-like australopith fossils such as Sts 19 appear to be older than the supposedly more primitive Sts 5, which is the youngest currently defined *A. africanus* fossil at ~2.04 Ma. The non-*A. africanus* fossil StW 573 (Clarke et al. 2003; Clarke 2008) is contemporary with the *A. africanus* fossils of STER/M4 and STER/JC and suggests that two species of *Australopithecus* were present at Sterkfontein between 2.6 and 2.2 Ma. Moreover, the *Homo*-like *A. sediba* fossils (Pickering et al. 2011a) are only slightly younger than these two specimens and similar in age to *A. africanus* fossil Sts 5 at 2.0 Ma suggesting two species of *Australopithecus* were contemporary at this time period and that three different species of *Australopithecus* are seen in South Africa between 2.6 and 2.0 Ma. If StW 53 is also considered as *Australopithecus* (Clarke 2008; Berger et al. 2010) then *Australopithecus* survived until at least 1.8 Ma. The fossils from Gladysvale seem to fall in the temporal range of those younger specimens from Sterkfontein. The time range for *Australopithecus* in South Africa can currently be estimated to sometime between 3.0 and 1.8 Ma.

The current youngest ages for a definitive species of *Australopithecus* (~2.0 Ma) in South Africa is around 0.7–0.5 Ma younger than the last representative of the genus (*Australopithecus garhi*; Asfaw et al. 1999) from eastern Africa [unless, following the suggestion of Wood and Richmond (2000), the oldest early *Homo* fossils from eastern Africa should be re-classified as *Australopithecus*; including those attributed to *Homo habilis* and *Homo rudolfensis*]. Most researchers would suggest that specimens attributed to both *Paranthropus* and *Homo* first occur in eastern Africa from ~2.7 to 2.6 and ~2.5 to 2.3 Ma, respectively (Walker et al. 1986; Feibel et al. 1989; Kimbel et al. 1996; Suwa et al. 1996, 1997; Ramirez Rozzi et al. 1997; Kullmer et al. 1999). In contrast, specimens attributed to *Homo* (Sk 847 from Swartkrans Member 1 and StW 53 from Sterkfontein Member 5A) do not appear to occur in southern Africa until after 2.0–1.8 Ma (Herries et al. 2009; Pickering et al. 2011b). If the Swartkrans Member 1 *Homo* fossils are older than 2 Ma as suggested by some ESR and the U-Pb ages (Herries et al. 2009; Pickering et al. 2011b) then it makes it impossible for *A. sediba* to be ancestral to *Homo,* as suggested by Berger et al. (2010), unless older fossils of this species are discovered. Pickering et al. (2011b) argue that the Swartkrans Member 1 fossils are not older than 1.9–1.8 Ma based on the fauna, but Herries et al. (2009) suggest that some fauna and ESR ages suggest an age of at least 2 Ma for some of Swartkrans Member 1. The U-Pb ages of capping and underlying speleothem make both scenarios possible and only more refinement in the dating will establish if *Australopithecus, Paranthropus* and *Homo* were on the landscape at the same time in South Africa. So far, *Australopithecus* has not been definitively identified from the same deposits as *Paranthropus* and *Homo* in South Africa, suggesting a major turnover in hominin species sometime between 2.2 and 1.8 Ma and perhaps suggesting they were not contemporary. This turnover is perhaps related to a period of increasing aridity in southern Africa at this time (Dupont et al. 2005). However, this may also be in part a lack of identification of these species in the various deposits that are now suggested to be temporally very close in age.

This paper has provided a current perspective on the formation of a regional chronology for *Australopithecus* in southern Africa (Table 3.2) that is at least not entirely

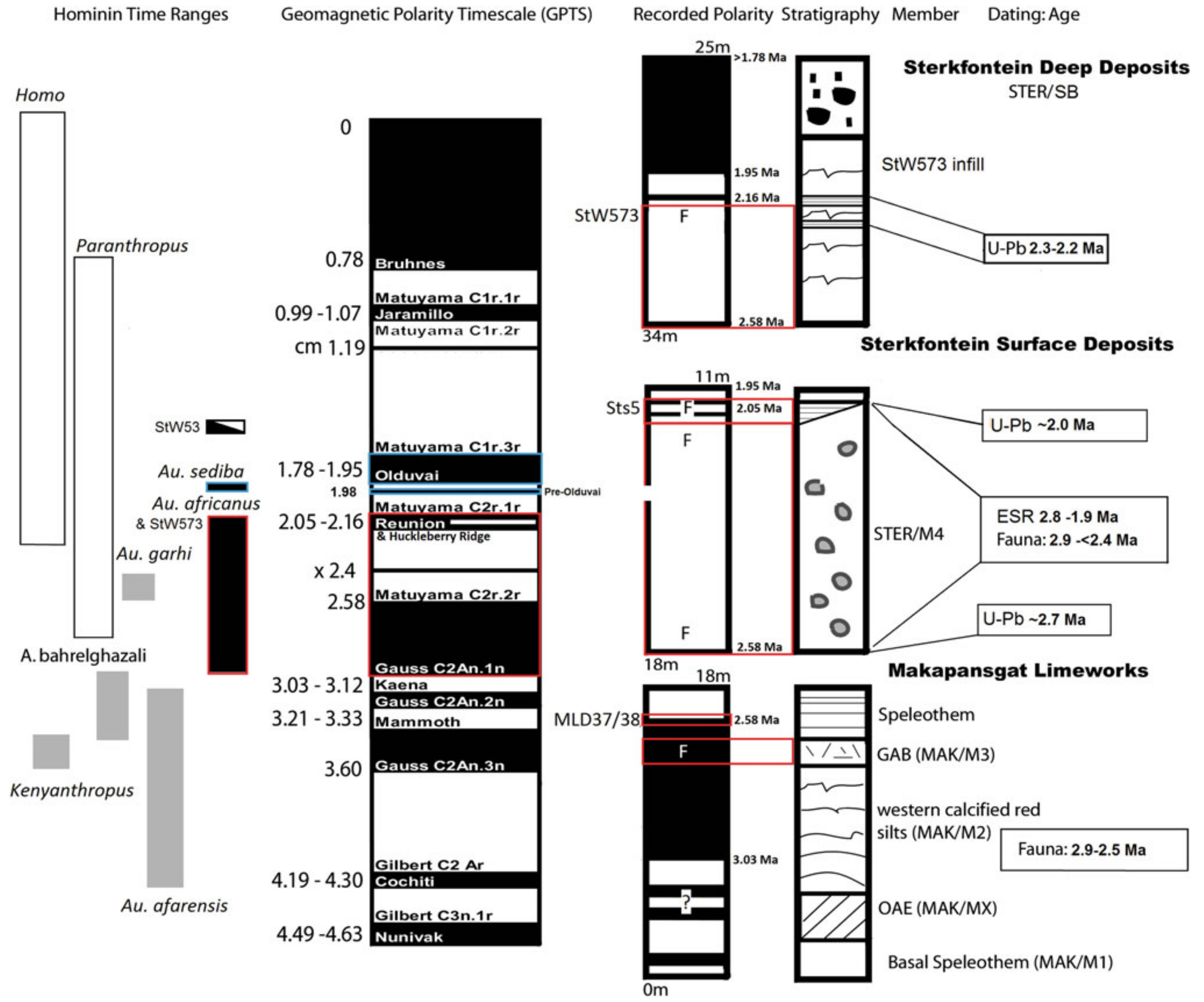

Fig. 3.7 Geomagnetic Polarity Time Scale (GPTS) and hominin age ranges set against the stratigraphy, radiometric dates (U-Pb (uranium-lead); ESR (electron spin resonance)) and faunal age estimates of the australopith-bearing Sterkfontein and Makapansgat paleocave deposits. STER/SB: Silberberg Grotto

dependent on faunal correlations with eastern Africa. Only further breakthroughs in radiometric dating methods or continued detailed U-Pb/palaeomagnetic comparisons will produce a fully independent chronology. The establishment of an independent southern African dating framework is needed to further clarify the differences between eastern and southern African climate pulses, species and faunal turnover.

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Chapter 4
Reconstructing the Habitats of *Australopithecus*: Paleoenvironments, Site Taphonomy, and Faunas

Anna K. Behrensmeyer and Kaye E. Reed

Abstract Hominin paleoecology is reconstructed using many types of evidence from fossils and their geological context. This evidence is limited by vagaries of the fossil and geological record. What questions can be asked regarding *Australopithecus* ecology given these limitations? We address this topic by reviewing the major issues concerning hominin synecology and taphonomy and discuss methods for deriving ecological information from fossil assemblages and their geological context. We provide basic information about the context of the six *Australopithecus* species known from 22 collecting sites and review their environment of deposition and other paleoecological evidence. Using this information we attempt to answer a series of questions, such as whether we can determine the habitat preferences of the different species, and whether more than one *Australopithecus* species shared an ecosystem at any given place and time. We conclude that *Australopithecus* as a genus was eurytopic because of the wide range of well-documented habitat reconstructions, but only *Australopithecus afarensis*, and possibly *Australopithecus anamensis*, have enough time range and fossil material to support the interpretation that these species were eurytopic. The dietary differences between east and south African species are intriguing given microwear analyses differentiating the two groups, although the carbon isotope data are similar. Further evidence of the ecological context of these species is needed and should be standardized using an appropriate scale of evidence (temporal and spatial) for the desired scale of habitat reconstruction.

Keywords Fauna • Paleoecology • Taphonomy

Introduction

Ecological adaptations of early hominins and how these changed over time are fundamental to understanding human evolution. Hominin paleoecology can be reconstructed through various types of evidence contained in fossils and their geological context. Basic information about hominin autecology—diet, locomotion, body size dimorphism, etc.—can be inferred from their anatomy and the isotope geochemistry of the fossils themselves. Hominin synecology, i.e., reconstructions of population structure and abundance, habitat preferences and associations with other organisms in natural communities, is more elusive, in large part because hominins are rare components of most fossil assemblages. Much effort has been devoted to inferring hominin habitats based on evidence from associated organisms (e.g., co-occurrence with arboreal mammals indicating that they lived in a forest community) and geological evidence for the physical environments and climatic conditions. Fewer attempts have been made to assess other aspects of hominin paleoecology, such as population structure or abundance relative to other taxa.

What do we want to know about the ecology of *Australopithecus*, and how much of what we would like to know is actually possible, given the limitations of the geological and paleontological record? These two questions provide the framework for this paper, which focuses primarily on synecology and approaches to reconstructing the habitats in which *Australopithecus* lived. We review the major issues regarding hominin paleo-synecology and taphonomy and discuss methods for distilling ecological information from fossil assemblages and their geological context. We draw upon examples from the East African record showing how researchers address various aspects of the ecological life and times of *Australopithecus*, and we also review current interpretations of paleohabitats at

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African *Australopithecus* sites. Using different scales of information ranging from documentation of paleoecological features at individual sites to global-scale climate records provide a secondary theme for this paper.

The study of *Australopithecus* synecology draws heavily upon inferred ecological characteristics of animals, particularly mammals that were preserved with these hominins. Information on the sedimentary environments of the sites and taphonomic attributes of these fossil assemblages also is necessary for credible interpretations of the associated fauna. This three-component approach can be applied to habitat reconstructions for particular fossil assemblages and also to document habitat variation relating to mammalian turnover patterns and adaptive shifts associated with different types of habitats. An apparent change in faunal composition through time can be caused by a shift in depositional environment or a change in taphonomic processes that select for or against certain types of organisms and skeletal parts. If these confounding variables can be addressed and corrected for, then it is possible to assess biological processes that caused turnover, such as the dispersal of species out of a region or into a region from elsewhere, by local speciation and extinction events, and changes in the relative abundance of persistent lineages. Conversely, long temporal ranges, broad geographic distributions of species, or stable patterns of relative abundance are useful for identifying the persistence of similar habitats through time or across the landscape. Examination of such patterns in the fossil record can lead to testable hypotheses regarding the interaction of climate change, local and regional tectonic processes, and the living communities of plants and animals, thereby providing ecological information necessary for understanding large-scale processes driving hominin evolution.

We begin by outlining major questions regarding *Australopithecus* paleoecology that, ideally, we would like to answer. We then introduce what is known about the *Australopithecus* fossil record, and present three major integrated approaches to inferring hominin habitats—taphonomy, paleoenvironmental (geological) context, and faunas. This is followed by summaries of current interpretations of *Australopithecus* paleoecology and recommendations for future research to refine and test these interpretations.

Questions About *Australopithecus* Paleoecology

1. What was the range of habitats associated with the genus *Australopithecus*, and is it possible to discern each species' preferred habitat? Did this genus initially live in forests, woodlands, or other types of closed habitats, or was it adapted to a mix of open and closed habitats from its beginnings?
2. What were the important limiting ecological variables (e.g., food, water, shelter, competition with other species, predator avoidance, intra-species interactions) for *Australopithecus*?
3. Did the habitats occupied by *Australopithecus* species vary across different regions? Was there more than one *Australopithecus* species sharing an ecosystem at any one place and time? How did the later species of *Australopithecus* co-exist with *Paranthropus* and early *Homo*?
4. Was *Australopithecus* a maker and user of stone tools? Did any *Australopithecus* species incorporate significant meat into its diet?
5. Is there evidence of change through time in a habitat where the same species continued to exist? Did niche breadth increase or decrease within the genus *Australopithecus* as it evolved?
6. How might global or continental-scale climate change between 4.5 and 2.0 Ma have affected the paleoecology of *Australopithecus*? What was happening in the environments of southern versus eastern versus central Africa, and how do these regional variations compare with later African climate changes associated with northern hemisphere glaciation?

These questions represent both possible and impossible goals for what we can expect to learn from the fossil record. Answers to many of them depend on both autecological and synecological evidence. Anatomical data, dental microwear, and isotopic readings from the hominin fossils themselves address some of the critical questions regarding australopith autecology—i.e., what these hominins were functionally capable of (morphology) and what they actually did in terms of substrate use, resource use, and other behaviors (microwear, isotopes, etc.). We do not attempt to review the vast array of such autecological evidence in this paper. Instead, we focus on geological context, taphonomic analysis, and associated fauna, which provide evidence for: (1) the physical environments and vegetation habitats occupied by *Australopithecus*, (2) taphonomic processes that affected their skeletal remains in the transition from biosphere to lithosphere, and (3) their distribution through time relative to changes in paleoenvironments and other organisms. Sampling biases, especially those relating to differential preservation of species and time-averaging, limit what we can know about synecology (see examples below). One of taphonomy's important contributions is to indicate what questions can be realistically pursued with the

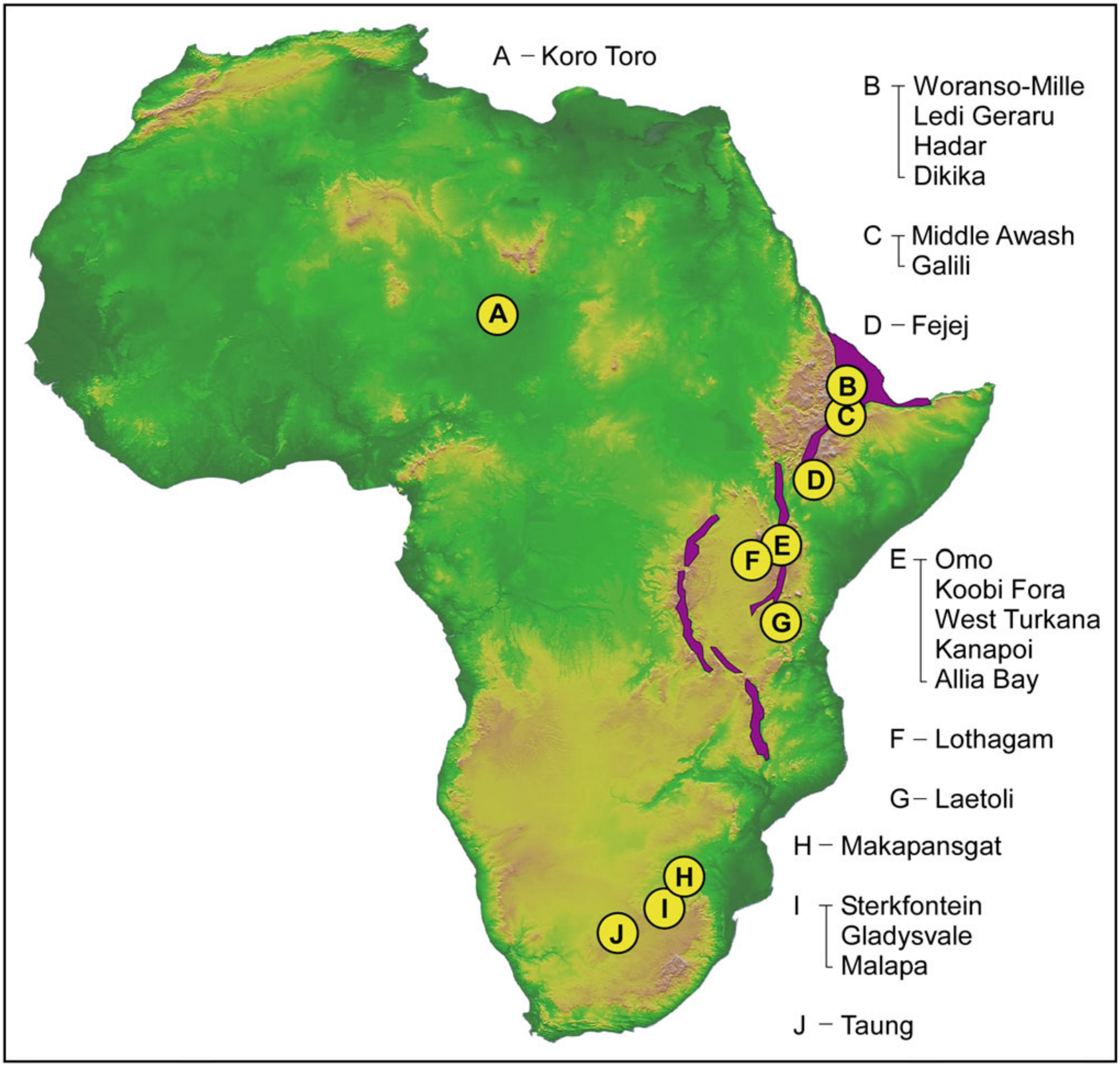

Fig. 4.1 Map of Africa showing regions and sites in Table 4.1

evidence we have, or are likely to have, from multi-disciplinary field and laboratory research.

What We Know: The Basics

At present, six species of early *Australopithecus* have been named from three sub-continental regions and ~22 collecting sites on the African continent (Figs. 4.1, 4.2; Table 4.1). Remains are relatively abundant in some of these sites, including Hadar (Ethiopia) and Sterkfontein (South Africa), fewer but relatively complete in some such as Malapa (South Africa), and sparse and fragmentary in many others. In some cases, fragmentary hominin remains from the currently documented range of *Australopithecus*, i.e., between ~4.2 and ~2.0 Ma, cannot be certainly identified as belonging to this genus (see Table 4.1). Much of what we currently know about the site taphonomy and paleoecology of *Australopithecus* is based on a sub-sample of these sites, including the greater Awash Basin (Hadar, Maka, Asa Issie, Dikika, Woranso-Mille, Bouri), Laetoli, and the South African cave sites (Makapansgat, Sterkfontein).

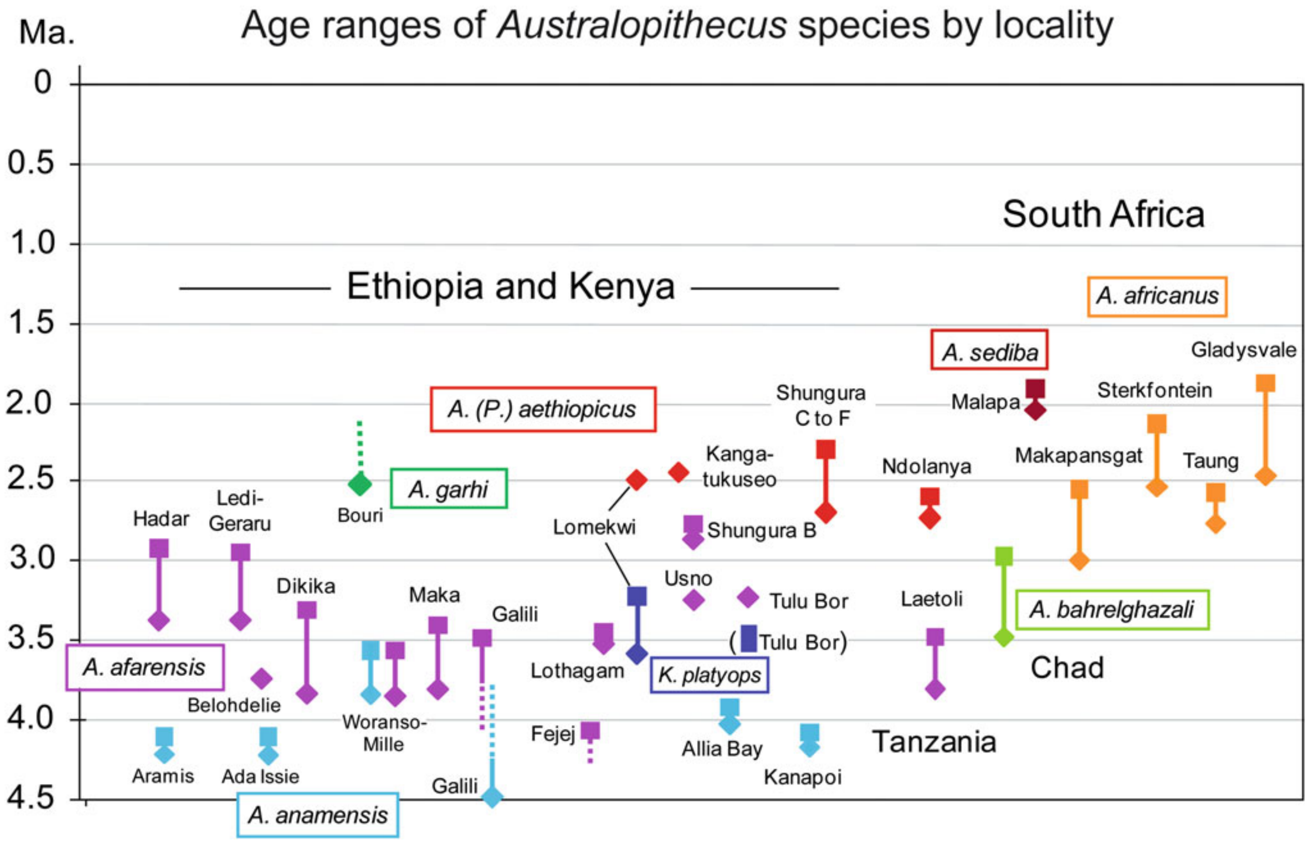

Fig. 4.2 Chronostratigraphic ranges of species of the genus *Australopithecus* (*color coded*) based on information from published hominin-bearing deposits. *Dashed lines* indicate uncertainty in range limit. See Table 4.1 for references

Documented Depositional Contexts for Australopithecus

- Volcaniclastic plains and paleosols (Laetoli)
- Fluvial channels and floodplains (Lothagam, Kanapoi, East and West Turkana, Omo Shungura Formation, Hadar, Dikika, Middle Awash)
- Lake margins (East and West Turkana, Hadar, Middle Awash, Chad)
- Karst terrain and cave deposits (Makapansgat, Sterkfontein, Taung, Gladysvale, Malapa).

Scales and Types of Evidence for Australopithecus Ecology

The evidence from geological and fossil records includes a wide range of temporal and spatial scales, each of which can provide different types of information bearing on hominin paleoecology (see also Table 4.2):

- *Footprints* preserve an instant in time, evidence for hominin behavior such as foraging and social behavior, and ecological characteristics of contemporaneous (i.e., within hours to days) flora and fauna.
- *Partial skeleton(s)* anatomically informative, represents the life span of an individual, and if associated in a contemporaneous death assemblage may provide information on group structure.
- *Excavation* ($10^{1–4}$ m^2) provides detailed evidence of the burial environment and circumstances of the hominin and any contemporaneous associated fauna and flora, usually within a short period of time-averaging ($\sim 10^1$–10^3 years).
- *Surface assemblage* Fragmentary bones and teeth of single individuals collected from a surface fossil assemblage derived from one or more eroding sedimentary layers; each specimen represents the life and death of a single individual but the combined (time-averaged) faunal assemblage may represent $\sim 10^2$–10^5 years.
- *Locality* (e.g., 10^4–10^6 m^2) general paleoenvironmental context and associated fauna from a limited area and stratigraphic thickness.
- *Collecting area, stratigraphic member or sub-member* more time and space typically represented in the combined fossil evidence from these entities, e.g., 10^4–10^5 years.

Table 4.1 Pliocene sites in Africa with fossils assigned to the genus *Australopithecus*, including some for which these records are not certain based on fragmentary remains, or are likely but not yet published

Collecting area	Sites	Country	Habitat interpretation	Lower age	Upper age	Taxon	References
Northern Awash Basin	Hadar	Ethiopia	Bushland, open woodland, wooded grassland	3.4	2.9	*A. afarensis*	Campisano (2007), Campisano and Feibel (2008), Reed (2008)
Northern Awash Basin	Dikika	Ethiopia	Woodland, open grasslands	3.8	3.4	*A. afarensis*	Alemseged et al. (2006), Wynn et al. (2006)
Northern Awash Basin	Ledi-Geraru	Ethiopia	Bushland, open woodland, wooded grassland	3.4	2.95	*A. afarensis*	Geraads et al. (2012)
Northern Awash Basin	Woranso-Mille	Ethiopia	Mix of riparian forest, open woodland, grassland	3.8	3.57	*A. anamensis, A. afarensis*	Haile-Selassie et al. (2010a, b)
Middle Awash Basin	Asa Issie	Ethiopia	Closed to grassy woodland	4.2	4.1	*A. anamensis*	White et al. (2006)
Middle Awash Basin	Aramis	Ethiopia	Grassy woodland savanna	4.2	4.1	*A. anamensis*	White et al. (2006)
Middle Awash Basin	Maka	Ethiopia	Woodland-bushland	3.78	3.42	*A. afarensis*	White et al. (1993)
Middle Awash Basin	Bouri	Ethiopia	Lake margin with grasslands	2.52	2.1?	*A. garhi*	Asfaw et al. (1999)
Middle Awash Basin	Belohdelie	Ethiopia	No information	3.7?	3.7?	*A. afarensis*	Asfaw (1987)
Southern Awash Basin	Galili	Ethiopia	Woodland to bushland	4.5	3.5	*A. anamensis, A. afarensis*	Kullmer et al. (2008)
Turkana Basin	Fejej	S. Ethiopia	No information	4.2?	4.06	*A. afarensis*?	Kappelman et al. (1996)
Turkana Basin	East Turkana	Kenya	Riparian forest, wet grassland, woodland	4.3	2.7	*A. afarensis*	Kimbel (1988), Brown et al. (2013)
Turkana Basin	East Turkana – Allia Bay	Kenya	Mosaic of closed woodland and open grasslands	4.1	3.8	*A. anamensis*	Macho et al. (2003), Schoeninger et al. (2003)
Turkana Basin	West Turkana	Kenya	Woodland and forest- edge; riparian woodland	4.3	2.5	*A. afarensis, Kenyanthropus platyops, Australopithecus* sp.	Brown et al. (2013), Leakey et al. (2001)
Turkana Basin	Lothagam	Kenya	Mix of riparian forest, open woodlands, grassland	6.5	5.5	*A. afarensis*?	Hill et al. (1992), McDougall and Feibel (1999)
Turkana Basin	Lothagam	Kenya	Open, seasonally dry	3.5	3.5	*A. afarensis*	Leakey and Walker (2003)

(continued)

Table 4.1 (continued)

Collecting area	Sites	Country	Habitat interpretation	Lower age	Upper age	Taxon	References
Turkana Basin	Kanapoi	Kenya	Mix of wooded and open grassland	4.17	4.07	*A. anamensis*	Harris et al. (2003)
Turkana Basin	Omo (Shungura, Usno)	Ethiopia	Riparian forest and woodland	3.44	2.44	*A. afarensis*? *A. garhi*?	Brown et al. (2013), Suwa et al. (1996), White (2002)
Laetoli	Laetolil Fm.	Tanzania	Mosaic of woodland, shrub-Land, bushland, grassland	3.8	3.5	*A. afarensis*	Harris et al. (1987), Su and Harrison (2008), Kovarovic and Andrews (2007)
Bahr el Ghazal		Chad	Open grassland and lake margin	3.5	3	*A. bahrelghazali*	Brunet et al. (1996)
Cave	Sterkfontein	South Africa	Open woodland, riparian forest, bushland	2.8	2.2	*A. africanus, A. sp*?	Clarke (2013), Herries et al. (2013)
Cave	Makapansgat	South Africa	Mosaic of riparian woodland, bushland, edaphic grassland	3.5	?	*A. africanus*	Dart (1952), Reed (1997), Herries et al. (2013)
Cave	Taung	South Africa	Dense woodland	3	2.0?	*A. africanus*	Dart (1925), Berger and Clarke (1995)
Cave	Gladysvale	South Africa	Closed/open vegetation	2.5	1.9	*A. africanus*	Berger and Tobias (1994)
Cave	Malapa	South Africa	No information	2.1	~1.9	*A. sediba*	Berger et al. (2010), Dirks et al. (2010)

- *Basin* a tectonic depression that has accumulated a thick sequence of sedimentary deposits, representing 10^5–10^6 years and providing information on environmental and paleontological change through time for one sub-region.
- *Region* tectonic and latitudinal context, comparisons of different hominin-bearing (and non-hominin-bearing) habitats through time or across space.
- *Continent* range of environments, latitudes, habitats, first and last appearances of hominin species.
- *Global* climate variation over space and trends and/or cycles through time.

Paleoenvironments, Taphonomic Biases and Research Strategies

The paleontological record is imperfect, and taphonomy often has to provide “reality checks” on assumptions about the biological fidelity of this record and what we can and cannot know about the past. For australopiths, these limitations may result from the following potential sources of bias:

1. Small samples of fragmentary remains for any given hominin taxon may not represent the average or modal characteristics of that taxon.
2. Even in large samples, selective preservation of hominin population sub-samples, such as robust individuals and/or body parts, could skew the range of body sizes and anatomical features that are available for collection and study relative to the once-living populations.
3. Available samples of depositional and paleogeographic contexts where fossil remains of this large-sized primate occur are likely only partially representative of the range of habitats and geographic areas where it actually lived.
4. Available assemblages of associated fossil mammals and hominins represent different degrees of time-averaging and spatial sampling from the original ecosystems. This blurs the meaning of “paleocommunity” and may bias comparisons of diversity and other ecological properties in faunas from different areas, depositional settings, and time periods (including comparisons to modern faunas).
5. Ecological indicator species may be unevenly preserved in the fossil record or are difficult to interpret in terms of their ecological requirements, either due to lack of modern analogues or to missing body parts.

Table 4.2 Types of evidence relating the paleoecology of *Australopithecus*, at increasing spatial and temporal scales, with examples of autecological and synecological data that can be inferred from this evidence

Evidence	Temporal scale	Spatial scale	Examples	Autecology of hominins	Synecology of hominins
Trackways	Seconds, minutes	10^0–10^1 m	Laetoli footprint layers	Presence in specific habitat, on a specific substrate, behavioral information	Contemporaneous fauna, within hours to days
Single individual with associated skeletal parts	Lifetime of the individual	Habitat of the individual	Sterkfontein "Little Foot", Hadar "Lucy", Dikika "Salem"	Taxonomic, ecomorphic, isotopic information on body size, diet, locomotion, etc.; burial environment	Taphonomic evidence of scavengers, trauma in life (e.g., damage to teeth)
Multiple associated individuals of a single taxon	Combined life span of individuals in the group	Habitat of group	Hadar "First Family", South African Malapa site(?)	Sexual dimorphism, demography, body size, diet, locomotion, burial environment and circumstances	Taphonomic evidence of scavengers, trauma in life (e.g., damage to teeth)
Single or multiple hominin specimens from a locality, collecting area, or well-defined stratigraphic interval	10^3–10^5 years	Habitat area sampled by organic remains, e.g., 10^2–10^5 km^2	South African cave sites, East Turkana, West Turkana, Lothagam, Kanapoi, Hadar, Bouri, Chad, Laetoli, etc.	Habitat based on ecomorphology of associated fauna and/or co-occurrence with specific ecological indicator taxa	Community structure and ecological preferences inferred from co-occurring vertebrate taxa
Combined sample from a geological formation and region	10^5–10^6 years	Area covered by fossiliferous deposits and their source areas, e.g., 10^4–10^6 km^2	Hadar, Middle Awash, Omo, East and West Turkana, Lothagam, Kanapoi, Sterkfontein, Makapansgat	Persistence, abundance, disappearance of individual hominin taxa through a stratigraphic interval	Through-time patterns of mammalian taxonomic richness, major group dominance, evenness, relationships to environmental parameters, evidence for immigration events
Basin with a thick, partially continuous stratigraphic record	10^5–10^6 years	Basin-scale	Turkana Basin, Awash Basin (Afar Depression)	Depositional context, taphonomy, and ecomorphology of hominin specimens within a single basin through time	Variation in time and space of faunas and paleocommunities, correlation with shifting physical environments
Region with multiple localities and sequences	10^5–10^6 years	Sub-continental scale	East Africa, South African Cave Sites	Variation in depositional context, taphonomy, and ecomorphology of hominins among regions	Variation in mammalian diversity and community structure in different tectonic settings, latitudes, climatic zones

We can address the problems above with taphonomic and paleoenvironmental data in a variety of ways. Obviously, more data collecting and the opening up of new areas will help with points (1) and (3), though there will never be enough fossils to resolve many finer-scale questions about regional variation and hominin occupation of areas lacking a paleontological record (i.e., most of the African continent). Understanding the limitations of the samples that we have, however, is a big step toward learning how effectively to tackle the questions that can be answered with the data in hand. There are ways to calibrate the degree of bias in the preservation of different body parts, body sizes, and taxa in order to address Point (2) above. An "isotaphonomic" approach that compares samples from specific, well-documented paleoenvironmental contexts such as fluvial channel lags or lake margin paleosols can help to control for ecological and taphonomic variables that differ across environments (Points (3) and (4)). The use of "taphonomic control" taxa, i.e., species with body

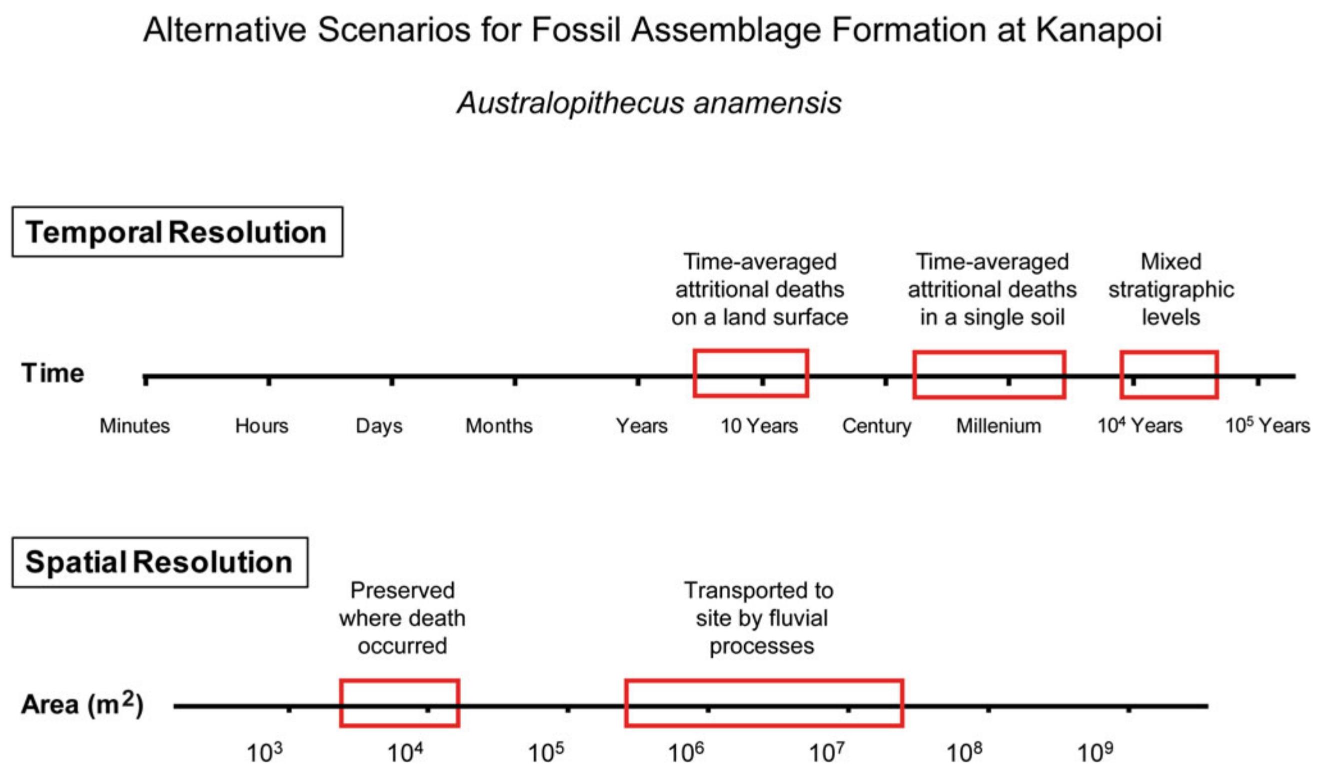

Fig. 4.3 Scale bar showing the different amounts of time-averaging implied by the paleosol context of each of the two levels at the Kanapoi *Australopithecus anamensis* site (*left gray box*) and the combined sample of hominins and associated faunal remains from both levels (*right gray box*)

size and morphology similar to hominins, such as baboons, can help to identify variations in abundance of species that are more likely to be biologically meaningful rather than taphonomically altered (Point (5)).

The "taphonomic control" approach was used to compare similar-age portions (Sidi Hakoma (SHT) and Tulu Bor tuffs) of the Hadar and East Turkana sequences (Behrensmeyer et al. 2004). *Australopithecus* is common at Hadar and rare at East Turkana, but is this the effect of a smaller fossil sample at East Turkana or a bias against primate preservation in this area? In both areas, the extinct baboon *Theropithecus* and *Australopithecus* co-occur through the 3.4–2.8 Ma time interval. Similar controlled survey fossil samples from these two areas indicate that, relative to the number of specimens of *Theropithecus* and other large monkeys recorded in the Hadar Formation and the Tulu Bor Member of the Koobi Fora Formation, there should be 2.5 hominin specimens in the East Turkana sample *if* hominins were as common relative to baboons as they are at Hadar (Behrensmeyer et al. 2004). However, only one hominin (a tooth fragment) was found in the Tulu Bor Member. This suggests (but does not prove) that *Australopithecus* was less common in the East Turkana region around 3.4 Ma than at Hadar. More tests of this kind could improve understanding of taphonomic versus ecological causes of hominin fossil abundance.

Two Examples of Site-Based Studies of *Australopithecus* Habitats

The types of evidence that feed into habitat reconstructions, as well as the limitations on inferences imposed by the fossil record, are illustrated in the following two examples of well-studied *Australopithecus* sites in East Africa.

Kanapoi

The Kanapoi locality in the southwestern Turkana Basin, Kenya, provides evidence for the paleoecology of *Australopithecus anamensis*, primarily from fossils preserved in fluvial sands and paleosols deposited within a time interval between 4.17 and 4.07 Ma (Harris et al. 2003). These deposits lie above and below a lacustrine interval, and the fauna is a time-averaged sample from two similar alluvial land surfaces (paleosols) that may have been formed tens of thousands of years apart (Fig. 4.3). Ecodiversity analysis of the faunas indicates that the two levels are only slightly different in terms of the percentage of terrestrial (ground-dwelling) mammals and the percentage of fresh grass grazers, i.e., mammals eating more water-dependent/seasonal wetlands grasses (Harris et al. 2003: Figs. 32 and 33; Behrensmeyer et al. 2007). The combined fauna is used to characterize the paleoecology of Kanapoi at the time of *A. anamensis* and is interpreted as a closed woodland habitat based on comparisons with analogue environments using ecological structure analysis (Reed 1997). Other lines of evidence suggest the existence of open habitats as well, based on stable isotopic signals in tooth enamel, possible non-arboreal monkeys, and micromammals, and characteristics of the paleosols (Wynn 2000; Manthi 2006). Whether these different habitat types were associated with each other across space, representing a persistent mosaic environment, or changed through the interval of time-averaging cannot be resolved with these analyses.

The amount of time represented by the Kanapoi faunal samples is clearly long by modern ecological standards and could include numerous habitat shifts across the areas of fossil accumulation. Also, the characteristics of the soils are superimposed on parent sediment that could represent ecological circumstances different from those during the period of pedogenesis. The Kanapoi *A. anamensis* remains (Leakey et al. 1995) could have been buried (1) during the initial sedimentary event(s), (2) during the early stages of pedogenesis affecting this parent material, or (3) later in the hundreds to thousands of years represented in the two fossiliferous units (Behrensmeyer et al. 2007).

Was *A. anamensis* associated with closed woodland, more open areas, or a mix of these habitat types? This is an important question from the standpoint of hominin evolution because it would indicate either habitat flexibility or specificity at ~4.2 Ma. In the case of shifting habitats through time, *A. anamensis* and other species could be closely tied to one habitat versus another, but still occur as mixed-habitat fossil assemblages. In the case of a mosaic of both closed and open habitats, species would have more opportunities, and perhaps also more selective pressure, to adapt to a variety of contemporaneous resources and substrates.

The Kanapoi hominins and associated fauna provide one of the most age-constrained and carefully documented examples of paleoecological evidence available at present, but it is still not possible to discriminate between alternative habitat models because of the amount of ecological time represented by the combined faunal sample. Mixed-habitat faunas do not necessarily mean mixed-habitat adaptations for the species on the faunal list. To improve temporal resolution, we need better ways of assessing the relative probabilities of these alternatives, such as more precise documentation of the depositional and taphonomic history of the fossil remains in each of the source paleosols, or stable isotope data from hominin and associated mammals' tooth enamel (Levin et al. 2011).

Hadar A.L. 333: Environmental Context of the "First Family" Locality

This example shows how the combination of detailed geological analysis and information from associated faunas contribute to reconstructing the context of an important accumulation of at least 15 *Australopithecus afarensis* individuals (W. Kimbel, personal communication). The A.L. 333 locality in the Denen Dora Member of the Hadar Formation is dated at ~3.2 Ma and has produced over 260 surface and excavated specimens of *A. afarensis* (Behrensmeyer et al. 2003; Behrensmeyer 2008; Harmon et al. 2003). Most of the hominin fossils were collected along with other faunal remains from an area of approximately 40 m × 80 m (3200 m^2) on steep slopes up to the stratigraphic level of 19 excavated specimens. It has long been assumed that the surface hominin fossils were derived from the same sedimentary unit as the in situ remains, and that this unit was part of a distinct, carbonate-rich paleosol (Aronson and Taieb 1981). Further study has shown that the in situ hominin fossils were buried prior to the formation of overlying paleosols (Behrensmeyer 2008).

Preserved bedding structures in the fine-grained, hominin-producing strata provide evidence that the abandoned channel swale continued to aggrade before sustained pedogenesis. The reconstructed paleodrainage of the DD-2 sandstone is oriented south to north with a trunk channel ~40 m wide and 3–5 m deep connecting a tributary system south of A.L. 333 to a distributary system to the north, which likely ended on the deltaic plain associated with the basin's depositional center. The burial of the hominin remains in the upper part of the channel involved fine-grained deposition indicating low-energy, seasonal flood events, and there is no sedimentological evidence for a high-energy, catastrophic flood that caused the demise of the hominins (Behrensmeyer 2008).

Although there is no direct record of vegetation at the A.L. 333 site, other than $CaCO_3$ root casts associated with pedogenesis, palynological research in the lower Denen Dora Member (DD-1 sub-member) suggests that the regional habitat prior to DD-2 and A.L.333 was predominantly a dry grassland (Bonnefille et al. 2004). Researchers (Aronson and Taieb 1981; Bobe and Eck 2001; Reed 2008) note that fossils of the genus *Kobus* (waterbuck) and other reduncines, which indicate moist substrates with "fresh grass" forage (Reed 1997), are common in the Denen Dora

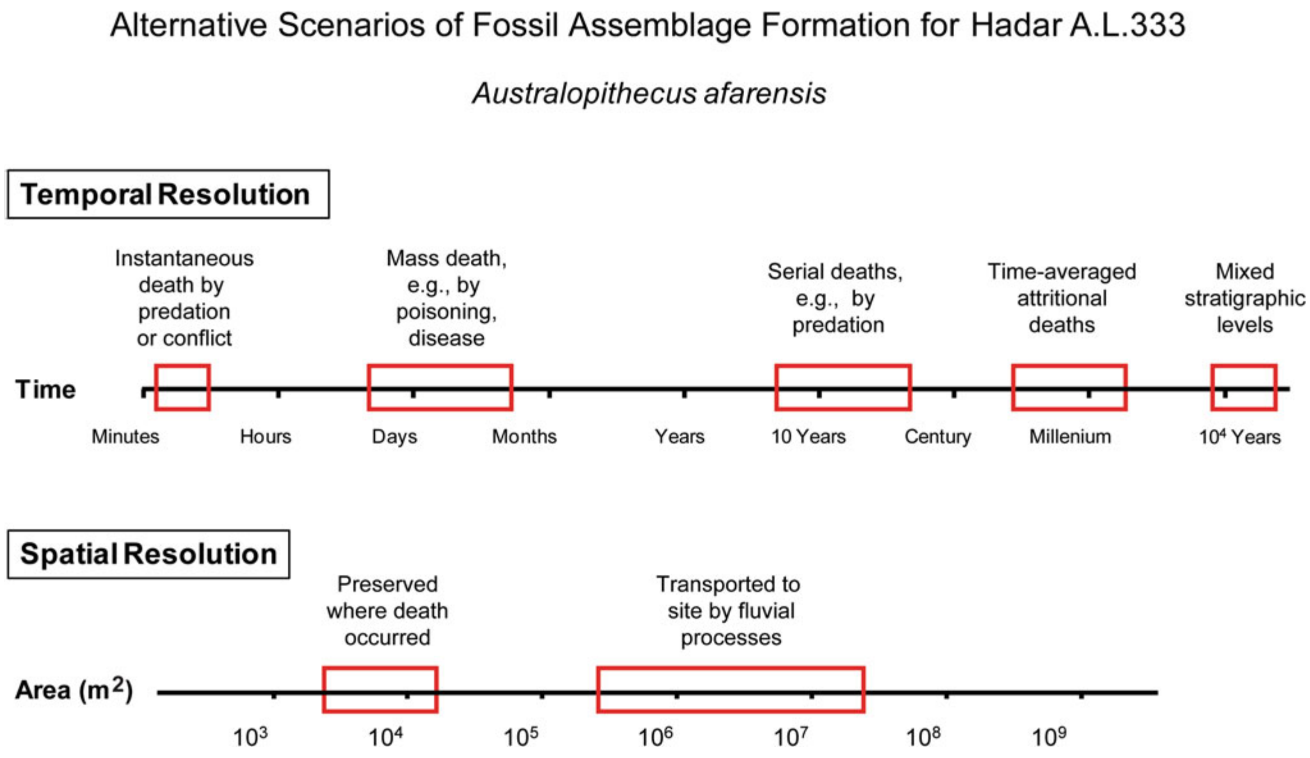

Fig. 4.4 Scale bar showing the different amounts of time-averaging that would be implied by alternative scenarios for the taphonomic origin of the A.L.333 *A. afarensis* assemblage. The biological and behavioral meaning of this as a population sample depends on which scenario is supported by paleoenvironmental context and taphonomic evidence

Member. Recent geo-faunal analysis by Campisano (2007; Campisano and Feibel 2008) indicates paleogeographic differences in the DD-2 sub-member, with edaphic grasslands and marshy conditions to the east and more closed, bush or woodland habitats to the west in the vicinity of A.L. 333. This agrees with stable isotope analysis of pedogenic carbonates at the excavation site indicating 30–34 % C_4 grassland (Hailemichael 2000), which is a relatively low proportion of grass compared with Hailemichael's other samples from the Denen Dora Member.

The in situ hominin remains at A.L. 333 can be related to a death—and possibly life—association of multiple hominin individuals with an abandoned channel swale that crossed an alluvial plain several kilometers from a paleolake to the north or northeast. The combined evidence indicates that both wooded and open grassland habitats were present in the DD-2 sub-member (Reed 2008), with a gradient from more closed in the west to more open edaphic grasslands to the east (Campisano 2007; Campisano and Feibel 2008). Hominins and other animals may have moved along linear depressions left by abandoned channels when they ventured across open savanna environments or used such areas for foraging and shelter. Therefore, as in the Kanapoi example, it is difficult to specify either open grassland or more bush to woodland as a "preferred" habitat for the A.L. 333 *A. afarensis*; the conservative interpretation is that they were associated with a mix of these types of vegetation.

Paleoenvironmental context provides only part of the history of the A.L. 333 hominin assemblage, and ongoing research is investigating alternative scenarios for the accumulation of the hominins based on taphonomic evidence from the fossils themselves, their spatial patterns of preservation, and co-occurring organisms (Behrensmeyer et al. 2003; Harmon et al. 2003). These scenarios cover a range of temporal scales and processes of death and burial (Fig. 4.4) and additional taphonomic analysis likely will shed new light on the paleoecology of this unusual fossil hominin accumulation.

Using Faunas to Infer Hominin Habitats

Today African habitats range from rain forests to deserts. The amount of rainfall, temperature, sunlight, evapo-transpiration, soil type, landscape physiography, and weather patterns/seasonality are the abiotic factors that cause differentiation in habitats. Floras and faunas are sensitive indicators of these environmental conditions, even on a relatively small spatial scale. Thus, ecological analysis of fossils provides a window into past habitats, which in turn can be used to reconstruct climatic conditions (Archibold 1995; Andrews 2006). In the tropical belt, the seasonal pattern and the amount of rainfall are the most important determining factors of the vegetation physiognomy (Hawkins et al. 2003). Habitats of various types often occur together in a particular spatial region because of changes in soil types, subterranean water, etc. For example, it is possible to have forests along rivers adjacent to near desert-like habitats, a condition that occurs where the present-day Awash River flows through the Afar hominin fossil beds in Ethiopia. These habitats are either called ecotonal or mosaic. Often mosaic habitats are indicated by ecological analysis of fossil assemblages; if this is due to time averaging of shifting habitats then the reconstruction of a contemporary mosaic of habitats could be incorrect. On the other hand, varying faunal compositions from time-synchronous collections over a broad spatial area, would lend support to the interpretation of a mosaic habitat structure. Occasionally, it is possible to reconstruct the habitat associated with hominin remains in a small spatial region and arrive at an interpretation for a non-mosaic (homogeneous) habitat at this scale (e.g., White et al. 2009).

Patterns of species occurrence at particular sites and their persistence and turnover through stratigraphic successions, combined with ecomorphic features of these species, provide evidence for ecological characteristics of hominin species and even for different populations of the same species (e.g., *A. afarensis* at Laetoli and Hadar; Su and Harrison 2008). Regional patterns can be combined in studies of larger-scale biogeographic and ecological patterns across the African continent. When compared with independently documented habitat shifts, species turnover patterns at individual sites may provide information on the eurytopic ("adaptable") and stenotopic ("specialized") nature of lineages, including hominins. One might expect that eurytopic species would occur consistently through time, despite habitat shifts, and across the landscape in a variety of habitats. In contrast, stenotopic species may only be recovered if particular habitats are sampled and may be consistently fewer in fossil assemblages, perhaps suggesting movement in and out of regions through time in response to habitat fluctuations. Over time stenotopic lineages may exhibit higher extinction and diversification rates (Vrba 1980; Badgley et al. 2008).

Because of collection practices, time-averaging, and spatial restrictions, it is probable that most fauna-based habitat reconstructions of Pliocene hominin localities represent a temporal (time-averaged) scale of 10^4–10^5 years, as illustrated in the Kanapoi example above, a relatively coarse level of resolution that may incorporate numerous shorter-term ecological shifts. On the other hand, reconstructions based on paleosols and pollen from specific sites may signal habitats of small area or short duration that may or may not be associated with the place and time where the sampled vertebrate fauna or hominins actually lived.

Paleoecological Evidence and Current Interpretations of *Australopithecus* Sites

The following section reviews various *Australopithecus* taxa (Table 4.1) and the information that is known about the paleoecological context of each locality.

Sites with Hominins of Uncertain Taxonomic Assignment

- *Lothagam Hill, Kenya*. There is abundant fauna from Lothagam, but hominins are very rare throughout the 7.0–3.5 Ma time span. Only two teeth are known from ~6.5–5.5 Ma in the upper Nawata Formation and one poorly preserved mandible from the overlying Apak Member of the Nachukui Formation (Leakey and Walker 2003). The bovid fauna of the upper Nawata is dominated by aepycerotins, alcelaphins, and reduncins, indicating a mix of gallery forest, open woodlands and grasslands. Fewer alcelaphins and more tragelaphins in the Apak Member as well as an increase in colobines provide evidence for a more closed habitat at ~5.0 Ma (Leakey and Harris 2003), although δ^{13}C analysis of Apak Member bovid tooth enamel indicates a significant component of C_4 vegetation (Cerling et al. 2003). The loss of *Etheria* (oyster) reefs in the Apak Member indicates a change to an ephemeral flow regime. Carbon isotope analysis of pedogenic carbonates and tooth enamel through the Lothagam succession indicates "a mosaic ecosystem with stands of pure C_3 vegetation interspersed with mixed C_3/C_4 floras" but no pure C_4 grasslands (Cerling et al. 2003). Given the number and excellent preservation of other mammalian fossils, the scarcity of hominins throughout the Nawata Formation indicates this group was rare to absent in Lothagam's late Miocene paleocommunity (Leakey and Harris 2003).
- *Omo (Shungura Formation), Ethiopia*. There are thousands of faunal specimens from this locality, largely consisting of isolated teeth, including some attributed to *Australopithecus* (Suwa et al. 1996) or more recently to *Australopithecus garhi* (White et al. 2002). Through the 1.2 Myr of likely *Australopithecus* occupation of this environment, the fossils

derive from fluvial depositional settings associated with the paleo-Omo River. The habitats associated with the hominins include riparian forest and woodland habitats from 3.2 to 2.0 Ma; alcelaphins and antilopins are a notably small component of the fauna during this time, indicating that open grassland habitats were limited in extent in the paleo-Omo River Valley (Bobe and Eck 2001; Bobe et al. 2002; Alemseged et al. 2007).

- *West Turkana, Kenya*. A number of hominin remains are identified as *A. afarensis* (Leakey et al. 2001), and at least 42 catalogued, but unpublished, specimens are assigned to *Australopithecus* (E. Mbua, personal communication). The fossils are mostly teeth from above the 3.4 Ma Tulu Bor Tuff, in the Lomekwi Member of the Nachukui Formation. *Kenyanthropus platyops* also occurs in the Lomekwi and underlying Kataboi Member, indicating the presence of two contemporaneous hominin genera. Based on the bovid fauna, the habitat of the lower through upper Lomekwi members has been interpreted as a mosaic dominated by woodland and forest-edge vegetation (Harris et al. 1988; Leakey et al. 2001). This is supported by abundant *Theropithecus brumpti*, a species regarded as indicating more closed habitats than *T. darti*, which is common in the contemporaneous Hadar Formation in Ethiopia (Leakey et al. 2001).

A. bahrelghazali

- *Bahr el Ghazal, Chad*. This site is dated between 3.0 and 3.5 Ma and is the only central African site from which any *Australopithecus* species has been recovered. The fauna associated with this hominin lacks tragelaphins and aepycerotins but has abundant alcelaphins, reduncins, and antilopins, indicating open grassland and lake margin habitats (Geraads et al. 2001).

A. anamensis

- *Allia Bay, Kenya*. Hominin remains consisting mostly of isolated teeth are preserved in a fluvial channel lag context associated with the base of the Moiti Member at ~4.0 Ma. Based on analysis of stress lines in the enamel of fossil herbivore teeth from this channel deposit, Macho et al. (2003) suggest that the habitat of *A. anamensis* was quite seasonal and similar to Masaai Mara in Kenya today. Schoeninger et al. (2003), using carbon and oxygen stable isotope analysis of tooth enamel, infer a mosaic habitat of closed woodland and grasslands with higher rainfall than the region receives today.
- *Kanapoi, Kenya*. A total of 59 specimens of *A. anamensis* have been reported from this locality. The abundant associated fauna is derived from floodplain paleosols and distributary sands that span an estimated total time period of about 100 kyr (see earlier discussion about Kanapoi time-averaging and habitat reconstruction) (Harris et al. 2003). Faunal eco-diversity analyses of these two levels are similar and indicate either wooded habitat or a mosaic with wooded and more open areas, while stable isotopes, the possible non-arboreal monkeys, and micromammals indicate presence of open grasslands. Wynn (2000) suggests, based on the characteristics of the paleosols where hominin remains were recovered in situ, that *A. anamensis* at least occasionally was associated with open conditions within a spatially variable ecosystem, typified by a mosaic of habitats, ranging "from forb-dominated edaphic grassland to gallery woodland, providing a larger view of the mixed ecosystem in which *A. anamensis* lived."
- *Aramis and Asa Issie, Ethiopia*. White et al. (2006) recovered *A. anamensis* from two localities near Aramis in the Middle Awash. The Asa Issie fauna has high percentages of colobine monkeys and tragelaphine bovids as well as forest-adapted avifauna and micromammals leading these authors to interpret the habitat as closed to grassy woodlands. The Aramis *A. anamensis* locality lacks other fauna but stable carbon analysis of pedogenic carbonate provide an average of ~25–35 % C_4, interpreted as indicating a "humid, grassy, woodland savannah environment." (White et al. 2006: 885).
- *Woranso-Mille, Ethiopia*. Haile-Selassie et al. (2010b) report a sample of 26 hominin remains of *Australopithecus*, recovered from the northernmost locality in the Afar thus far and dated to ~3.57–3.8 Ma. These fossils consist of isolated teeth and partial mandibles and maxillae that exhibit features of both *A. anamensis* and *A. afarensis*, thus a possible transitional form. The fauna from four collection sites indicates a mix of riverine forest, open woodland and grassland habitats, based on relatively abundant *Theropithecus oswaldi* aff. *darti* and tragelaphin, aepycerotin, and bovin bovids, which Haile-Selassie et al. (2010a) note is more similar to the older Kanapoi fauna than that of age-contemporaneous Laetoli (see below).
- *Galili, Ethiopia*. This site has produced *Australopithecus* teeth and a femur (Kullmer et al. 2008; Viola et al. 2008) identified as most similar to *A. anamensis*. The fauna suggest a comparable date with Kanapoi, and the Kataboi Member of the Nachukui Formation, although there are some similar fauna with the younger lower Hadar Formation. Galili proboscideans are primarily grazers, but browsing rhino (*Diceros*) and giraffe also are present, and bovids are dominated by tragelaphins followed by bovins

and reduncins. The habitat is reconstructed as primarily woodland to bushland, although open grassland is indicated by the grazing proboscideans and equids (Kullmer et al. 2008).

- *Fejej, Ethiopia*. Although originally described as *A. afarensis*, Van Couvering (2000) suggests that these specimens may be *A. anamensis*, but only based on their age (Kappelman et al. 1996).

A. anamensis summary. Faunal and other paleoecological evidence from seven different areas indicate a range of habitats from closed woodland (Assa Issie) to open grassland (Kanapoi). Wynn's (2000) assessment that this hominin "thrived in varied ecosystems" seems appropriate based on current evidence. As discussed in Haile-Selassie et al. (2010a), the mammalian species recovered in the Woranso-Mille are different from those at Kanapoi, Allia Bay, and other deposits of the approximately the same age. Whether this is due to differences in environment or reflects a larger-scale biogeographic phenomenon requires further study.

A. afarensis

- *Lothagam, Kenya*. Four isolated teeth found in the fluvially deposited Kaiyumung Member of the Nachakui Formation, dated at ~3.5 Ma, have been attributed by Leakey and Walker (2003) to *Australopithecus* cf. *A. afarensis*. The dominant bovid tribes of this member, aepycerotins, alcelaphins, and bovins, indicate relatively open and seasonally dry conditions (Harris et al. 2003). This interpretation is supported by a decrease in Colobinae and an increase in *Theropithecus* relative to the underlying Apak Member.
- *Laetoli, Tanzania*. *Australopithecus* fossils are relatively rare in the Laetolil deposits in Tanzania. According to Su and Harrison (2008), the Laetoli environment during *Austrolopithecus'* times was a mosaic of woodland, shrubland, and grassland with ephemeral streams and/or ponds. In contrast, Kovarovic and Andrews (2007) reconstruct it towards the wooded end of the savanna spectrum, i.e., a mosaic of dense woodland and bushland. In either case, there are no aquatic animals, and thus no evidence of permanent water, which may have contributed to low numbers of *A. afarensis* on the landscape as well as in the fossil assemblages.
- *Woranso-Mille, Ethiopia*. Haile-Selassie et al. (2010a) describe a partial skeleton of *A. afarensis* from the Korsi Dora vertebrate locality that has an estimated age of ~3.58 Ma. Additional fragmentary hominin remains are assigned to *A. afarensis* but also bear traits of *A. anamensis*. Over 1500 vertebrate specimens from this paleontological study area (Haile-Selassie et al. 2010b) indicate a mix of riverine forest, open woodland and grassland habitats (see discussion under *A. anamensis*).
- *Dikika, Ethiopia*. This locality has sediments of the Basal and lower Sidi Hakoma members of the Hadar Formation. Wynn et al. (2006) suggest that the fossils of *A. afarensis* are associated with a delta and a wooded environment, although certain species indicating open grasslands were also present. This site may have cut marked bones, which are controversial but if confirmed would show that this species incorporated meat or animal products into its diet (McPherron et al. 2010; for alternative viewpoint see Dominguez-Rodrigo et al. 2010).
- *Hadar, Ethiopia*. *A. afarensis* occurs in three successive members of the Hadar Formation, persisting through ~500 kyr in spite of shifts in the fauna and vegetation (Bonnefille et al. 2004; Campisano 2007).
    - Sidi Hakoma Member. The Sidi Hakoma deposits range in time from ~3.42–3.26 Ma (Campisano 2007). The deposits in the lowermost part of the unit indicate higher annual rainfall and less seasonal environments than found in any other Hadar sub-member (Reed 2008). The rest of the Sidi Hakoma Member fluctuates between bushland and open woodland with a riverine component until the top of the member when there is a transgression of paleolake Hadar into the collection areas.
    - Denen Dora Member. The entire Denen Dora Member encompasses only about 56 kyr (Campisano 2007). There is a major increase in the abundance of reduncine bovids in the middle part of this time period, indicating extensive wetland and floodplain habitat. After this episode, there is faunal evidence for open wooded grassland (Campisano et al. 2004; Behrensmeyer 2008; Reed 2008) (see earlier discussion of the A.L. 333 locality).
    - Kada Hadar Member. There are two collection units that encompass ~3.2–2.94 Ma separated by the Bouroukie Tuff 1 (BKT-1) at ~3.12 Ma (Campisano 2007). The separation is important as the habitats shift from open woodland with some edaphic grassland to more arid and scrub woodland habitats. The KH-2 fauna also has high proportions of antilopin and alcelaphin bovids, which indicate more arid environments (Vrba 1975), especially when contrasted with other Hadar Formation sub-members (Reed 2008).
- *Ledi-Geraru, Ethiopia*. Two *A. afarensis* molars were recovered from the Denen Dora Member of the Hadar Formation (Wood 2011). They were recovered with reduncin bovids indicating a lakeshore environment, as well as antilopins and alcelaphins that indicate more shrubland and grassland habitats (Reed et al., in preparation).

- *Maka and Belohdelie, Ethiopia*. White et al. (1993) conclude from faunal evidence that there was woodland-bushland at the time of deposition of the Maka material, which is similar to the faunal interpretation for the Denen Dora Member of the Hadar Formation. *A. afarensis* has also been assigned to the frontal from Belohdelie, but no information is available for the ecological context of the find (Asfaw 1987).
- *East Turkana (Koobi Fora), Kenya*. The older deposits (Tulu Bor and Lokochot members) have a moderately large faunal collection but *Australopithecus* is rare. The Tulu Bor Member of the Koobi Fora Formation is contemporaneous with the entire Hadar Formation in time (3.4–2.7 Ma) but has yielded only a few *A. afarensis* specimens (Kimbel 1988; Campisano et al. 2004). Feibel et al. (1991) described the depositional environment during Tulu Bor times as fluvial with floodplain lakes. Harris (1991) suggested that the habitat at this time included gallery forests amid floodplains, wet grasslands and woodlands. Controlled paleontological surveys of the Lokochot and Tulu Bor members at East Turkana support the comparative scarcity of *Australopithecus* fossils at East Turkana (Behrensmeyer et al. 2004), suggesting that the pattern is ecological or paleobiogeographic rather than taphonomic.
- *West Turkana, Kenya*. As mentioned previously, at least 42 catalogued but unpublished specimens are assigned to *Australopithecus*, and at least some of these are assigned to *A. afarensis*. These derive from above the Tulu Bor Tuff and other fauna indicates gallery forest and woodland (Leakey et al. 2001).
- *Fejej, Ethiopia*. Hominin specimens from this site were the oldest assigned to *A. afarensis* at 4.0–4.2 Ma (Kappelman et al. 1996), although some are now regarded as *A. anamensis* (Delson et al. 2000), but this is based solely on the age of the remains. There is no available information on the associated fauna or paleoenvironment.

A. afarensis summary. White et al. (1993) suggested broad habitat tolerance for *A. afarensis*, and the geological and faunal evidence from ~12 different localities from northern Ethiopia to Tanzania supports this earlier assessment; the fossil remains of this species are associated with habitats ranging from relatively open grassland to woodland, shrubland and riparian forest. There is no evidence that *A. afarensis* preferred any particular habitat, although low relative abundance at Laetoli and scarcity at East Turkana suggests some limits on its ecological flexibility. Given that this species was widespread and ecologically eurytopic (Reed 2008), then what caused its disappearance or extinction at ~2.7 Ma? This question could possibly further examined if: (1) the parameters of the reconstructed habitats could be refined in terms of abiotic factors (e.g., seasonal extremes in temperature and moisture), (2) patterns indicating competition or niche-partitioning could be reconstructed for other eurytopic mammalian species coexisting with *A. afarensis* (e.g., via stable isotope analysis) and (3) morphological changes within the lineage (Lockwood et al. 2000) could be associated with responses to habitat change.

Australopithecus or Paranthropus aethiopicus

- *Omo (Shungura Formation), Ethiopia*. Suwa et al. (1996) assign 19 isolated hominin teeth from a total sample of 48 to this species between 3.0 and 2.0 Ma. These occur from members C–F, i.e., between 2.9 and 2.3 Ma; later relatively robust teeth are assigned to *Australopithecus* (*Paranthropus*) *boisei*. This species co-occurs with a "non-robust" hominin, represented by teeth that could belong to *A. afarensis*, *A. africanus*, or early *Homo*. The environment was predominantly riparian forest and woodland based on associated faunas, which lack a strong open grassland-adapted component until after 2.0 Ma (Bobe and Eck 2001; Bobe et al. 2002; Alemseged et al. 2003; see earlier section).

A. africanus

- *Makapansgat, Member 3, South Africa*. This deposit contains an extremely large number of mammalian specimens (greater than 30,000), of which 24 are *A. africanus*. The deposit was accumulated in the cave by fossil hyaenid and porcupine species (Maguire et al. 1980). Mammalian community structure suggests that this region was a habitat mosaic that contained riparian woodland, bushland, and edaphic grassland (Reed 1998). Other habitat reconstructions range from woodland (Vrba 1980) to forest (Cadman and Rayner 1989).
- *Makapansgat, Member 4, South Africa*. *A. africanus* is represented by only three out of a total of 257 mammalian specimens. Cercopithecine monkeys make up 80 % of the collection; and the likely accumulators were birds of prey and leopards (Reed 1996). Member 4 fossil deposits suggests a more wooded habitat than Member 3, but this could be a function of sample size and predation bias rather than an actual change of habitat at the site. As Members 3 and 4 are roughly contemporaneous, both assemblages probably represent a similar woodland–bushland habitat mosaic.
- *Sterkfontein, Member 2, South Africa*. The skeleton of Stw 573 has been attributed, thus far, to *Australopithecus* sp. but is still embedded in rock, preventing thorough

taxonomic analysis (Clarke 1999). Dating for the locality ranges from 2.8 to 2.6 Ma (Pickering and Kramers 2010). The fauna recovered with Stw 573 thus far is mostly cercopithecoids and carnivores with very few ungulates (Pickering et al. 2004). These researchers suggest an open woodland habitat in a valley setting surrounded by rolling hills covered with rocks and shrubs. A riverine forest is also proposed based on the presence of numerous monkeys and a leopard. The fauna, other than the hyaenid *Chasmaporthetes*, is also present at Sterkfontein Member 4 and other younger localities in South Africa. Thus, if the deposit overlaps in time with Sterkfontein Member 4 (see below), there may be two *Australopithecus* species present at roughly the same time. It is worth noting that Pickering et al. (2004) state that most of the fauna recovered are "climbers" and this may have implications for Stw 573 as well.

- *Sterkfontein, Member 4, South Africa*. This member has been dated to between 2.2 and 2.6 Ma (Herries et al. 2013). The faunal community suggests a habitat of open woodland, with bushland and thicket areas (Reed 1997). Other habitat reconstructions of this member at Sterkfontein have indicated medium density woodland (Vrba 1975) and an ecotone between dry sandy highveld grassland and Kalahari thornveld (Avery 2001). Bamford (1999) notes the presence of lianas, which indicate fairly dense riverine forest.
- *Taung and Gladysvale, South Africa*. The single specimen of *A. africanus* from Taung was likely incorporated into a meal of a bird of prey. The eagles suggested as the predator range in their hunting regions from forests through deserts (Berger and Clarke 1995). The other fauna associated with this deposit suggests a habitat that is fairly dense woodland (e.g., *Tragelaphus*, *Cephalophus*, *Panthera*, cercopithecoids). The hominin teeth recovered from Gladysvale are associated with other fauna recovered from the ex situ material that indicate deposition during a period of relatively wet climate and closed vegetation (Berger and Tobias 1994; Plug and Keyser 1994).

A. africanus summary. Although there is some evidence for closed forest habitats (e.g., fossil wood, lianas), the associated fauna recovered with this species indicates a mosaic of habitats ranging from forest to open grassland. Certainly the higher latitude of these deposits means important climatic differences compared with those nearer to the equator, especially with respect to seasonal temperature fluctuations. Also, the irregular upland terrain of the South African limestone plateau contrasts with the lower, more even topography of the aggrading rift basins in East Africa

A. sediba

This species, recently discovered at the site of Malapa in South Africa, is represented by relatively complete remains of a number of juvenile and adult specimens from a cave fill dated to ~1.9 Ma. Thus far, no other fauna has been published from the locality, but remains of other species are present, and information on the paleoecology will no doubt be forth-coming (Berger et al. 2010; de Ruiter et al. 2013; Dirks et al. 2010).

Kenyanthropus platyops

This taxon was recovered from the Nachukui Formation on the west side of Lake Turkana (Leakey et al. 2001). According to these researchers, fauna recovered near the specimens suggest a habitat that is more wet and closed than habitats at Hadar. We include this taxon because, though not placed in the genus *Australopithecus*, it is from the same time interval as early *Australopithecus* in East Africa.

A. garhi

- *Bouri, Ethiopia*. This species has been recovered from the Hata Member of the Bouri Formation, and is a late East African (2.5–2.1? Ma) representative of the genus (Asfaw et al. 1999). The fauna associated with *A. garhi* indicates the presence of a shallow lake surrounded by grasslands (de Heinzelin et al. 1999). Cut marked bones were found in the same strata as *A. garhi*, and meat-eating behavior is attributed to this species (de Heinzelin et al. 1999). White (2002) has suggested that some of the teeth from the Omo Shungura Formation are *A. garhi* and as such would be found in the more closed woodland habitats of the region (Bobe and Eck 2001; Bobe et al. 2002; Alemseged et al. 2003).

Discussion: *Australopithecus* Paleoecology

Returning to the questions that were posed at the beginning of this paper, what can we say about the paleoecology of australopiths in light of current taphonomic, paleontological, and geological information from the many known occurrences of *Australopithecus* in the African fossil record?

1. *What was the range of habitats associated with* Australopithecus*, and is it possible to discern each species' preferred habitat*? Even the earliest records for the genus include evidence for diverse habitats, from forests and woodlands to more open vegetation, suggesting eurytopic ecological adaptations from the beginning. This evidence is time-averaged over ecologically long time intervals, thus limiting what we can infer about habitat preferences within the available vegetation mosaics. We also do not yet know whether any of the species in this genus preferred one of these habitat types or a mix of open and closed habitats. However, Campisano (2007) has shown that across similar time intervals at Hadar, *A. afarensis* is more abundant in drier regions. The documented existence of *Australopithecus* from Chad to Ethiopia to South Africa indicates continent-scale distribution, considerable seasonal temperature tolerance, and adaptability to different topographic settings.
2. *What were the most important limiting ecological variables (e.g., food, water, shelter, competition with other species, predator avoidance, intra-species interactions) for the australopiths*? There is a possibility that the genus was limited by climatic conditions and associated vegetation types that disappeared at Hadar during the 2.8–2.35 Ma interval of increased aridity, when it went locally extinct. Relative scarcity of *A. afarensis* fossils at Laetoli suggests dependence on water sources and vegetation associated with water. Otherwise, understanding of these variables remains unknown.
3. *How did habitats vary among australopith species and across different regions*? There is evidence from regional faunal differences for some degree of either habitat variability or biogeographic isolation among the different species. Contrary to the hypothesis that hominin evolution is linked with retreating forests and expanding grasslands, the habitats of the earliest species, *A. anamensis* have been reconstructed as rather open, followed by a mosaic of open and closed habitats for *A. afarensis*. *A. bahrelghazali* appears to have existed in the most open grassland habitat, which is interesting considering its location in a lake basin in central Africa. *A. africanus* appears also to have been associated with mosaic habitats, although the habitats contributing to the mosaic change through time in southern Africa. There is as yet no overlap in species between South and East Africa during the temporal range of *Australopithecus*, evidence that this hominin genus was one of the most widely distributed members of the Pliocene mammalian fauna of Africa. Differences in its patterns of occurrence among basins within East Africa and, indeed, among localities on the west and east side of Lake Turkana, also suggest that *Australopithecus* was a eurytopic genus. These observations and supporting data provide a foundation for developing and testing hypotheses regarding responses to climate change experienced on local and regional scales. New research to obtain high resolution drill core records of environmental change from Plio-Pleistocene paleolakes along the East African Rift can also be applied to these hypotheses.
4. *Was there more than one* Australopithecus *species sharing an ecosystem at any given place and time*? This appears possible given the evidence from West Turkana, Omo, Galili, Woranso-Mille, and Sterkfontein (Table 4.1), but at present there is hard evidence for only one species at any one stratigraphic level and site. Time-averaging of hominin remains from different time periods may create the appearance of co-occurrence in a paleocommunity. Further fieldwork and taxonomic research are needed on deposits that may include different hominins.
5. *Was* Australopithecus *a maker and user of stone tools*? There are tantalizing occurrences of purported cutmarks on bones at two *Australopithecus* sites, Dikika and Bouri, but these finds are contested. More in situ evidence is needed, including the artifacts themselves, to provide a definitive answer to this question.
6. *Was there change in habitat use through time*? *Did niche breadth increase or decrease within individual lineages as* Australopithecus *evolved*? We do not know the answers yet, but higher resolution paleoecological research, additional hominin sites, and stable isotope studies of hominin enamel through sequences such as the Hadar Formation could provide new information bearing on these questions.
7. *How might global or continental-scale climate change between 4.5 and 2.0 Ma have affected the paleoecology of* Australopithecus? Some degree of climate forcing is probable, but understanding this will take careful study of regional variability in paleoclimates in southern versus eastern versus central Africa and comparisons with deep sea and continental lake records of global and continental-scale climate change. These data, in turn, can be used in paleoclimatic models of more localized regions to arrive at better models of climatic change through the Pliocene.

Habitats

The localities where the different species of *Australopithecus* have been documented provide evidence for varying amounts of closed woodland to forest as well as open grassland and shrubland habitats. This evidence is based primarily on associated fauna and stable isotopes, with some input from the paleobotanical record. The genus *Australopithecus* can be characterized as eurytopic because its species are found in deposits that have faunal and isotopic evidence for a wide range of habitats. It is not clear, however, whether individual species were eurytopic or stenotopic with respect to the inferred spectrum of vegetation types because hominin sample sizes are generally too small to show statistically significant associations with particular ecological indicator taxa (e.g., Bobe et al. 2002). The one exception where there is enough hominin fossil material at one locality to begin to examine this questions is *A. afarensis* at Hadar, which persists for ~500 kyr though changing environmental conditions, indicating eurytopy with respect to these conditions (Bonnefille et al. 2004; Reed 2008). That the microwear of *A. afarensis* indicates little variability in diet (Grine et al. 2006a, b), however, may indicate that although the species inhabited different environments, it ate something similar in all of them (see below).

Given limited samples of hominins and known biases introduced by taphonomic processes, pinning down an association of a particular hominin species with a "preferred" habitat may be possible using quantitative analysis associations with ecological indicator taxa. Progress in this approach will require more data points consisting of carefully controlled associations of hominins and faunal or other proxies to allow higher temporal and spatial resolution of the consistency of these associations. Growth in understanding ecological indicator species associated, or not associated, with hominins will also help this approach. Autecological investigations including expanded stable isotope analysis of hominin tooth enamel using minimally destructive laser-ablation technology could also provide direct evidence of dietary preferences and variability. Microwear and anatomical traits indicating adaptation for climbing, walking, etc., could also support higher resolution inferences about preferred habitats.

Diet and Food Procurement

There has been recent research that sheds light on the diet of some *Australopithcus* species but also brings up further questions. It has long been known that *A. africanus* microwear indicates a variable diet, but not as variable as *Paranthropus robustus* recovered from the same geographic region. In contrast, *A. anamensis* and *A. afarensis* appear to have been more limited in their selection of foods due to the low variation in the fine scratches that appear on their teeth through time (Grine et al. 2006a, b). Stable isotopes of *Australopithcus* taxa are discussed in Sponheimer (2013) and Grine et al. (2012), but indicate both C_3 and C_4 plants were consumed. Finally, evidence suggests that some of these hominins may have been consuming meat or marrow (de Heinzelin et al. 1999; McPherron et al. 2010). Thus, while there is interesting autecological evidence provided for many of these taxa, there are still many questions as to how they were utilizing their habitats.

Conclusion and Future Research

We know much more about the paleobiology of *Australopithecus* than we did 30 years ago, and in spite of taphonomic and time-averaging caveats, the large number of documented sites now provides convincing evidence that the genus had an impressive breadth of tolerance for varied habitats and climates. Better-coordinated research in faunal analysis, habitat reconstruction, spatial distribution, and taphonomic biases of the hominin fossil record at local, regional, continental, and global scales, as well as additional new sites, should greatly expand this knowledge in the coming decades.

Used in conjunction with species turnover patterns and evidence for abiotic environmental change, the evidence provided in this paper can serve as a baseline for continuing research on the ecological context of hominin evolution. Further advances in habitat reconstruction for *Australopithecus* will depend on careful attention to the scale of the evidence (temporal and spatial) versus the scale of the desired reconstruction. Particular caution is needed to avoid interpreting ecological features of a time-averaged faunal list as a "snapshot" (single time-plane) sample of the habitat of *Australopithecus* or any other hominin.

In a succession of fossiliferous strata, we usually are dealing with varying proportions of different habitats (e.g., closed vs. open, or wetter vs. drier habitats) rather than the extremes of one or the other. How these habitat "mosaics" are recorded in the fossil record depends on the spatial scale of the sample as well as the amount of time represented. Shifts of an ecotone across a depositional area through time can also result in a similar mixed habitat signal (Behrensmeyer et al. 2007). There is no simple solution to the problem of time-averaged ecological signals, but in some fossil-bearing sequences there are ways to calibrate the scale of habitat patches and evaluate the adaptations of individual species. These include:

1. Higher resolution sampling and morphological analysis of faunas associated with *Australopithecus*-bearing strata, including intra- and inter-basin comparisons of mammalian species associated most commonly with *Australopithecus.* What are the morphological and abundance similarities and differences among species that co-occur, or do not co-occur, with *Australopithecus*?

To the same end, analyses of tooth wear patterns and stable isotopes in the same species across space and/or through time at individual localities will give us information regarding diets that may be consistently different in particular basins.

2. Coordinated lateral sampling of faunas and paleoenvironmental variables in Pliocene sequences where *Australopithecus* is common versus uncommon or absent (e.g., Hadar vs. Turkana Basin, Omo Shungura vs. Tugen Hills vs. Lothagam).

While pursuing increased resolution and refinement of taphonomic and ecological evidence, it also will be important to adjust the spatial and/or temporal scale of paleoecological interpretations to take account of the inevitable limitations of the record. Much remains to be learned about resolving ecological information in the fossil record of *Australopithecus,* or any other intriguing extinct mammalian genus.

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Part II
Sites and Species

The articles in this section provide descriptions and discussions on the species of *Australopithecus* in different areas or different individual sites. They provide the critical systematic background for the broader discussion on paleobiology in later sections.

In Chap. 5, "*Australopithecus* in Ethiopia", Zeresenay Alemseged reviews the distribution and documented ages for the three species of *Australopithecus* found in Ethiopia: *Australopithecus anamensis*, *Australopithecus afarensis*, and *Australopithecus garhi*. Fossil attributed to *Australopithecus* are found in many parts of Ethiopia from the north to the southernmost part of the country. The first appearance of the genus in Ethiopia is slightly over 4 million years ago, and does not seem to be associated with any major climatic or geological event. He reviews what is known about each of the species, and then focusses on many of the critical, unknown aspects of the biology and relationships of the different taxa.

In Chap. 6, "The Alpha Taxonomy of *Australopithecus africanus*" Fred Grine reviews the long, complex, and convoluted taxonomic history of fossils commonly attributed to *A. africanus* from Makapansgat, and especially Sterkfontein. For decades, researchers have debated how many different taxa are present at these sites and which specimens are likely males and which are females, with little consensus. Much of the debate, he notes, centers on immature specimens, and often lacks quantification of the anatomical features under discussion. He emphasizes the need to resolve basic issues of taxonomy at the species level before broader questions of adaptation and biogeography can be properly considered, and suggests that new technologies may help to settle the ongoing debates about what constitutes *A. africanus*.

In Chap. 7, Ronald Clarke offers his interpretation of "*Australopithecus* from Sterkfontein Caves, South Africa." He argues that two species of *Australopithecus* can be identified at that site—*A. africanus* and *Australopithecus prometheus*. The second species, originally described from Makapansgat is now known from a nearly complete skeleton found in Member 2 in the Silberberg Grotto. A wide range of conflicting dates between 4 and 2 Ma have been reported for these deposits, but he suggests that it seems likely that they date to roughly 3 Ma. Both species are present in Member 4 between 2.5 and 2.14 Ma. He also asserts that the StW 53 cranium, often identified as *Homo habilis*, belongs to *A. africanus*. He reviews the taphonomic situation that led to the accumulations of hominin remains and also the likely environments during which the different members were deposited.

In Chap. 8, "*Australopithecus sediba* from Malapa, South Africa", Darryl deRuiter, Steven Churchill, and Lee Berger report on the most recently described species of *Australopithecus*. They review the history of the discovery of the fossils, the geology and reconstructed taphonomy of the site, and details of the bony elements preserved. They then outline how *A. sediba* can be distinguished from other species of *Australopithecus*, and the philosophical choices involved in placing a fossil taxon with intermediate morphologies in either *Australopithecus* or *Homo*. The discovery of *A. sediba* with a precise date of between 2.0 and 1.95 Ma has important implications for the taxonomic identification and phylogenetic placement of numerous early hominin fossils of similar age in both southern and eastern Africa.

In Chap. 9, “Variation in Mandibular Postcanine Dental Morphology and Species Diversity in *Australopithecus*”, Fred Grine, Marcia Delanty, and Bernard Wood address the question of whether multiple species are found in the deposits of Member 4 at Sterkfontein, discussed in earlier chapters by Grine and by Clarke. They find that compared with a sample of teeth from the lowland gorilla, *Gorilla gorilla*, the samples of mandibular premolars and molars from Member 4 at Sterkfontein are slightly more variable, but the differences are significant for only a few cusp dimensions. While their analyses suggest great variability in the fossil sample, they do not identify any specimens as distinct outliers in all features. Thus, they do not reject the null hypothesis of a single taxon, *A. africanus*, in Member 4.

The Editors

Chapter 5
Australopithecus in Ethiopia

Zeresenay Alemseged

Abstract *Australopithecus* in Ethiopia is currently represented by three species: *Australopithecus anamensis, Australopithecus afarensis* and *Australopithecus garhi* ranging in age from about 4.2 to 2.5 Ma. The genus is encountered from Hadar and environs in the North to Fejej in the southernmost part of the country. The relationship among the three species appears to be an anagenetic link going from the oldest to the youngest, but there is not enough evidence to relate the genus directly to any known ancestral species, which renders its origin difficult to pinpoint. Of the three, *A. afarensis* is by far the best known in terms of its paleobiology and paleoecology, and further research is required to reconnoiter the paleobiology of *A. anamensis* and *A. garhi* as well as to shed light on the ancestor of the genus in general.

Keywords *Australopithecus afarensis* • *Australopithecus anamensis* • *Australopithecus garhi*

The Genus *Australopithecus*

The genus *Australopithecus* is the first fossil hominin genus named from Africa (Dart 1925). The type species, *Australopithecus africanus*, recovered from many South African cave sites, represents one of the best documented and relatively well known early hominin species and was the only "gracile" *Australopithecus* taxon widely recognized until 1978, when it was joined by *Australopithecus afarensis* (Johanson et al. 1978). The proliferation of fieldwork in different parts of Africa over the past four decades has shown that the genus was not only diverse but also had greater antiquity than previously thought (Brown et al. 2013). The spatial and temporal distribution of its species reveals that *Australopithecus* was successful in occupying a wide range of environments and geographic areas in southern, eastern and northern parts of Africa for over 1.7 Myr between ca. 4.2 and 2.5 Ma (Brown et al. 2013). Currently, *Australopithecus* comprises six species though authors have differing views on this: *Australopithecus africanus*, *Australopithecus afarensis*, *Australopithecus bahrelghazali*, *Australopithecus anamensis*, *Australopithecus garhi*, and *Australopithecus sediba*, when the "robust" forms are assigned to *Paranthropus.*[1]

Three of these species—*A. anamensis, A. afarensis*, and *A. garhi*—are found in Ethiopia (Fig. 5.1). The earliest evidence for *Australopithecus* in Ethiopia comes from the sites of Asa Issie and Aramis in the Middle Awash dated to ∼4.1–4.2 Ma, and from 4.0 to 4.18 Ma site of Fejej in the south (Kappelman et al. 1996; White et al. 2006). The fragmentary nature of the Fejej remains does not allow firm taxonomic attribution, but in their announcement the authors noted that the Fejej teeth are virtually identical in their preserved anatomy to A.L. 198-1 (Fig. 5.2), which belongs to *A. afarensis* (Fleagle et al. 1991). Yet, the recently discovered fossils from the Middle Awash assigned to *A. anamensis*, though fragmentary, document a more secure first appearance datum (FAD) of the genus in Ethiopia, and are nearly as old as the material from Kanapoi in Kenya (Leakey et al. 1995). Evidence for the last appearance datum (LAD) of the genus comes from the Hata Beds at Bouri in the Middle Awash region of Ethiopia and is represented by *A. garhi* fossils at about 2.5 Ma (Asfaw et al. 1999). The temporal range of the genus can therefore be bracketed between ca. 4.2 and 2.5 Ma in Ethiopia, and geographically the genus occupied the whole range of the Ethiopian Great Rift Valley region from Hadar and environs in the north to Fejej in the southernmost part of the country.

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[1] The robust species are placed in the genus *Paranthropus* for convenience. The author does not think that there is adequate evidence or consensus to accept or reject *Paranthropus* monophyly.

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Vertebrate Paleobiology and Paleoanthropology, DOI: 10.1007/978-94-007-5919-0_5,

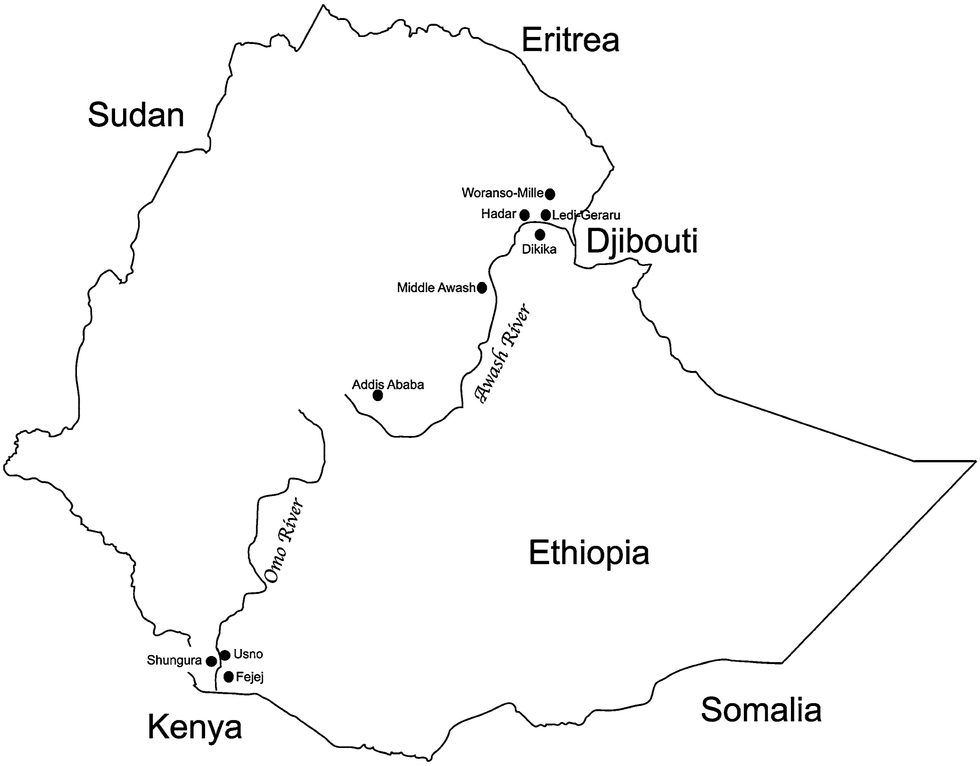

Fig. 5.1 Schematic map of Ethiopia noting sites from which *Australopithecus* has been recovered. The Middle Awash area includes the subareas of Aramis, Asa Issie, Belohdelie, Bouri, Maka, and Wee-ee

The three *Australopithecus* species encountered in Ethiopia have generalized morphologies differentiating them from species of the genus *Homo,* including a prognathic face, small brain, megadont postcanine teeth, relatively large canines and primitive upper limbs (not known for *A. anamensis*). Moreover, they can be differentiated from *Paranthropus* species because they lack the derived dentognathic features of those taxa, such as enlarged post-canine dentition, reduced anterior teeth, etc. They can also be readily distinguished from the earliest putative hominins species (*Ardipithecus, Sahelanthropus* and *Orrorin*) because they possess many derived features, including larger molars, smaller canines and undoubted bipedalism, shared with other later hominins.

It is apparent that the masticatory apparatus of the first representatives of the genus appears better adapted to a more heavily chewed and/or abrasive diet (Teaford and Ungar 2000; but see also Sponheimer 2013). This might point to a shift in dietary adaptation of the earliest members of the genus *Australopithecus* and their venturing into more open environments, though they lived mainly in rather closed and wooded settings (Reed 1997; White 2006). Yet, the emergence of the genus just prior to 4.0 Ma does not seem to correspond to any known global climatic change. Understanding the external causes for the adaptive shift toward early hominin megadontia therefore deserves further investigation. As to their locomotor repertoire, there is no question that the three Ethiopian species of this genus were bipedal; however, they retained many primitive and ape-like features, particularly on the upper part of the skeleton, that are difficult to interpret from a functional point of view (Larson 2013; Harmon 2013). Some propose that members of the genus included arboreality in their locomotor behavior, particularly *A. afarensis* (Senut and Tardieu 1979; Stern and Susman 1983; Alemseged et al. 2006; Green and Alemseged 2012) while others suggest that these primitive characters were retentions from the common ancestor without any significant relevance to the locomotor adaptation of these species (Lovejoy 1981; Latimer 1991; Ward 2013). Reconciling these differing interpretations will require further research into the functional anatomy of the “primitive” features within the context of extant primate morpho-functional diversity.

Questions About the Genus

Several important questions concerning *Australopithecus* in Ethiopia are not fully answered because of the fragmentary nature of the fossil evidence and small sample size. As shown by Kimbel et al. (2006: 148), “currently available character-state and stratigraphic data are consistent with the hypothesis that Early Pliocene *A. anamensis* was ancestral to Middle Pliocene *A. afarensis*, and further suggest that

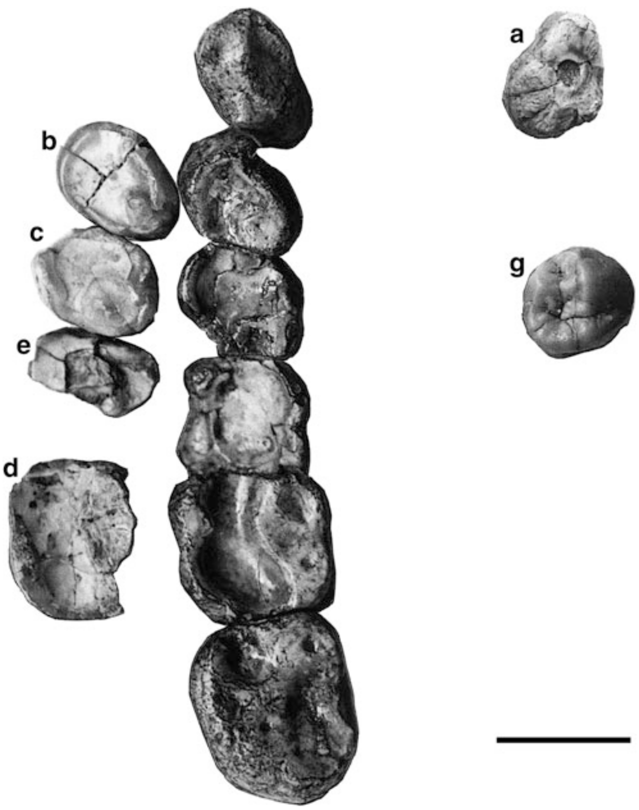

Fig. 5.2 Occlusal view of the Fejej mandibular teeth (FJ-4-SB-1 (**a**–**e**, **g**); FS-4-SB-2 (**g**)) compared with a cast of *A. afarensis* (A.L. 198-1) from Hadar. Reprinted with permission from Wiley-Liss

these taxa constituted an anagenetically evolving lineage." This claim appears to be supported by the available data coming from Kenyan, Tanzanian and Ethiopian fossil sites. What's more, based on new fossils from the site of Woranso-Mille, in Ethiopia, Haile-Selassie (2010) suggests that there is no compelling evidence to falsify the ancestor–descendant relationship between *A. anamensis* and *A. afarensis*. Further these temporally and morphologically intermediate fossils are interpreted to indicate that the species names *A. afarensis* and *A. anamensis* do not refer to two real species, but rather to earlier and later representatives of a single phyletically evolving lineage (Haile-Selassie 2010). The ca. 4.1 Ma fragmentary Fejej fossil material from locality FJ-4 is sometimes discussed as possibly attributable to *A. anamensis* (Kappelman et al. 1996; White 2002), though it cannot be morphologically distinguished from the 3.2 Ma A.L. 198-1 (*A. afarensis*) (Fleagle et al. 1991). The taxonomic attribution of the Fejej fossil is critical in light of questions pertaining to the mode of speciation in the *A. anamensis*–*A. afarensis* lineage. If indeed the FJ-4 fossil belongs to the latter, it would mean that the two species overlapped in time and that *A. afarensis* was the result of a cladogenetic speciation event. However, given the results obtained by Kimbel et al. (2006) on the polarity of characters among the two species' different site samples, and in the absence of diagnostic features, it is more reasonable to consider the FJ-4 fossils as part of the *A. anamensis* hypodigm pending a more firm taxonomic identification or further discovery.

Yet, resolving whether there was in situ anagenesis in the *A. anamensis*–*A. afarensis* lineage in Ethiopia requires additional evidence. Given that the Kenyan and Ethiopian *A. anamensis* site samples are close to each other in age, and that the *A. afarensis* hypodigm is encountered in Tanzania, Kenya and Ethiopia, one cannot establish precisely where and from which ancestor *Australopithecus* emerged as a genus, and where the transition between *A. anamensis* and *A. afarensis* occurred.

As pointed out by White et al. (2006, 2009), there is a clear difference between *Ardipithecus ramidus* and *A. anamensis*, in their dentognathic configurations as well as their paleoenvironmental settings among many other differences, which reflects adaptations for different diets and probably different ecological niches. If the two taxa are directly related, the emergence of these new adaptations must have happened within a relatively short geologic time, because *Ar. ramidus* and *A. anamensis* are encountered in sedimentary layers dated to 4.4 and 4.2 Ma, respectively. There is no evidence for major paleoenvironmental or paleoclimatic changes around this time explaining these major morphological and dietary shifts. Factors that triggered the possible transformation from the thinner-enameled putative ancestors (*Ar. ramidus*; White et al. 2006) to the megadont and thick enameled *Australopithecus* just before 4.0 Ma remain unclear. Though, additional research at sites dated to around 4.0 Ma could help answer these questions, the striking contrast between *Ar. ramidus* and *Australopithecus* (White et al. 2009) in terms of their feet morphology and overall locomotor repertoire, dental and cranial anatomy, environmental and dietary adaptation and patterns of sexual dimorphism in addition to their temporal proximity makes their ancestor–descendant relationship less likely rendering the direct ancestor of *Australopithecus* and its origin elusive.

The Three Species

Australopithecus anamensis

Diagnostic remains of this species were found at the sites of Allia Bay and Kanapoi in Kenya (Leakey et al. 1995), though the first discovery of fossils of this taxon occurred in the Kanapoi region in 1965 by a Harvard University expedition (Patterson and Howells 1967). The suite of dentognathic features observed on these fossils, including the morphology of the mandibular symphysis, orientation of the dental row, size and form of the upper canine and traits on the lower third premolar clearly demonstrate the integrity of the species, and show that the FAD for genus *Australopithecus* was earlier than previously thought (Laetoli 3.7 or Belohdeli: ca. 3.8 Ma). *A. anamensis* was not known from Ethiopia with certainty until 2006, when its presence in the Middle Awash was reported (White et al. 2006). The contribution of the Ethiopian *A. anamensis* material was that in addition to increasing the size of the species' hypodigm, which is critical for a poorly sampled species such as this one, it also expanded its known geographical range further by about 1,000 km to the north in the Afar, and added new paleoenvironmental and paleoecological information about the species. At the Ethiopian sites the species was a regular occupant of a wooded biome, which differs from the mosaic environmental settings reconstructed at Allia Bay and Kanapoi, increasing the known ecological range of the species (Leakey et al. 1995; White et al. 2006).

Questions About *A. anamensis*

In addition to some dental features, the Middle Awash maxilla (ARA-VP-14/1) is anatomically similar in preserved parts to the KNM-KP 29283, with straight tooth rows and vertically implanted canines (White et al. 2006). But the authors point out that the Asa Issie canine size relative to molar size and canine shape is intermediate between *Ar. ramidus* and known *A. anamensis* conditions. These observations probably indicate geographic variation within *A. anamensis*, which could be related to differences in ecological niches in Ethiopia and Kenya. Paleoenvironmental reconstructions show that the species lived in different types of settings. Given that the two site samples are dated to around the same time, one cannot establish the patterns of dispersal or paleobiogeography of this ancient species. Among the important questions regarding the Ethiopian *A. anamensis* sample are: (1) What does it tell us about variation and the biogeography of the species? and (2) What do we learn from the apparent differences in the type of biome occupied by the Ethiopian *A. anamensis* compared to the Kenyan sample? (3) Is *A. anamensis* an earlier representative of an already known species (Haile-Selassie 2010). More fossils are required to elucidate these issues.

Australopithecus afarensis

Australopithecus afarensis is one of the best-known Pliocene hominin species along with *A. africanus*. Its earliest occurrence (FAD) is documented at the site of Belohdelie, Ethiopia, dated to ca. 3.8 Ma (Asfaw 1987). It is also encountered at the site of Laetoli, dated to ca. 3.7 Ma, in Tanzania, where the holotype (L.H. 4) was found and recently at the site of Woranso-Mille, Ethiopia at around the same time (Haile-Selassie et al. 2010). However, the last occurrence (LAD) of this species is problematic. *A. afarensis* has been found at all levels of the Hadar Formation that span from just over 3.4 Ma up to ca. 2.9 Ma (Kimbel et al. 2004; Alemseged et al. 2005; Kimbel and Delezene 2009). However, in the lower Awash, there is a widespread unconformity between ca. 2.9 and 2.7 Ma, after which the Busidima Formation, distinct from the Hadar Formation (Fig. 5.3), is deposited in a different geotectonic setting (Quade et al. 2004; Wynn et al. 2006). So it is not obvious whether ca. 2.9 Ma is the actual LAD for the species or is an artifact of missing sediments. The 2.9–2.7 Ma interval is represented in the Shungura Formation of the lower Omo basin (Brown and de Heinzelin 1983), but the "*A. afarensis*-like" hominin remains from there are fragmentary and not diagnostic (Suwa et al. 1996). Future field research in this time interval will shed light on this important problem.

The morphology of *A. afarensis* is reasonably well known from fossils that come from the sites of Hadar, Dikika, Maka and Belohdelie (Johanson et al. 1978; Asfaw 1987; White et al. 1993; Kimbel et al. 2004; Alemseged et al. 2005, 2006), and exhibits substantial cranial and dental variation accompanying significant sexual dimorphism (Kimbel et al. 2004; Fig. 5.4). The seemingly high degree of variation has led some researchers to suggest the presence of multiple species within the Hadar sample (Senut 1983). Yet, the single species hypothesis has not been demonstrably rejected. In addition to the fact that *A. afarensis* is a sexually dimorphic species mainly in regards to body size, it is probable that the relatively large sample size from Hadar, spanning ca. 500 kyr, would result in a high degree of observed variation. Equally important in this regard is the observation on temporal trends by Lockwood and others (Leonard and Hegmon 1987; Lockwood et al. 2000) whereby the overall mandibular size increased through time, particularly with specimens from the last temporal rank of the Hadar Formation becoming larger. This pattern shows that time also contributed to the range of variation. But other visible variations such as the morphology of the lower P3 (uni- vs. bi-cuspid) and the mandibular symphysis (angled vs. vertical) do not show a clear temporal trend and are observed throughout the sample.

Fossil evidence from Hadar and other sites shows that *A. afarensis* was a habitual biped, and most researchers accept this. However, there is still heated debate as to the importance of arboreality in the species (Ward 2002, 2013). Most of the questions arise from the fact that *A. afarensis* retains several ape-like features including primitive limb proportions, long and curved fingers, gorilla-like scapulae

Fig. 5.3 Reconstructed skulls of a male (A.L. 444-2 (cast), *left*) and female (A.L. 822-1 (actual skull), *right*) *A. afarensis*. Photographs by W. H. Kimbel

and ape-like wrist bones, among others (Susman and Stern 1991; Stern 2000; Alemseged et al. 2006; Tocheri et al. 2007; Green and Alemseged 2012). The issue is further complicated by the difficulty in interpreting primitive characters, and by the lack of clear understanding of the function of many postcranial elements (and muscle attachments and inferred muscle configuration and function) in comparative extant primates.

Despite the abundant *A. afarensis* fossil material from Hadar, the proportion of juvenile specimens is very small and fragmentary, notwithstanding the sample of immature remains from the A.L. 333 locality at Hadar (see Harmon 2013). Moreover, up to now most investigations looking at development and growth patterns in early hominins have been conducted on South African fossils mainly because of problems of "fossil material availability" to researchers using recently developed techniques that are often employed to explore internal structures and juvenile dentition. As a result, compared to the wealth of knowledge that we have about the adults in the Ethiopian *Australopithecus,* little is known about the infants of *A. afarensis* and nothing about those of *A. anamensis* and *A. garhi*. The discovery of an almost complete skeleton of a juvenile *A. afarensis*, DIK-1-1, has shed fresh light on questions pertaining to ontogeny, and further detailed studies promise to add an unprecedented amount of data to investigate growth and development in early hominins (Fig. 5.5) (Alemseged et al. 2006).

At Hadar, the species *A. afarensis* is generally found in wet woodland habitats (Reed 1997, 2008), and in the adjacent site of Dikika the vertebrate fauna indicates the presence of a woodland-grassland landscape close to water and with frequent flooding (Alemseged et al. 2005; Wynn et al. 2006). In addition, the Maka mandible is associated with fauna similar to that encountered in the Denen Dora Member of the Hadar Formation (White et al. 1993). Thus, it could be concluded in general that *A. afarensis* lived in a wooded environment within the proximity of water, at least in Ethiopia. The diet of *A. afarensis* can be described as generalist-herbivore, however recent reports show that *A. afarensis* may have at least sporadically included animal tissue (meat and bone marrow) in its diet (McPherron et al. 2010). Cutmarked bones from the site of Dikika are currently the earliest evidence for meat eating and tool use in the species. Because the current evidence is fragmentary, further fieldwork and additional experimental research will be required to acquire new data and elucidate the tempo and mode of tool use and meat consumption in our family.

Finally, the general consensus on the phylogenetic position of the Ethiopian *A. afarensis* hypodigm is that it represents a morphologically generalized but variable basal early hominin species which is ancestral to all subsequent hominins,

Fig. 5.4 Composite stratigraphic section of the Hadar Formation (courtesy of Chris Campisano). Sidi Hakoma, Denen Dora, and Kada Hadar Member section adapted from Campisano and Feibel (2008), Basal Member section adapted from Wynn et al. (2006). Preliminary Basal Member paleomagnetic interpretation provided by Mark Sier (unpublished)

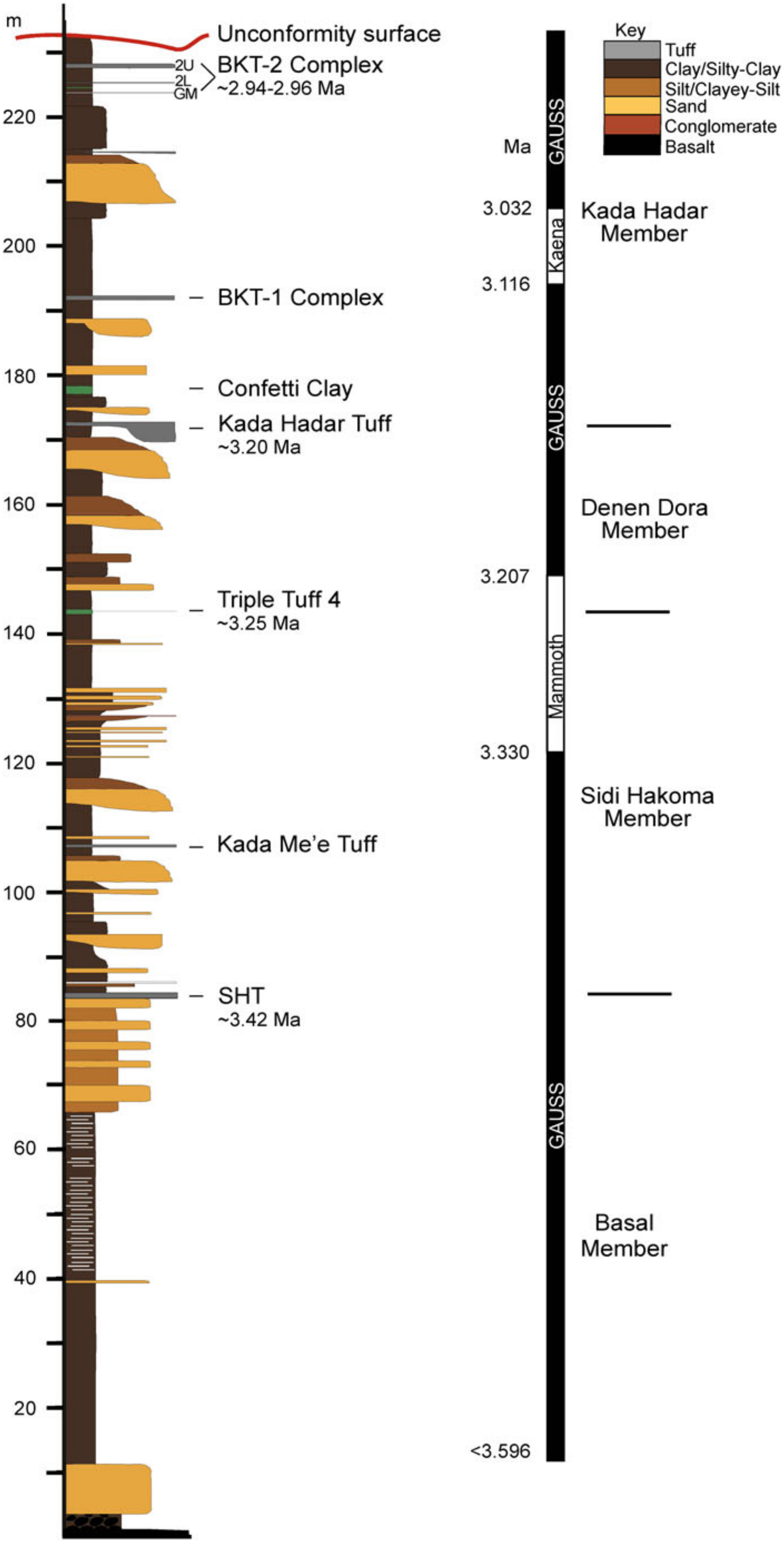

Fig. 5.5 DIK 1-1, a juvenile *A. afarensis*, nicknamed "Selam", skull and partial vertebral column and the glenoid cavity of the right scapula shown

including the genus *Homo* (Johanson et al. 1978; Strait et al. 1997; Kimbel et al. 2004; Strait and Grine 2004, Kimbel and Delezene 2009), although Leakey et al. (2001) have presented fossil evidence for *Kenyanthropus platyops* representing a possible second Pliocene hominin species. In addition to abundant morphological evidence that supports this hypothesis, its temporal and spatial placement is consistent with this proposition. Some researchers, however, argue that this species could not be ancestral to our genus because it is too derived in its general morphology (Senut 1983) and in some aspects of its ramus morphology (Rak et al. 2007).

Questions About A. afarensis

(1) What is the temporal range of *A. afarensis* (FAD and LAD) considering the widespread unconformity in the lower Awash Basin after 2.9 Ma and the taxonomic uncertainty about the Fejej material? (2) How valid is the suggestion that there are multiple species at Hadar? (3) Which features clearly relate *A. afarensis* to the robust clade? (4) What are the features linking *A. afarensis* to *Homo*? (5) What is the evidence to argue that *A. afarensis* is too derived, and thus must represent a dead-end branch? (6) Why do we see many primitive features on the upper part of the skeleton? What was the function of these features and how arboreal was *A. afarensis*? (7) What is known about ontogeny, life history and social structure in this species? (8) How is this species related to *K. platyops*? (9) What was the pattern and extents of tool use and meat eating in the species?

Australopithecus garhi

Australopithecus garhi is the youngest species of the genus from Ethiopia and is known so far only from the Hata sediments dated to ca. 2.5 Ma at the Bouri Peninsula of the Middle Awash research area (Asfaw et al. 1999). The extent of its temporal and spatial distribution will remain unclear until more fossils are recovered (White 2002). Its cranial and dental morphology are intriguing. This species differs from its putative ancestor, *A. afarensis*, by absolutely larger but morphologically similar postcanine teeth and a less asymmetric upper P3. On the other hand, its small cranial capacity, prognathic subnasal region, presence of sagittal crest and frontal trigon, convex clivus and canine fossa are shared with *A. afarensis*, though differing in some details. *A. garhi* can be distinguished from *A. africanus* and *Paranthropus* by its primitive facial, palatal and subnasal morphology (Asfaw et al. 1999). These authors suggested that this species is placed in the right place and time to be the ancestor of early *Homo*; and contemporary (but not associated) postcranial remains display a derived human-like humeral/femoral (intermembral) ratio and an ape-like forearm/upper arm (brachial) ratio. The shape of the premolars and the size ratio of the canines to the molars resemble early *Homo*. Moreover, close spatial and temporal association between *A. garhi* and behaviors such as stone tool use and exploitation of animal resources, thought to characterize *Homo,* provide additional circumstantial support (de Heinzelin et al. 1999). *A. garhi* was found in a lake margin environment, frequented by open grazers and water-dependent species. However, in a cladistic analysis Strait and Grine (2004) found no support for the hypothesis that *A. garhi* is specifically ancestral to *Homo*.

Questions About A. garhi

There are more questions about *A. garhi* than answers! Many important aspects of this species remain completely unknown, including variation, temporal and spatial distribution, cranial and postcranial association, stone tool use, to mention some. The only thing that seems to be clear, based on phenetic similarity, is that the species descended from *A. afarensis*.

(1) It was claimed that *A. garhi* shows that a non-robust species persisted in East Africa until at least 2.5 Ma, but can we say that it is any less robust than we can say it is robust? And could *A. garhi* be linked to megadont early *Homo* specimens such as ER 1590, 1470, 1802, UR 501 or Omo 75-14 (White 2002). (2) The behavioral evidence and postcranial material are implicitly associated, but what is the impact of this on our interpretation of the species' paleobiology? (3) Meat-eating is inferred for the species (de Heinzelin et al. 1999), but megadontia is often associated with a hard and abrasive diet, so how do we explain this apparent conflict? (4) Is it likely that *A. garhi* could be the ancestor of *Homo*? How accurate is this suggestion (Asfaw et al. 1999; Strait and Grine 2004; Strait et al. 2007)?

Conclusion

The genus *Australopithecus* in Ethiopia contains three species that probably have an ancestor–descendant relationship, but diverse morphological, locomotor and behavioral attributes. All three have a primitive cranium with a prognathic face, small brain size, large canines and megadont postcanine teeth. The geographic origin of the genus is currently hard to establish as is it difficult to link it to any know ancestral species. Whether the transition from its ancestor occurred in Ethiopia is not clear, because *A. anamensis* is primarily known from Kenya. More fossils from the time periods of 3.5–4.5 and 2.5–3.0 Ma, and further comparative investigation of the whole hypodigm will shed light on these important questions. Moreover, additional fossils from *A. garhi* or from the 2.5 Ma time period are crucial to understanding the role of this species in our evolutionary history.

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Chapter 6
The Alpha Taxonomy of *Australopithecus africanus*

Frederick E. Grine

Abstract The identification of species in the fossil record has long vexed paleontologists because of its inherent difficulty, and it has long preoccupied them because of its fundamental significance. *Australopithecus africanus* exemplifies this difficulty and importance. This species, as commonly defined, is viewed by some as having played a role in the evolution of the genus *Homo*, while others consider it to have been uniquely related to *Paranthropus*. A third opinion places it near the base of the evolutionary divergence of the "robust" australopith and human lineages. Various analyses find *A. africanus* to be phylogenetically unstable, and this is almost certainly owing to its craniodental variability. This has led to questions concerning the taxonomic homogeneity of the assemblages from Taung, Sterkfontein, and Makapansgat that comprise its hypodigm. Initial discoveries at these sites were attributed to different species and possibly genera, but subsequent studies suggested that these fossils represent a single, albeit variable taxon. This paradigm has become current conventional paleoanthropological wisdom, but observations about the degree and pattern of variability evinced by these fossils have raised anew the possibility that the *A. africanus* hypodigm is taxonomically heterogeneous. Various workers have proposed that at least some of these fossils belong to a different taxon, but there is notable lack of agreement over the manner in which they should be sorted. Morphometric studies tend to find little, if any, support for taxonomic heterogeneity, but they may not have directly addressed those features that have been suggested to differ. Novel innovative technological and quantitative approaches are required to adequately address the possible taxonomic heterogeneity of the *A. africanus* hypodigm.

Keywords Sterkfontein • Makapansgat • Taung • Species • Morphology • Variation • Sexual dimorphism • Stratigraphy • *Australopithecus* • *Homo* • *Paranthropus* • Cranium • Dentition • Postcranium

Alun R. Hughes (1916–1992). This contribution is dedicated to the memory of Alun R. Hughes, whose tireless efforts at Sterkfontein from December 1966 until 1991 provided the scientific community with a treasure trove of hominin fossils. It was indeed a privilege to have known him and to have worked with him

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Introduction

The identification of species in the fossil record has long vexed paleontologists because of its inherent difficulty, and it has long preoccupied them because of its fundamental importance. Ghiselin (1974) and Hull (1976, 1978) have presented cogent arguments that the key attribute of a species is that it be a fully individuated historical entity. Moreover, this entity should be diagnosably distinct from other such entities (Eldredge and Cracraft 1980; Wiley 1981; Cracraft 1987; Nixon and Wheeler 1990). There are a number of operational criteria by which species might be delimited empirically (Sites and Marshall 2004), but because paleontologists deal almost exclusively with morphological characters, most alpha-level taxonomic studies are concerned with character distribution and the determination of seemingly fixed diagnostic differences (Eldredge and Cracraft 1980; Wiley 1981; Nixon and Wheeler 1990; Davis and Nixon 1992).

Of course, what determines "diagnosable" in a paleontological context is commonly problematic because population character limits must be inferred from numerically restricted and/or temporally heterogeneous samples. Indeed, Wiens and Servedio (2000) have demonstrated that determining character fixation is generally impossible with samples comprising fewer than hundreds or even thousands of individuals. Accordingly, a more realistic and practical criterion for character based species delimitation would recognize at least some frequency of polymorphisms in the diagnostic characters.

Measures of character variability (e.g., the coefficient of variation, or CV) are commonly employed in assessments of the taxonomic homogeneity (versus heterogeneity) of fossil samples (e.g., Cole and Smith 1987; Kimbel and White 1988; Donnelly and Kramer 1999; Skinner et al. 2006; Humphrey and Andrews 2008; Lague et al. 2008; Macaluso 2010). Unfortunately, simulation experiments with neontological data have shown that these methods may fail to detect the presence of multiple species in a sample (Cope and Lacy 1992; Cope 1993; Plavcan 1993). Moreover, the notion that excessive variation in a fossil sample may serve to falsify a single-species hypothesis is rooted in the assumption that extinct taxa were no more variable than the modern ones employed as references. This supposition has been challenged both theoretically and empirically (Kelley and Plavcan 1998; Plavcan and Cope 2001).

Generally, the choice of extant reference taxa has been based on phylogenetic propinquity, since degree of evolutionary relatedness will potentially serve to constrain morphology. Although this is neither the only nor even a necessary criterion by which extant reference species should be chosen (Aiello et al. 2000; Plavcan 2002), most researchers have employed extant hominids and, in particular, the most sexually dimorphic of them—*Gorilla* and/or *Pongo*—to assess variation among fossil hominins (Johanson and White 1979; Wood 1985; Richmond and Jungers 1995; Grine et al. 2013). However, elevated levels of variation in fossil samples may simply suggest an even greater degree of sexual dimorphism in some species in the past (Scott and Lockwood 2004; Skinner et al. 2006). As such, it has been argued that any living catarrhine primate that is the most sexually dimorphic or perhaps polymorphic might provide a better alternate model (Baab 2008; Scott et al. 2009). Of course, this might be extended to suggest that any mammal species, regardless of its degree of relatedness, could be employed to explore the limits of variability. As such, the rationale for including papionins but excluding miroungins (elephant seals) as comparators in the study of fossil hominins is rather obscure.

Another potential problem with the use of extant species as models is that they represent an instant in geological time, whereas most paleontological assemblages have accumulated over many millennia. The consequences of time-averaging on phenotypic variation in fossil samples have been examined for a variety of taxa. Bell et al. (1987), MacFadden (1989), and Bush et al. (2002) found comparable levels of morphometric variation in time-averaged fossil assemblages and recent samples of the same or closely related species of fish, horses, and bivalves. Cronin (1985) and Hunt (2004a) found only slight increases in morphometric variance with respect to samples of marine crustaceans that derived from a single stratigraphic horizon and those that were time averaged across different horizons. The temporal spans over which averaging was sampled ranged from 100 yr to 500 kyr (Cronin 1985; Hunt 2004a). Hunt (2004b) found that variance observed in time-averaged samples of Quaternary mammals is typically only slightly inflated (approximately 5 %) relative to extant population-level values. Of course, comparison of variance in modern and fossil samples of closely related species is bedeviled by the fact that the former have been used to establish morphological and/or morphometric variability that define the latter. As such, the results of such studies are perhaps not wholly unexpected. Put simply, fossil assemblages that differ by more than a given amount from other such samples may be referred to different species.

As an interesting alternative, Wood (1991a) has suggested that extinct species might be used to model intraspecific variation in other fossil assemblages. In particular, he used *Paranthropus boisei* to assess the degree of variation exhibited by assemblages from South Africa held to be attributable to *Paranthropus robustus* and *Australopithecus africanus*. *Paranthropus boisei* is a reasonable choice for comparison for several reasons: it is characterized by a number of distinctive apomorphies, it has a reasonably deep temporal record (c. 1.0 Myr), and there is relatively little disagreement about its hypodigm. Similarly, the abundant Pliocene record for *Australopithecus afarensis* might suggest itself as a reasonable choice for comparison with other paleontological assemblages. Although there has been considerable debate over the taxonomic homogeneity of its hypodigm (Olson 1981, 1985a, b; White et al. 1981; Senut and Tardieu 1985; Kimbel et al. 1985; Falk 1988; Kimbel and White 1988), the weight of evidence has led to a general (if not universal) consensus that a single species is represented by these fossils (Kimbel and Delezene 2009). At the same time, however, arguments that stressed the fundamental similarity of the earlier (Laetoli) and later (Hadar) assemblages (e.g., White et al. 1981; Kimbel et al. 1985) have given way to those that view the former as morphologically intermediate between fossils attributed to *Australopithecus anamensis* and those from Hadar (Kimbel et al. 2006; Haile-Selassie 2010; Haile-Selassie et al. 2010; Ward et al. 2010).

Although there are undoubted and perhaps inescapable problems associated with the use of one fossil species assemblage to assess the range of variation in another (e.g., the possibility that such comparisons can become wholly circular), paleontological samples provide a unique opportunity to incorporate temporal depth in the assessment of variation. As such, they provide a valuable source of comparative information. In a word, *P. boisei* and *A. afarensis* may inform *A. africanus*.

The Status of Australopithecus africanus

The initial period of discovery of hominin fossils from the South African sites of Taung, Sterkfontein, and Makapansgat saw them attributed to three species partitioned between two or possibly three genera (Dart 1925a, 1948a; Broom 1936, 1938, 1950). This was followed by a period of rationalization, wherein all were regarded as representing a single taxon, *A. africanus*. This view gained ascendency through the influential work of Robinson (1954), Le Gros Clark (1955, 1964), Tobias (1967), Brace (1973) and Wolpoff (1974), and has become conventional paleoanthropological wisdom (e.g., White et al. 1981; Rak 1983; Wood and Richmond 2000; MacLatchy et al. 2011). Nevertheless, questions persist about the degree and pattern of craniodental variability exhibited by the fossils that constitute its hypodigm. The possibility that the *A. africanus* assemblage subsumes two (or more) species has significant implications for the interpretation of hominin evolution.

Phylogenetic (i.e., cladistic) analyses have concluded variously that *A. africanus*, as conventionally defined, occupies one of three positions: (1) it is the sister taxon to *Paranthropus* (Chamberlain and Wood 1987), (2) it is the sister of a clade containing both *Paranthropus* and *Homo* (Strait et al. 1997; Strait and Grine 2004), or (3) it is a member of an unresolved trichotomy involving *Homo* and *Paranthropus* (Kimbel et al. 2004). Indeed, *A. africanus* is one of the least stable species in such studies (cf. Skelton et al. 1986; Chamberlain and Wood 1987; Skelton and McHenry 1992; Strait et al. 1997; Strait and Grine 2004; Kimbel et al. 2004). This is largely owing to the fact that it is variable in so many craniodental characters (Strait et al. 1997), which has enabled this species to be viewed in quite different ways, depending upon the features that are chosen for emphasis. Thus, Robinson (1967) and Olson (1981, 1985a) argued that *A. africanus* lacks features that are distinctive of *Paranthropus*, and that its more generalized morphology is consistent with it being a member of the *Homo* lineage. On the other hand, White et al. (1981), Rak (1983), and Kimbel et al. (2004) focused on features they regarded as indicating nascent masticatory specialization to proclaim *A. africanus* as a being uniquely related to the "robust" australopiths. Clarke (1988a, b, 1994a, 2008, 2013) has argued that these seemingly contradictory phylogenetic conclusions result from the presence of two species in the *A. africanus* hypodigm; one being more closely related to *Homo* and the other to *Paranthropus*. The question of whether the *A. africanus* hypodigm is taxonomically heterogeneous revolves principally (though not wholly) around the interpretation of specimens from Sterkfontein.

Because of the pivotal role that *A. africanus* plays in all interpretations of hominin evolution, a review of the history and evidence for the taxonomic composition of the Sterkfontein and Makapansgat assemblages seems a worthy undertaking.

Australopithecus africanus*: A Taxonomic History*

In 1924, Raymond Dart obtained the fossilized skull of a juvenile hominoid from the Buxton lime quarry at Taung (then Taungs), in the Northern Cape Province of South Africa. Dart (1925a) recognized that it represented a hitherto unknown "extinct race of apes intermediate between living anthropoids and man," for which he proposed the name *Australopithecus africanus*. Robert Broom (1925a, b) was an early and ardent supporter of Dart's claims for the Taung fossil. In 1936, Broom, who had recently taken a scientific post at the Transvaal Museum, Pretoria, was given a small collection of fossils (including several baboons) by two of

Dart's students, G. W. H. Schepers and H. le Riche, who had obtained them from the lime-mine at Sterkfontein. Broom immediately visited the site with Schepers and le Riche, and asked the manager of the lime-quarrying operation there to "keep a sharp look out" for any fossils that might resemble the Taung skull. A week later (August 17), Broom was handed the "blasted out natural brain cast of an anthropoid," and after "much further hunting" he recovered the base of the skull to which it belonged together with the associated maxillae and upper postcanine teeth. This specimen, catalogued as TM 1511 (TM refers to "Transvaal Museum," the original name for what became the Northern Flagship Institution and is now known as the Ditsong National Museum of Natural History), was described by Broom (1936) under the name *Australopithecus transvaalensis*. The specific distinction from the Taung skull was based in part on his observation that "the brain cast …is considerably wider, especially in the frontal region, and the [upper first permanent] molar teeth differ in a number of important details." This differentiation was supported by Broom's assessment that "the associated animals found at Taungs are all different from those found at Sterkfontein" and his conclusion that Sterkfontein was geochronologically younger.

Two years later, Broom (1938) transferred the Sterkfontein species to a new genus, *Plesianthropus*, following the discovery of a juvenile mandibular symphysis that he considered to differ in shape from that of Taung. This fossil is catalogued under two numbers: TM 1516 (the mandibular fragment together with the mesial part of a Ldm$_1$) and Sts 50 (an unerupted LC crown that fits into TM 1516). Over the course of the next year, that is, until the suspension of work at Sterkfontein with the onset of World War II, Broom recovered a few more fossils which added to the collection that he had assembled from the "Type Site." The dozen or so specimens uncovered by this first phase of activity (1936–1939) at Sterkfontein were described and illustrated by Broom (1946).

Broom renewed work at Sterkfontein in 1947 with the assistance of J. T. Robinson. This second phase of activity continued until 1949 and resulted in the recovery of the bulk of material (c. 54 specimens) from the "Type Site" curated by the Ditsong Museum. This collection includes a number of significant cranial specimens (e.g., Sts 5, Sts 17, Sts 19, Sts 71 and Sts 52) (Sts, or STS, refers to "Sterkfontein Type Site"). Broom and Robinson (1950) and Robinson (1956), who described these fossils, were of the opinion that they belonged to one species.

The fossils recovered at Sterkfontein by Broom (1936–1939) and subsequently by Broom and Robinson (1947–1949) derive from excavation (generally feather and wedge, but also explosive excavation) or from the mine rubble-dumps of what was referred to variously as the "old red sand breccia," "pink breccia," "lower breccia," and the "Type Site breccia" of the Type Site deposit (Robinson 1952, 1962). This clastic sedimentary unit was designated Member 4 of the Sterkfontein Formation by Partridge (1978). The vast bulk of hominin material recovered from Sterkfontein comes from these sediments in the Type Site deposit. As such, discussions over potential morphological differences among the majority of australopith fossils from Sterkfontein have not involved issues of their stratigraphic derivation.

In some instances, however, the derivation of particular specimens, either from other karst catchments (e.g., Silberberg Grotto or Jacovec Cavern) that are potentially older or especially from contiguous deposits that are potentially younger (e.g., Member 5 Extension Site), has entered into taxonomic discussions. Where the issue of stratigraphic derivation of the fossils is germane to questions of hominin alpha taxonomy at Sterkfontein, this will be discussed more fully.

Also in 1925, a few fossils were found in the rubble dumps at the lime-mine at Makapansgat by Wilfred Eitzman, a schoolteacher in the nearby town of Mokopane (formerly Potgietersrus). Soon after the announcement of the Taung skull, Eitzman sent them to Dart. In the first published reference to the site, Dart (1925b) described the bones, most of which were very fragmentary and unidentifiable. Some 20 years later (1945–1946) a series of research expeditions to the Makapansgat Limeworks were undertaken by Dart's students (the first being led by P. V. Tobias), which resulted in the recovery of additional fossils from the rubble dumps left behind by the miners. These discoveries led the Bernard Price Foundation to provide Dart with funds to begin systematic survey and excavation at the cave complex. This work was initiated in 1947 under the field leadership of J. W. Kitching, A. R. Hughes, and G. Gardiner. In September of that year, Kitching discovered a hominin occiput in a block of "grey breccia" among the dumps. This specimen (designated MLD 1, where MLD refers to "Makapansgat Limeworks Dumps") was described by Dart (1948b) as representing a novel species of *Australopithecus*, *Australopithecus prometheus*.

Dart (1948b) cited several differences between Sts 5 and MLD 1, but doubted Broom's proposed generic separation of the Sterkfontein assemblage (as *Plesianthropus*) from *Australopithecus*. Dart (1948b: 278–279) opined that "the Taungs infant had an uncomplicated occipital sutural system and it seems more probable that the *Australopithecus* of Makapansgat, although closely akin, was a different species…; he certainly hunted bigger game and had a more varied dietary [*sic*]. Even if there were none of these differences the locality and the novel evidence it affords would justify reference of the specimen to a new species." An additional two-dozen craniodental fossils were subsequently recovered from the "grey" and "pink stoney" breccia deposits at Makapansgat; all were described by Dart (1949a, b, 1954, 1959, 1962a, b, 1965). A few postcranial fragments have also been recovered from these same deposits (Dart 1949c, 1958, 1962c; Reed et al. 1993). Partridge (1979) designated the "grey" or "Lower Phase I" breccia of Brain (1958) as Member 3, and the "pink stoney" or "Upper Phase I" breccia as Member 4 of the Makapansgat Formation. To date, the issue of their stratigraphic derivation has not played any role in discussions concerning the possible specific heterogeneity of the hominin assemblage from Makapansgat.

While Dart envisioned the Makapansgat and Sterkfontein fossils as representing distinct species, Broom (1950) suggested that they could be separated at the subfamilial level owing to differences in the ischial tuberosities of Sts 14 and MLD 8. The former was seen to be "a little like that of a chimpanzee" and the latter "almost exactly as in Man." On the other hand, Robinson's (1954) analyses suggested strongly that the specimens from Makapansgat and Sterkfontein represented the same species—indeed, even the same subspecies (*A. africanus transvaalensis*)—and that these samples differed at most at the subspecific level from the Taung skull (*A. africanus africanus*). Robinson's view of the conspecificity of the australopiths from these three sites gained support from his subsequent detailed assessment of the teeth (Robinson 1956), and Tobias's (1967) analysis of the cranial remains.

At the same time, however, Tobias (1967: 244) drew attention to some "robust" australopith features in the fossils from Makapansgat, stating that "in these respects, the Makapansgat specimens seem to show a somewhat nearer approach to *A. robustus* than do the Sterkfontein specimens." Aguirre (1970) took this further, suggesting that at least some of the Makapansgat fossils attested to the presence of two species—*A. africanus* and *P. robustus*—at the site. With regard to the latter, he argued that the MLD 2 mandible represented an "adolescent male of *Paranthropus*." Aguirre (1970) also speculated that the presence of two species might apply to the Sterkfontein assemblage. As such, he presaged Clarke's (1988a) interpretation by nearly two decades, but his proposal received little, if any support. Tobias (1967) had earlier concluded that those traits reminiscent of the "robust australopithecines" at Makapansgat simply attest to polymorphism within *A. africanus*.

Although Broom (1950) argued "the case of the splitter of the South African ape-men," recognizing three taxa to accommodate the fossils from Taung (*A. africanus*), Sterkfontein (*Plesianthropus transvaalensis*), and Makapansgat ("*Australopithecus*" *prometheus*), he nonetheless recognized no taxonomic distinction among those from Sterkfontein, or among those from Makapansgat. Rather, he saw sexual dimorphism as accounting for at least some of the variation in these samples.

The issue of sexual dimorphism is an important aspect of morphological and morphometric variation within the *A. africanus* hypodigm (and especially the Sterkfontein assemblage) that has been discussed or at least alluded to by a number of workers. Thus, for example, Kimbel and White (1988), noting that greater facial prognathism and robusticity are expected for males in sexually dimorphic hominids, argued that the comparatively gracile, but highly prognathic facial skeleton of Sts 5 is unlikely to be explained on the grounds of sexual dimorphism alone. Because Sts 71, a comparatively orthognathic cranium, was regarded by them as male on the basis of "facial robusticity and postcanine tooth size," they observed that "if Sts 5 is a female, as is commonly thought, then the differences in facial prognathism between these specimens is opposite that which characterizes the sexes in great apes" (Kimbel and White 1988: 185).

Sexual Dimorphism and Species Identification

Broom and Robinson (1950: 26) noted that some of the Sterkfontein crania differ "very considerably" from one another. Sexual dimorphism was held to account for at least some this variation, with specimens such as TM 1511,[1] TM 1512, Sts 5, Sts 17, Sts 71, and Sts 19 being regarded as female, and TM 1514, TM 1516/Stw 50, Sts 7, and possibly TM 1515 as male (Table 6.1). The principal grounds for sexual attribution were overall specimen size and especially canine size. Thus, according to Broom and Robinson (1950: 39),

> skull No. 7 [i.e., Sts 71] has the canine socket measuring 9.7 mm by about 7 mm. There thus seems to be little doubt that the skulls No. 1, No. 5, No. 6 and No. 7 [i.e., TM 1511, Sts 5, Sts 17 and Sts 71] are all female skulls. In No. 8 [i.e., Sts 19] we have no front teeth, but the brain is not much larger than in these others, and it is thus probably also a female skull. We have thus at present no good male skull.

With reference to the purported male specimens, Broom (1946) had earlier recognized the TM 1516/Sts 50 mandibular fragment as that of a juvenile male, and the TM 1514 maxilla as an "old male." He also considered the poorly preserved TM 1515 mandible as possibly that of an "old male" on the basis of canine size. Broom and

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[1] Broom (1946) initially regarded TM 1511 as being not improbably a young male, but following the discovery of an "excellent upper canine of a male," Broom and Robinson (1950) came to view TM 1511 as female because of the size of its canine alveolus. However, this "excellent upper canine" (Sts 3) of Broom and Robinson (1950: Fig. 14), was later identified by Robinson (1956) as a mandibular tooth.

Table 6.1 Sexual attribution of cranial and mandibular specimens from Sterkfontein and Makapansgat

Specimen	Remains	Sex	Reference	Notes
Sterkfontein				
TM 1511	Cranial	Male	Broom (1946)	Specimen S1
		Female	Broom and Robinson (1950)	Skull 1
		Male	Rak (1983, 1985)	
		Male	Lockwood (1997, 1999)	
		Male	Clarke (2008)	
		Male	Grine et al. (2012)	
TM 1512	Cranial	Female	Broom (1946)	Specimen S2
		Female	Rak (1983, 1985)	
		Female	Kimbel and White (1988)	
		Female	Lockwood (1997, 1999)	
		Female	Clarke (2008)	
TM 1514	Cranial	Male	Broom (1946)	Specimen S3
TM 1515	Cranial	? Male	Broom (1946)	Specimen S4
TM 1516/Sts 50	Mandibular	Male	Broom (1946)	
Sts 5	Cranial	Female	Broom and Robinson (1950)	Skull 5
		Female	Wolpoff (1975)	
		Male	Rak (1983, 1985)	
		Indeterminate	Lockwood (1997, 1999)	See text (female)
		Male	Thackeray (2000)	
		Female	Clarke (2008)	
		Female	Grine et al. (2012)	
Sts 7	Mandibular	Male	Broom and Robinson (1950)	
Sts 17	Cranial	Female	Broom and Robinson (1950)	Skull 6
		Male	Rak (1983, 1985)	
		Female	Lockwood (1997, 1999)	
		Female	Grine et al. (2012)	
Sts 19	Cranial	Female	Broom and Robinson (1950)	Skull 8
Sts 36	Mandibular	Male	Wallace (1972)	
Sts 52	Facial	Male	Wallace (1972)	
		Male	Wolpoff (1975)	
		Female	Rak (1983, 1985)	
		Male	Clarke (2008)	
		Male	Grine et al. (2012)	
Sts 53	Cranial	Female	Rak (1983, 1985)	
		Female	Kimbel and White (1988)	
		Female	Lockwood (1997, 1999)	
		Female	Grine et al. (2012)	
Sts 63	Cranial	Female	Lockwood (1997, 1999)	
Sts 71	Cranial	Female	Broom and Robinson (1950)	Skull 7
		Male	Wallace (1972)	
		Male	Wolpoff (1975)	
		Male	Rak (1983, 1985)	
		Male	Kimbel and White (1988)	
		Female	Lockwood (1997, 1999)	

(continued)

Table 6.1 (continued)

Specimen	Remains	Sex	Reference	Notes
		Female	Clarke (2008)	
		Female	Grine et al. (2012)	
Sts 73	Cranial	Female	Lockwood (1997, 1999)	
Stw 13	Cranial	Male	Rak (1983, 1985)	
		Indeterminate	Lockwood (1997, 1999)	See text (female)
		Female	Grine et al. (2012)	
Stw 53	Cranial	Male	Clarke (2008)	
		Female	Thackeray et al. (2000)	
Stw 73	Cranial	Female	Grine et al. (2012)	
Stw 183	Cranial	Male	Grine et al. (2012)	
Stw 252	Cranial	Male	Clarke (2008)	
		Male	Grine et al. (2012)	
Stw 369	Cranial	Male	Grine et al. (2012)	
Stw 391	Cranial	Male	Clarke (2008)	
Stw 573	Cranial	? Male	Clarke (2008)	
Stw 505	Cranial	Male	Lockwood (1997, 1999)	
		Male	Lockwood and Tobias (1999)	
		Male	Clarke (2008)	
Makapansgat				
MLD 1	Cranial	? Female	Dart (1948b)	
		Male	Dart (1962b)	
MLD 2	Mandibular	Male	Dart (1948a)	
MLD 6	Cranial	Female	Dart (1949a)	
		Female	Lockwood (1997, 1999)	
MLD 9	Cranial	? Female	Dart (1949b)	
		Male	Lockwood (1997, 1999)	
MLD 18	Mandibular	Female	Dart (1954)	
MLD 22	Mandibular	? Female	Dart (1962a)	
MLD 29	Mandibular	? Male	Dart (1962a)	
MLD 37/38	Cranial	Female	Dart (1962b)	
MLD 40	Mandibular	Male	Dart (1962a)	
MLD 45	Cranial	Male	Lockwood (1997, 1999)	

? = the determination is indicated as being ‘probable’

Robinson (1950) identified the Sts 7 mandible as male on the basis of its overall “massive” size.

The problem of sexing the craniodental remains from Sterkfontein and Makapansgat has been addressed by a number of workers. For the most part they have followed Broom and Robinson in using overall specimen and especially canine (or inferred canine) size to assign sex. However, other criteria, such as the differential expression of structures considered to be derived and the timing of dental development, have been relied upon as well. Thus, Wallace (1972) argued that Sts 52 is a male based on the relative timing of canine emergence, and Rak (1985) suggested that specimens exhibiting “fewer structures interpreted as derived [e.g., anterior pillars, a flat nasoalveolar clivus] are regarded as females.” According to this criterion, TM 1512, Sts 52 and Sts 53 were identified as female. Rak’s (1983, 1985) descriptions of TM 1511, Sts 5, Sts 17, Sts 71 and Stw 13 would see them classified as male. However, Lockwood and Tobias (1999) argued that males of *A. africanus* do not preferentially evince derived “robust” australopith-like features. Lockwood (1997, 1999) also noted that while the males of two dimorphic species likely differ from one another to a greater degree than the females of those species, the infraorbital region of the Sterkfontein and Makapansgat fossils does not support Rak’s (1983, 1985) inference. This is because specimens as disparate in size as

Sts 17 and Stw 505 (small and large respectively) possess anterior pillars, and the face of the latter is heavily buttressed despite its comparatively diminutive size.

Lockwood (1997, 1999) used two quantitative approaches—a CV-based method and a bootstrap method—in the assessment of sexual (size) dimorphism in the Sterkfontein and Makapansgat samples. He found that both approaches yielded estimates of the degree of dimorphism in linear dimensions to be about 13.2 %—being less than in gorillas, but more than in chimpanzees and humans. Lockwood (1997, 1999) found Sts 5 and Stw 13 to be indeterminate on the basis of probability of assignment because of inferential disagreements between metrical and non-metrical features. However, he also observed that his estimate of 13.2 % size dimorphism in the sample was maintained when Sts 5 and Stw 13 were interpreted as females rather than males. As such, he was inclined to the view them both as female.

Over 30 fossils from Sterkfontein and Makapansgat have been assigned sex by at least one worker, and 11 of these (nine from Sterkfontein and two from Makapansgat) have been addressed by more than one researcher (Table 6.1). Of these, there is consensus of opinion over only five (ignoring Broom and Robinson's (1950) attribution of TM 1511, based on the misidentification of Sts 3 as an upper canine). There has been a notable lack of consensus over Sts 5, Sts 17, Sts 52, Sts 71, Stw 13, and MLD 9; all but Stw 13 and MLD 9 have featured prominently in discussions over the alpha taxonomy of the *A. africanus* assemblage.

Because of its state of preservation, the sex assignment of Sts 5 has implications for other specimens. It has traditionally been regarded as female following Broom and Robinson (1950: 14), who argued primarily from the size of its canine alveoli that "there is no reasonable doubt that the skull is that of a female." Hence the sobriquet "Mrs. Ples." Dart altered his view of the sex of the MLD 1 occipital from probable female (Dart 1948b) to male (Dart 1962b) on the basis of comparisons with it.

The well-buttressed facial skeleton of Sts 5 was cause for Rak (1983, 1985) to suggest that "Mrs. Ples" is more likely male. Rak's suggestion has been taken up by Thackeray and colleagues in a series of publications (Loth et al. 1995; Thackeray 1997a, 2000; Prat and Thackeray 2001; Thackeray et al. 2002; Potze and Thackeray 2010) that posit Sts 5 to be a juvenile male. Thackeray's arguments have been refuted by Grine et al. (2012). Not only is his "evidence" for a developing sagittal crest on Sts 5 wholly imaginary, there is no evidence from the third molar roots for its purported immaturity. Moreover, it is clear that the dimensions of the right canine alveolus of Sts 5 are a reasonable proxy for those of its canine root, and these are among the smallest recorded for any Sterkfontein australopith (Grine et al. 2012). If maxillary canine roots and their alveolar dimensions were sexually dimorphic among the Sterkfontein australopiths, as they are in *A. anamensis* and *A. afarensis* (Ward et al. 2010; Manthi et al. 2012), the diminutive canine socket of Sts 5 provides strong support for Broom's initial identification of this specimen as female.

As noted above, the identification of Sts 5 as an adult female has taxonomic implications. Thus, for example, Kimbel and White (1988: 186) argued that if Sts 5 is a female, "it is unlikely that the total variation in facial morphology in the Sterkfontein Type Site collection is attributable to sexual dimorphism."

Does the *Australopithecus africanus* Hypodigm Subsume Two or More Species?

Following Clarke's (1985a, b) suggestion that the Sterkfontein sample possibly includes two australopith species, a number of workers have addressed this issue. Different approaches and different anatomical parts have been assessed, and while these efforts have clearly focused on the cranium and dentition, the postcranial skeleton has not been ignored completely.

Cranial Variation in the Sterkfontein Type Site Assemblage

Kimbel and White (1988) suspected that the Sterkfontein crania could be divided into two groups, with one including the prognathic Sts 5 and the other the comparatively orthognathic specimens Sts 52 and Sts 71 (Table 6.2; Fig. 6.1). They were, however, hesitant to ascribe these groups to different taxa, and did not elaborate upon their membership beyond these three fossils.

Following the recovery of the fragmentary Stw 252 partial cranium, Clarke (1988a, b) argued that the species to which it belonged was ancestral to *Paranthropus*. The other Sterkfontein species was represented by specimens such as Sts 5. He also opined that these same two australopith taxa were represented at Makapansgat as well. However, Clarke's (1988a) division of the fossils differed from that of Kimbel and White (1988) in that he grouped Sts 52 with Sts 5 (Table 6.3). According to Clarke's scheme, *A. africanus*—Taung, Sts 5, Sts 17, Sts 52 and MLD 6—has smaller cheek teeth, a thick supraorbital margin and prominent nasal skeleton, while the "second species"—Stw 252, Sts 71, Sts 36, and MLD 2—is characterized by a thin supraorbital margin, a flat or concave nasal skeleton and larger teeth (Fig. 6.2). The principal diagnostic differences given by Clarke (1988a, et seq.) between *A. africanus* and the "second species" are enumerated in Table 6.4.

Table 6.2 Attribution of the hominin fossils from Sterkfontein to groups by Kimbel and White (1988)

Group 1	Group 2
Sts 5	Sts 52
	Sts 71

Clarke (1988a) argued that these two groups do not simply correspond to a sexual division because the morphological associations (i.e., a thick supraorbital margin coupled with small teeth vs. a thin supraorbital margin combined with large teeth) run opposite to normal patterns of hominin sexual dimorphism. He also noted that Stw 252 resembles Sts 71 and differs from Sts 5 in its anteriorly positioned malars and high, gently curved occipital profile. However, the latter resemblance is certainly open to question owing to the fact that the occipital of Stw 252 is largely, if not entirely, reconstructed *ad fingum*. Moreover, the profile of the Sts 71 occipital, as noted by Broom and Robinson (1950: 25), is "most likely due to slow post-mortem crushing without very manifest breaking of the bones." Lockwood and Tobias (1999) concurred with Broom and Robinson's assessment, and Holloway (1972) has pointed out additional evidence for deformation of the occipital and other parts of this cranium from his study of its endocranial aspect. Holloway's (1972) observations, in turn, are supported by the computed tomography (CT) analysis of Conroy et al. (2000).

Earlier, Clarke (1985a: 175) had commented upon differences between "the more lightly structured cranium of Sts 17 to the more rugged Sts 71." He noted that Sts 17 had been excavated by Broom and Robinson from near the top of the Type Site deposit, suggesting that it might therefore have been temporally close to the "morphologically similar" Stw 53 cranium. At that time, Clarke accepted the attribution of Stw 53 to *Homo*, and thus questioned whether Sts 17 might therefore represent *Homo habilis* rather than *A. africanus*. Clarke (1988a) subsequently attributed Sts 17 to *A. africanus*, and later (Clarke 1995) proposed that Stw 53 is also a specimen of *Australopithecus*, and finally (Clarke 2008, 2013) that it represents *A. africanus*.

Clarke (1994a) expanded the list of specimens from Sterkfontein and Makapansgat that he attributed to his two taxa, and upon his characterization of the "second species" (Table 6.3). Thus, he used the high position of nasion, the

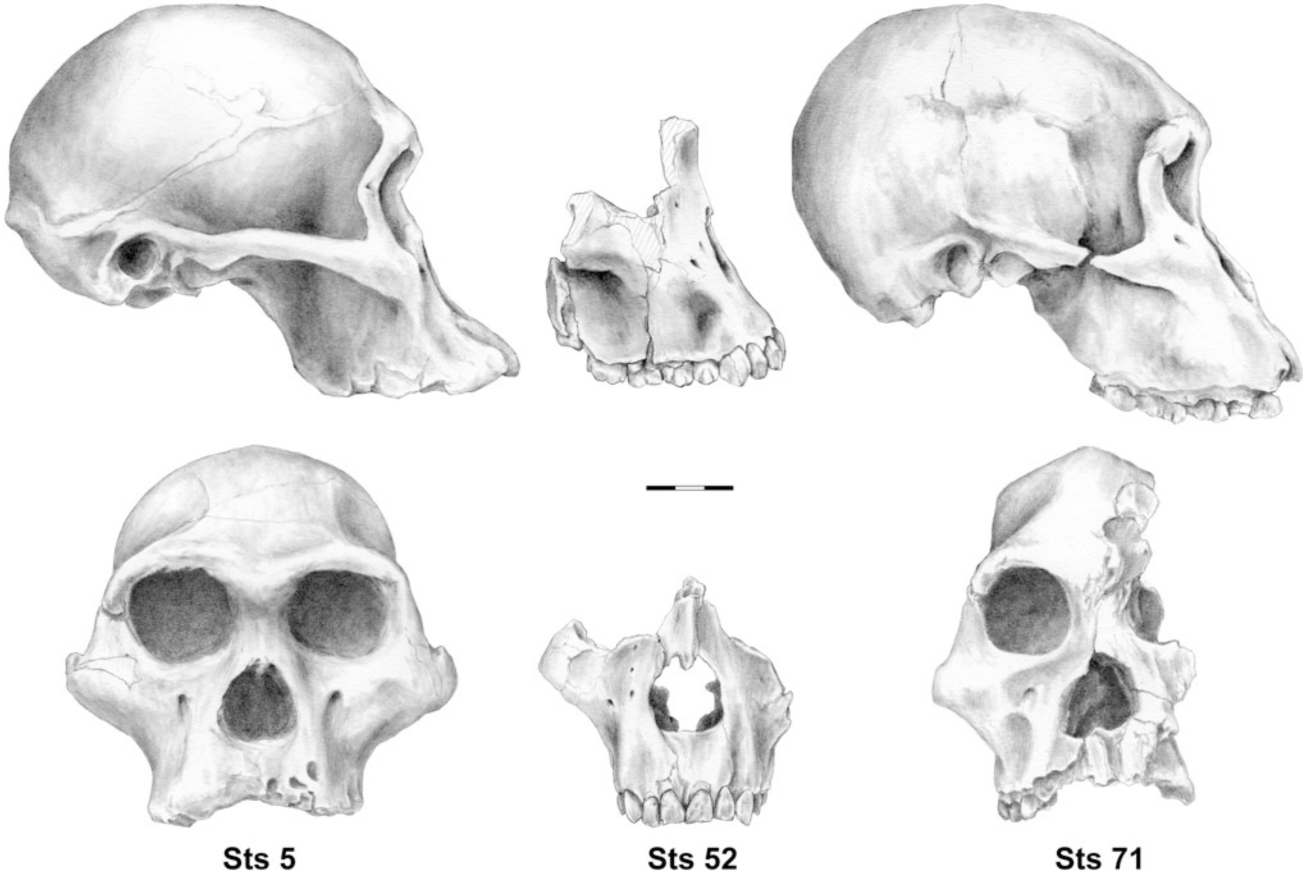

Fig. 6.1 Comparison of Sts 5, Sts 52, and Sts 71 in lateral and facial views. Scale in cms

Table 6.3 Attribution of the hominin fossils from Taung, Sterkfontein and Makapansgat to groups by Clarke (1988a, et seq.)

A. africanus	Second species	Reference
Taung	Sts 36	Clarke (1988a)
Sts 5	Sts 71	
Sts 17	Stw 252	
Sts 52	MLD 2	
MLD 6		
TM 1511	TM 1516	Clarke (1994a)
TM 1512	Sts 1	
TM 1514	Sts 7	
Stw 404	Sts 28	
	Stw 14	
	Stw 384	
	Stw 505	
	MLD 1	
	MLD 9	
	MLD 27	
	MLD 29	
	Stw 578	Partridge et al. (2003)
Stw 53	Stw 183	Clarke (2008)
Stw 391	Stw 498	
	Stw 573	

Only those specimens that are newly added to each group are listed for each reference. As such, individual specimens referred to in these and other articles by Clarke that duplicate the list up to that time are not given for each reference

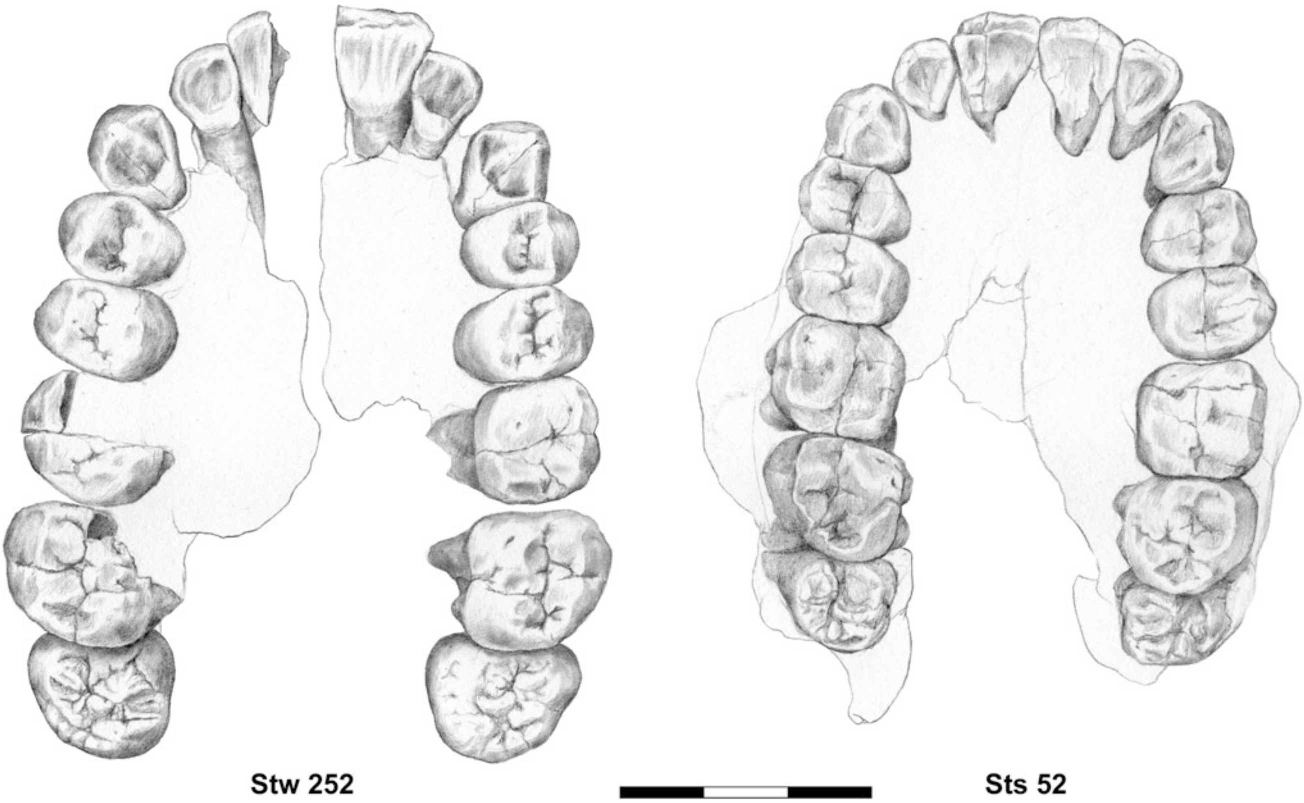

Fig. 6.2 Comparison of the Stw 252 and Sts 52 maxillary dentitions. Scale in cms

Table 6.4 Clarke's (1988a, 1994a, 2008) diagnostic differences between specimens regarded by him as being attributable to *Australopithecus africanus* and the 'second species' at Sterkfontein and Makapansgat

Craniodental feature	*A. africanus*	'Second species'
Tooth size	Smaller teeth	Larger teeth
Molar cusp shape	Higher, more pointed	Lower, bulbous
Molar cusp position	Tips point vertically	Tips point towards crown center
Supraorbital margin	Thick	Thin
Glabellar prominence	Strong	Weak
Frontal squame	Slightly convex behind glabella	Slightly concave behind glabella
Nasal skeleton	Prominent	Flat
Position of nasion	Below frontomaxillary suture	Above frontomaxillary suture (close to glabella)
Position of malar root	Posterior	Anterior
Zygomatic arch	Gracile	Robust
Central face	Projecting	Hollow
Sagittal crest (in males)	Absent	Small, posteriorly restricted
Occipital profile	Low, convex	High, gently curved
Taxonomic affinity	*Homo*	*Paranthropus*

See Table 6.3 for the specimens assigned to each group

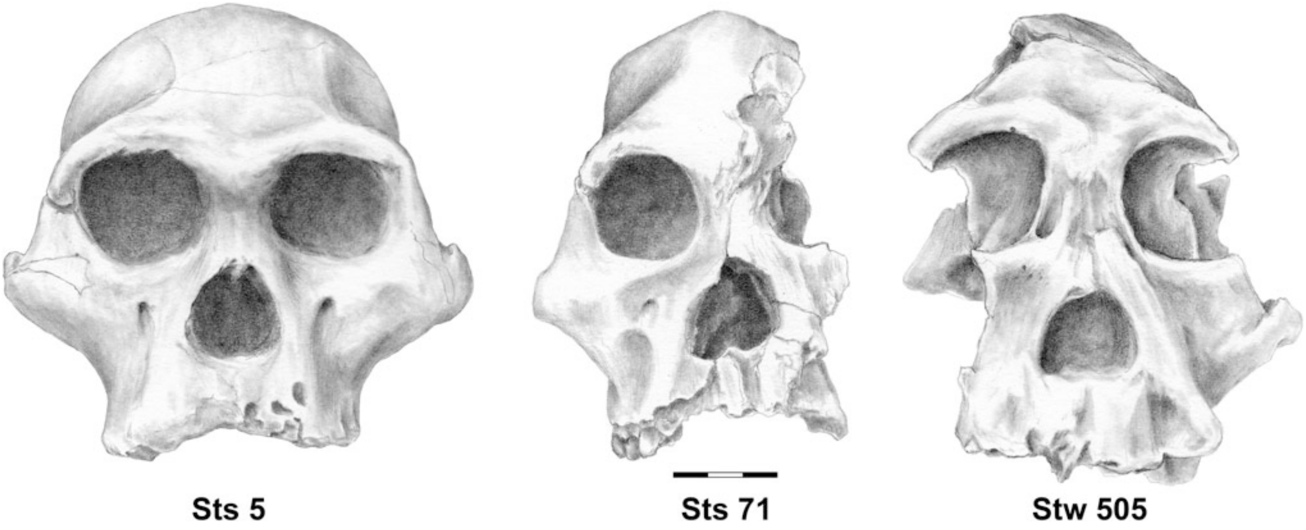

Fig. 6.3 Comparison of Sts 5, Sts 71, and Stw 505 in facial view. Scale in cms

lack of glabellar prominence and the slight concave frontal squama to group the large, presumptive male cranium Stw 505 with the smaller Sts 71, contrasting them with Sts 5 (Fig. 6.3). Clarke (1994a: Fig. 10.6) also contrasted the Stw 404 and Stw 384 mandibular cheek teeth, remarking that the discrepancy between them is comparable to that between jaws of *H. habilis* (OH 7) and *P. boisei* (Peninj 1) respectively. The teeth of these two Sterkfontein specimens are illustrated in Fig. 6.4. These differences were considered further evidence that *A. africanus* and the "second species" were ancestral to, or at least on separate lineages leading to *Homo* and *Paranthropus* respectively.

Clarke (1994a) also drew favorable comparisons between the MLD 1 occipital and those of Sts 71 and Stw 252, considered to represent the "second species." Because Dart (1948b) had designated MLD 1 as the holotype of *A. prometheus*, Clarke (1994a) suggested that this name be used in reference to the "second species." At the same time, he argued that the Taung skull was an ontogenetic precursor of Sts 5 in the configuration of its frontal bone. However, a 3D geometric morphometric analysis of craniofacial ontogeny by McNulty et al. (2006) found that between Sts 5 and Sts 71, the latter is more likely to resemble the adult form of the Taung child.

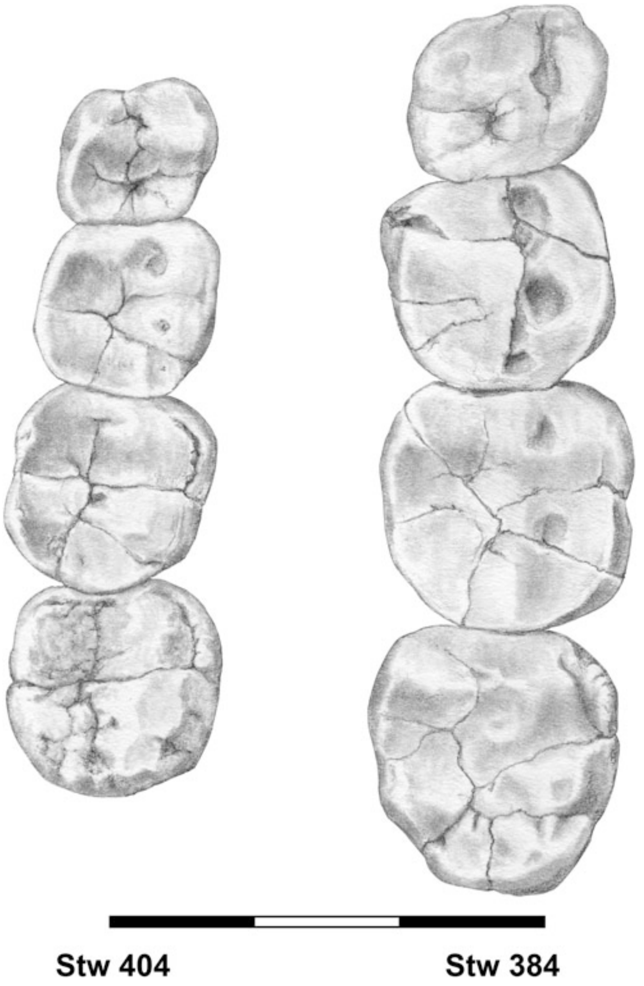

Fig. 6.4 Comparison of the Stw 404 and Stw 384 mandibular postcanine dentitions (P_4–M_3). Scale in cms

Table 6.5 Attribution of the hominin fossils from Sterkfontein to groups by Lockwood (1997)

Group 1	Group 2	Group 3
Sts 5	TM 1511	Stw 183
Stw 13	Sts 71	
	Stw 505	

Groups 1 and 2 are recognized as "subgroups" that did not incorporate more fragmentary remains and were therefore not clearly differentiated. The Stw 183 maxilla (Group 3) is recognized as the best evidence for a separate taxon in the Sterkfontein Type Site (Member 4) assemblage

Lockwood (1997) remained uncommitted over the recognition of separate morphological groups among the Sterkfontein and Makapansgat fossils. While he regarded the strongest evidence for distinct "subgroups" within the Sterkfontein Type Site assemblage to be Sts 5 and Stw 13 representing one, and TM 1511, Sts 71 and Stw 505 representing another (Table 6.5), he noted that because they do not incorporate more fragmentary, intermediate fossils they are not necessarily clearly differentiated. As a result, he concluded that taken together they most likely represent the range of variation attributable to a single species.

The immaturity of Stw 252 (aged by Lockwood to between 7 and 9 years, using the dental development chart for *Australopithecus* by Beynon and Dean (1988)) affects several of the features employed by Clarke (1988a, 1994a) in his characterization of it and of the "second species." In particular, this affects his observations about its supraorbital and glabellar morphologies. On the other hand, Lockwood (1997) was cautious about the specific attribution of Stw 252 owing to Spoor's (1993) analysis of the Stw 255/Stw 266a temporal bones that are likely part of the same individual. As a result, he concluded that Stw 252 is "probably best regarded as *Australopithecus* sp. indet. until the well-preserved dental remains are thoroughly analyzed" (Lockwood 1997: 284).

Lockwood (1997: Table 10.1) also provided cogent observations regarding inconsistencies in the distribution of a number of the morphologies considered by Clarke (1988a, 1994a) as diagnostic among the specimens allocated by him to each. At the same time, however, Lockwood suggested that the Stw 183 maxilla (Fig. 6.5) might represent a separate taxon (Table 6.5). Even in this instance, however, the immature nature of the specimen makes such an attribution extremely tentative.

Lockwood and Tobias (2002) described 27 cranial specimens excavated under the aegis of the University of the Witwatersrand from the Sterkfontein Type Site. Working on the premise that Stw 505 and all of the fossils recovered in the earlier excavations by Broom and Robinson (1936–1939, 1947–1949) belonged to *A. africanus*, they classified each new fossil into one of four categories:

1. it is attributable with confidence to *A. africanus*,
2. it is clearly distinguishable from *Paranthropus* and broadly similar to *A. africanus* and early *Homo*, but could not be assigned specifically because it lacked sufficient diagnostic morphology,
3. it differs substantively from *A. africanus*, being suggestive of a different or new species, or
4. it is not taxonomically identifiable beyond being a hominin.They refrained from assigning Stw 252 to any group, stating that its definitive description was being prepared by R.J. Clarke. They also refrained from assigning the Stw 498 maxilla to any group for the same reason, although Lockwood (1997) had earlier argued that attribution to *A. africanus* "was appropriate" for this specimen.

Lockwood and Tobias (2002) assigned a few of the more complete elements—Stw 13, Stw 73, Stw 370, Stw 591—to *A. africanus*, and while the Stw 391 maxillary fragment was placed in Group B, they considered it to be "strongly suggestive" of *A. africanus* (Table 6.6). About half of the

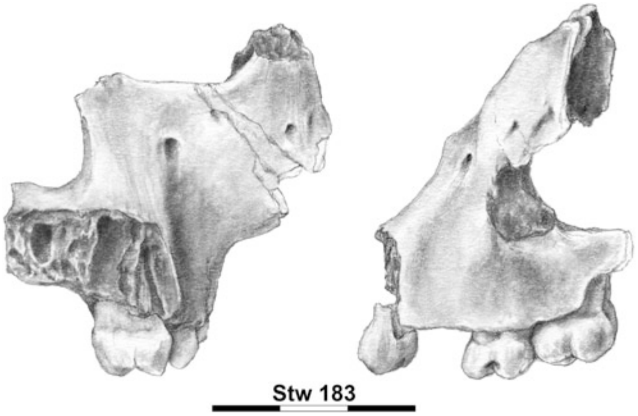

Fig. 6.5 The Stw 183 juvenile maxilla in facial and lateral views. Scale in cms

Table 6.6 Attribution of the hominin fossils from Taung, Sterkfontein and Makapansgat to groups by Lockwood and Tobias (2002)

A. africanus	Group C	"Unique"
Taung	Stw 183	Stw 98
TM 1511	Stw 255	Stw 187
TM 1512		Stw 329
TM 1514		
Sts 5		
Sts 17		
Sts 52		
Sts 53		
Sts 61		
Sts 63		
Sts 71		
Sts 3009		
MLD 1		
MLD 6/23		
MLD 9		
MLD 37/38		
MLD 45		
Stw 505		
Stw 13		
Stw 73		
Stw 370		
Stw 579		
? Stw 391		

Specimens in Group C are held to "differ substantively from *A. africanus*, being suggestive of a different or new species." Each of the specimens in the "unique" category "shows a unique pattern of differences from 'typical' *A. africanus* specimens"

fossils—including Stw 18, Stw 49, Stw 69, Stw 151, Stw 298, Stw 299, Stw 391, and Stw 509—were attributed to Group B, while two—the Stw 183 juvenile maxilla and the Stw 255/Stw 266a temporal fragments—were thought to suggest a "distinct phenon." The Stw 183 maxilla was seen as reminiscent of *P. robustus* in the development of an incipient maxillary trigone and its rounded inferolateral orbital margin (Fig. 6.5). Although Stw 183 was felt to constitute the strongest evidence for a second species, they were hesitant to consider it as definitive evidence because of its ontogenetic immaturity.

They opined that Stw 255 (which may belong to the remainder of the Sts 252 cranium) shows resemblances to *P. boisei* in the relationship of the tympanic to the postglenoid and mastoid processes, but that "on the whole, Stw 255 suggests the appearance of the temporal bone in KNM-WT 17000" (Lockwood and Tobias 2002: 446). This is an intriguing statement because the temporals of *P. boisei* and *Paranthropus aethiopicus* (the species to which KNM-WT 17000 is attributed by most authorities) differ in the relationship of the tympanic plate to the postglenoid process. The two are appressed in *P. boisei* and separated in *P. aethiopicus*. Spoor (1993) discussed the possible orientation of the Stw 255 petrous pyramid, suggesting that its posterior surface might have had a rather more coronal axis than is evident for other Sterkfontein homologues, resembling more closely specimens of *Homo* and *Paranthropus*.

However, the Stw 255 temporal resembles other Sterkfontein homologues in the presence of a prominent, club-like Eustachian process, and Lockwood and Tobias (2002) considered this to be significant in as much as it has been argued to be a singular feature of *A. africanus* (e.g., Kimbel and Rak 1993; Kimbel et al. 2004). It is particularly manifest on Sts 5 and MLD 37/38, although it is also evident on the type specimen of *P. robustus* (Dean 1985). Nevertheless, Lockwood and Tobias (2002) tentatively suggested that Stw 255 and Stw 183 may represent a distinct "phenon" as they "deviate from the *A. africanus* sample in the same direction." That is, in the direction of *Paranthropus*. As such, they regarded these two fossils as "potentially the best cranial evidence for taxonomic heterogeneity within Member 4."

Lockwood and Tobias (2002: 447) drew attention to three other specimens—Stw 98, Stw 187, and Stw 329—as meriting further attention because "each shows a unique pattern of differences from 'typical' *A. africanus* specimens" (Table 6.6). Stw 98 is a partial temporal bone, Stw 187 is a partial neurocranium comprising parietal and occipital fragments of an immature individual, and Stw 329 is part of a juvenile temporal bone.

With reference to Stw 98, Lockwood and Tobias (2002) observed that the opening for the vestibular aqueduct exhibits a configuration that is rare in hominin specimens except those attributed to *P. boisei*. However, they noted that "all else about Stw 98 suggests clear differences" from that species (2002: 411). They saw the Stw 187 basioccipital fragment as having closest overall resemblance with OH 24 (attributed to *H. habilis* by most workers), but it was also seen to differ from early *Homo* "in the direction of *A. africanus*" in the pronounced tubercles for the attachment of the longus capitis muscles. Indeed, they observed that this may be a unique feature of *A. africanus*. The Stw 329 temporal was considered to differ from *A. africanus* homologues in the form of its tympanic, which is concave medially and exhibits only a rudimentary Eustachian process. Although Stw 329 lacks a prominent, club-like Eustachian process, it is from a juvenile individual, and it is not clear whether this affects the expression of this trait. Lockwood and Tobias (2002) present no argument that would support a view that these three specimens, despite their deviations from modal morphologies, are attributable to anything other than *A. africanus*.

Thus, of the five specimens regarded by Lockwood and Tobias (2002) as being potentially suggestive of a distinct phenon, or taxon, all are of doubtful veracity. This is owing either to their ontogenetic immaturity (Stw 252/255/266a, Stw 183, Stw 187, Stw 329), the questionable distinctiveness of particular morphological features (e.g., the opening of the vestibular aqueduct), or the erroneous assessment of morphological configurations in other hominin taxa (e.g., the relationship between the postglenoid process and the tympanic in *P. aethiopicus* and *P. boisei*).

Moreover, it is important to note that Lockwood and Tobias (2002) did not consider any aspect of dental morphology in their assessments, and they stressed that such an analysis would undoubtedly influence specimen assignments. Studies that have considered aspects of the dentition will be reviewed below.

STET and Cranial Variation in the Sterkfontein Type Site Assemblage

Wolpoff and Lee (2001, 2006; Lee and Wolpoff 2005) have applied a variant of the approach to testing conspecificity proposed by Thackeray et al. (1995, 1997; Thackeray 1997b). This employs the standard error of pairs of measurements from a bivariate slope relating one specimen to another, where the standard error of the slope assumes the role of taxonomic arbiter. Thackeray refers to this as "s.e.$_{m}$" (standard error of the m-coefficient in the formula for a straight line (i.e., $y = mx + c$)), while Wolpoff and Lee call it "STET" (standard error test of the null hypothesis of no taxonomic difference). Whereas Thackeray (1997b, 2007) subscribes to a given "s.e.$_{m}$" value (e.g., the log value of -1.61) as a "biological species constant," Wolpoff and Lee (2001, 2006; Lee and Wolpoff 2005) apply STET in a comparative context. Here, the distribution of STET values among conspecifics in other samples sets the limits for the possible rejection of conspecificity among unknowns. Although the objectives of the studies by Wolpoff and Lee were the evaluation of variation among Late Pleistocene Levantine fossils (Wolpoff and Lee 2001) and Early Pleistocene East African "habiline" crania (Lee and Wolpoff 2005; Wolpoff and Lee 2006), specimens from Sterkfontein were employed as pairwise comparators because they were assumed to represent a single species.

Six Sterkfontein crania were thus used: TM 1511, Sts 5, Sts 19, Sts 71, Stw 505, and Sts 25. Pairwise comparisons among the first five yielded STET values between 1.34 (TM 1511 vs. Sts 71) and 3.25 (Sts 5 vs. Stw 505). The latter is similar to the values they obtained for Skhul 5 versus Skhul 9, and KNM-ER 1813 versus OH 16. What is of potential interest in the present context is the fact that notably higher STET values were obtained for comparisons involving Sts 25 (Wolpoff and Lee 2001; Lee and Wolpoff 2005). In these comparisons, Sts 25 versus Sts 71 yielded a value of 5.49, and Sts 25 versus Sts 5 resulted in one of 5.62. Wolpoff and Lee (2001; Lee and Wolpoff 2005) noted that the STET values pertaining to Sts 25 fall well above the maxima recorded by them for samples of chimpanzees ($n = 44$; max. STET = 3.10) and living humans ($n = 113$; max. STET = 4.11).

As a result, they omitted Sts 25 from the Sterkfontein sample in the second iteration of their "habiline" taxonomy study (Wolpoff and Lee 2006). This was explained by them as follows: "An earlier compilation of the Sterkfontein data included Sts 25. This was not an appropriate comparison, as the specimen is quite young, and Sts 25 is not included here" (Wolpoff and Lee 2006: 79). Wolpoff (personal communication) has confirmed that "young" refers to ontogentic rather than geochronological age. However, I am not aware of any evidence to the effect that Sts 25 is anything other than a small adult calvaria. Indeed, Kimbel and Rak (personal communication) have observed that the patency of its ectocranial sutures is comparable to that of MLD 37/38, in which the third molars are heavily worn (Dart 1962b). If Sts 25 is indeed an adult, its apparent morphometric difference from other Sterkfontein specimens (i.e., Sts 5 and Sts 71) could be of potential interest.

Dental Variation in the Australopithecus africanus *Hypodigm*

As noted above, Clarke's perception of considerable molar size variation in the Sterkfontein Type Site assemblage led him to suggest that a "small-toothed, less specialized form of *Australopithecus* was contemporary with the large-toothed *A. africanus*" (1985b: 295).[2] Following this proposal, Kimbel and White (1988) observed that the buccolingual (BL) diameters of M^2s from Sterkfontein and Makapansgat yield a bimodal, non-overlapping frequency distribution, and a higher CV than samples of other australopith species, including *A. afarensis* and *P. robustus*. However, they did not find such bimodality at any other tooth position in either the maxilla or mandible, and the M^2 CV value was seen to be not "unusually high" by comparison with those for extant species samples.

Wood (1991a) compared variation in the conventional *A. africanus* hypodigm for a variety of cranial, mandibular and dental dimensions against that in *Gorilla gorilla* and *P. boisei*. As such, his comparators comprise the most dimorphic extant hominid and potentially provide for time-averaged variation in a sexually dimorphic extinct hominin. With the exception of some mandibular incisor diameters, he found no evidence for excessive variability in the Sterkfontein assemblage. Calcagno et al. (1999) examined odontometric variability in the Sterkfontein australopith assemblage using the CV, and determined that only in the M^2 did variation exceed that of a *Gorilla* sample. Although their observation regarding the M^2 is reminiscent of that of Kimbel and White (1988), Calcagno et al. (1999) concluded that they could not recommend rejection of the single species hypothesis on this basis alone. The CV has also been employed in subsequent analyses of crown dimensions for larger dental samples from Sterkfontein (Moggi-Cecchi 2003; Moggi-Cecchi et al. 2006), and these studies concluded that the Sterkfontein values do not provide evidence for more than one taxon in the Type Site assemblage.

Moggi-Cecchi and Boccone (2007) recorded cusp proportions for samples of *A. africanus* and *P. robustus* maxillary molars, and observed that both had "remarkably high" levels of variability in absolute areas, with CV values above 15 % in all instances. However, data for dimorphic extant taxa were not provided by which these values could be evaluated, and the fact that almost all of the *A. africanus* and *P. robustus* CVs are of comparable magnitude does not suggest that the hypodigm of the former is any more taxonomic heterogeneous than that of the latter.

Grine et al. (2013) examined overall crown size and proportional cusp areas of the mandibular postcanine teeth, which constitute the bulk of the Sterkfontein Member 4 assemblage, in order to determine whether the degree of variation in it exceeds that of *G. gorilla*. Variation in the Sterkfontein (and combined Sterkfontein + Makapansgat) sample is significantly greater than in *Gorilla* for P_3 and P_4 crown areas, the MD diameter of the P_4, and the relative size of the P_3 metaconid. While the differences in the P_3 can be attributed to functional differences in this tooth between *Gorilla* and *Australopithecus*, the exaggerated P_4 size variation at Sterkfontein defies such explanation. The Sterkfontein sample also exhibits significantly greater variability in the expression of accessory molar cuspulids (the C6 and/or C7) and the protostylid. However, because these features vary in both frequency and expression in other extinct hominin species (e.g., *P. boisei* and *A. afarensis*) and among modern human populations (Scott and Turner 1997; Hlusko 2004; Guatelli-Steinberg and Irish 2005), Grine et al. (2013) concluded that it would be imprudent to attribute such variation to taxonomic heterogeneity in the *A. africanus* assemblage.

Clarke (2008) added the Stw 53 cranium and Stw 391 maxilla to his *A. africanus* sample, and Stw 183, Stw 498, and Stw 573 to the hypodigm of his "second species" (Table 6.3), and expanded upon his characterization of the latter as having molars with low, bulbous cusps, the tips of which are orientated towards the crown center (Table 6.4). Fornai et al. (2010) attempted to evaluate Clarke's (2008) proposal of cusp differences using a 3D geometric morphometric analysis of landmarks determined from standard (i.e., medical) computed tomography (CT) scans of maxillary molars. Although their results suggested support for the existence of two molar morphs in the Sterkfontein Member 4 assemblage, conventional CT scan data do not usually permit accurate identification of tooth enamel boundaries; especially in specimens that are scanned dry (Grine 1991). This inaccuracy results from beam hardening artifacts at object borders (Joseph 1981; Rao and Alfidi 1981), and tooth enamel seems to be especially problematic in this regard. While these effects can be reduced by X-ray beam filtration (Meganck et al. 2009) or the use of ray-casting instead of standard image thresholding algorithms (Sherf and Tilgner 2009), this is rarely (if ever) done in studies of fossils.

Taxonomic Absurdity at Sterkfontein and Makapansgat

Schwartz and Tattersall (2005) have presented an extraordinarily confusing picture of what they perceive as discrete "morphs" in the australopith assemblages from Sterkfontein and Makapansgat, proposing that well over a dozen such groups can be identified. Some of these pertain only to fossils from Makapansgat, some refer only to Sterkfontein, and others comprise specimens from both.

It would seem that some of this multitude of groups could be combined through commonality of membership, although Schwartz and Tattersall (2005) eschew this. Thus,

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[2] This must be a typographical error. In later publications, Clarke (1988a, b, 1994a, 2008) clearly regards *A. africanus* as having smaller teeth than the "second species."

for example, Sts 5, Sts 19, and the temporal bones (but not the other parts) of both Stw 53 and Stw 252 belong to their "pseudostyloid" group, while MLD 37/38 belongs to their "Sts 5 cranial morph." Since MLD 37/38 and Sts 5 belong to the same cranial morph, it would seem reasonable to assume, therefore, that MLD 37/38 also belongs to the "pseudostyloid" group. Similarly, because the facial component of Stw 53 is listed as the sole Sterkfontein member of their "SK 48 facial morph" group, and because both Stw 53 and Sts 53 are listed as members of the "DNH 7/SK 48-like upper dental and facial morph" at Sterkfontein, one might reasonably assume that these "morphs" are one and the same. Unfortunately, given Schwartz and Tattersall's (2005) treatment of the fossils, it is not possible to assume anything of the sort.

For example, Schwartz and Tattersall (2005) recognize SK 48 and DNH 7 morph(s) at Sterkfontein, and two separate TM 1517 morphs at Makapansgat.[3] Since SK 48 and DNH 7 are recognized widely as probable male and female specimens of *P. robustus* (Lockwood et al. 2007; Moggi-Cecchi et al. 2010), and the left hemi-cranium and right hemi-mandible of TM 1517 comprise the type of *P. robustus*, one should expect that the "TM 1517 facial and upper dental morph," the "TM 1517 lower dental morph," and the DNH 7/SK 48 morph would be one and the same. However, with reference to TM 1517, Schwartz and Tattersall (2005: 167) are of the remarkable opinion that "probably the cranium and mandible do not represent the same individual or even taxon." They cite the existence of "four fragmentary teeth" (at least one of which is misidentified by them by type) that are "allegedly associated" with the cranium, but there are actually *five* teeth in question—an incomplete RP^3, an incomplete RP^4, small parts of a RM^1, a complete RM^2 and a complete RM^3 (not two "RM^{3}s" as claimed by them)—as illustrated by Broom (1946: Plate IX, Fig. 86). These are clearly the antimeres of the teeth preserved in the TM 1517 maxilla, being almost perfect mirror images in morphology as well as size, as observed by Robinson (1956). Moreover, they occlude perfectly with the teeth in the TM 1517 right mandibular corpus (Wallace 1972). There is, therefore, little reason beyond lack of familiarity with the material, dental misidentification, and morphological myopia to believe that the cranium and mandible that constitute the type of *P. robustus* represent more than a single individual, let alone more than one species.

As a result, I have generously conflated the two TM 1517 "morphs" and the DNH 7/SK 48 morph(s) to a single group, referred to here simply as the "*Paranthropus*-like" morph. Recognition of a single "*Paranthropus*-like" morph serves to reduce the number of "morphs" to only ten. Aguirre's (1970) arguments, and Clarke's (1988a, b) suggestion that one of the australopith species represented at Sterkfontein and Makapansgat is ancestral to this genus makes Schwartz and Tattersall's (2005) attributions of some possible interest. Since two of the Sterkfontein "morphs" differ only in the expression of the maxillary molar cingulum, and because even Schwartz and Tattersall (2005) acknowledge that they may represent a single group, we might possibly conflate them, thus reducing the number further.

Schwartz and Tattersall (2005) acknowledge that some of the fossils from Makapansgat (n = 9) and Sterkfontein (n = 6) are "unassignable to morph." Thus, one might conclude that there are nine "morphs" for the most of the fossils from Taung, Sterkfontein and Makapansgat, together with a tenth group for those that cannot be readily assigned to one of the foregoing. The ten groups that I have been able to construct from Schwartz and Tattersall (2005) are:

1. Taung facial and dental morph (Sterkfontein and Makapansgat)
2. *Paranthropus*-like facial and dental morph (Sterkfontein and Makapansgat)
3. pseudostyloid group (Sterkfontein and Makapansgat)
4. MLD 2 lower dental morph (Sterkfontein and Makapansgat)
5. "Upper molar cingulum development" group (Sterkfontein only)
6. Stw 151 upper and lower dental morph (Sterkfontein only)
7. Stw 505 facial morph (Sterkfontein only)
8. Stw 252-like morph (Makapansgat and Sterkfontein)
9. Non-hominid/*Pongo*-like morph (Sterkfontein only)
10. Unassignable to morph at (a) Sterkfontein and (b) Makapansgat.

Given the phylogenetic hypothesis to which Schwartz (2004; Grehan and Schwartz 2009) subscribes, it is perhaps not unexpected that one of those recognized is a "non-hominid/*Pongo*-like morph."

A good number of fossils belong to two or even three separate groups simultaneously (Table 6.7). For example, the facial skeleton of Stw 53 belongs to the *Paranthropus*-like facial morph and its basicranium belongs to the "pseudostyloid" group, while its zygoma and braincase evince morphologies that render them unassignable. Schwartz and Tattersall (2005) also maintain that the composite juvenile specimen Sts 24 belongs to two morphs (the

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[3] Schwartz and Tattersall (2005) recognize a number of Makapansgat fossils as conforming to their "TM 1517 facial and upper dental morph." Although they do not explicitly recognize any Sterkfontein fossil as a member of this group, they inadvertently do so in their discussion of the hominin remains from Kromdraai (Schwartz and Tattersall 2005: 167–168), where they mistakenly identify TM 1512 as coming from that site.

Table 6.7 Attribution of the hominin fossils from Taung, Sterkfontein and Makapansgat to "morphs" or groups by Schwartz and Tattersall (2005)

Group 1	Group 2	Group 3	Group 4	Group 5
Taung	TM 1512	Sts 5	MLD 2	(Moderate)
Sts 2	Sts 53	Sts 19	Stw 327	Sts 22
Sts 8	Stw 53*	Stw 53*	Stw 404	Sts 35
Sts 17	MLD 4	Stw 183*	Stw 451	Stw 73
Sts 24*	MLD 6	Stw 252*		
Sts 32	MLD 9	Stw 498*		(Marked)
Sts 42	MLD 11	MLD 37/38		Sts 12
Sts 52	MLD 12			Sts 24*
Stw 183	MLD 18			Sts 28
Stw 252*	MLD 19			Sts 37
Stw 384	MLD 23			
Stw 498*	MLD 24			
MLD 5	MLD 28			
	MLD 30			
	MLD 41			
	MLD 44			
	MLD 45			

Group 6	Group 7	Group 8	Group 9	Group 10
Stw 14	Sts 71	Stw 252*	Stw 277	Sts 7
Stw 104	Stw 505	MLD 42	Stw 278	Sts 36
Stw 151		MLD 43		Stw 53*
				Stw 151*
				Stw 252*
				Stw 498*
				MLD 1
				MLD 3
				MLD 10
				MLD 22
				MLD 27
				MLD 29
				MLD 31
				MLD 34
				MLD 40

The columns represent their ten major "morphs" or groups
Specimens designated with an asterisk (*) are attributed simultaneously to more than one "morph" or group
Group 1 Taung morph (*A. africanus*)
Group 2 *Paranthropus*-like morph
Group 3 'pseudostyloid'/Sts 5 group
Group 4 MLD 2 dental morph
Group 5 Upper molar cingulum development
Group 6 Stw 151 dental morph
Group 7 Stw 505 facial morph
Group 8 Stw 252-like morph
Group 9 nonhominid/*Pongo*-like morph
Group 10 unassignable to morph

deciduous first molars belong to the Taung morph, while the remainder of the specimen belongs to another morph) because of the misguided notion that it represents more than one individual. It does not (Grine 1981).

Notwithstanding the patent taxonomic absurdity that results from application of their scheme, Schwartz and Tattersall (2005) seemingly recognize at least two groups—viz. *A. africanus* (the Taung morph) and a *P. robustus*-like group—whose existence at Makapansgat and/or Sterkfontein has been posited by others (e.g., Aguirre 1970; Clarke 1988a, 2008). Unfortunately, membership in these two groups according to Schwartz and Tattersall (2005) does not conform to the specimen allocations of other workers (cf. Tables 6.3 and 6.7).

Other Sterkfontein Australopith Fossils: Silberberg Grotto and Jacovec Cavern

As noted above, the vast bulk of fossils recovered at Sterkfontein by Broom (1936–1939), by Broom and Robinson (1947–1949) and subsequently by the University of the Witwatersrand initiative (1966–present) derive from mine rubble-dumps or excavation of clastic sediments (calcified or decalcified "breccia") from the Type Site deposit. These sediments comprise Member 4 of the Sterkfontein Formation (Partridge 1978). The Type Site, which was widened by lime-mining activity and subsequently deepened by paleontological exploration, exposes a large area of Member 4 breccia. In 1956, C. K. Brain discovered stone artifacts in "loose breccia" about 18 m west of the Type Site in an area that was called the Extension Site by Robinson (1957, 1959, 1962) and Mason (1957, 1962), who undertook its excavation. The Extension Site sediments, which were referred to alternately as the "red-brown breccia" or "middle breccia," comprise Partridge's (1978) Member 5. Like Member 4 in the Type Site, this unit is also exposed on the surface (Fig. 6.6). Partridge (2000) subsequently recognized three units for Member 5 (A–C) as a result of Clarke's (1994b) excavations. Several isolated teeth ascribed to *Homo* cf. *Homo erectus* and *Paranthropus* have been recovered in the Lincoln Cave "South" sediments. However, these appear to have eroded from Member 5B, where other fossils of these two have been identified, and to have been redeposited in the younger, unconsolidated sediments of Lincoln Cave (Reynolds et al. 2003, 2007). The details concerning the relationship of Member 4 and Member 5 will be discussed below, as they relate to discussions over the attribution of a number of fossils to either *Australopithecus* or *Homo*.

In addition to the Extension Site Member 5 deposits, there are two other fossiliferous repositories at Sterkfontein that are variably individuated from the sedimentary units that comprise the Type Site deposit. These underground cavern systems are the Silberberg Grotto and the Jacovec Cavern (Fig. 6.6).

The Silberberg Grotto (also referred to as the Daylight Cave) has been known to be fossiliferous from the time of Broom's initial work at Sterkfontein, having yielded in 1942 parts of the skull of the long-legged running, or hunting, hyena, *Chasmaporthetes*, to H. K. Silberberg. It was investigated more fully by Tobias (1979) and subsequently by Clarke (1998) for its paleontological potential. Partridge (1978, 2000) identified stratigraphic units (e.g., members 2 and 3) in the Silberberg Grotto predating those exposed on the surface in the Type Site. Clarke found conjoining hominin foot bones in the rubble that had resulted from lime-mining activity in the Silberberg Grotto (Clarke and Tobias 1995), and these were subsequently found to be part of a nearly complete skeleton (Clarke 1998). The skeleton, Stw 573, derives from a stoney breccia that Partridge had designated as Member 2 (Partridge et al. 1999, 2000, 2003).

This deposit has been argued to be separated from Member 4 by a considerable thickness of sediment—designated as Member 3—which itself accumulated atop the flowstone that covers Member 2 (Partridge and Watt 1991). Member 3 has been calculated to be at least 8 m thick. As such, the Member 2 deposit in the Silberberg Grotto has been regarded as considerably older than the Type Site Member 4 breccia (Clarke and Tobias 1995; Partridge et al. 1999, 2000, 2003; Muzikar and Granger 2006; Clarke 2008). Although the identification of Member 3 as a separate lithostratigraphic unit from Member 4 has been questioned by Pickering and Kramers (2010), the Silberberg Grotto deposit is certainly much deeper than the surface exposures from which the bulk of australopith fossils have been recovered (Fig. 6.6). This would suggest that, regardless of the nomenclature applied to the intervening strata, a considerable amount of time could have elapsed between the deposition of the sediments in Silberberg Grotto and the Type Site (Clarke 2013).

Partridge et al. (1999) obtained several paleomagnetic signatures from flowstones in the Silberberg Grotto, and argued primarily from faunal estimates for the age of Member 4 and the apparently primitive characteristics of *Chasmaporthetes nitidula* from Member 2 (Turner 1997), that the Member 2 deposit could be placed within an interval between the termination of the Mammoth subchron and the Gauss–Gilbert reversal boundary (i.e., between approximately 3.2 and 3.6 Ma). They provided a "best estimate" of 3.3 Ma for the age of the Stw 573 skeleton. Subsequently, Partridge et al. (2003) recorded ^{26}Al and ^{10}Be measurements of quartz grains for three samples of Member 2 breccia in the Silberberg Grotto that yielded a date of some 4.2 Ma. This would indicate that the paleomagnetic estimate had placed the sequence two reversals too young.

The comparative antiquity of the Stw 573 skeleton has been questioned by Walker et al. (2006) and Pickering and Kramers (2010) on the basis of U-Pb dates for speleothems that they believe bracket it. However, Clarke (2006, 2013) personal communication) has expressed very good reasons to doubt this purported association. Moreover, although U-Pb methodology may be effective at dating carbonates under certain conditions (Cole et al. 2005; Polyak et al. 2008; Rasbury and Cole 2009), it is far from clear that its uncritical application to the speleothems that formed in karst caves within the Precambrian Malmani dolomitic limestones of the Bloubank valley has yielded meaningful dates. This method would seem especially vulnerable in these settings to the differential erosion of the parent dolomites, and the mobility of different and sometimes quite substantial amounts of uranium through them and the deposits they surround (Rink 1997, 2000; Ludwig and Renne 2000). Moreover, given the differential erosion and infilling that characterizes these caves, it is far from clear how the speleothems actually relate in all instances to the clastic sediments they purportedly constrain. Indeed, the dates published by Pickering et al. (2011) for speleothems that supposedly bracket the fossiliferous Member 1 deposit at Swartkrans would see *A. africanus* at Sterkfontein and *P. robustus* at Swartkrans as contemporaneous. This is patently ridiculous.

The other repository of hominin fossils at Sterkfontein is the Jacovec Cavern (Fig. 6.6).[4] This large cave contains several generations of fill that are not contiguous with those of the main deposit (Wilkinson 1983, 1985; Partridge et al. 2003). Wilkinson (1985: 169) argued that the Jacovec deposits are an "older basal mass" underlying the main deposit, and that they are not "simply an extension downslope of higher-lying members." A fragmentary hominin cranium (Stw 578) was discovered in a hanging remnant of "orange sandy breccia" that adheres to the ceiling of the cave, and additional hominin bones were recovered from the same breccia that had collapsed into a debris cone that fills much of the chamber. Partridge et al. (2003) determined burial ages for this fossiliferous breccia on the basis of two ^{26}Al and ^{10}Be measurements, obtaining a date of some 4.0 Ma. Partridge et al. (2003) observed that the burial ages of the Jacovec Cavern sediments are indistinguishable from those in the Silberberg Grotto. If the two deposits are, indeed, of equivalent age, it is possible that they accumulated from a common source, although this is by no means certain.

Stw 573 from the Silberberg Grotto

As noted above, Clarke (2008, 2013) attributed the Stw 573 skeleton from the Silberberg Grotto to membership in his "second species." In particular, he regarded the skull as having a stronger resemblance to *A. afarensis* than *A. africanus* (Clarke 2006). He has compared it favorably to Stw 252 and Stw 505 on the basis of its robust zygomatic arch, lack of supraorbital thickening, and the presence of a small, posteriorly restricted sagittal crest (Clarke 2008, 2013).

Stw 578 from Jacovec Cavern

The Stw 578 cranium from Jacovec Cavern was favorably compared by Partridge et al. (2003) to Stw 252 and contrasted with Sts 5 in terms of its frontal morphology (Table 6.3). Thus, Stw 578 was aligned by Partridge et al. (2003) with Clarke's "second species;" they also observed the strong posterior slope of its tympanic "differs from all other *Australopithecus* temporals from Member 4." Clarke (2013) has suggested that this temporal is more like that of *A. afarensis*. Although the Jacovec and Silberberg crania were considered to be penecontemporaneous, neither Partridge et al. (2003) nor Clarke (2013) have drawn direct comparisons between them (beyond the fact that both have some resemblance to Stw 252).

Among the dozen other isolated hominin bones and teeth recovered from the orange breccia of Jacovec Cavern are a proximal femur, a distal humerus, and a partial clavicle. As discussed below, Partridge et al. (2003) also contrasted the morphology of the femur and clavicle with homologues from the Type Site deposit.

The Postcranial Remains from Sterkfontein

In only a few instances have postcranial bones featured in discussions concerning australopith taxonomy at Sterkfontein. In the first instance, Partridge et al. (2003) drew attention to differences between specimens recovered from Jacovec Cavern and those from the Type Site. They contrasted the long neck and small head of the Jacovec femur (Stw 598) with one Type Site specimen (Stw 522), but noted its similarity to another (Stw 99). More meaning was attributed to the Jacovec clavicle (Stw 606), with the form

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[4] The spelling of the name of this cavern varies. It was initially called the "Terror Chamber" or "Terror Cave" by M. Justin Wilkinson, and although this name was used by him in passing, he more formally referred to it as Jakovec Cavern (Wilkinson 1973; see also Wilkinson 1983, 1985). This spelling has been used by Pickering and Kramers (2010) and Herries et al. (2010), whereas Jacovec is the spelling employed by most others (e.g., Partridge and Watt 1991; Kibii 2001, 2007; Martini et al. 2003; Partridge et al. 2003; Clarke 2006).

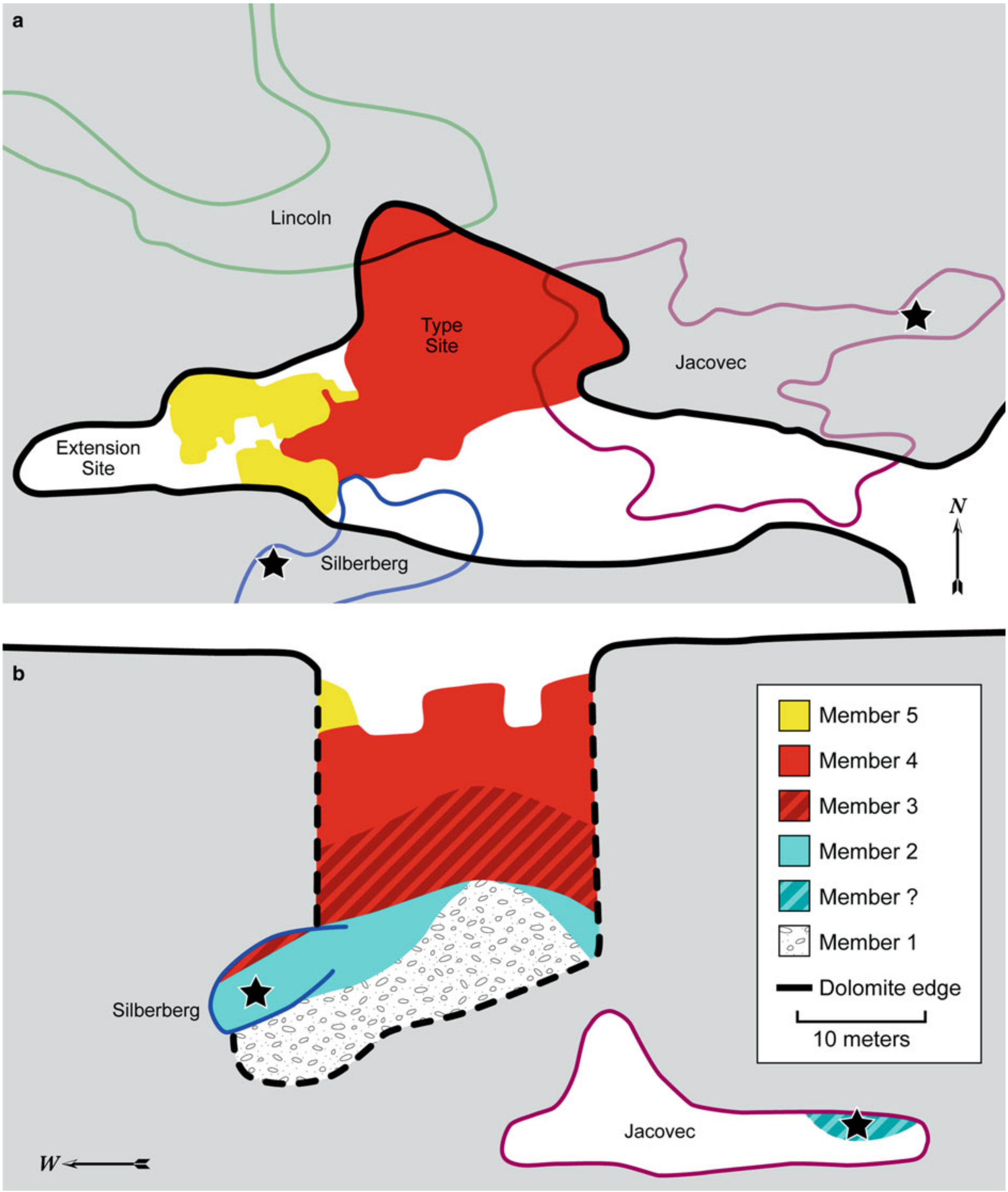

Fig. 6.6 Plan view and schematic East–West section through Sterkfontein depicting the relationship of the fossiliferous exposures of the Type Site and Extension Site, and those of Lincoln Cave, the Silberberg Grotto, and Jacovec Cavern. The plan view shows the approximate extent of the Member 4 and Member 5 deposits that are exposed on the surface (bounded by the edges of the now eroded dolomite roof), and their horizontal relationships with the hominin fossils that have been found in the underground caverns. The schematic (hypothetical) East–West section depicts the vertical and horizontal separation of the fossils from the Silberberg Grotto and Jacovec Cavern and the fossil-bearing sedimentary units that have been excavated at the surface. The extent and disposition of the different members deep to the surface exposure should not be taken as a precise reconstruction. Whether Member 3 represents a separate stratigraphic unit from Member 4 has been questioned (Pickering and Kramers 2010). The stars in the Silberberg Grotto and Jacovec cavern indicate the approximate locations of the Stw 573 skeleton and Stw 578 cranium respectively. Plan view adapted from Kuman and Clarke (2000), Partridge et al. (2003), and Reynolds et al. (2007). Schematic East–West section adapted from Partridge and Watt (1991, Figs. 2 and 4), Partridge (2000), and Clarke (2006)

of its conoid tubercle contrasted with those on all other Sterkfontein homologues.

Another case in which the postcranial skeleton has featured in discussions of taxonomy is with reference to the Stw 431 pelvis (Berge et al. 2007). The Stw 431 composite skeleton comprises 18 postcranial bones of what is manifestly a single individual; all were recovered in situ from decalcified Member 4 sediments (Kibii and Clarke 2003; Toussaint et al. 2003). This specimen has been attributed to *A. africanus* by most workers, either by consideration of its morphology (e.g., Toussaint et al. 2003) or simply by convention (e.g., Dobson 2005). However, analysis of the reconstructed pelvis suggested to Berge et al. (2007) that its ilium differs from that of *A. africanus* (Sts 14) and resembles purported *Paranthropus* fossils from Kromdraai and Swartkrans. Berge et al. (2007) concluded that this observation "confirmed the hypothesis" of the presence of a species of *Australopithecus* contemporaneous with *A. africanus* that was "probably at the origin" of *P. robustus*.

Clarke (2013) has suggested that two distinct morphologies are represented by the Stw 562 and Stw 595 hallucial metatarsals. The former is said to be more human-like and the latter more ape-like in that the articular surface on the head does not extend dorsally (suggesting to Clarke that the individual could not toe-off while walking).

There are comparatively few postcranial remains from Makapansgat, and no worker who has studied them has suggested that they represent more than a single hominin species (e.g., Dart 1949c, 1958, 1962c; Robinson 1972; Reed et al. 1993).

Australopithecus or *Homo*?

The stratigraphic and potential chronological separation of the Silberberg Grotto and Jacovec Cavern fossils from those of the Type Site (Member 4) deposit has almost certainly been a factor in their taxonomic assessment. Other instances in which the provenience of particular fossils has been pertinent to discussions of hominin taxonomy at Sterkfontein relate to their attribution to *Australopithecus* or *Homo*. Indeed, stratigraphic considerations have been involved in taxonomic discussions at Sterkfontein for over half a century, following the recovery of the first teeth and stone tools from the "Extension Site."

Member 4, Member 5, and Taxonomy at Sterkfontein

Following Brain's discovery of stone artifacts in the "loose breccia" of what became known as the "Extension Site," excavations by Robinson and Mason in 1957–1958 uncovered in situ an additional 286 lithic artifacts and one bone tool. This work also resulted in the discovery of a juvenile maxillary fragment and four isolated hominin teeth (these fossils are curated by the Ditsong National Museum of Natural History with the prefix SE, for "Sterkfontein Extension"). Robinson (1957, 1958, 1962) considered them to be attributable to *Australopithecus*, although he argued that the stone-tool-maker was most likely a more advanced taxon (i.e., *Telanthropus*, or *H. erectus*). Tobias (1965: 187), on the other hand, observed that some of the SE tooth crowns "fall outside the *A. africanus* range of variation for several metrical features…, but can be comfortably accommodated within the *H. habilis* range." He concluded that they represented the more advanced, tool-making hominin of the Extension Site.

The deposits exposed in the Extension Site comprise Partridge's (1978) Member 5 (Fig. 6.6). Partridge (2000) subsequently recognized three units for this Member (A–C) as a result of Clarke's (1994b) excavations there. According to this revised scheme, Member 5A sediments had collapsed into "swallow hole" that had formed in Member 4, and this created space for the accumulation of the subsequent 5B sediments. According to Clarke's (1994b) interpretation, Member 5A comprises a "stoney breccia," the Member 5B deposit contains Oldowan artifacts, and Member 5C incorporates Early Acheulean tools.

In 1976, A. R. Hughes excavated the Stw 53 partial cranium from what was interpreted as Member 5 (Hughes and Tobias 1977). This specimen, together with several small, isolated finds (Stw 19, Stw 27, Stw 42) from rubble-dumps that likely represented Member 5 debris, was provisionally assigned to *Homo* (Hughes and Tobias 1977; Tobias 1978). More particularly, part of the Stw 53 cranium was recovered from calcified sediments lining the walls of a sinkhole in Member 4, while the remainder of the specimen was found in decalcified sediments within the sinkhole (Tobias 1978). Tobias (1978: 247) observed that "a few pieces of foreign stone have been found in the same sinkhole." He was also of the opinion that quartzite artifacts recovered from adjacent solution pockets "at about the same level" were coeval with the cranium. The Stw 53-bearing deposit comprises Partridge's (2000) Member 5A.

Clarke (1994b) noted that the "stoney breccia" must have accumulated subsequent to the deposition of Member 4. Kuman and Clarke (2000) further argued that the "Stw 53 Infill," which they perceived as being devoid of lithic artifacts, was intermediate in time between Member 4 and what they came to regard as Member 5 (i.e., the lithic-tool-bearing deposits—5B and 5C of Partridge). Importantly, both Kuman and Clarke (2000) and Partridge (2000) observed significant differences in environmentally sensitive fauna between Member 4 and the "Stw 53 Infill" (e.g., a preponderance of grazing antelopes in the latter). In particular, Kuman and Clarke (2000) noted that “there are good faunal reasons [primarily the presence of *Theropithecus oswaldi*, which is absent from Member 4 but present in Member 5B] to suggest that this infill is later in time than Member 4.” Herries and Shaw (2011) have also opined that the “Stw 53 Infill” is intermediate in age between Member 4 and the rest of Member 5, but the only data they cite in support of this assertion pertain to ESR dates from mammalian tooth enamel. Given the notorious fallibility of ESR dates derived from open-system biogenic apatites (Grine 2005), their assertion is of little moment.

However, Clarke (2008) subsequently altered his earlier view on the temporal relationships among the Member 4, “Stw 53 Infill,” and Member 5B deposits, coming to regard the “Stw 53 Infill” as a hanging remnant of Member 4. However, Clarke’s argument that Stw 53 derives from Member 4 because the infill from which it derives is devoid of stone tools loses cogency given Tobias’s (1978) observation, and the fact that the inferolateral aspect its zygomatic process displays unmistakable evidence of stone-tool cut marks (Pickering et al. 2000). Moreover, Partridge (2000) clearly regarded Member 5A as distinct from Member 4, aligning it with the 5B and 5C because he perceived no sedimentological difference among them.

In addition to being a point of contention with regard to the specific assignation of Stw 53, the issue of stratigraphic derivation from either Member 4 or Member 5 has been raised in reference to the taxonomy of several other hominin fossils, including Sts 17, Sts 19, and Stw 151.

Sts 17

Clarke (1985a: 175) commented upon differences in cranial morphology between “the more lightly structured cranium of Sts 17 [and] the more rugged Sts 71.” He noted that Sts 17 had been excavated by Broom and Robinson from near the top of the Type Site deposit, and suggested that it might therefore have been temporally close to the “morphologically similar” Stw 53 cranium. At the time, Clarke was in agreement with the opinion held by Tobias (1978) and others that Stw 53 was attributable to *Homo*. As a result, Clarke (1985a) questioned whether Sts 17 might actually represent *H. habilis* rather than *A. africanus*.

Subsequently, Clarke (1988a, 1994a) identified Sts 17 as a member of *A. africanus*, but still regarded Stw 53 as *H. habilis*. Stw 53 was interpreted by him as belonging to *Australopithecus*, and specifically of *A. africanus* only later (Kuman and Clarke 2000; Clarke 2008). Apart from Clarke’s (1985a) suggestion of differences between Sts 17 and Sts 71, I am unaware of any other reference to Sts 17 as differing in any way from other Type Site fossils.

Sts 19

The taxonomic affinity of the Sts 19 cranial base has been discussed for over a quarter century without resolution (Clarke 1977; Kimbel and Rak 1993; Ahern 1998; Kimbel 2009; Petersen 2010). It was attributed to *A. africanus* by Broom and Robinson (1950), but they observed that it attested to a “considerable degree of variation” in that species. They also noted that it was “found in an old dump” rather than in their excavation of the in situ Type Site breccia. Clarke (1977) observed that its temporal has several features in common with *Homo* rather than *Australopithecus*, and was prompted to speculate that if (as seemed likely to him) it was a specimen of *Homo*, it may therefore have derived from Member 5.

A morphometric analysis led Dean and Wood (1982) to concur with Broom and Robinson (1950) that Sts 19 simply indicates a rather wide range of variation in *A. africanus*. They saw Sts 19 as more *Homo*-like and Sts 5 as more ape-like. The cranial bases of Sts 5 and Sts 19 are compared in Fig. 6.7. The distribution of states for thirteen basicranial characters led Kimbel and Rak (1993; see also Kimbel 2009) to conclude that this specimen’s affinities reside with early *Homo* rather than *A. africanus*. Ahern (1998), on the other hand, found that in eleven of twelve of these features the variation between Sts 19 and other specimens of *A. africanus* did not exceed that in chimpanzees. Most recently, a morphological and morphometric study by Petersen (2010) concluded that Sts 19 is “the specimen most likely to be distinct” from *A. africanus*” among the fossils from Sterkfontein.

Following Kimbel and Rak (1993), Strait et al. (1997) included Sts 19 in their hypodigm of *H. habilis.* However, it alone accounted for over a third of the characters that were coded as being variable in that species, and in three features it differs from all East African specimens attributed to *H. habilis* sensu stricto (Grine 2001). Thus, if Sts 19 belongs to a taxon other than *A. africanus*, it is not clear that it is early *Homo*.

Stw 53

The Stw 53 cranium was provisionally assigned to *Homo* by Hughes and Tobias (1977; Tobias 1978). Indeed, Clarke (1985b: 175) remarked that it looks “almost identical to the cranium O.H. 24,” which has been referred to *H. habilis* by nearly all workers following Leakey et al. (1971) (e.g., Tobias 1991; Wood 1993; Kimbel 2009). The attribution of Stw 53 to *Homo* has been subscribed to by a number of workers (e.g., Wood 1991b; Kimbel and Rak 1993; Clarke 1994a; Grine et al. 1996; Kimbel et al. 1997, 2004; Smith and Grine 2008; Kimbel 2009; Curnoe 2010). In general,

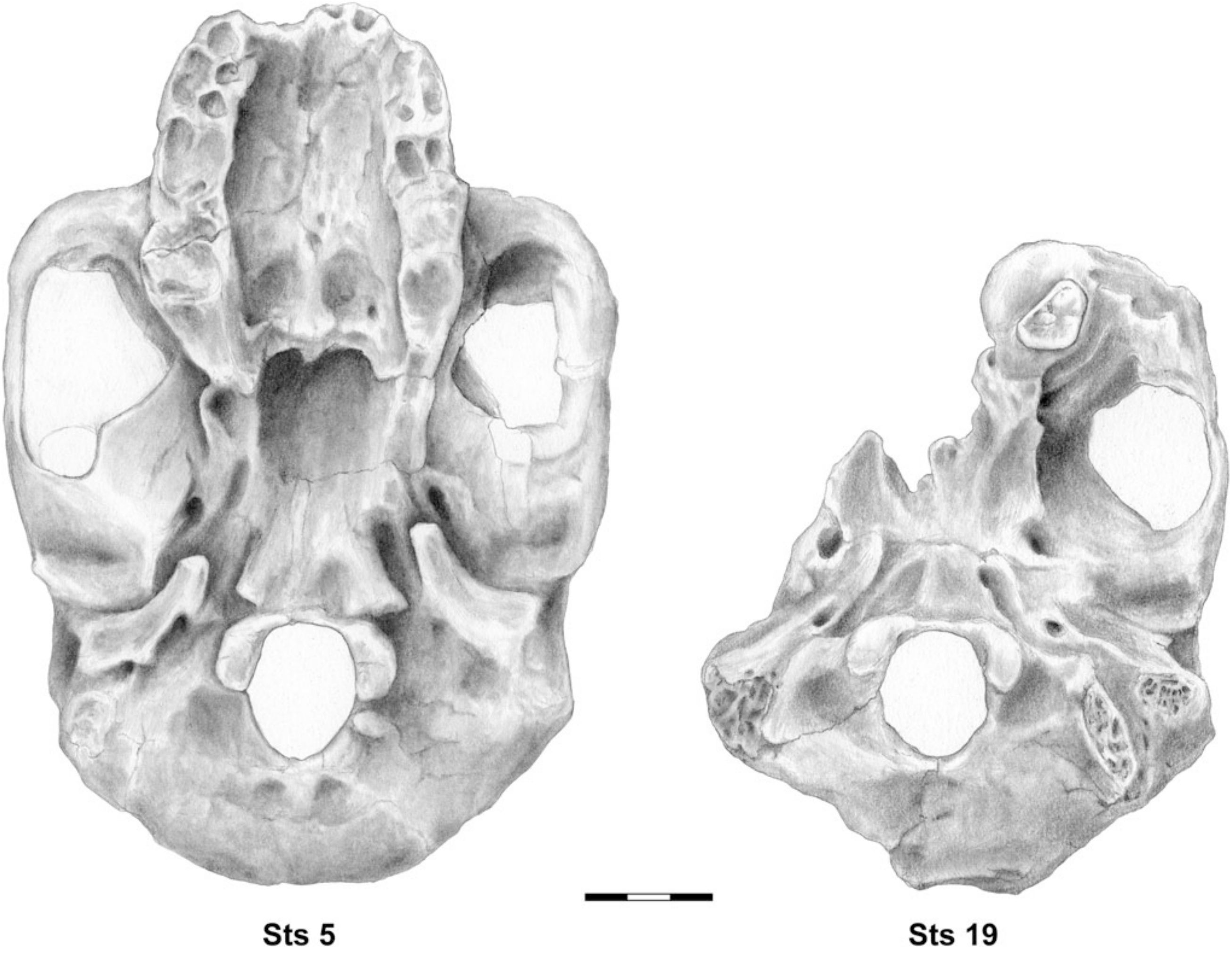

Fig. 6.7 Comparison of the Sts 5 and Sts 19 cranial bases. Scale in cms

there has been a tendency to compare Stw 53 more favorably with fossils from East Africa that are attributed to *H. habilis* than to any other species.

On the other hand, Kuman and Clarke (2000) attributed Stw 53 to *Australopithecus*, remarking on its small cranial capacity, narrow frontal and flat nasal skeleton, and Clarke (2008, 2013) has ascribed it specifically to *A. africanus*. The facial morphology of Sts 5 and Stw 53 is compared in Fig. 6.8. With regard to Clarke's (1985b) earlier observation that Stw 53 looks almost identical to OH 24, he has come to view all of the gracile hominin fossils from Bed I and lower Bed II of Olduvai Gorge (e.g., OH 13, OH 24 and OH 62) as representing *Australopithecus* rather than *Homo*. Thus, Blumenschine et al. (2003: 1220) suggested that these specimens "phenetically may be thought of as a gracile form of australopithecine." As such, Clarke's changed views on the attribution of the Olduvai Gorge fossils are consistent with his conclusion that the Stw 53 cranium is a male specimen of *A. africanus*.

The attribution of Stw 53 to *Australopithecus* has been supported by Thackeray et al. (2000), who compared a series of linear measurements for it and Sts 5 using a least-squares linear regression analysis. However, this same bivariate approach resulted in Sts 5 being seen as conspecific with both OH 24 and KNM-ER 1470 using the 95 % confidence limits (CL) for a chimpanzee sample, and conspecific with KNM-ER 406, KNM-ER 1813, and KNM-ER 3733 using extant catarrhine intraspecific samples (Aiello et al. 2000). As such, this approach would find conspecificty of Sts 5 with crania usually attributed to *H. habilis*, *Homo rudolfensis*, *H. erectus*, and *P. boisei*. Understandably, this approach has not gained acceptance as a meaningful taxonomic tool.

Berger et al. (2010) have also opined that Stw 53 represents *A. africanus* rather than *Homo*. However, their reasons for this rely almost entirely upon anatomy that has been reconstructed by Clarke (1985a) wholly *ad fingum* (e.g., the orientation of the frontal process of the zygomatic and the form of the inferolateral corner of the orbital

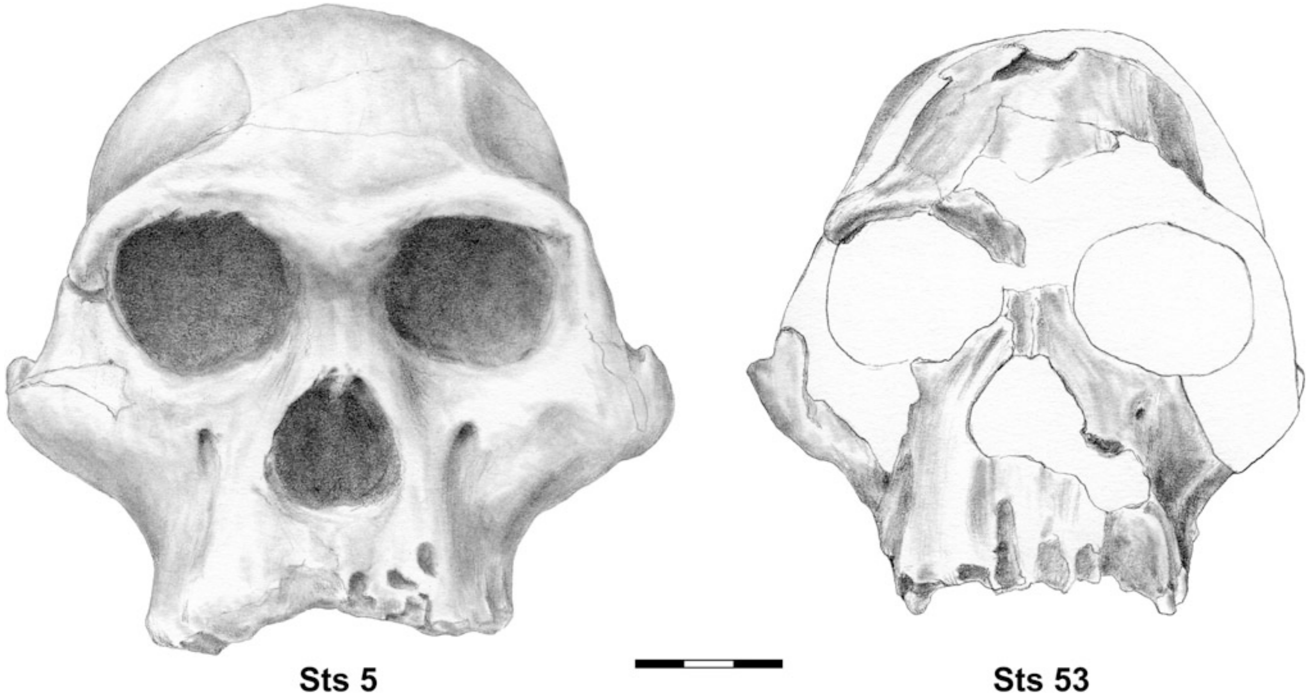

Fig. 6.8 Comparison of Sts 5 and Stw 53 in facial view. Scale in cms

margin) inasmuch as its lacks any osseous basis whatsoever. It would seem that Berger et al. (2010) have failed to differentiate plaster from bone.

Spoor (1993; Spoor et al. 1994) observed that the proportions of the semicircular canals in the Stw 53 temporal "are not seen in any of the other fossil or extant hominids or great apes," but are similar to those of "large cercopithecoid" monkeys. Spoor et al. (1994: 648) even went so far as to suggest that this meant that Stw 53 "relied less on bipedal behavior than the australopithecines." While one can imagine some workers' (e.g., Sarmiento 1988) delight at such a suggestion, it would appear that the criterion employed by Spoor—semicircular canal radius—is not actually correlated with locomotor behavior (Malinzak et al. 2011, 2012).

Stw 151

Moggi-Cecchi et al. (1998) argued that Stw 151 represents a hominin more derived towards early *Homo* than the rest of the Member 4 *A. africanus* hypodigm. Spoor (1993) had earlier commented on the orientation of the posterior surface of its petrous pyramid, noting that it is more like the modern human condition than in other Sterkfontein specimens (including Sts 19 and Stw 53). Moggi-Cecchi et al. (1998) observed that the petrous crest also more closely resembles the condition in early *Homo* than *A. africanus* (e.g., Sts 5 and MLD 37/38), but they likened Stw 151 to Stw 53. They also regarded the entoglenoid process to be more *Homo*-like. Nevertheless, Moggi-Cecchi et al. (1998) concluded that because the developmental pattern evidenced by the Stw 151 dentition accords with that ascribed to *A. africanus* rather than early *Homo* (where there is closer correspondence in the timing of I1 and M1 emergence), attribution to the latter is perhaps unwarranted.

As noted by Moggi-Cecchi et al. (1998), the pieces that constitute Stw 151 were recovered from partly decalcified in situ "breccia" in a solution pocket at a relatively shallow depth, and in close proximity to grid squares that yielded *Theropithecus* fossils. Thus, they suggested that Stw 151, with its apparent mixture *Australopithecus* and *Homo*-like features could have derived from Member 5.

Towards a Resolution: Some New Approaches

Despite well over a quarter century of study and opinion, it would seem that we have not yet satisfactorily resolved the question of whether the *A. africanus* hypodigm contains fossils of more than one species. This is likely owing to several factors.

In the first instance, a good part of the evidence that has been put forth in support of taxonomic heterogeneity has taken the form of anecdotal observations relating to a restricted bit of anatomy and/or a small number of specimens. Thus, it is common for a particular morphological feature (be it cranial, mandibular, or dental) to be contrasted between two specimens without consideration of others that may display intermediate configurations. In the second instance, not a few of the specimens that have been singled out as displaying potentially divergent traits are immature, and the ontogenetic changes that may affect these particular morphologies have not been explored satisfactorily. In the third instance, the vagaries of preservation leave a fossil record comprised of variably incomplete and/or distorted specimens. As a result, it may be possible to construct scenarios relating to dental differences between some specimens and basicranial differences between others, but linking teeth and temporals may be difficult, if not impossible. In the fourth instance, much of the discussion over morphology has been decidedly subjective. Thus, while Clarke (1988a, 1994a, 2008) has differentiated specimens according to a number of features that are readily amenable to measurement (e.g., tooth size, supraorbital margin thickness, glabellar prominence, zygomatic arch development, etc.), there has been little if any quantitative assessment of these traits. Similarly, although Lockwood and Tobias (1999) were in notable disagreement with Kimbel and Rak (1993) over the placement of the thickest part of the supraorbital torus, no morphometric analysis was undertaken by them.

This is not to say that quantitative and sometimes very sophisticated statistical analyses are wholly lacking. Thus, Wood (1991a), Moggi-Cecchi and Boccone (2007), and Grine et al. (2013) have evaluated morphometric variables, but these have been restricted to one or two dimensions, and in some cases (e.g., tooth crown cusp proportions) the features are not necessarily those that have been proposed as being taxonomically relevant.

Advances in technology (e.g., the advent of precise micro-CT scanning and high definition laser scanning) and quantitative methods (e.g., 3D geometric morphometrics, surface watershed analyses, etc.) may permit these issues to be addressed in a more satisfactory manner. In particular, innovative quantitative approaches which permit testing of the variation in different anatomical units against extant, sexually dimorphic hominid taxa and other fossil hominin species with deep geochronological records (e.g., *A. afarensis*) can be applied from representational data using a variety of geometric morphometric tools (e.g., landmarks, semi-landmark lines, surface patches). Analyses of more complete cranial and mandibular fossils would enable the inclusion of those specimens which lack standard osteometric landmarks. Detailed models of covariation among the various anatomical regions could then be used to predict the shapes of missing regions in the more incomplete fossil specimens.

In addition, recent work by Skinner et al. (2009) has demonstrated the efficacy of mandibular molar dentine-enamel junction topography to discriminate among species of living apes. It has also been shown to effectively distinguish the lower molars in *A. africanus* and *P. robustus* (Skinner et al. 2008). Although that study entailed only a small number of isolated molars (two M1s, six M2s and five M3s) from Sterkfontein, its application to larger samples, and especially teeth associated with crania that have been the focus of taxonomic discussion might shed valuable light on the question.

Other potentially informative approaches to this question might involve aspects of biology other than those related to the expression of particular morphological traits. Thus, clues about diet might be gleaned from dental microwear and light stable isotopes, and this information might be evaluated in light of morphologies that have been proposed to be taxonomically diagnostic.

For example, occlusal microwear data have been recorded and analyzed for only ten M2s from Sterkfontein (Grine 1986; Grine and Kay 1988; Scott et al. 2005). Comparison of these data with those for *P. robustus* and *A. afarensis* (Grine 1986; Grine and Kay 1988; Scott et al. 2005; Grine et al. 2006; Ungar et al. 2010) provides the tantalizing observation that the Sterkfontein sample exhibits somewhat greater variability in some parameters (e.g., greater variation in anisotropy than in *P. robustus*, and greater variation in complexity than *A. afarensis*). Such variation could reflect greater dietary variability in the species *A. africanus*, or it could also relate to two groups of hominins that differed in diet and microwear. Moreover, there might well be differences in the microwear patterns of the anterior versus the postcanine teeth among specimens that could relate to differences in dietary proclivity and habit. To date, the large sample of specimens recovered from Sterkfontein through the University of the Witwatersrand excavations has not been examined for microwear.

Similarly, carbon isotope data have been obtained for four australopith specimens from Makapansgat (Sponheimer and Lee-Thorp 1999) and 18 from Sterkfontein (van der Merwe et al. 2003; Sponheimer et al. 2005). Comparable data have been gathered for 22 specimens of *P. robustus* (21 from Swartkrans and one from Kromdraai) (Lee-Thorp et al. 1994, 2000; Sponheimer et al. 2005, 2006). The range of published δ^{13}C values for the Sterkfontein + Makapansgat sample (mean = −6.45; SD = 2.32; CV = 36 %; obs. range = −1.8 to −11.3) is substantially higher than that for the *P. robustus* sample (mean = −7.48; SD = 1.19; CV = 16 %; obs. range = −5.4 to −10.0). Although, as noted by Lee-Thorp and Sponheimer (2006) and Cerling et al. (2011), the δ^{13}C data for both australopith species are more variable than virtually all modern and extinct taxa that have been examined in South Africa, these data might still be brought to bear on the issue of the taxonomic homogeneity of the *A. africanus* hypodigm. To date, there has been no attempt to relate any of the carbon isotope data to individual specimens as they might relate to the proposed taxonomic groupings. Considered in conjunction, these different sources of dietary information may speak to this issue.

Given the new approaches that can be employed and the novel technologies that can be applied, there is reason to be optimistic that the questions relating to the alpha taxonomy of *A. africanus* can be answered with at least some degree of satisfaction.

Conclusions

The Early Pleistocene hominin *A. africanus* exemplifies the problem and importance of species identification in the paleontological record. This taxon has been viewed as having occupied a variety of important evolutionary roles: related to the origin of *Homo*, the origin of *Paranthropus*, or at the base of their divergence. Its instability in phylogenetic studies is owing to the fact that it is variable in so many craniodental characters (Strait et al. 1997). Is this variation attributable to taxonomic heterogeneity of the *A. africanus* hypodigm? This question goes beyond the immediate local issue of alpha taxonomy because it has significant implications for the interpretation of early hominin evolution (Lockwood and Tobias 1999; Kimbel et al. 2004).

Historically, taxonomic assessments of the fossils from Taung, Sterkfontein, and Makapansgat have undergone three phases: initial splitting, rationalization, and renewed questions about homogeneity. Initial discoveries saw the fossils attributed to different species and possibly genera (Dart 1925a, 1948a; Broom 1936, 1938, 1950). Subsequent studies suggested that they all represented a single, albeit variable species (Robinson 1954, 1965; Le Gros Clark 1955, 1964; Tobias 1967). More recently, the possibility that the *A. africanus* hypodigm comprises specimens of two (or more) species has been raised anew (e.g., Clarke 1985a, 1988a, 1994a, 2008, 2013; Kimbel and White 1988; Kimbel and Rak 1993; Lockwood 1997; Moggi-Cecchi et al. 1998; Lockwood and Tobias 1999, 2002).

The issue revolves largely, though not wholly, around the interpretation of fossils from Sterkfontein. Although various studies have proposed that at least some of them can be attributed to more than a single group and/or taxon (Clarke 1988a, 1994a, 2008; Kimbel and White 1988; Lockwood 1997; Lockwood and Tobias 2002; Schwartz and Tattersall 2005), there is a notable lack of agreement among workers as to their sorting. Morphological differences certainly exist between some specimens, but most of the fossils are incomplete, such that it has proven difficult to relate differences in one anatomical region with those in another.

Statistically grounded morphometric studies have generally yielded results that are not necessarily consistent with the hypothesis of taxonomic heterogeneity (e.g., Wood 1991a; Lockwood 1997; Moggi-Cecchi and Boccone 2007; Grine et al. 2013). However, the morphometric analyses that have been undertaken to date may not have necessarily sampled those features held to reflect taxonomic differentiation. Innovative quantitative approaches that enable testing of variation in different anatomical units are required to address the question of heterogeneity in the *A. africanus* hypodigm. Recent technological advances in areas such as surface laser-scanning and micro-CT scanning will permit novel and relevant data to be analyzed through the use of sophisticated geometric morphometric tools. It is also possible that data from dental microwear and stable light isotopes (i.e., the ratios of $^{13}C/^{12}C$) might be brought to bear on the question. If the basic question relating to the alpha taxonomy of *A. africanus* cannot be addressed with satisfaction, many other avenues of paleoanthropological enquiry will remain closed to fruitful exploration.

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Chapter 7
Australopithecus from Sterkfontein Caves, South Africa

Ronald Clarke

Abstract Since the discovery by Robert Broom of the first adult *Australopithecus* at Sterkfontein in 1936, a large quantity of fossil remains of this genus, consisting of crania, teeth and postcranial bones, has been excavated from those cave infills. They have generally been considered as belonging to one species, *Australopithecus africanus*, but there is now abundant proof that a second species is represented by many of the fossils. This second species should be classified as *Australopithecus prometheus*, the name given by Raymond Dart in 1948 to such fossils from Makapansgat (MLD 1 and MLD 2). *A. prometheus* is distinguished from *A. africanus* by having a more vertical occiput, larger, bulbous-cusped cheek teeth, a flatter face, lower frontal squame, and sagittal crest in the males. An almost complete skeleton of *Australopithecus* (StW 573) from an early deposit in the cave belongs to this second species, and for the first time this discovery made it possible to indisputably associate postcranial anatomy with specific cranial anatomy. It is also now possible to clearly distinguish males and females of each species, and to state with conviction that StW 53, a cranium excavated in 1976 and widely identified as *Homo habilis*, is in fact a male *A. africanus*, virtually the same as the TM 1511 cranium found by Broom 40 years earlier.

Keywords *Australopithecus prometheus* • *Homo habilis* • Makapansgat • StW 53 • Taxonomy • Taung

Introduction

It was on 17th August 1936 that Dr. Robert Broom discovered at Sterkfontein Caves, South Africa, the first known adult *Australopithecus* cranium to add to the only other *Australopithecus* known at that time, which was the child skull from Taung, the type specimen of *Australopithecus africanus*. Broom (1936) placed his specimen (TM 1511) into a new species, *Australopithecus transvaalensis,* but following his discovery in 1938 of a child symphyseal fragment (TM 1516 with canine Sts 50), he created a new genus, *Plesianthropus*, for the Sterkfontein fossils (Broom 1938) and with subsequent discoveries (Broom and Schepers 1946; Broom et al. 1950) suggested that there were large-toothed males (e.g., Sts 7) and smaller-toothed females (e.g., Sts 5, TM 1512) represented in the assemblage. Robinson (1954) placed all the Sterkfontein specimens into *A. africanus* and, later still, Robinson (1972) was to include them in the genus *Homo* as *Homo africanus*, a move that has not gained acceptance.

The first adult *Australopithecus* (TM 1511), from Sterkfontein, was badly crushed and its main contribution to the understanding of *Australopithecus* morphology has been its natural endocranial cast (Sts 60), its facial structure and its cheek teeth (Fig. 7.1). The incisors and canines were missing, but recently the missing left third molar and right second premolar (Fig. 7.2) were recovered from a lime miner's dump (Clarke 2007, Clarke and Partridge 2010). With the discovery of more *Australopithecus* fossils, Broom and Robinson had to counter the arguments of some colleagues that the fossils were merely a variety of ape that had nothing to do with human ancestry. Hence they had to emphasize their human-like features. They also considered the fossils all to belong to one species that came from one Sterkfontein stratum, the Lower Breccia of Robinson (1962), now called Member 4 of the Sterkfontein Formation (Partridge 1978). It was further assumed that all of the hominid postcranial bones that were found in that deposit belonged to that same species (*Plesianthropus transvaalensis*, now termed

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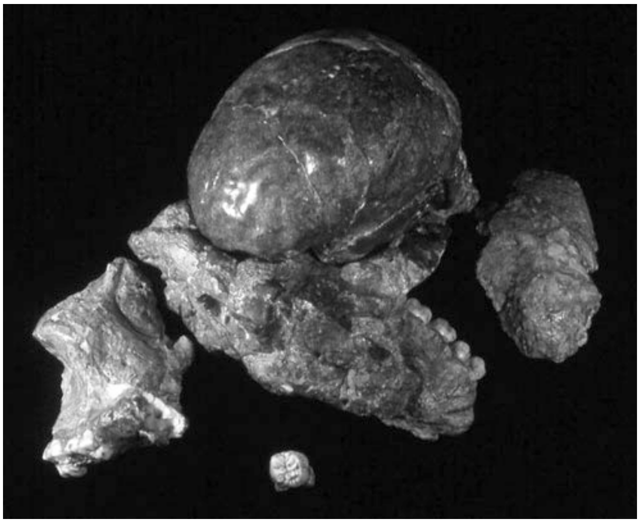

Fig. 7.1 TM 1511 with Sts 60 endocranial cast. The first discovered adult *Australopithecus*

Fig. 7.2 Dentition of TM 1511 *Australopithecus africanus* with the recently discovered left M^3 and right P^3

A. africanus). This lumping of all the fossils into one species has led over the years to three different perceptions of the phylogenetic position of *A. africanus* (see also Grine 2013). Some researchers concentrated on the *Homo*-like features and saw them as ancestral to *Homo* (Robinson 1967, 1972; Olson 1985), others concentrated on the larger teeth and jaws within the sample and saw them as ancestral to *Paranthropus* (Johanson et al. 1981; Rak 1983), and the third view was that *A. africanus* was ancestral to both *Homo* and *Paranthropus* (Tobias 1980; Skelton et al. 1986). The one-*Australopithecus*-species concept for Sterkfontein has been the accepted view until recently. However, excavations at Sterkfontein since 1966 have now revealed that there are at least three *Australopithecus*-yielding infills apparently of different ages—Member 4, Member 2, and Jacovec Cavern (Partridge 1978; Partridge et al. 2003; Clarke 2006) (Fig. 7.3)—with at least two different species of *Australopithecus*. The main infill, Member 4, which is at least 8 m thick, could cover a long time-span of perhaps 300 kyr (Partridge and Watt 1991) and has provided a large sample of more than 500 *Australopithecus* fossils. It has been claimed that in addition to *A. africanus* there is a second distinct species of *Australopithecus* present in Member 4 (Clarke 1985, 1989, 1994a), and one of the lower infills (Member 2) contains an *Australopithecus* skeleton (StW 573) that appears not to belong to *A. africanus* but rather to the second species (Clarke 1998, 2008). The *Australopithecus*-bearing deposits of Sterkfontein possibly cover a period from about 3.3 to 2.14 Ma (Partridge 2005).

Member 4

This massive infill of breccia has yielded hundreds of *Australopithecus* fossils (Broom and Schepers 1946; Broom et al. 1950; Deloison 2003; Pickering et al. 2004a; Moggi-Cecchi et al. 2006). When Broom first visited Sterkfontein in 1936, the lime miners were working in a surface quarry and blasting out fossil-rich breccia of what is now known as Member 4 of the Sterkfontein Formation (Partridge 1978). It was from this quarry area that the type specimen of *A. transvaalensis* (TM 1511) was recovered by Broom on the 17th of August 1936 (Figs. 7.1, 7.2). Hence the quarry locality later became known as the Type Site to distinguish it from other Sterkfontein cave localities. Many *Australopithecus* specimens, as well as other fauna, were recovered during ensuing years from this quarry site. In 1937, four other specimens were recovered from an area of solid breccia that was lower than and slightly to the east of the Type Site, but which appears to be the same body of breccia (Fig. 7.4): a well-preserved right maxillary fragment (TM 1512), a distal femur (TM 1513), a left maxilla (TM 1514) and a capitate (TM 1526). Here the lime miners had begun blasting in the area that now forms the exit chamber from the tourist route through the caves. After 1966, A. R. Hughes and P. V. Tobias began systematic excavations and recovered more *Australopithecus* specimens from dumps of lime miners' breccia that derived from Member 4. Their in situ excavations in the Type Site, as well as in the decalcified breccia adjacent to and southwest of the Type Site, produced a large sample of *Australopithecus* fossils, as well as other fauna and fossil wood that have provided information on the environment of *Australopithecus* (Bamford 1999). The fossils of Broom and Robinson are housed in the Transvaal Museum, Pretoria (with catalogue numbers prefixed by TM, Sts, and Se), and those of Tobias and Hughes in the School of Anatomical

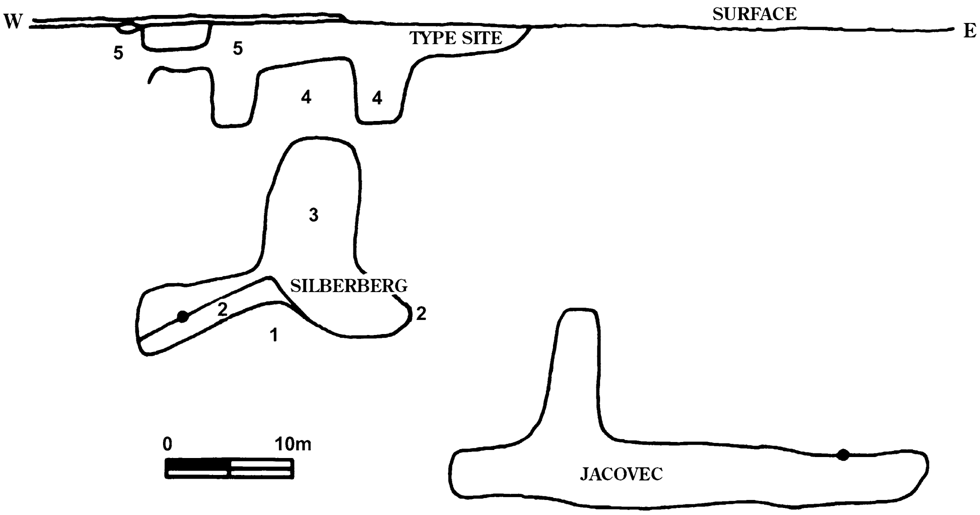

Fig. 7.3 Schematic West–East section of the main Sterkfontein fossil deposits to show relative positions of the stratigraphic Members 1–5, as well as the Type Site, Silberberg Grotto and Jacovec Cavern. Positions of the Member 2 and Jacovec hominids are shown by *large dots*. Other *Australopithecus* fossils occur throughout Member 4

Fig. 7.4 TM 1512 maxilla (*top left*), TM 1513 distal femur (*bottom left*), TM 1514 crushed maxilla (*top right*), and TM 1526 capitate (*bottom right*)

Sciences of the University of the Witwatersrand, Johannesburg (with catalogue numbers prefixed by StW). When all of these hominid fossils are considered, they provide a wealth of information on *Australopithecus* anatomy, including variation within the cranial sample. Some of this variation most reasonably represents males and females of *A. africanus*, whilst other variation represents males and females of a second, larger-toothed, flatter-faced species of *Australopithecus* (Clarke 1989, 2008).

The type specimen of *A. africanus* is the child skull from Taung (Dart 1925), and when the *Australopithecus* cranial fossils from Member 4 are compared to this type specimen, there are some that clearly match the morphology, such as Sts 5 cranium, Sts 52 maxilla and mandible, and TM 1512 and StW 391 maxillary portions (Fig. 7.5). Of these, Sts 5 and TM 1512 have small canines and thus appear to be female, whilst Sts 52 and StW 391 have larger canines and appear to represent males (Fig. 7.6).

There are other specimens, however, that do not fall within this *A. africanus* morphology, and Clarke (1985, 1989, 1994a, 2008) has suggested that they represent a second, larger-toothed species of *Australopithecus*. These are well represented by Sts 71 cranium, Sts 1 maxilla, StW 183 maxillary portion, StW 252 cranium, StW 498 maxilla and mandible, StW 384 mandible, Sts 36 mandible and StW 505 cranium (Fig. 7.7). There are several other specimens within the Sterkfontein sample that undoubtedly belong in this second species. Clarke (1989) noted that the differences between the large-toothed and small-toothed *Australopithecus* are not simply a matter of size and cannot be attributed to sexual dimorphism (Fig. 7.8). First, there are morphological differences in the teeth, in that the larger teeth have more inflated, bulbous cusps, approaching the *Paranthropus* morphology. A geometric morphometric study on the maxillary molars by Fornai (2009; Fornai et al. 2010) confirmed that there are indeed two distinct morphologies. Secondly, the larger-toothed cranium represented by StW 252 has a thin brow ridge, whereas the smaller-toothed cranium represented by Sts 5 has a thicker brow ridge. Among primates, including humans, the large-toothed males have more prominent brow ridges whilst the smaller-toothed females have less pronounced, or thinner, brow ridges. The larger-toothed *Australopithecus* has more anteriorly situated cheekbones that give it a flattened, or slightly hollowed nasal region (Sts 71 and StW 252). This contrasts with the more posteriorly situated cheekbones in the smaller-toothed form, such as Sts 5. The larger-toothed cranium has an incipient supraglabellar hollowing and a more vertical, rounded occiput. Broom et al. (1950) noted that whilst their skull number 6 (Sts 17) agreed closely with skull number 5 (Sts 5), skull number 7 (Sts 71) differed considerably. They observed that, in side view, the latter skull was relatively short and the occipital region was rounded rather than angled. However, they thought that this different morphology was probably due to slow post mortem crushing. Whilst it is true that such crushing does occur with some Sterkfontein fossils, this does not seem to be the case with Sts 71, especially as the uncrushed StW 252 shows the same morphology. Conroy et al. (2000) made CT scans of Sts 71 in order to digitally reconstruct the cranium and calculate the endocranial capacity. They found that the high resolution CT scans through the occipital confirmed the observation by Broom et al. (1950) that there was no obvious breakage of the bone. Thus one would have to postulate slow plastic deformation to account for the rounded profile of the occipital if one does not accept it as normal morphology. Conroy et al. (2000) did not refer to the work of Clarke (1990) where, following his cleaning and some reconstruction of the cranium, he observed that Sts 71 “differs from Sts 5 in being less prognathic, having a thinner supraorbital margin, flat upper nasal region, more bulbous cheek region, less of a step from the anterior malar

Fig. 7.5 *Australopithecus africanus* child from Taung (*left*), adult female TM 1512 and adult male StW 391 (*upper right*), and adult male Sts 52 (*lower right*)—not all to same scale. Note the similarity of the facial profiles and note the larger canine and canine socket in the males Sts 52 and StW 391 respectively

Fig. 7.6 Palatal view of TM 1512 female *A. africanus* (*left*) and StW 391 male *A. africanus* (*right*). Note the larger canine socket and wider premolars in the male

surface to the canine root eminence, more medially-directed temporal lines, and a larger canine socket. The canine socket is 7.5 mm in mesiodistal diameter, whereas the Sts 5 canine socket is 5.6 mm." In all of these features, which cannot be ascribed to plastic deformation, Sts 71 corresponds with the morphology of StW 252. Thus it is highly likely that the more vertical, rounded occiput, which also corresponds with StW 252 morphology, is a feature characteristic of this second species.

The existence of this second species was actually recognized at Makapansgat by Dart (1948a–c). The first *Australopithecus* from there was an occiput, MLD 1, which Dart found to be different from that of Sterkfontein "*Plesianthropus.*" Although, at the time, this may have seemed an insufficient basis on which to create a new species, it does currently seem that Dart was correct, as the occiput more closely resembles those of the second species such as StW 252 and Sts 71 than it does Sts 5 (*A. africanus*). Furthermore, the temporal lines approach each other so closely that there was probably a sagittal crest on the parietals, as there is in StW 505 (a male of the second species) and the StW 573 skull, which also seems to belong to this species, as discussed later on. The second *Australopithecus* found at Makapansgat was the juvenile mandible MLD 2, which has the typical large bulbous-cusped molars characteristic of the Sterkfontein second species. Dart named this Makapansgat species *Australopithecus prometheus*. Although this name has not been generally used in many years, it was I believe a valid name and should be used for the second species, as tentatively suggested by Clarke (1994a).

There is a reluctance of some researchers to accept that two species of one genus of hominid (*Australopithecus*) could be living in the same location and be preserved as fossils in the same breccia. However, such a scenario is not unusual in the animal kingdom, for example lion (*Panthera leo*) and leopard (*Panthera pardalis*) being two species of one genus of carnivore live in overlapping territories and both are preserved as fossils in the Sterkfontein Member 4 and Post-Member 6 (Kuman and Clarke 2000; also called

Fig. 7.7 Comparison of dentition of *A. africanus* mandible Sts 52 (*far left*) and mandible of large-toothed species StW 384 (*left*), as well as maxillae of large-toothed species Sts 1 and StW 183 (*right* and *far right*)

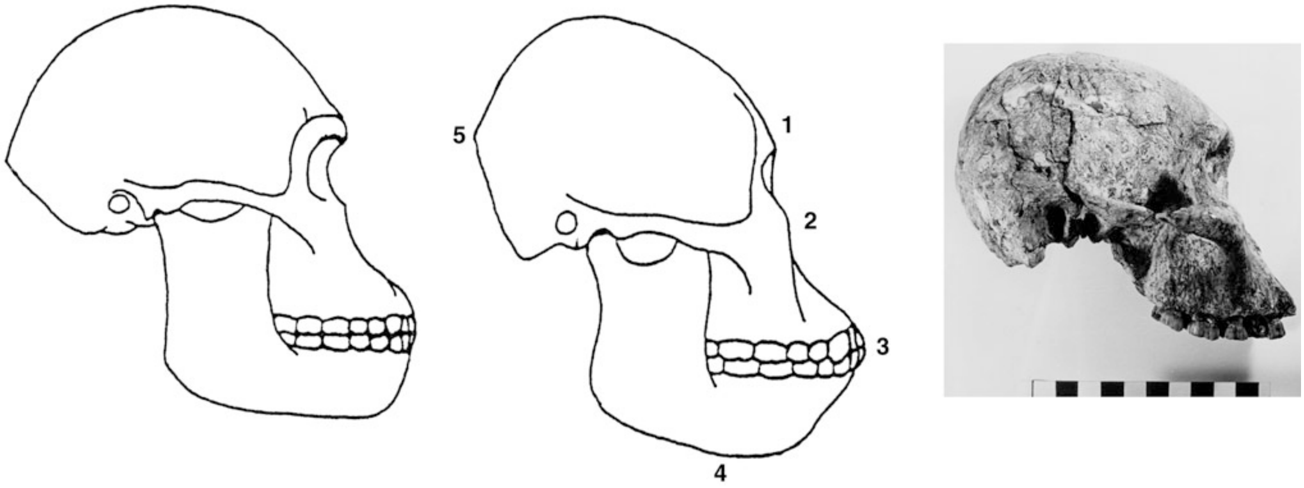

Fig. 7.8 Reconstructed profiles of *A. africanus* female based on Sts 5 (*left*), and second species male based on StW 252 (*center*), with female cranium of second species Sts 71 (*right*). *Numbers* indicate major features of second species to contrast with *A. africanus*. *1* Thin supraorbital margin and incipient supraglabellar depression. *2* Anteriorly situated cheekbone. *3* Large canines and large anteriorly projecting incisors in male. *4* Large but slender-bodied mandible. *5* Vertical, rounded occiput

"Post-Member 5" breccia in Turner 1997) breccias and in Swartkrans Member 2 (Brain 1981). Furthermore, we know that among the primates, two species of *Parapapio* (*Parapapio broomi* and *Parapapio jonesi*) inhabited the same areas and were preserved as fossils in the Sterkfontein Member 4 breccia (Brain 1981).

The dental differences between *A. africanus* and the second species of *Australopithecus* are such that they suggest different feeding strategies, and indeed some dental and cranial similarities of the second species to *Paranthropus* indicate the possibility that it could well be close to the ancestral stock from which *Paranthropus* evolved. Aguirre

(1970) was so impressed with the *Paranthropus*-like morphology of the MLD 2 dentition that he even proposed placing it in that genus. However, the large canines and incisors of the second species, together with the cranial morphology, show that although it is *Paranthropus*-like it belongs within *Australopithecus*.

In addition to the many dental, maxillary and mandibular fossils of *Australopithecus* from Member 4, there are several adult and sub-adult partial crania and one near-complete cranium (Sts 5). The partial crania are TM 1511 (crushed and with endocast), Sts 17 (face, palate and parietal), Sts 19 (cranial base with StW 73 palate), Sts 52 (lower face with palate and mandible), Sts 67 (calvaria), Sts 71 (right side of cranium), StW 13 (crushed face with maxilla and left parietal), StW 53 (fragmented cranium with teeth), StW 252 (fragmented cranium with teeth), StW 498 (mandible, maxilla and parietal fragments) and StW 505 (face with left side of braincase). Of these, the StW 53 cranium requires some detailed explanation because it is a very important specimen and has frequently, but erroneously, been referred to in the literature as *Homo habilis* from Member 5 (see also Grine 2013).

In 1976, at the southwestern end of his Sterkfontein excavation, Alun Hughes recovered hominid teeth and cranial fragments of one individual (StW 53) from the decalcified breccia within a solution pocket. The right posterior portion of the braincase was embedded in solid breccia in the wall of the solution pocket, thus indicating the exact location and breccia type from which the other fragments had been decalcified and scattered. The breccia at that western end was, at the time, thought to be all Member 5 with an overlying exposure of Member 6 in a small area on the northern side. As Member 5 had yielded abundant early stone tools, and as no stone tools whatsoever had occurred in Member 4, Hughes and Tobias (1977) believed that StW 53 must be a cranium of early *Homo*. Subsequently, it was frequently referred to as *H. habilis* because of its supposed similarity to the OH 24 "*Homo habilis*" from Olduvai Gorge Bed 1 (Leakey et al. 1971; Clarke 1985). Later stratigraphic investigation by Clarke (1994b) showed that StW 53 did not in fact come from tool-bearing Member 5, but from a hanging remnant of Member 4 (Kuman and Clarke 2000). Furthermore, at a conference in Orce, Spain, in 1995, Clarke (1999a) observed that StW 53 and supposed *H. habilis* specimens OH 13, OH 24, and KNM-ER 1813 had small brains and flat noses like those of *Australopithecus*, and in these respects differed greatly from the much larger-brained OH 7 type specimen of *H. habilis*, as well as from KNM-ER 1470 *H. habilis* which has a prominent nasal skeleton. He also referred to the work of Spoor (1993; Spoor et al. 1994) who found that the bony labyrinth of the StW 53 temporal was unique among hominid fossils and had similarity to large cercopithecoids, suggesting arboreality. In other words, there was nothing in its anatomy to suggest that StW 53 was anything but an *Australopithecus* and it certainly came from the non-tool-bearing Member 4, just like the other *Australopithecus* fossils from Sterkfontein (Kuman and Clarke 2000).

Clarke (1985) made a reconstruction of the StW 53 cranium "based solely on anatomical considerations and symmetry." This was the only reconstruction of StW 53 Clarke ever made (see below), but Curnoe and Tobias (2006) incorrectly claimed that Hughes and Clarke had made two reconstructions differing from each other, and Curnoe and Tobias used this imaginary discrepancy to justify their making a "new reconstruction." Clarke (2008) published a detailed criticism of their methods, their incorrect claims, and their results. Some of the main points made were that they had widely separated a near-contact, unrealistically flexed joints and bone contacts, and unnaturally extended the gap between front and back to produce a braincase that is wider, higher, and longer than it should be. Furthermore, the cranium was now deformed. Thus their construction is not a reconstruction because it has not followed the anatomical guidelines and contours and therefore does not reflect the original form of the cranium. It is a construct of how they considered it should be, rather than a reconstruction of how it actually was. In their own words, Curnoe and Tobias (2006) admit that "our reconstruction differs in important respects from the earlier one, especially in terms of neurocranial length, breadth, and height. However, given that StW 53 exhibits extensive damage, these dimensions are most likely prone to much error in reconstruction." Despite this, they have still maintained that the maximal cranial length of their "reconstruction" is virtually identical to the *H. habilis* cranium KNM-ER 1470 (their Fig. 18) and their overall conclusion based on their artificially enlarged and deformed StW 53 braincase, as well as their interpretation of the anatomy, is that it is a representative of *H. habilis*.

The Clarke (1985) reconstruction, which was based on anatomy and contours of the bones (which contra Curnoe and Tobias do not "exhibit extensive damage"), shows that the StW 53 cranial size and shape does not differ significantly from *A. africanus* in the form of Sts 5 (Fig. 7.9). The facial structure of the two is very similar with small, narrow muzzle, small nasal aperture and flat nasal skeleton, and both have a narrow, rectangular palate. The frontal bones of both resemble each other in size and form with a prominent metopic ridge. The StW 53 frontal bone fits very closely on the Sts 60 endocranial cast of the first adult *Australopithecus* TM 1511 and is very obviously not that of a large-brained *Homo*, but of a small-brained *Australopithecus*. The wider intermastoid breadth in StW 53 when compared to Sts 5 is undoubtedly because it is a male *A. africanus*, whilst Sts 5 is a female. This is indicated also in the dentition. Sts 5 has smaller canine and cheek teeth sockets than does StW

Fig. 7.9 Clarke reconstruction of StW 53 male *A. africanus* (*top left*) compared to Sts 5 female *A. africanus* cast (*top right*), Endocranial casts of StW 53 (*lower row left*) and Sts 5 (*lower row right*)

53, which more resembles Sts 52 and StW 391. In its small canine and premolar sockets Sts 5 is similar to TM 1512 which is also undoubtedly a female. The larger canine socket in the apparent males has caused the socket to bulge more anteriorly, which can contribute to a less pronounced appearance of the premaxillary region.

There is in fact nothing in the anatomy of StW 53 to align it with *H. habilis* (in the form of OH 7, KNM-ER 1470, and OH 65) rather than with *Australopithecus* (see Blumenschine et al. 2003). The type specimen of *H. habilis* is Olduvai Hominid 7 (OH 7), consisting of the two parietals and mandible of a juvenile (Leakey et al. 1964). The parietals alone indicate a much larger-brained hominid than any *Australopithecus*, and these parietals match in size and shape those of the near-complete cranium KNM-ER 1470 (Leakey 1973). Hence, the 1470 cranium cannot be distinguished from *H. habilis*, and there is no justification for its having been placed in a separate species, *Homo rudolfensis* (e.g., Groves 1989; Wood 1992). The discovery of a complete dentition in the maxilla of OH 65 from Olduvai Gorge Bed 1 (Blumenschine et al. 2003) supports the placement of KNM ER 1470 in *H. habilis*. The maxilla of OH 65 matches in shape and size that of 1470, and the cheek tooth crowns, though small by comparison with *Australopithecus*, have widely-flaring roots like those of KNM-ER 1470. The palates of both fossils are broad and horseshoe-shaped, thus differing radically from the narrow, rectangular palates of *Australopithecus* Clarke (2012).

It is rather the smaller-brained, more *Australopithecus*-like fossils OH 13, KNM-ER 1813, and OH 24 which should be removed from the taxon *H. habilis* as they have no similarity to *H. habilis* as represented by the type specimen OH 7, the cranium KNM-ER 1470, and the maxilla OH 65. The question of whether the smaller-brained forms should be classed as *Homo* or *Australopithecus* is debated. While most textbooks and research papers classify them as *H. habilis*, Richard Leakey (1974; Leakey et al. 1978; Leakey and Lewin 1992) classed them as *Australopithecus* (see also Leakey 1979). Ferguson (1995) made ER 1813 the holotype of his new species *Homo microcranous*.

Member 4 Postcranial Fossils

In 1946, after the discovery of many cranial fossils from Sterkfontein, Broom (in Broom and Schepers 1946) wrote “it is very remarkable that, as in the caves in China, postcranial bones are very rare.” In spite of the wealth of *Australopithecus* fossils discovered since that time, the situation has not much changed. In other words, relative to the quantity and state of completeness of cranial and dental fossils, the postcranial fossils are few and mostly fragmentary. Considering that for one skull of a human skeleton there are 174 postcranial elements, one would normally expect a greater amount of postcranial fossils to accompany the numerous cranial specimens at Sterkfontein. Even allowing for fragmentation of long bones by carnivores and by the crushing effect of rocks in the talus cone of the cave, there should be a greater quantity of articular ends and of the smaller and more compact bones such as those of the wrist, hand, ankle and foot. The relative paucity of such elements compared to cranial and dental remains is a taphonomic question that needs further investigation (Clarke 2007). It is noteworthy that monkey postcranial fossils are much better represented.

Nevertheless, there are now several informative hominid postcranial fossils (Table 7.1). Notably, there are two partial skeletons, Sts 14 (Robinson 1972) and StW 431 (Kibii and Clarke 2003; Toussaint et al. 2003), from Member 4 (Fig. 7.10), some well-preserved articular ends of limb bones, and some complete foot and hand bones. Most importantly there is now a practically complete *Australopithecus* skeleton with skull (StW 573) from Member 2, providing a near-total *Australopithecus* skeletal morphology of a single individual against which the other fragmentary fossils can be compared (Clarke 1998, 1999b, 2002, 2008).

Broom (Broom and Schepers 1946) was so impressed by the human-like characters of a distal femur (TM 1513) and a capitate (TM 1526) that he raised the question of whether they might belong to a human rather than to *Australopithecus*. He concluded, however, that they were almost certainly those of *Plesianthropus* (i.e., *Australopithecus*). As the sample of cranial and postcranial fossils recovered from Sterkfontein Member 4 has increased over the years, it has become clear that there are no cranial or dental remains of *Homo* and that the postcranial bones are, as Broom said, almost certainly those of *Australopithecus*. However, the

Table 7.1 *Australopithecus* postcranial fossils from Sterkfontein Member 4

Skeletal part	Catalog number(s)	Details/notes
Partial skeleton	Sts 14	9 thoracic and 6 lumbar vertebrae, complete pelvis, proximal left femur minus head
	StW 431	4 thoracic and 5 lumbar vertebrae, partial pelvis with partial sacrum and parts of both ilia, lateral half of right clavicle shaft, lateral margin of left scapula, distal half of right humerus and proximal halves of right radius and ulna
Vertebra	Sts 73	Partial vertebra
	StW 8/41	2 thoracic and 4 lumbar vertebrae conjoined
	StW 642	Partial column of 12 thoracic and lumbar and 1 cervical vertebrae
Clavicle	StW 616	Left shaft fragment
	StW 582	Right shaft
Scapula	StW 162	Left proximal portion
	StW 366	Left spine of scapula
	StW 612	Left spine of scapula
	Sts 7	Right proximal portion
Humerus	StW 124, 150	Left distal portions
	Sts 7	Right head and proximal shaft
	StW 328 and 517	Right heads
	StW 38, 182, 339, Sts 2198a	Right distal portions
Radius	Sts 68	Left proximal quarter
	StW 626a	Left shaft
	StW 627	Left shaft fragments
	StW 46	Left distal end
	StW 354	Left distal end with partial shaft
	StW 348, 528	Right shafts
	StW 105	Right proximal third of an adolescent
	StW 139	Right proximal portion
	Sts 2198b	Proximal fragment
	StW 125	Fragment of a shaft
	StW 516	Proximal portion
Ulna	StW 108, 398, 613, 632	Left proximal ends
	StW 113	Left proximal half
	StW 626b	Left shaft portion
	StW 399 (398b)	Left distal end
	StW 380, 390	Right proximal third
	StW 571	Right proximal end
	StW 349, 577	Right shaft portion
	StW 326	Right shaft and distal end
	StW 125	Proximal end
	StW 340	Shaft portion
Wrist	TM 1526, StW 624	Right capitate
	StW 618	Left scaphoid
Metacarpals	StW 583	Left 1st, distal portion
	StW 382	Left 2nd
	StW 64	Left 3rd
	StW 394	Left 3rd, distal portion
	StW 330	Left 4th, missing distal epiphysis
	StW 26, 292	Left 4th, distal portion
	StW 63	Left 5th
	StW 68	Right 3rd
	StW 27	Right 3rd, distal portion
	StW 65	Right 4th, proximal portion
Hand phalanges	StW 293	Left 2nd, proximal portion
	StW 294	Right thumb, distal portion
	StW 331	Right 3rd, middle
	StW 400	Right 3rd, proximal portion
	StW 28	Right 5th, proximal
	StW 617	Thumb, distal portion
	StW 29, 597	Proximal
	StW 122	Proximal, eroded
	StW 635	Phalanx
Pelvis	StW 611	Left ischium
	Sts 65	Right ilium
Femur	TM 1513	Left distal end
	StW 522	Right neck and head
	StW 367	Right neck and shaft
	StW 99	Right head, neck and shaft
	StW 614	Right distal end of shaft
	Sts 34	Right distal end
	StW 318	Right distal fragment
	StW 25, 30, 31, 361, 392, 527	Heads
	StW 403, 479, 501	Neck and head
	StW 610	Neck
	StW 121, 448	Shaft
	StW 615	Portion of shaft
	StW 129	Distal end
Tibia	StW 181	Left distal fragment
	StW 358, 389	Left distal end
	StW 396	Right proximal portion
	StW 514	Proximal portion
	StW 515	Distal portion
Fibula	StW 356	Left shaft
Ankle	StW 88, 102, 486	Right talus
	StW 347, 363	Left talus
	StW 352	Right calcaneum
	StW 643	Right calcaneum fragment
	StW 638	Right cuboid
	StW 623	Left navicular

(continued)

Table 7.1 (continued)

Skeletal part	Catalog number(s)	Details/notes
Metatarsals	StW 89, 377	Left 2nd
	StW 477, 496	Left 3rd
	StW 387	Left 3rd, proximal half
	StW 485	Left 4th, proximal portion
	StW 634	Left 5th
	StW 562, 595	Right 1st
	StW 595c	Right 2nd
	StW 435	Right 3rd
	StW 388, 595d	Right 3rd, proximal half
	StW 596	Right 4th
	StW 114	Right 5th
Foot phalanges	StW 478	Proximal left of 1st ray
	StW 355	Proximal left of 2nd, 3rd or 4th ray
	StW 470	Proximal right of 1st ray
	StW 595b	Right proximal phalanx of hallux

question of association between cranial and postcranial fossils has to be considered in the light of the demonstration that two species of *Australopithecus* might be represented by the cranial remains.

Two first right metatarsals that I excavated from Member 4 are relevant to this question because I observed that one (StW 595) is very ape-like, and the other (StW 562) has some more human-like characters. In particular, on StW 595, as in the chimpanzee, the articular surface for the first phalanx does not extend onto the dorsal surface, indicating that it could not toe off in walking. By contrast, StW 562 is rather less ape-like in morphology than StW 595 and has an articular surface for the first phalanx that does extend onto the dorsal surface, indicating that it could toe off in walking (Fig. 7.11). Hence there seem to be two types of locomotion represented in these foot bones of *Australopithecus*. If that is the case, then they would represent two species and clearly one cannot make assumptions about the postcranial anatomy and locomotive behavior of *A. africanus* until postcranial remains can be definitely associated with *A. africanus* cranial fossils. This is pertinent to the study by Proctor (2010).

When Robinson (1972) published his work on early hominid posture and locomotion, he noted that there was no known fossil material of the *Australopithecus* foot, but he went on to claim that the Olduvai foot and other fossils of *H. habilis* represent the same kind of creature as *Australopithecus*. From this he deduced that *Australopithecus* could "stand, walk and run essentially as man does" and that it "was probably capable of running and walking fast." The two recently discovered foot bones just mentioned from Sterkfontein show that Robinson was not entirely correct in this deduction and that at least one *Australopithecus* species had a foot anatomy that would not have permitted running. One can only make some general statements about the postcranial anatomy and locomotion of the genus *Australopithecus* at Sterkfontein. We can say, for example, that the two species of *Australopithecus* were both upright walkers and that they had hands proportioned like those of modern humans with a long, powerful, opposable thumb relative to short palm and fingers. This is further discussed below in the section on Member 2.

Fig. 7.10 StW 431 *Australopithecus* partial skeleton

Surprisingly, despite the relative rarity of *Australopithecus* postcranial fossils at Sterkfontein, two important and informative postcranial bones represented the third and fifth *Australopithecus* specimens recovered from there. These were a

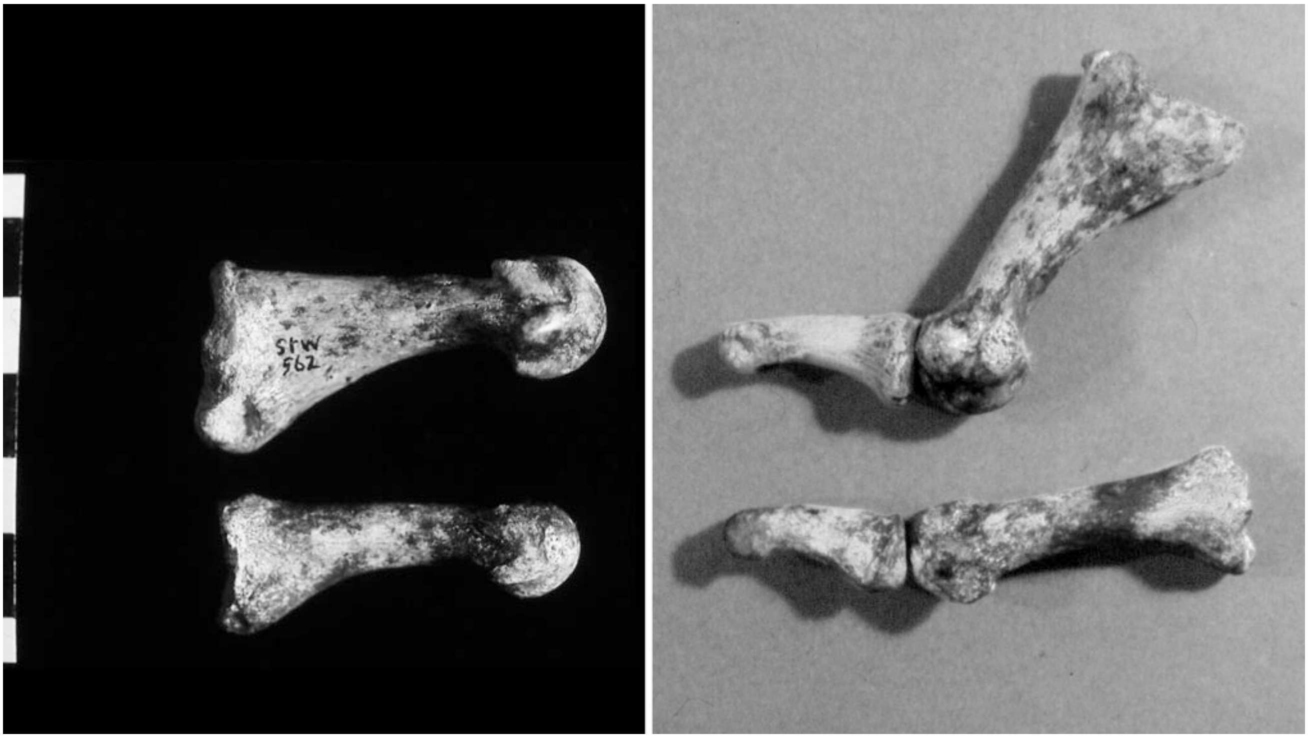

Fig. 7.11 Two morphologically different right first metatarsals from Sterkfontein Member 4, StW 562 (*top left*) and StW 595 (*bottom left*). Same bones articulated with chimpanzee proximal phalanx and StW 595b proximal phalanx at right to show that StW 562 can extend its big toe (*top right*), whilst StW 595 cannot (*bottom right*)

distal femur (TM 1513) and a capitate (TM 1526) found in 1937. Both of these were crucial elements in that they provided information on the locomotion of *Australopithecus*. Broom (in Broom and Schepers 1946) concluded that "the femur is that of an animal that walked as does man, entirely or almost entirely on its hind feet." Although Broom found that the capitate had some ape-like as well as human-like characters, he observed that the articulation for the second metacarpal was large and this suggested to him that, if the second metacarpal was better developed than that of an ape, then the thumb metacarpal would also have been better developed. He concluded that "as the proximal end of the second metacarpal must have been still more like that of man than that of the living anthropoids, we may not be wrong in suspecting that *Plesianthropus* had a useful thumb, or at least a better thumb than in any of the living anthropoids." Subsequent discoveries of hand bones in Member 4 and in particular the discovery of a complete *Australopithecus* hand in Member 2 (Clarke 1999b) have shown that indeed Broom was not wrong in his deduction. *Australopithecus* did have a well-developed thumb.

The discovery of a complete pelvis in the partial skeleton (Sts 14) in 1947, as well as the partial pelvis of StW 431 and some finds of proximal femur fossils have confirmed Broom's initial observation, based on the distal femur TM 1513, that *Australopithecus* walked bipedally, although not in exactly the same fashion as modern humans. The ilia are more laterally flared (Fig. 7.12) and some femoral necks are long with relatively small heads. Furthermore, the legs of *Australopithecus* had not become as elongated relative to the body size as they are in modern humans.

The Sterkfontein *Australopithecus* fossils recovered by Broom and Robinson, including the Sts 14 partial skeleton, were studied in detail by Robinson (1972). The StW 431 partial skeleton has been described by Toussaint et al. (2003) and the StW 431 pelvis by Kibii and Clarke (2003).

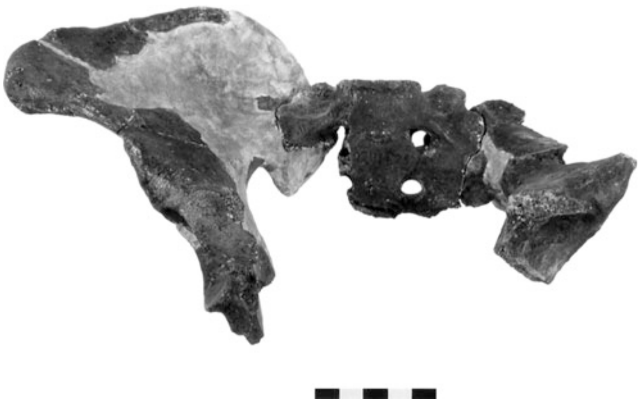

Fig. 7.12 Pelvis of StW 431 *Australopithecus* as reconstructed by Kibii and Clarke

In addition to various studies on different aspects of *Australopithecus* postcranial anatomy, which have included references to Sterkfontein fossils, there have also been detailed studies of *Australopithecus* hand bones by Ricklan (1988), thoracic and lumbar vertebrae by Benade (1990), the shoulder girdle by Berger (1994), foot bones by Deloison (1993, 2003), and distal humeri and proximal radii and ulnae by Menter (2002).

Member 2

Member 2, exposed in the Silberberg Grotto, represents (with the Jacovec Cavern) one of the oldest major fossil-bearing deposits at Sterkfontein and contains a near-complete *Australopithecus* skeleton, StW 573, initially dated by paleomagnetism to 3.3 Ma (Clarke 1998; Partridge et al. 1999; see "Dating"). It was discovered in situ in 1997, and subsequent excavation has revealed a complete skull (Fig. 7.13), complete left arm and hand (Fig. 7.14), crushed and broken right arm and hand, complete right scapula and clavicle, crushed pelvis and scattered ribs and vertebrae, both legs complete though broken (Fig. 7.15), and a partial left foot and one right lateral cuneiform (Clarke and Tobias 1995; Clarke 1998, 1999b, 2002; Deloison 2003). At present, some of the skeleton is still embedded in concrete-like breccia and is being slowly uncovered whilst parts of the skeleton including the left arm and the skull have been lifted in blocks so that final cleaning can be done in a laboratory with the aid of microscopes. Thus, only general observations can be made. The skull differs from those of *A. africanus*. It has a deep anterior zygomatic arch, prominent nuchal crest and inion, and a posterior sagittal crest. It has resemblance to StW 505, a large male *A. prometheus*. The hands are proportioned like those of modern humans, with short palm and fingers and long thumb. There is a strong curvature to the phalanges and powerful muscle attachments. The arms are of approximately equal length to the legs, i.e., not proportioned like either apes (with long arms relative to legs) or humans (with long legs relative to arms). The complete right scapula has some human-like and some ape-like features. The foot bones have a mixture of ape and human characters, and in particular, the big toe shows slight divergence and some mobility at the metatarso-cuneiform articulation (Clarke and Tobias 1995). All of this indicates that *Australopithecus* at Sterkfontein was adept at tree-climbing in an upright posture and that hominids (meaning *Australopithecus, Paranthropus, Homo*, and related forms, excluding apes) did not evolve from a knuckle-walking ancestor (contra Richmond and Strait 2000) but were upright in the trees and walked upright on the ground (Clarke 1999b). The Laetoli footprints of bipedal *Australopithecus afarensis* show that the foot had some ape-like characters, including a slightly divergent big toe (Deloison 1991, 1993), and the foot bones of StW 573 from Sterkfontein Member 2 have the kind of anatomy that could have made the Laetoli footprints (Clarke 1999b).

Fig. 7.13 StW 573 *Australopithecus* skull and left humerus

Jacovec Cavern

In 1995, a Sterkfontein deposit in the Jacovec Cavern separate from, but adjacent to, the main Sterkfontein deposits (Wilkinson 1983; Kibii 2000, 2004) began yielding *Australopithecus* fossils that seemed to be of similar age to the skeleton of Member 2 (Partridge et al. 2003). These specimens include a partial cranium (StW 578) with a temporal bone that again differs from *A. africanus* and is more like that of *A. afarensis*, and a partial clavicle (StW 606) that is more ape-like than either *A. africanus* or *A. afarensis*, both of which are similar to modern humans. A proximal left

Fig. 7.14 StW 573 *Australopithecus* left forearm and hand, with hand enlarged at bottom right

femur (StW 598) from this deposit is the best preserved *Australopithecus* femur from Sterkfontein (Fig. 7.16). Similarly, a complete distal left humerus (StW 602) is the best preserved of *Australopithecus* from Sterkfontein (Partridge et al. 2003). The Jacovec fossils were recovered partly from in situ breccia (part of the cranium) and partly from a debris cone of collapsed material (other fragments of the cranium and other hominid fossils). This cone seems to be of considerable depth and has yielded other faunal material including *Chasmaporthetes* limb bones in very good condition. There is thus much potential for the recovery of more well-preserved *Australopithecus* fossils, including highly informative postcranial material.

Dating

Until recently, the only way of dating the Sterkfontein *Australopithecus* fossils was by general comparison of the fossils of Members 4 and 5 and the stone tools of Member 5 with the well-dated deposits of East Africa. Thus if the early Acheulean and *Homo ergaster* of Member 5 date to about 1.6 Ma and the Oldowan tools and *Paranthropus* teeth of lower Member 5 date to nearly 2 Ma, it could be proposed that the *Australopithecus*-bearing Member 4 deposit beneath, with no stone tools and no *Homo* fossils, is probably older than 2 Ma. Through consideration of the stratigraphy it was further estimated that the *Australopithecus* of Member 2 could be 3–3.5 Ma, and Partridge et al. (1999) provided a paleomagnetic date of 3.3 Ma. Now various other dating methods have been applied to the breccias. One of the methods (cosmogenic nuclide burial dating) has given dates for Member 2 and Jacovec Cavern that seem too old, ca. 4 Ma (Partridge et al. 2003), and another (uranium-lead dating) has given dates for Member 2 that seem too young, 2.2 Ma (Walker et al. 2006; Pickering and Kramers 2010). A paleomagnetic date for the top of Member 4 (Partridge 2005; Herries 2013) has provided an age of 2.14–2.15 Ma, which is a reasonable age when stratigraphy and faunal comparisons are taken into account. If one then considers the 16 m of cave breccia between this dated

Fig. 7.15 StW 573 *Australopithecus* left lower leg and foot and right lower leg

Fig. 7.16 *Australopithecus* fossils from Jacovec Cavern: StW 606 lateral half of left clavicle (*top right*), StW 598 proximal half of left femur (*left*), StW 600 5th lumbar vertebra (*center middle*), StW 605 hand phalanx (*lower middle*), and StW 602 distal end of left humerus (*lower right*). Note long neck and small head of femur and chimpanzee-like morphology of clavicle

horizon and the much lower Member 2 skeleton, an age of around 3 Ma for the skeleton seems quite reasonable (but see Herries 2013 and also Grine 2013). Although under certain conditions rapid infill of an underground cavern could be possible, it seems unlikely in the case of Sterkfontein which, during *Australopithecus* times, was most probably no lower than the surrounding terrain. The landscape was heavily vegetated with gallery forest (Bamford 1999). The combination of these features would have made for a more stable land surface, not prone to fast infilling of caverns through surface erosion. A major problem with both the paleomagnetic dating and the uranium-lead dating of Member 2 is that they were based on the flowstones, and it is clear that the flowstones around the skeleton were formed after a collapse that took place, displacing parts of the hominid and leaving cavities that were subsequently filled with flowstone. Thus a date on the flowstone does not give a date for the skeleton. This fact is particularly well emphasized by the formation of flowstone on the wall of the Silberberg Grotto and the surface of Member 2 that began only in January 1999 and which has been increasing every year during the rainy season. It is obvious a date on this flowstone would not give the age of Member 2.

Paleoenvironment

Hundreds of fragments of fossil wood were recovered from Member 4 in association with *Australopithecus*. Many of these have been sectioned and shown to belong to a liana, *Dichapetalum mombuttense*, that grows now only in tropical forests of central and western Africa (Bamford 1999) and which requires large trees for support. Such a forest scenario for *Australopithecus* accords with the presence in the deposit of many large monkeys (*Parapapio* and *Cercopithecoides*), as well as the fossils of *Makapania*, a bovid with skull and feet similar to those of the takin (Pickering et al. 2004b), which inhabits woodland in the Himalaya foothills. The fauna of Member 4 contrasts with that of the succeeding Member 5 that contains elements such as horse, spring hare, and ostrich indicative of a more open grassland environment (Vrba 1976; Reed 1997; Kuman and Clarke 2000; Luyt 2001; Luyt and Lee-Thorp 2003; Kibii 2004).

Taphonomy

In 1950, Broom, Robinson, and Schepers wrote: "There seems to be little doubt that the quarry which yielded our best *Plesianthropus* specimens is the upper part of a large cave which for many years had been the lair or lairs of sabre-tooths and that the bones had been introduced by them." The extensive excavations since that time have shown that such an explanation does not fit the facts. First, the entrances to the caves during the time of *Australopithecus* were vertical shafts and the caves were not accessible for use as dens until the talus infill had nearly reached the roof. Secondly, we know that there were many other large carnivores in the vicinity at that time, e.g., leopards, lions, hyenas, and the long-legged hunting hyena *Chasmaporthetes*. Any or all of these, in addition to the sabre-toothed cats could have been a contributing factor to the bone accumulation. If an *Australopithecus* did fall prey to a carnivore, then it would have been consumed on the surface and some of its bones could have entered the cave either through slope wash or by being dropped by cats feeding in overhanging trees. However, to judge from the paucity of tooth marks on the Sterkfontein hominid remains (Pickering et al. 2004a), this was probably not the main reason for their accumulation. Another way in which animal and hominid remains entered the caves is by natural death trap, i.e., by falling into one of the vertical shafts. The Member 2 deposit in the Silberberg Grotto is a particularly good example of this, where articulated skeletal parts of carnivores and monkeys have been recovered (Pickering et al. 2004b), in addition to the complete *Australopithecus* skeleton (Fig. 7.17). A similar death trap area was excavated by this author in Member 4 in the 1990s consisting of several partial skeletons and skulls of monkeys. It is indeed possible that natural death traps contributed to much of the *Australopithecus* accumulation in Member 4 but that subsequent disturbance of the talus through roof fall and partial collapse into lower chambers and movement of the talus slope resulted in the breaking up and scattering of once-complete skeletons (Clarke 2007).

Fig. 7.17 Sketch by R.J. Clarke of StW 573 *Australopithecus* body in Member 2 talus slope, based on position of fossilized skeletal elements in the breccia

Fig. 7.18 Internal aspect of right posterior braincase of StW 53, as exposed by decalcification in the breccia. *Arrow* points to sharp-edge chert block in the area of the zygomatic arch. Note many chert blocks surround the cranium

Raymond Dart's (1949a, b, 1957) concept of *Australopithecus* as a bone-tool using cannibalistic killer has in recent years been discounted because it has been shown that the so-called osteodontokeratic bone tool culture of Makapansgat had nothing to do with hominids but resulted from hyena and porcupine activity (Hughes 1954, 1961; Brain 1981). Similarly, the damaged monkey skulls from Taung which Dart originally attributed to *Australopithecus* activity have been shown to have been damaged by eagle beaks and talons (Berger and Clarke 1995). No stone tools have been found in association with *Australopithecus* at Sterkfontein (Kuman and Clarke 2000), even though *Australopithecus* had the manual ability to make them and in East Africa stone tools occur as long ago as 2.6 Ma, which was the time when *Australopithecus* was living in southern Africa.

This issue is particularly relevant to the case of StW 53, an *Australopithecus* cranium originally classed as early *Homo* (Hughes and Tobias 1977) but which I have demonstrated (Clarke 2008) to be a male *A. africanus*. This hominid comes from upper Member 4 and is said to bear cut marks (Pickering et al. 2000). Those authors have presented a case for considering them as manmade cut marks. In the context of the Sterkfontein breccias, different sized blocks of stone, including sharp quartz and chert can be forced against bone surfaces either during talus formation or during collapse episodes. A Member 4 *A. prometheus* mandible, StW 498, also has cut marks similar to those of StW 53. Thus one could question whether cut marks made by a handheld flake would differ from cut marks made by a natural stone forced against the bone in a debris slope.

In fact, the cut marks on StW 53 were, I believe, produced naturally by a small chert block in the area of the zygomatic arch and which moved against the bone under pressure in the talus slope. A block was there when the cranium was discovered and can be seen in a cast made at the time (Fig. 7.18). Although there is no proof of stone tools made by *Australopithecus*, there still remains an intriguing question of whether any of the *Australopithecus* remains could have resulted from predation by hominids. We know that in parts of Africa humans have had the habit of killing and eating chimpanzees (Himmelheber and Himmelheber 1958), and thus it would not be surprising if early *Homo* killed and ate *Australopithecus*. So perhaps we need to look again at Dart's early hypothesis, not to resurrect the osteodontokeratic, but to consider whether there could have been, on occasion, the possible involvement of hominids in the accumulation of other hominid remains.

Conclusion

The picture we have of *Australopithecus* at Sterkfontein is that between 3.5 and 2.14 Ma, in what was generally a forest-fringe environment, there were at least two species represented. The earliest representative of one species, *A. prometheus* from Member 2, dates to probably about 3 Ma. Then in Member 4, dating between 2.5 and 2.14 Ma, *A. prometheus* and *A. africanus* are represented.

It is apparent from the anatomy of *Australopithecus* from Sterkfontein that it shared with modern humans the following attributes: (1) a similar though larger dentition with relatively small canines compared to those of the apes; (2) upright posture with a similar pelvis to that of humans and a foot with some human-like modifications; (3) a basically unspecialized hand with short palm and fingers but with a relatively long thumb which is specialized for opposability. All of these features uniting *Australopithecus* and *Paranthropus* with humans differ from those of the apes. As Hooton (1931: 132) stated: "The possession of a human foot makes an animal a man." The apes do not have a human foot, do not have a human hand, and do not have human teeth, and therefore it is highly misleading and confusing to classify them with the human-like forms as Hominidae. Hence there seems no justification for the current trend in paleoanthropology to group the apes together with humans and australopithecines in the family Hominidae, and I prefer to retain that family name only for the human-like primates.

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Chapter 8
Variation in Mandibular Postcanine Dental Morphology and Hominin Species Representation in Member 4, Sterkfontein, South Africa

Frederick E. Grine, Marcia M. Delanty, and Bernard A. Wood

Abstract The hominin fossils from the Member 4 deposit at Sterkfontein, South Africa are most commonly attributed to *Australopithecus africanus*. However, a number of studies have suggested that they represent more than one species, although there is no consensus among those who recognize two (or more) taxa in this sample as to the allocation of individual specimens. We examine crown size and proportional cusp areas of the mandibular postcanine teeth, which constitute the bulk of the Sterkfontein Member 4 assemblage, to determine whether the degree of variation in it exceeds that of a single, highly dimorphic hominid species, *Gorilla gorilla*. The Lewontin CV ratio test, the Fligner-Killeen test and ordination of taxonomic distances via multidimensional scaling were employed to evaluate the degree of variation in the fossil and recent samples at each premolar and molar position. Sterkfontein (and combined Sterkfontein and Makapansgat) sample variation is significantly greater than that of the gorilla with regard to crown areas of the P_3 and P_4, relative P_3 metaconid size, and the MD diameter of the P_4. While the difference in P_3 metaconid size variability can be attributed to functional differences in this tooth between *Gorilla* and *Australopithecus*, the exaggerated premolar size variation at Sterkfontein defies such explanation. Those instances in which the Sterkfontein molar sample exhibits significantly greater variability are related to the expression of accessory cuspulids (C6 and/or C7) and the protostylid. Because these same features vary in incidence and expression in other fossil hominin species and among modern human populations, it would seem imprudent to attribute such variation to taxonomic heterogeneity in the Sterkfontein assemblage. Variation in Sterkfontein premolar crown size is intriguing and, perhaps in concert with the size variation that has been documented for Sterkfontein M^2s, may hint at taxonomic heterogeneity. However, it may also be related to temporal heterogeneity if the Sterkfontein Member 4 deposit comprises a substantial time aggregate, as has been suggested. Indeed, time and heightened levels of sexual dimorphism have been cited in explanation for exaggerated variability in other fossil hominin assemblages that are interpreted as representing a single species. In this light, our results do not necessarily contradict the hypothesis that a single, polymorphic species, *A. africanus*, is represented in the Sterkfontein Member 4 deposit.

Keywords *Australopithecus* • *Australopithecus africanus* • Sterkfontein • Makapansgat • Taung • Dentition • Fligner-Killeen test • Lewontin CV ratio test

Introduction

The ascription of morphological variation in a fossil assemblage to intraspecific di- or polymorphism, as opposed to taxonomic mixing continues to be a matter of debate and discovery (e.g., Kimbel and White 1988; Lieberman et al. 1988; Kelley and Etler 1989; Miller 1991, 2000; Wood 1991b, 1993; Wood et al. 1991; Uchida 1992; Cope 1993; Kramer 1993, Kramer et al. 1995; Plavcan 1993, 2002; Grine et al. 1996; Kelley and Plavcan 1998; Donnelly and Kramer 1999; Aiello et al. 2000; Plavcan and Cope 2001; Moggi-Cecchi 2003; Scott and Lockwood 2004; Lee 2005; Villmoare 2005; Schrein 2006; Schwartz and Tattersall 2006; Taylor 2006; Baab 2008). For good reason, extant species are most often employed as models by which to interpret variability in fossil hominin assemblages. Because

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intraspecific variation in living primates is commonly related to sexual dimorphism (Wood et al. 1991; Uchida 1992; Plavcan 2002), the most dimorphic extant hominids, *Gorilla* and/or *Pongo*, are generally employed in comparisons with fossil hominin assemblages (Johanson and White 1979; Wood 1985; Richmond and Jungers 1995; Lockwood et al. 1996; Lockwood 1999). Comparing the variation in a fossil sample to that exhibited by an extant species allows the test of the null hypothesis that the two samples do not differ. If this hypothesis is not contradicted, it would be consistent with the suggestion that a single species is represented in the paleontological sample (Richmond and Jungers 1995; Miller 2000). This approach has been used extensively in assessing the taxonomic homogeneity of fossil hominid assemblages (Richmond and Jungers 1995; Lockwood et al. 1996; Kelley and Plavcan 1998; Miller 2000; Schrein 2006; Skinner et al. 2006; Baab 2008).

Although fossil samples that exceed the limits imposed by extant species samples are commonly inferred to contain more than one taxon, there are differences in the units of comparison. The samples of the extant species represent an instant in geological time, whereas the fossil samples express variation that has accumulated over many millennia. For this and other reasons, there is no reason to expect the maximum level of sexual dimorphism that can be (or has been) expressed in the skeleton or dentition of an extinct hominid is sampled among living gorillas or orangutans (Kelley and Plavcan 1998). Indeed, comparatively high levels of variation in fossil samples have been interpreted as suggesting a greater degree of sexual dimorphism in some species in the past (Kelley and Xu 1991; Richmond and Jungers 1995; Lockwood et al. 1996). Thus, Plavcan and Cope (2001) have observed that it is not possible to falsify the single-species hypothesis for a fossil sample on the basis of relative variation alone. Nevertheless, there is reasonable consensus that morphological variability in proximately related extinct and extant species should be of comparable degree, unless there are compelling reasons to otherwise interpret excessive variation in some feature in a fossil sample as being nonetheless intraspecific in nature (Plavcan and Cope 2001).

A large number of hominin fossils have been recovered in situ from calcified and decalcified Member 4 sediments at the site of Sterkfontein, as well as from "breccia" dumps attributed to Member 4 (Tobias and Hughes 1969; Partridge 1978; Wilkinson 1983; Partridge and Watt 1991; Clarke 1994; Moggi-Cecchi et al. 2006). The question of whether these specimens represent a single taxon, *Australopithecus africanus*, or more than one species continues to be debated (Clarke 2013; Grine 2013). Studies that have focused largely on cranial morphology and overall dental dimensions have reached different conclusions regarding the degree of variation within the sample. Even among those workers who have postulated the existence of two (or more) taxa in the Sterkfontein assemblage, there is disagreement over the specimens that should be attributed to them (Grine 2013).

Taxonomic Homogeneity of the Sterkfontein Member 4 Hominin Assemblage

Kimbel and White (1988) observed that the buccolingual (BL) diameter of the M^2s from Sterkfontein Member 4 displays a bimodal, non-overlapping frequency distribution, and the highest coefficient of variation (CV) among fossil hominin taxa including *Australopithecus afarensis, Paranthropus robustus*, and *Paranthropus boisei*. They proposed that this variation was not related to sexual dimorphism, since even highly dimorphic extant hominids display considerable size overlap between the sexes in molar dimensions. Noting that greater facial prognathism and robusticity are expected for males in sexually dimorphic hominids, Kimbel and White (1988) argued that the comparatively gracile, but highly prognathic facial skeleton of the Sts 5 cranium is unlikely to be explained on the grounds of sexual dimorphism alone. Kimbel and White (1988) divided the Sterkfontein specimens into two groups: one included Sts 71 and Sts 52, while the other included Sts 5.

Clarke (1988, 1994, 2013) also has argued that the Sterkfontein fossils represent two taxa, but his division of the material differs from that of Kimbel and White (1988). He observed that *A. africanus*, as represented by Taung, Sts 5, Sts 17, Sts 52, and MLD 6, has a thick supraorbital margin and prominent nasal skeleton, and holds that Stw 252, Sts 71, Sts 36, and MLD 2 belong to a second species, characterized by a thin supraorbital margin, flat nasal skeleton and larger teeth.

The composite juvenile specimen, Stw 151, has also been invoked to argue for the existence of a second taxon in the Sterkfontein Member 4 assemblage (Spoor 1993; Schwartz 1997; Moggi-Cecchi et al. 1998). Spoor (1993) and Moggi-Cecchi et al. (1998) suggested that it belonged to a form more derived than *A. africanus* on the basis of the orientation of the posterior surface of its petrous pyramid and its pattern of dental development. Schwartz (1997) opined that it represents an intermediate form between *A. africanus* and *P. robustus* on the basis of its molar enamel thickness.

Kimbel and Rak (1993), on the other hand, discussed facial variation among the Sterkfontein fossils, but argued that the apparently random pattern of variation precludes them from being easily divided into separate groups.

Lockwood's (1997, 1999) analysis of cranial morphology also led him to conclude that only one species is represented in the Sterkfontein Member 4. He determined that the pattern of variation conforms to that found in extant hominoids, and that the degree of size variation is not extreme in comparison to highly dimorphic species, such as *Gorilla gorilla*, or to other fossil taxa, such as *P. boisei*. Lockwood (1997, 1999) obtained the same results when the Sterkfontein assemblage was considered alone, and for a sample that included specimens from both Sterkfontein and Makapansgat. Lockwood and Tobias (1999) noted that the large Stw 505 cranium extends the range of variation of the Sterkfontein assemblage, but attributed it to the same species (*A. africanus*) as the other specimens from the site.

Subsequently, however, Lockwood and Tobias (2002) described 27 new cranial specimens from Sterkfontein Member 4, and while they did not recognize a second species in this assemblage per se, they argued that specimens such as Stw 183 and Stw 255 differ in like manner from the rest of the *A. africanus* sample.

Calcagno et al. (1997) suggested that a multiple species interpretation best fit their Sterkfontein odontometric data. However, in a subsequent study (Calcagno et al. 1999), in which the CV was employed to analyze variation in larger sample of Sterkfontein teeth, they determined that only in the M^2 diameters did variation exceeded that of a *Gorilla* sample. They concluded that they could not recommend rejection of the single species hypothesis on this basis alone. The CV has also employed in later analyses of crown dimensions for further enhanced dental samples from Sterkfontein (Moggi-Cecchi 2003; Moggi-Cecchi et al. 2006). These studies concluded that in comparison to samples of other extinct hominin species, the CVs do not provide evidence for more than one taxon in the Sterkfontein Member 4 assemblage.

Ungar et al. (1999) investigated occlusal relief in Sterkfontein and Makapansgat M_2s, and observed that MLD 2 and Stw 412 exhibit "shearing quotients" nearer the mean for chimpanzees than for the other fossil hominin molars in their sample. They suggested that these differences warrant further scrutiny.

To date, analyses of the comparatively abundant Sterkfontein dental remains have been limited to comparisons of overall crown dimensions (Kimbel and White 1988; Calcagno et al. 1997, 1999; Moggi-Cecchi 2003; Moggi-Cecchi et al. 2006), or they have employed techniques that require unworn teeth and therefore severely limit sample size (Ungar et al. 1999). No statistical analysis of the variation displayed by the Sterkfontein Member 4 dental remains has considered details of occlusal morphology.

Cusp Proportions and Taxonomy

The utility of premolar and molar cusp proportions in taxonomic (species-level) comparisons has been explored in a number of studies (Corruccini 1977; Lavelle 1978; Hills et al. 1983; Hartman 1989; Uchida 1991, 1992, 1998a, b; Wood and Xu 1991; Matsumura et al. 1992; Smith 1999; Bailey 2004; Pilbrow 2007; Grine et al. 2009; Quam et al. 2009). These data have been shown to be useful in evaluations of Plio-Pleistocene hominin fossils from eastern Africa, where cusp proportions seem to be particularly effective for sorting mandibular postcanine teeth (Wood et al. 1983; Wood and Uytterschaut 1987; Suwa 1988, 1990; Wood 1991a; Suwa et al. 1994, 1996).

Although Wood (1991a) analyzed cusp proportions for a portion of the Sterkfontein dental sample (restricted to the Sts and TM specimens in the collection of the Ditsong Museum, Pretoria), an analysis of the entire Sterkfontein Member 4 assemblage that is currently available (including the abundance of specimens in the collection of the University of the Witwatersrand, Johannesburg) has not been undertaken.

The purpose of the present study is to assess the degree of variation exhibited by the full available sample of permanent mandibular premolars and molars from Sterkfontein Member 4 by examining overall crown size and individual cusp proportions. Mandibular teeth were chosen because of their relative abundance in the Sterkfontein (and Makapansgat) assemblage, because of their comparative efficacy in delineating taxonomic groups, and because they exhibit quite striking differences in size and morphology (Fig. 8.1). We address two questions: (1) Does the degree of morphometric variation exhibited by the Sterkfontein Member 4 assemblage exceed that of the most sexually dimorphic extant African hominid, *G. gorilla*? (2) Do the addition of specimens from Taung and Makapansgat affect the degree of variation in the Sterkfontein sample?

Materials and Methods

A total of 77 mandibular premolars and molars from Sterkfontein Member 4 representing some 45–47 individuals were included in this study (Table 8.1). Eight (those with Sts and TM catalogue designations) were recovered by R. Broom and/or J. T. Robinson in their excavation of the "Type Site" between 1938 and 1949, while all others (designated Stw) were recovered since 1966 through the efforts of A. R. Hughes, P. V. Tobias, and R. J. Clarke. These fossils

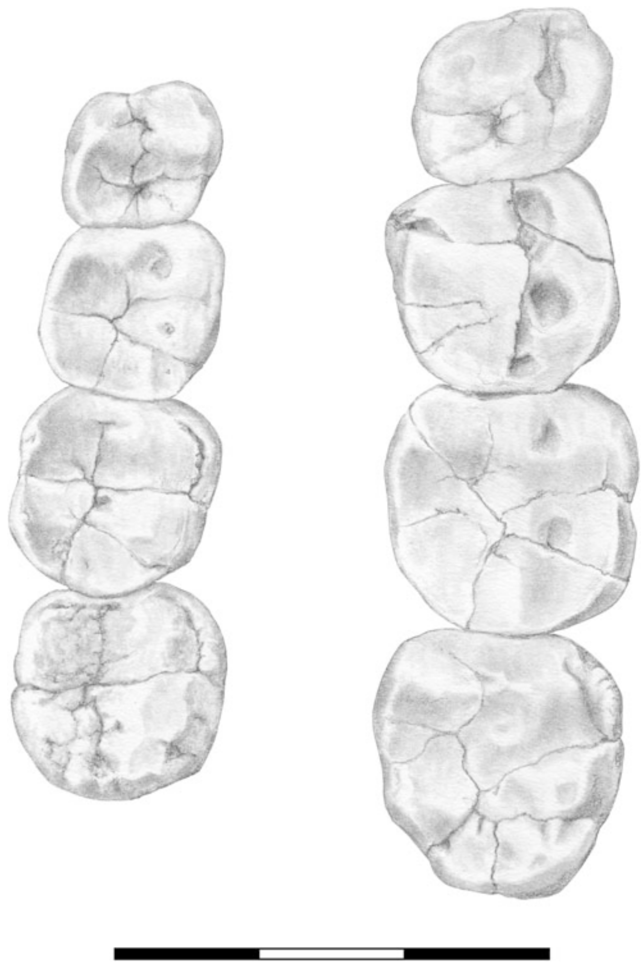

Fig. 8.1 Occlusal views of RP_4–M_3 of Stw 404 (*left*) and Stw 384 (*right*) illustrating the level of size and morphological variation present in the Sterkfontein Member 4 mandibular postcanine dental assemblage. Scale is in cms

have been described and illustrated by Robinson (1956) and Moggi-Cecchi et al. (2006). Two (Stw 145 and Stw 147) represent isolated tooth crowns considered by Moggi-Cecchi et al. (2006) as being possibly associated with one another, but no such associations have been proposed for the other fossils considered here.

As discussed above, Stw 151 has been argued to represent a second hominin—more derived than *A. africanus*—in the Sterkfontein Member 4 assemblage (Spoor 1993; Schwartz 1997; Moggi-Cecchi et al. 1998). Moggi-Cecchi et al. (1998) described this specimen as having been recovered from decalcified Member 4 deposits. Kuman and Clarke (2000), however, subsequently surmised that this particular part of the deposit may represent a late phase of Member 4, or be contemporaneous with what they refer to as the “Stw 53 Infill” (equivalent to Partridge’s 2000, Member 5A), although their reasons for these assertions are unclear.

Table 8.1 Mandibular teeth of South African fossil hominin specimens employed in this study

Specimen	P3	P4	M1	M2	M3
Stw 3				x	
Stw 7	x				
Stw 14	x	x		x	x
Stw 61				x	
Stw 106			x		
Stw 109				x	x
Stw 112		x			
Stw 116				x	
Stw 123a			x		
Stw 131		x			x
Stw 142					x
Stw 145			x		
Stw 147		x			
Stw 151			x		
Stw 193		x			
Stw 213	x	x		x	
Stw 234				x	
Stw 237					x
Stw 246			x		
Stw 280					x
Stw 285b				x	
Stw 291			x		
Stw 296			x	x	
Stw 327		x	x	x	
Stw 353					x
Stw 364			x		
Stw 384				x	x
Stw 401	x				
Stw 404	x	x		x	
Stw 412	x	x		x	
Stw 420	x		x	x	
Stw 487a		x			x
Stw 491			x	x	x
Stw 498				x	x
Stw 520					x
Stw 529				x	x
Stw 537		x		x	x
Stw 555				x	
Stw 560				x	x
Sts 4				x	
Sts 6				x	
Sts 7				x	
Sts 9	x		x		
Sts 24	x		x		
Sts 51	x				

(continued)

Table 8.1 (continued)

Specimen	P3	P4	M1	M2	M3
Sts 52	x	x	x	x	
TM 1523		x			
MLD 2	x		x	x	
MLD 4					x
MLD 18		x	x	x	x
MLD 19					x
MLD 24				x	
MLD 40	x	x	x	x	
Taung			x		

Despite the uncertainty surrounding its provenience, Stw 151 is included in the present study.

We also included the holotype of *A. africanus* from Taung and four fossils from Makapansgat that are referred to this species (Table 8.1). The teeth of the Taung and Makapansgat fossils have been fully described and illustrated (Abel 1931; Dart 1948, 1954, 1962; Robinson 1956). Eighteen specimens from Sterkfontein (possibly 19 if Stw 145 and 147 are associated), and three from Makapansgat are represented at more than one tooth position. Thus, a total of 89 mandibular cheek teeth from Sterkfontein, Makapansgat and Taung were included in our analysis (Table 8.2). With the exception of the M_2, the sample of which is nearly twice as large as that that for any other tooth, the other teeth are represented in nearly equal abundance.

A total of 92 mandibular premolars and molars of the western lowland gorilla, *G. gorilla*, were included as a comparative sample, with almost equal representation at each tooth position (Table 8.2). Males and females are nearly equally represented in the sample, and the numbers of specimens at each tooth position are similar to those in the fossil hominin sample. We maintained this level of similarity because the CV is sensitive to sample size, being biased to underestimate relative variation in smaller samples, especially those that consist of fewer than eight specimens (Plavcan and Cope 2001). Fortunately, the samples employed here all exceed 12 individuals (Table 8.2).

Table 8.2 Mandibular tooth samples employed in this study

Sample	P3	P4	M1	M2	M3
Sterkfontein	11	13	14	24	15
Makapansgat	2	2	3	4	3
Taung	0	0	1	0	0
Fossil hominin total	13	15	18	28	18
Gorilla gorilla	18	19	17	19	19

In all instances, teeth were excluded if occlusal cusp boundaries could not be distinguished clearly, and only a single tooth (usually the left) was employed when antimeres were present.

Dental Variables

In order to facilitate comparison with the results of other studies that have employed the CVs of absolute crown dimensions, the maximum MD and BL diameters of the fossil hominin teeth were recorded by one of us (FEG) on the original specimens.

Cusp areas were determined from photographs using methods employed in previous studies (Wood et al. 1983; Wood and Uytterschaut 1987; Suwa 1988; Suwa et al. 1994, 1996; Grine et al. 2009). Maximum occlusal area was determined according to the method employed by Suwa et al. (1994, 1996), in which the area of the occlusal fovea was maximized in order to define the reference plane. This differs somewhat from the methods employed by Wood and colleagues (Wood and Abbott 1983; Wood et al. 1983; Wood and Uytterschaut 1987), who used the “plane of the cervical line,” and by Bailey (2004), who used the buccal and distal cervices of upper molars for orientation. Such differences in orientation, however, result in measurement differences that are generally very slight, being comparable to intra-observer error rates using only a single method of measurement (Suwa et al. 1994; Bailey et al. 2004). Indeed, Bailey et al. (2004: 329) concluded that “if certain prescribed standards are employed then cusp and crown base areas measured by different workers can be pooled into a single database.” Data for the teeth from Makapansgat and Taung were taken from Wood (1991a).

The variables recorded for the mandibular premolars are indicated in Fig. 8.2; those recorded for the mandibular molar crowns are indicated in Fig. 8.3. Following Wood (Wood et al. 1983; Wood 1991a) and Suwa (Suwa et al. 1994, 1996), the areas of the accessory cusps (C6 and C7) were measured both as singular entities, and by dividing them with equal parts being added to the areas of the adjacent principal cusps. The protostylid was also measured both as a singular entity, and by adding it to the area of the protoconid.

While the 2D variables employed here have been shown to be efficacious in taxonomic studies (e.g., Wood et al. 1983; Wood and Uytterschaut 1987; Suwa 1988, 1990; Matsumura et al. 1992; Uchida 1992; Suwa et al. 1994, 1996; Smith 1999; Grine et al. 2009), variables that employ three dimensional data pertaining to occlusal relief (e.g., Hartman 1989; Ungar et al. 1999; Skinner et al. 2008a, b,

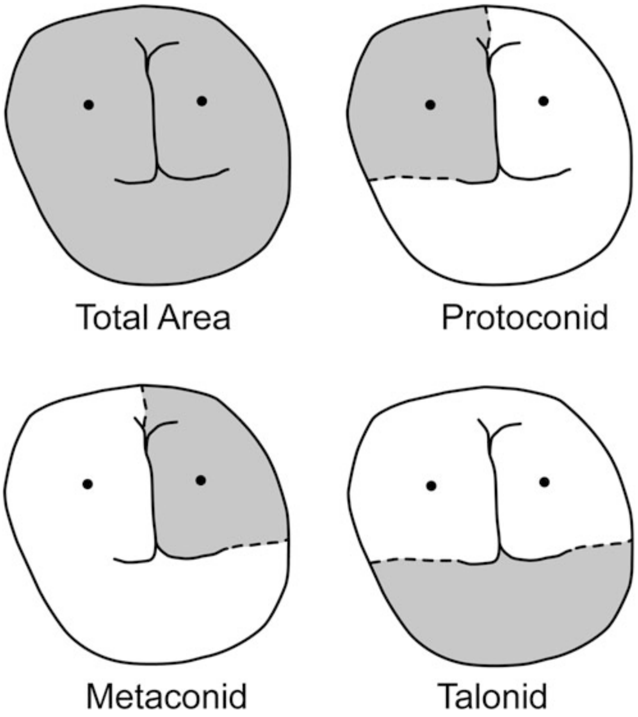

Fig. 8.2 Diagrams illustrating the occlusal area measurements recorded for mandibular premolars. Adapted from Wood and Uytterschaut (1987) and Suwa (1988)

2009; Benazzi et al. 2009) will, of necessity, capture additional information which may provide greater insights and precision in taxonomic assessments. Indeed, recent analyses of enamel-dentine junction (DEJ) topography in the mandibular molars of *Pan paniscus*, *Pan troglodytes*, *A. africanus*, and *P. robustus* indicate that it can generally serve to distinguish specimens of these taxa, and that it can discriminate first, second, and third molars within each species (Skinner et al. 2008a, b, 2009). Unfortunately, because techniques that employ 3D landmarks and semi-landmarks from the outer enamel surface rely upon unworn or very slightly worn teeth, they are of limited applicability in assessing intraspecific variation in paleontological samples where the majority of teeth are worn.

Statistical Evaluation of Variation

The method that most adequately determines whether a paleontological assemblage exhibits a significantly greater degree of variation than an extant comparative species sample cannot be sensitive to outliers, a problem that bedevils range-based statistics (Cope 1993; Cope and Lacy 1995; Donnelly and Kramer 1999; Plavcan and Cope 2001). At the same time, determining the statistical significance of differences in CVs is not always straightforward (Cope and Lacy 1992; Kramer 1993).

Lewontin (1966) described the use of logarithms to calculate trait variance for Fisher distribution tests, where the CV^2 approximates the variance of logarithms to base *e*. This provides a relatively simple F-test of significance for comparing two CVs, although one that is sensitive to departures from normality (Box 1953). Despite this potential drawback, the Lewontin CV ratio test was performed here because of its power (Donnelly and Kramer 1999), and because it provides useful comparison with previous studies that have been based on the CV (e.g., Kimbel and White 1988; Calcagno et al. 1997, 1999; Moggi-Cecchi 2003).

Donnelly and Kramer (1999) reviewed several methods for comparing CVs, and determined that the weighted-means test for equal dispersion, which is a modified version of the Fligner-Killeen test (Fligner and Killeen 1976), maintained power and robusticity while minimizing type I and type II errors. Of particular importance to paleontological application, it does not rely upon normally distributed samples (Plavcan 1994; Rehg and Leigh 1999), and it maintains power even when the samples under comparison have dissimilar distributions (Donnelly and Kramer 1999). Based on these considerations, the Fligner-Killeen test was also employed in the present study even though it is a more conservative and possibly less powerful statistic than the Lewontin CV ratio test.

Average taxonomic (= average Euclidean) pair-wise distances (d) calculated from the relative cusp areas were also computed among specimens. The resultant d values were summarized by ordination via multidimensional scaling (MDS) analysis (Rohlf 1972). The results of MDS closely approximate those found through other ordination analyses, such as principal coordinates or principal components analysis (Rohlf 1972). Finally, Pearson product-moment (PPM) correlations were calculated between the coordinates for each dimension of the MDS plot and the relative cuspal areas in order to illuminate those variables that contributed maximally to the differences in both plot dimensions. Because the MDS analyses require a complete dataset for each tooth, some fossil specimens could not be included in these plots because damage and/or occlusal attrition precluded the accurate determination of one (or more) of the variables.

The fossils were analyzed first using only the specimens from Sterkfontein, and subsequently by combining the teeth from Sterkfontein, Makapansgat and Taung.

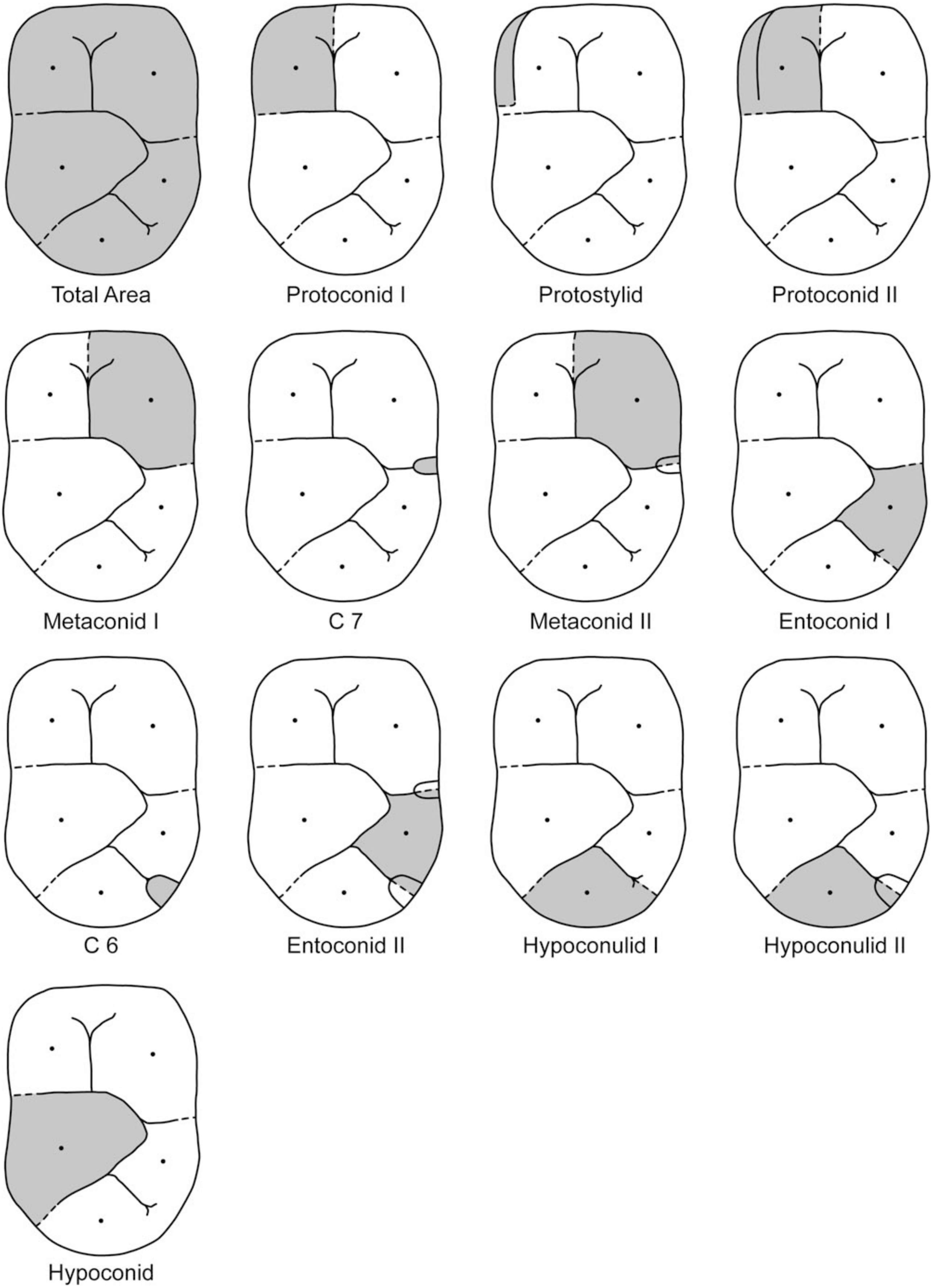

Fig. 8.3 Diagrams illustrating the occlusal area measurements recorded for mandibular molars. Adapted from Wood et al. (1983)

Table 8.3 Fossil hominin and *Gorilla* sample statistics for the mandibular P3

	Sterkfontein			Sterkfontein/Makapansgat			*Gorilla*		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
MD diameter	10.1	1.3	12.9	10.1	1.2	12.1	12.6	1.7	13.4
BL diameter	11.1	1.2	11.0	11.2	1.1	10.2	14.2	1.7	12.2
Total crown area	88.3	19.9	22.5	88.2	18.4	20.8	136.9	17.8	13.0
Metaconid area	26.7	7.0	26.1	26.7	6.6	24.8	29.2	4.7	16.1
Protoconid area	48.3	5.5	11.5	48.7	5.4	11.1	49.3	4.5	9.1
Talonid area	28.1	6.8	24.2	27.2	6.9	25.5	23.9	4.6	19.3

Table 8.4 Results of Fligner-Killeen and Lewontin CV Ratio tests (p values) for the mandibular P3

	Fligner-Killeen		Lewontin CV Ratio	
	Sterkfontein versus *Gorilla*	Sterkfontein + Makapansgat versus *Gorilla*	Sterkfontein versus *Gorilla*	Sterkfontein + Makapansgat versus *Gorilla*
MD diameter	0.32	0.23	0.47	0.37
BL diameter	0.30	0.29	0.39	0.27
Total crown area	0.07	0.09	**0.02**	**0.04**
Metaconid area	0.44	0.38	**0.04**	0.06
Protoconid area	0.61	0.54	0.20	0.22
Talonid area	0.65	0.73	0.20	0.15

Statistically significant values in boldface

Results

Mandibular Third Premolar

The statistics pertaining to the variables recorded for the P_3 in the Sterkfontein, combined Sterkfontein/Makapansgat, and *Gorilla* samples are recorded in Table 8.3, and comparisons between the fossil and recent samples are provided in Table 8.4.

The Lewontin CV ratio test indicates significantly greater levels of variation in total area and relative metaconid area in the Sterkfontein than in the *Gorilla* sample. The inclusion of the Makapansgat teeth does not substantially alter these results. The Fligner-Killeen test indicates no significant difference in variation for any of the measurements, although total crown area borders on significance between the Sterkfontein and *Gorilla* samples ($p = 0.07$).

Figure 8.4 depicts the results of the MDS analysis of the fossil and *Gorilla* P_3s. There is one notable outlier among the fossils; Stw 7 occupies an extreme position along dimension 1. With regard to the palaeontological sample, PPM correlation of dimension 1 coordinates reveals significant association with protoconid ($r = -0.954$; $p < 0.01$) and talonid ($r = 0.992$; $p < 0.01$) areas. The PPM correlation of the dimension 2 coordinates reveals a significant association with metaconid area ($r = 0.920$; $p < 0.01$).

Mandibular Fourth Premolar

The statistics pertaining to the variables recorded for the P_4 in the Sterkfontein, combined Sterkfontein/Makapansgat, and *Gorilla* samples are recorded in Table 8.5, and comparisons between the fossil and recent samples are provided in Table 8.6.

The Lewontin CV ratio test indicates significant differences between the fossil and extant samples in MD diameter and total crown area. The Fligner-Killeen reveals no significant difference in variation between the Sterkfontein and *Gorilla* samples, or between the Sterkfontein/Makapansgat and *Gorilla* samples.

Figure 8.5 depicts the results of the MDS analysis of the fossil and *Gorilla* P_4s. There are two notable outliers among the fossils; Stw 537 and Stw 14 occupy extreme positions along dimensions 1 and 2, respectively. The PPM correlations reveal significant association between metaconid

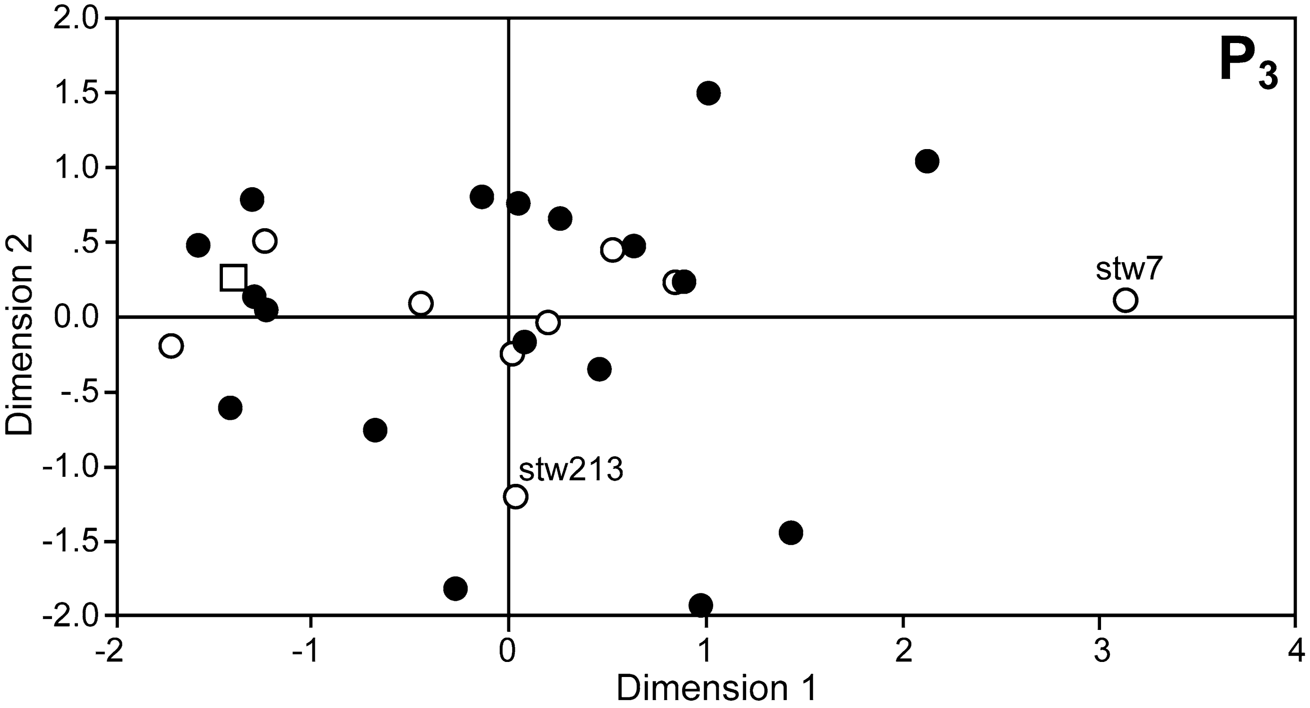

Fig. 8.4 Multidimensional scaling plot of fossil hominin (*open symbols*) and *Gorilla* (*solid symbols*) mandibular P3s. *Open circles* Sterkfontein specimens; *open square* Makapansgat specimen. Protoconid and talonid areas are significantly associated with dimension 1 coordinates; metaconid area is significantly associated with dimension 2 coordinates

Table 8.5 Fossil hominin and *Gorilla* sample statistics for the mandibular P4

	Sterkfontein			Sterkfontein/Makapansgat			*Gorilla*		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
MD diameter	10.8	1.2	11.4	10.6	1.3	12.0	11.7	0.8	7.1
BL diameter	11.2	1.1	9.8	11.3	1.0	9.2	12.1	0.8	6.9
Total crown area	103.8	20.4	19.6	104.2	18.9	18.1	121.7	12.8	10.5
Metaconid area	31.9	4.9	15.4	31.6	4.8	15.3	27.9	3.0	10.7
Protoconid area	39.1	4.5	11.6	39.2	4.3	11.1	36.9	3.5	9.3
Talonid area	31.1	5.2	16.6	31.1	4.9	15.9	37.6	4.8	12.9

Table 8.6 Results of Fligner-Killeen and Lewontin CV Ratio tests (p values) for the mandibular P4

	Fligner-Killeen		Lewontin CV Ratio	
	Sterkfontein versus *Gorilla*	Sterkfontein + Makapansgat versus *Gorilla*	Sterkfontein versus *Gorilla*	Sterkfontein + Makapansgat versus *Gorilla*
MD diameter	0.15	0.15	**0.03**	**0.02**
BL diameter	0.83	0.74	0.09	0.13
Total crown area	0.13	0.81	**0.01**	**0.02**
Metaconid area	0.72	0.76	0.08	0.08
Protoconid area	0.78	0.74	0.20	0.25
Talonid area	0.74	0.68	0.16	0.20

Statistically significant values in boldface

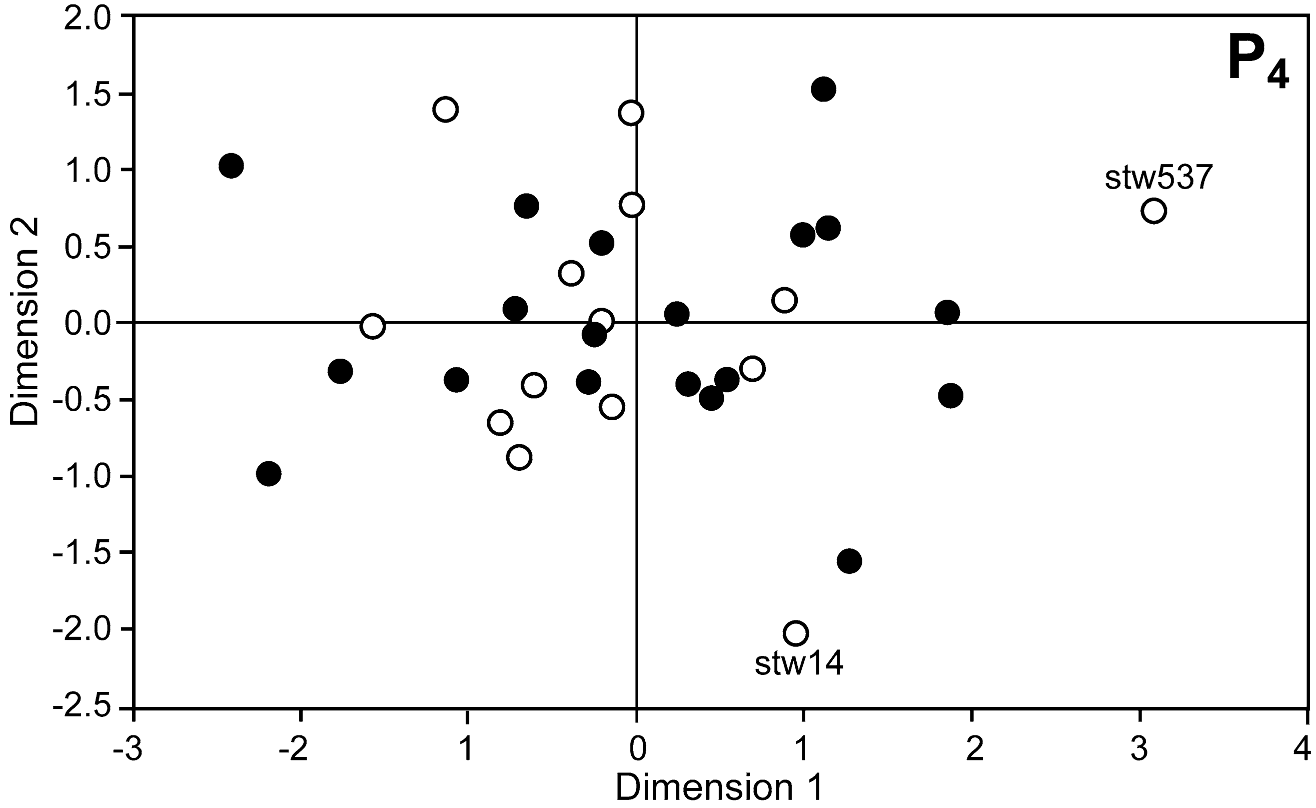

Fig. 8.5 Multidimensional scaling plot of fossil hominin (*open symbols*) and *Gorilla* (*solid symbols*) mandibular P4s. *Open circles* Sterkfontein specimens. Metaconid and talonid areas are significantly associated with dimension 1 coordinates; protoconid area is significantly associated with dimension 2 coordinates

($r = 0.864$; $p < 0.01$) and talonid ($r = -0.942$; $p < 0.01$) areas and dimension 1 coordinates, and a between protoconid area ($r = -0.985$; $p < 0.01$) and dimension 2 coordinates in the fossil sample.

Mandibular First Molar

The statistics pertaining to the variables recorded for the M_1 in the Sterkfontein, combined Sterkfontein/Makapansgat, and *Gorilla* samples are recorded in Table 8.7, and comparisons between the fossil and recent samples are provided in Table 8.8.

It should be noted that 19 % of Sterkfontein M_1s and 22 % of the combined fossil hominin sample exhibit a C6, whereas 44 % of Sterkfontein M_1s and 39 % of the combined fossil sample have a C7. The vast majority of Sterkfontein M_1s (87 %) and some 89 % of the combined fossil sample exhibit a protostylid. By contrast, the C6 is comparatively common on gorilla M_1s (38 %), while the C7 is comparatively rare (6 %). Only 11 % of *Gorilla* M_1s were seen to exhibit a protostylid, and it tends to be more weakly expressed than in the hominin sample.

The Lewontin and Fligner-Killeen tests reveal significantly greater variation in both fossil samples than in the gorilla sample with respect to entoconid I area. The difference is clearly related to this measurement being affected by the presence of a C6 and/or C7 adjacent to it, and the fact that the samples are polymorphic with regard to these accessory cuspulids. The Sterkfontein and combined fossil samples are associated with noticeably lower CVs than the gorilla sample with regard to the hypoconid and hypoconulid I areas, although these differences are not statistically significant. Here too, the differences between the fossil and extant samples are undoubtedly related to the variable presence of a C6.

Figure 8.6 depicts the MDS plot of the hominin and *Gorilla* M_1s. There is only one potential outlier to the fossil cluster; Stw 566 is somewhat separated from the others along dimension 2. It is noteworthy that Stw 151 and MLD 2 fall comfortably within the Sterkfontein sample distribution. Taung is a close neighbor of Stw 246.

With regard to the fossil sample, Pearson product-moment correlations reveal significant association between

Table 8.7 Fossil hominin and *Gorilla* sample statistics for the mandibular M1

	Sterkfontein			Sterkfontein + Makapansgat + Taung			*Gorilla*		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
MD diameter	14.3	0.9	6.3	14.1	0.9	6.7	15.8	1.0	6.6
BL diameter	12.4	0.8	6.5	12.6	0.8	6.7	13.1	0.9	7.1
Total crown area	152.7	18.6	12.2	153.7	17.5	11.4	180.9	24.0	13.2
Protostylid area	5.8	1.8	30.0	6.0	1.7	29.1	10.4	3.5	33.2
Protoconid I area	20.8	2.5	11.8	20.7	2.4	11.5	42.2	6.1	14.5
Protoconid II area	24.6	2.1	8.7	24.4	2.3	9.3	46.0	5.6	12.2
Metaconid I area	22.8	2.5	11.0	22.8	2.4	10.3	43.3	5.7	13.1
Metaconid II area	23.0	2.0	8.6	23.0	1.9	8.1	43.6	5.6	12.9
Entoconid I area	15.3	3.5	23.0	15.2	3.5	23.2	27.8	5.8	20.8
Entoconid II area	16.0	3.1	19.7	16.0	3.4	21.4	29.9	6.5	21.7
Hypoconid area	22.7	1.3	5.8	22.5	1.7	7.7	38.1	5.0	13.1
Hypoconulid I area	15.6	2.3	14.6	15.6	2.2	13.8	26.7	5.5	20.8
Hypoconulid II area	16.0	2.5	15.5	16.1	2.4	14.7	28.5	5.2	18.2
C6 area	4.5	0.9	20.6	4.8	1.0	20.5	4.2	2.3	27.2
C7 area	4.2	3.3	79.3	4.2	3.3	79.3			

Table 8.8 Results of Fligner-Killeen and Lewontin CV Ratio tests (p values) for the mandibular M1

	Fligner-Killeen		Lewontin CV Ratio	
	Sterkfontein versus *Gorilla*	Sterkfontein + Makapan + Taung versus *Gorilla*	Sterkfontein versus *Gorilla*	Sterkfontein + Makapan + Taung versus *Gorilla*
MD diameter	0.27	0.60	0.44	0.47
BL diameter	0.35	0.59	0.35	0.39
Total crown area	0.18	0.11	0.37	0.26
Protostylid area	0.35	0.36	0.31	0.34
Protoconid I area	0.24	0.81	0.18	0.15
Protoconid II area	0.81	0.12	0.24	0.16
Metaconid I area	0.77	0.31	0.10	0.15
Metaconid II area	0.77	0.30	0.18	0.24
Entoconid I area	**0.02**	**0.02**	**0.01**	**0.00**
Entoconid II area	0.11	0.20	0.10	0.25
Hypoconid area	0.11	0.67	0.10	0.42
Hypoconulid I area	0.61	0.50	0.44	0.35
Hypoconulid II area	0.93	0.10	0.13	0.17
C6 area	0.31	0.41	0.36	0.29

Statistically significant values in boldface

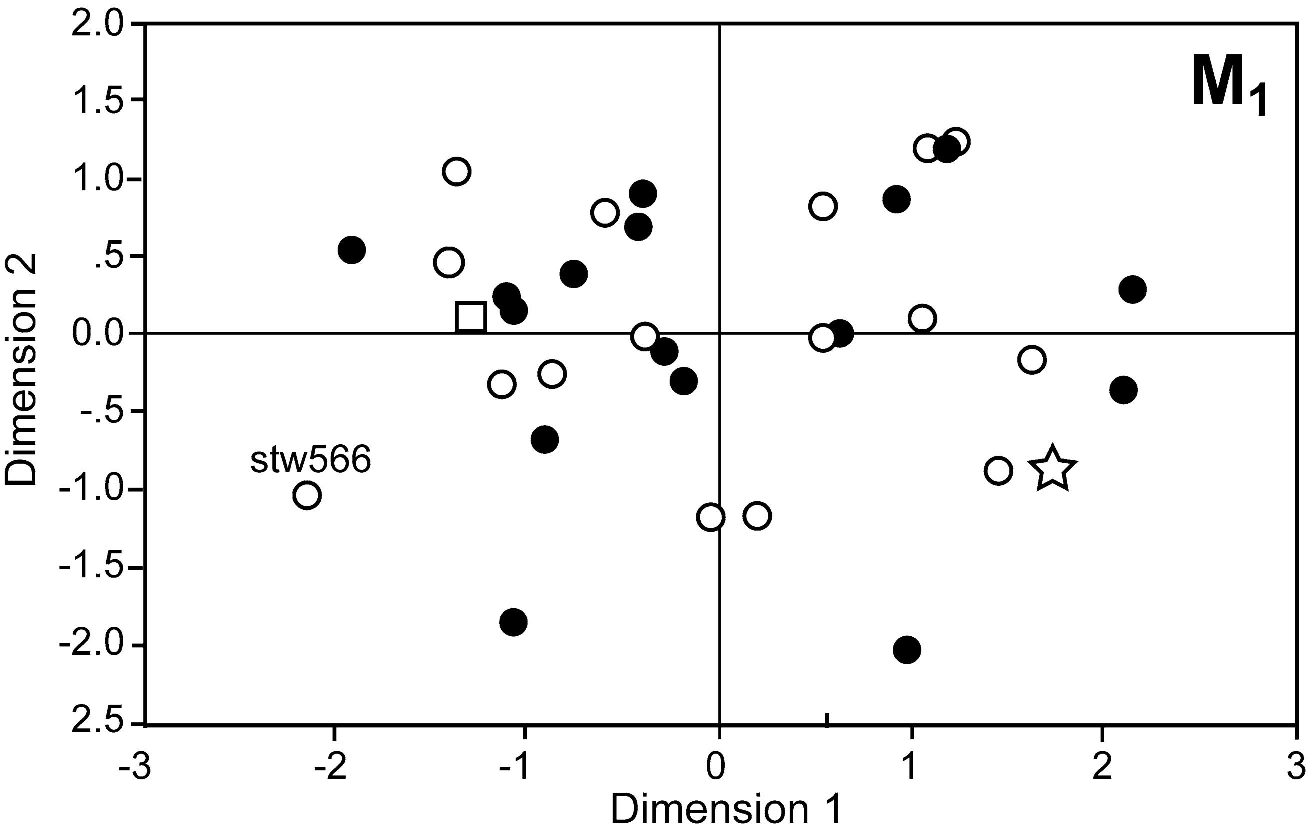

Fig. 8.6 Multidimensional scaling plot of fossil hominin (*open symbols*) and *Gorilla* (*solid symbols*) mandibular M1s. *Open circles* Sterkfontein specimens; *open squares* Makapansgat specimens; *open star* Taung specimen. Entoconid and hypoconulid areas are significantly associated with dimension 1 coordinates; metaconid and hypoconid areas are significantly associated with dimension 2 coordinates

entoconid ($r = 0.981$; $p < 0.01$ and $r = 0.957$; $p < 0.01$) and hypoconulid areas ($r = 0.591$; $p < 0.01$ and $r = 0.484$; $p < 0.01$) and dimension 1 coordinates, and between metaconid ($r = 0757$; $p < 0.01$ and $r = 0.775$; $p < 0.01$) and hypoconid areas ($r = -0.686$; $p < 0.01$ and $r = -0.784$; $p < 0.01$) and dimension 2 coordinates.

Mandibular Second Molar

The statistics pertaining to the variables recorded for the M_2 in the Sterkfontein, combined Sterkfontein/Makapansgat, and *Gorilla* samples are provided in Table 8.9, and comparisons between the fossil and recent samples are recorded in Table 8.10.

Some 50 % of Sterkfontein M_2s and 44 % of the combined fossil sample exhibit a C6, and in keeping with the first molar frequencies, 41 % of Sterkfontein and 42 % of Sterkfontein/Makapansgat M_2s have a C7. As with the first molars, the vast majority of Sterkfontein (80 %) and Sterkfontein/Makapansgat (81 %) M_2s evince a protostylid. The C6 is also comparatively common on *Gorilla* M_2s (58 %), whereas both the C7 are protostylid are absent from this molar sample.

The Lewontin CV and Fligner-Killeen tests indicate significant differences between the fossil and *Gorilla* samples in the amount of variation in relative protoconid area. The variable presence of the protostylid in the former and its complete absence in the latter is responsible for this observation. The Lewontin CV test also indicates significant differences in the entoconid and C6 areas. Inasmuch as the former is affected by the presence of the latter, it would appear that the variable occurrence of the C6 is responsible for this difference.

Figure 8.7 depicts the MDS plot of the hominin and *Gorilla* M_2s. There are two outliers among the fossils; Stw 3 is clearly separated from the cluster along dimension 1, and Stw 420 is somewhat isolated along dimension 2. With regard to its P_3, however, Stw 420 clusters comfortably among the other fossil specimens. It is noteworthy that MLD 2 and MLD 24 fall within the Sterkfontein sample distribution. The PPM correlations reveal significant

Table 8.9 Fossil hominin and *Gorilla* sample statistics for the mandibular M2

	Sterkfontein			Sterkfontein + Makapansgat			*Gorilla*		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
MD diameter	16.2	1.2	7.5	16.1	1.2	7.6	17.6	1.3	7.4
BL diameter	14.2	1.2	8.6	14.3	1.2	8.1	14.8	1.2	8.0
Total crown area	199.2	33.2	16.6	198.8	31.2	15.7	225.8	30.1	13.3
Protostylid area	6.2	3.1	49.8	6.2	3.1	49.8			
Protoconid I area	22.9	3.2	13.8	23.0	3.0	13.3	24.7	1.7	6.8
Protoconid II area	26.1	2.5	9.5	25.9	2.5	9.6	24.9	1.6	6.6
Metaconid I area	21.7	2.3	10.5	21.6	2.2	10.2	24.5	2.3	9.4
Metaconid II area	22.3	1.8	8.0	22.3	1.8	7.9	24.5	2.3	9.4
Entoconid I area	15.0	2.4	16.1	15.1	2.3	15.4	14.8	2.2	14.8
Entoconid II area	16.5	3.1	18.8	16.6	3.0	17.9	17.2	2.2	12.9
Hypoconid area	21.7	2.2	10.1	21.7	2.1	9.7	19.9	2.3	11.8
Hypoconulid I area	13.9	2.1	14.8	14.1	2.0	14.4	16.1	2.6	16.3
Hypoconulid II area	15.1	2.0	13.2	15.1	1.9	12.7	17.9	2.0	11.3
C6 area	4.7	2.5	52.9	4.7	2.5	52.9	6.5	1.7	26.2
C7 area	4.4	1.7	37.8	4.5	1.5	33.5			

Table 8.10 Results of Fligner-Killeen and Lewontin CV Ratio tests (p values) for the mandibular M2

	Fligner-Killeen		Lewontin CV Ratio	
	Sterkfontein versus *Gorilla*	Sterkfontein + Makapansgat versus *Gorilla*	Sterkfontein versus *Gorilla*	Sterkfontein + Makapansgat versus *Gorilla*
MD diameter	0.40	0.38	0.47	0.47
BL diameter	0.47	0.56	0.37	0.49
Total crown area	0.19	0.28	0.16	0.24
Protoconid I area	**0.00**	**0.00**	**0.00**	**0.00**
Protoconid II area	0.17	0.12	0.55	0.05
Metaconid I area	0.30	0.34	0.31	0.36
Metaconid II area	0.72	0.75	0.24	0.22
Entoconid I area	0.40	0.61	0.36	0.44
Entoconid II area	0.18	0.25	**0.05**	0.08
Hypoconid area	0.82	0.15	0.26	0.19
Hypoconulid I area	0.61	0.64	0.34	0.29
Hypoconulid II area	0.24	0.29	0.25	0.32
C6 area	0.10	0.10	**0.02**	**0.02**

Statistically significant values in boldface

association of protostylid ($r = -0.749$; $p < 0.01$), protoconid II ($r = -0.646$; $p < 0.01$), entoconid ($r = 0.796$; $p < 0.01$ and $r = 0.970$; $p < 0.01$), hypoconid ($r = -0.677$; $p < 0.01$) and C6 area ($r = 0.840$; $p < 0.01$) with dimension 1 coordinates. Only protoconid I area ($r = 0.912$; $p < 0.01$) is significantly associated with dimension 2.

Mandibular Third Molar

The statistics pertaining to the variables recorded for the M$_2$ in the Sterkfontein, combined Sterkfontein/Makapansgat, and *Gorilla* samples are given in Table 8.11, and comparisons between the fossil and recent samples are provided in Table 8.12.

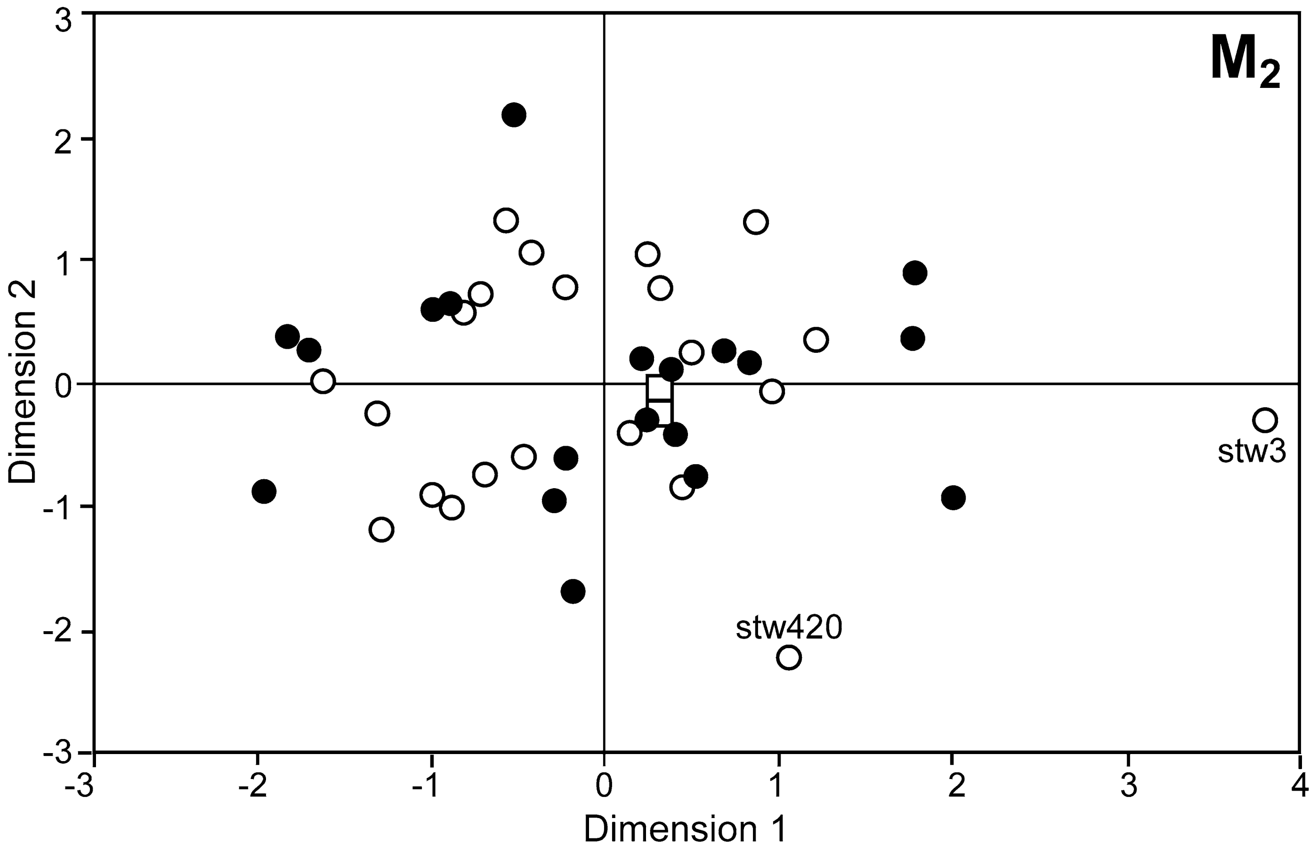

Fig. 8.7 Multidimensional scaling plot of fossil hominin (*open symbols*) and *Gorilla* (*solid symbols*) mandibular M2s. *Open circles* Sterkfontein specimens; *open squares* Makapansgat specimens. Protoconid II, protostylid, entoconid, hypoconid and C6 areas are significantly associated with dimension 1 coordinates; protoconid I area is significantly associated with dimension 2 coordinates

Table 8.11 Fossil hominin and *Gorilla* sample statistics for the mandibular M3

	Sterkfontein			Sterkfontein + Makapansgat			*Gorilla*		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
MD diameter	16.7	1.4	8.5	16.5	1.4	8.5	18.1	1.6	8.9
BL diameter	15.1	1.2	8.2	14.8	1.2	7.8	14.1	1.4	10.2
Total crown area	215.6	31.2	14.5	207.0	32.0	15.4	213.2	36.4	17.1
Protostylid area	6.0	2.2	36.2	6.0	2.2	36.2	3.4	0.4	10.3
Protoconid I area	23.0	2.8	12.2	23.3	2.7	11.6	25.1	3.7	14.9
Protoconid II area	27.2	3.8	13.9	26.6	3.6	13.6	25.4	3.4	13.3
Metaconid I area	21.3	3.3	15.4	21.2	3.2	15.3	22.9	3.5	15.1
Metaconid II area	22.6	2.5	11.1	22.5	2.6	11.8	24.0	3.3	13.8
Entoconid I area	13.3	2.6	19.4	13.5	2.6	19.3	12.4	2.0	16.2
Entoconid II area	16.9	3.0	17.7	17.2	3.2	18.5	15.1	3.1	20.3
Hypoconid area	19.9	2.5	12.7	19.5	2.4	12.4	19.4	2.1	11.1
Hypoconulid I area	12.9	4.1	31.8	13.0	3.7	28.4	17.0	4.3	25.4
Hypoconulid II area	15.2	3.6	24.0	15.2	3.5	22.7	18.5	3.5	19.1
C6 area	6.7	1.6	24.0	6.9	1.5	22.4	7.6	2.6	33.8
C7 area	6.2	3.0	47.6	5.6	2.8	50.2	6.4	1.8	28.5

Table 8.12 Results of Fligner-Killeen and Lewontin CV Ratio tests (p values) for the mandibular M3

	Fligner-Killeen		Lewontin CV Ratio	
	Sterkfontein versus *Gorilla*	Sterkfontein + Makapansgat versus *Gorilla*	Sterkfontein versus *Gorilla*	Sterkfontein + Makapansgat versus *Gorilla*
MD diameter	0.36	0.46	0.34	0.48
BL diameter	0.12	0.76	0.19	0.31
Total crown area	0.42	0.27	0.25	0.49
Protostylid area	0.76	0.24	**0.01**	0.22
Protoconid I area	0.73	0.67	0.22	0.14
Protoconid II area	0.28	0.34	0.42	0.49
Metaconid I area	0.24	0.23	0.47	0.49
Metaconid II area	0.54	0.52	0.20	0.23
Entoconid I area	0.20	0.23	0.23	0.27
Entoconid II area	0.62	0.63	0.31	0.32
Hypoconid area	0.40	0.39	0.29	0.29
Hypoconulid I area	0.36	0.44	0.18	0.36
Hypoconulid II area	0.17	0.12	0.18	0.25
C6 area	0.22	0.59	0.21	0.16
C7 area	0.88	0.07	0.12	0.12

Statistically significant values in boldface

The M_3 exhibits a high frequency of the C6 in the Sterkfontein (79 %) and combined Sterkfontein/Makapansgat (76 %) samples, and the C7 is present on 50 % of the Sterkfontein and 53 % of the combined sample molars. The vast majority of Sterkfontein (94 %) and Sterkfontein/Makapansgat (85 %) M_3s have a protostylid, and most are at least moderately developed. With regard to *Gorilla* M_3s, the C6 and C7 are moderately common (37 % incidence for both cuspulids). As with the M_1, only some 11 % of *Gorilla* M_3s exhibit a protostylid, and here too it tends to be more weakly expressed than on the hominin crowns.

The Lewontin CV ratio test reveals significantly greater variation in the Sterkfontein than the *Gorilla* samples with respect to the relative area of the protostylid. According to the Fligner-Killeen test, there is no significant difference in variation between the fossil and gorilla samples.

Figure 8.8 depicts the MDS plot of the hominin and *Gorilla* M_3s. There is one potential outlier among the fossils; Stw 498 shows some degree of separation along dimension 1. Stw 14, which was observed to be an outlier in the P_4 analysis, lies in the center of the Sterkfontein sample M_3 distribution.

With regard to the fossil sample, PPM correlations reveal significant association of protoconid ($r = -0.873$; $p < 0.01$ and $r = -0.503$; $p < 0.01$) and hypoconid ($r = 0.752$; $p < 0.01$) areas with the dimension 1 coordinates; only hypoconulid area ($r = -0.645$; $p < 0.01$) is significantly associated with dimension 2.

Discussion

Table 8.13 summarizes the mandibular premolar variables in which the fossil assemblages display significantly greater variation than a similarly sized *G. gorilla* sample. According to the Lewontin CV test, morphometric variation in the Sterkfontein (and the combined Sterkfontein and Makapansgat) samples is significantly greater for total crown area in both premolars; relative P_3 metaconid area and P_4 MD diameter are also more variable in the Sterkfontein sample. None of the differences between the Sterkfontein and *Gorilla* samples indicated by the CV ratio test is supported by the Fligner-Killeen mean dispersion test, but this might

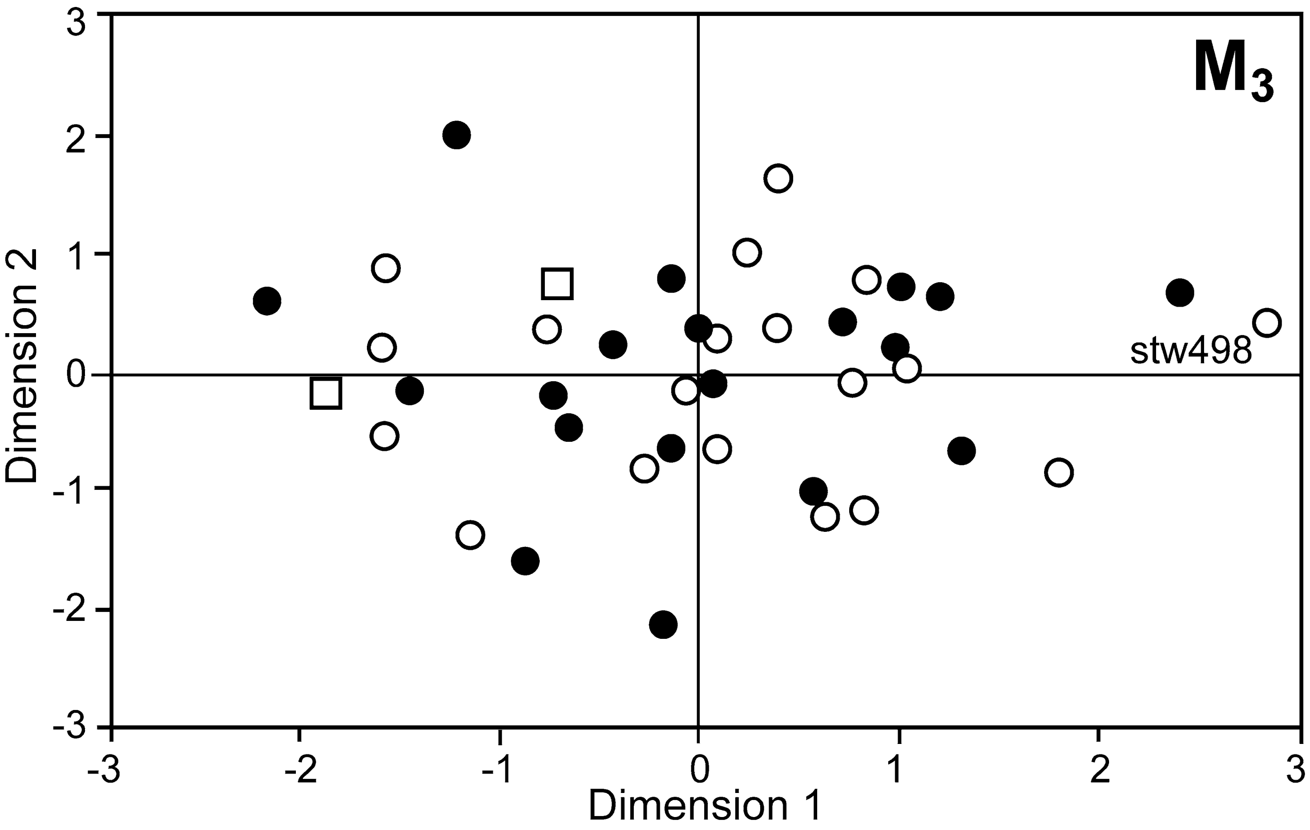

Fig. 8.8 Multidimensional scaling plot of fossil hominin (*open symbols*) and *Gorilla* (*solid symbols*) mandibular M3s. *Open circles* Sterkfontein specimens; *open squares* Makapansgat specimens. Protoconid and hypoconid areas are significantly associated with dimension 1 coordinates; hypoconulid area is significantly associated with dimension 2 coordinates

Table 8.13 Summary of mandibular premolar variables in which the Member 4 Sterkfontein hominin sample exhibits significantly greater variation than a similarly sized *Gorilla* sample (represented by XXX)

	P_3		P_4	
	CV Ratio	F-K Test	CV Ratio	F-K Test
MD diameter			XXX	
BL diameter				
Total crown area	XXX		XXX	
Metaconid area	XXX			
Protoconid area				
Talonid area				

be expected, given its more conservative nature (Donnelly and Kramer 1999).

The difference in the variation exhibited by P_3 metaconid size can be attributed to functional differences in this tooth between *Gorilla* and *Australopithecus*. Thus, the greater variability in the size of the metaconid in the Sterkfontein sample is simply related to the fact that gorilla P_3s are characterized by a greatly enlarged, honing protoconid and a tremendously reduced or absent metaconid. The greater variability in p_4 size in the Sterkfontein hominin sample, however, defies such explanation.

Table 8.14 summarizes the mandibular molar variables in which the Sterkfontein Member 4 sample displays significantly greater variation than a similarly sized *G. gorilla* sample. According to the Lewontin CV and Fligner-Killeen tests, the Sterkfontein (as well as the Sterkfontein + Makapansgat + Taung) M_1 sample is significantly more variable in the proportional area of the entoconid. This is almost certainly related to the fact that 44 % of Sterkfontein M_1s (and 39 % of the combined fossil sample molars) have a C7, whereas it is very rare (6 %) on gorilla homologues.

Similarly, according to the Lewontin CV ratio test, the Sterkfontein (and combined Sterkfontein and Makapansgat) M_2 sample exhibits significantly greater variation than the *Gorilla* sample in the proportional area of the entoconid. There is also a difference in C6 size variation. Whereas the C6 is present in roughly equivalent proportions of Sterkfontein (50 %) and *Gorilla* (58 %) M_2s. The variation in its proportional size differs significantly between them. A C7 occurs in 41 % of Sterkfontein individuals but is absent from the gorilla sample. Thus, the C7 would also seem to be

Table 8.14 Summary of mandibular molar variables in which the Member 4 Sterkfontein hominin sample exhibits significantly greater variation than a similarly sized *Gorilla* sample (represented by XXX)

	M_1		M_2		M_3	
	CV Ratio	F-K Test	CV Ratio	F-K Test	CV Ratio	F-K Test
MD diameter						
BL diameter						
Total crown area						
Protostylid area					XXX	
Protoconid area			XXX	XXX		
Metaconid area						
Entoconid area	XXX	XXX	XXX			
Hypoconid area						
Hypoconulid area						
C6 area			XXX			
C7 area						

at least partly responsible for the difference in entoconid size variability between the fossil and gorilla samples. The Lewontin CV and Fligner-Killeen tests indicate significantly greater variation in the Sterkfontein (and the combined Sterkfontein + Makapansgat + Taung) M_2 sample in the proportional area of the protoconid. This, in turn, is likely related to the difference in protostylid incidence, where the great majority of Sterkfontein M_2s (80 %) have it but it is wholly lacking in the gorilla sample.

In the third molar, the Sterkfontein sample exhibits significantly more variability than the *Gorilla* sample only with regard to the proportional size of the protostylid. Most Sterkfontein M_3s (94 %) have a protostylid, and it tends to be at least moderately developed, whereas only 11 % of *Gorilla* M_3s exhibit this trait, which tends to be more weakly expressed than on hominin homologues.

The results of the CV ratio and Fligner-Killeen tests do not support the molar size heterogeneity that has been suggested by previous studies (Kimbel and White 1988; Calcagno et al. 1999), although this has been attributed only to the maxillary M2. The greater degree of variation expressed in the mandibular molars from Sterkfontein appears to be related to the variable incidence and expression of the accessory cuspulids (C6 and/or C7) and the protostylid, and these features vary in incidence and expression in other fossil hominin species (e.g., *P. robustus* and *A. afarensis*) as well as among modern human populations (Keene 1994; Scott and Turner 1997; Pilbrow 2003; Hlusko 2004; Guatelli-Steinberg and Irish 2005; Bailey and Wood 2007; Skinner et al. 2008a, b). It would seem prudent, therefore, to follow a conservative interpretation of the morphometric variation exhibited by the Sterkfontein molars rather than to ascribe taxonomic heterogeneity to it.

No Sterkfontein specimen represented at more than one mandibular postcanine position was consistently positioned as an outlier to the others according to the MDS ordinations. Thus, for example, while the P_3 of Stw 213 is a comparative outlier, its P_4 and M_2 fall comfortably within the Sterkfontein sample clusters. This suggests that distinction at one tooth position does not imply distinction at another.

Although mandibular teeth are not available for every Sterkfontein specimen for which taxonomic distinction has been suggested, some of the fossils that have been so identified were included in this study. Thus, Clarke's (1988) argument that MLD 2 belongs to a separate group from Sts 52 and Taung is contradicted by the MDS scaling plots, which place MLD 2 in close proximity to Sts 52 with regard to all three of its teeth (P_3, M_1 and M_3). Similarly, in the MDS ordination of the M_1, Stw 151, which has been suggested to be derived in relation to other Sterkfontein Member 4 specimens (Spoor 1993; Schwartz 1997; Moggi-Cecchi et al. 1998), is close to the center of the Sterkfontein sample scatter.

While it might be argued that the CV ratio and Fligner-Killeen tests employed here (like all tests that involve the CV) cannot reliably falsify a single species hypothesis (Kelley and Plavcan 1998; Plavcan and Cope 2001), the results do not provide compelling evidence for rejection of the null hypothesis that the Sterkfontein Member 4 hominin assemblage comprises a single species. At the same time, however, it is noteworthy that of all the variables measured, in not a single instance was the *G. gorilla* sample found to be significantly more variable than the Sterkfontein sample. Similarly, while the differences in molar variability should probably not be viewed as attesting to multiple species in the Sterkfontein assemblage, the differences in premolar crown size are more intriguing. They—perhaps in concert with maxillary second molar size—may hint at taxonomic heterogeneity. However, they might also be related to temporal heterogeneity of the sample if the Sterkfontein Member 4 assemblage represents a considerable time aggregate, as suggested by Clarke (1985) and Kimbel and White (1988).

Until recently, age estimates for the Sterkfontein deposits have been based solely upon biochronological evidence (Cooke 1974; Vrba 1974, 1975, 1985, 1995; Delson 1988; McKee et al. 1995; Berger et al. 2002). However, these estimates have ranged rather widely for the Member 4 faunal assemblage (e.g., between ca. 3.0 and 2.4 Ma and between 2.5 and 1.5 Ma). One of the potential problems with the use of faunal remains from these deposits is the presence of some taxa that suggest considerable antiquity together with others (e.g., *Equus*, *Damaliscus*, and possibly *Papio*) that indicate a comparatively recent age. Recently, though, Clarke (2002) has dismissed the occurrence of at least some of the latter, citing taxonomic misidentification or admixture from Member 5.

Schwarcz et al. (1994) provided a wide range of dates (2.8–1.26 Ma) for Sterkfontein Member 4 based on ESR of tooth enamel, but opined that the bimodal distribution they obtained suggested a mixing of Member 5 and Member 4 fossils. Paleomagnetism studies have been applied also to this karst deposit (Brock et al. 1977; McFadden et al. 1979; Partridge et al. 2000a, b; Herries 2003a, b; Thackeray et al. 2004), but these determinations have not been wholly consistent and without controversy, and they are ultimately controlled by dates derived from biochronological estimates.

In some instances, the paleomagnetic signatures have even been used to interpolate sedimentation rates in the Sterkfontein deposits and these, in turn, have been used to infer ages for the hominin fossils (e.g., 3.3 Ma for Stw 573 from Member 2 (Partridge et al. 1999)). Terrestrial cosmogenic nuclides have been employed in an attempt to provide a depositional date for Sterkfontein hominin fossils (Partridge et al. 2003; Muzikar and Granger 2006; Walker et al. 2006), but these too have resulted in a wide range of values. Thus, ages for the underlying, hominin-bearing Member 2 deposit range from ca. 4.0 Ma on ^{26}Al and ^{10}Be measurements (Partridge et al. 2003) to some 2.2 Ma on ^{238}U/^{206}Pb determinations from speleothems (Walker et al. 2006). Unfortunately, neither the paleomagnetic estimates nor the nuclide dates that have been proposed for Sterkfontein seem to have provided finer resolution to the biochronological estimates for Member 4.

The temporal depth represented by the Sterkfontein Member 4 deposit need not be very great to accommodate a single species whose level of variation in a few morphometric features of the dentition appears to exceed that of the western lowland gorilla. As such, and under the caveat that only mandibular postcanine occlusal traits were examined here, the results of the present study would not necessarily seem to contradict arguments that a single, polymorphic species, *A. africanus*, is represented in the Sterkfontein Member 4 deposits. Indeed, temporal heterogeneity and/or exaggerated sexual dimorphism have been cited in analyses of other fossil assemblages to conclude that they comprise the remains of a single species (e.g., Kelley and Xu 1991; Richmond and Jungers 1995; Lockwood et al. 1996).

We recognize, of course, that the methods employed here would not be able to differentiate between two (or more) taxa if they do not differ (or differ only very subtly) in mandibular postcanine occlusal morphology. As noted by Moggi-Cecchi (2003), if two (or more) hominin taxa are present in the Sterkfontein Member 4 assemblage, they may not be represented equally by cranial and dental elements. As such, mandibular premolars and molars alone may not serve to rule out the possibility of the existence of two (or more) species in the assemblage. Furthermore, we have not tested the hypothesis of multiple species in the Sterkfontein assemblage against a mixed sample of extant taxa, and nor have we examined whether a mixed species sample (e.g., *Pan paniscus* and *Pan troglodytes*) could be successfully identified as such against the *Gorilla* sample employed here. These are intriguing approaches that should be addressed in future studies.

Conclusions

The hominin fossils from the Member 4 deposits at Sterkfontein, South Africa are most commonly attributed to *A. africanus*, although a number of studies have suggested that they represent more than one species. However, there is no consensus among those who recognize two (or more) taxa in this assemblage as to the allocation of individual specimens. Absolute crown dimensions as well as proportional cusp areas of the mandibular postcanine teeth, which constitute the bulk of the Sterkfontein Member 4 fossils, were examined to determine whether the degree of variation in this assemblage exceeds that of a living, highly dimorphic hominid species, *G. gorilla*. The Lewontin CV test and the Fligner-Killeen test were employed to evaluate the degree of variation within the fossil and recent samples at each premolar and molar position.

Morphometric variation in Sterkfontein (and in the combined Sterkfontein and Makapansgat) premolar sample is significantly greater than that of the gorilla with regard total crown area of the P_3 and P_4, relative metaconid area of the P_3, and the MD diameter of the P_4. While the difference in P_3 metaconid size variability can be attributed to functional differences in this tooth between *Gorilla* and *Australopithecus*, where gorilla P_3s are characterized by a greatly enlarged, honing protoconid and a tremendously reduced to absent metaconid the variability in premolar size in the Sterkfontein hominin assemblage defies such explanation.

Those instances in which the Sterkfontein molars exhibit significantly greater variability than gorilla homologues appear to be related to the variable expression of the accessory cuspulids (C6 and/or C7) and the protostylid. Inasmuch as these same features vary in incidence and expression in other fossil hominin species (e.g., *P. robustus* and *P. afarensis*) and among modern human populations (Keene 1994; Scott and Turner 1997; Pilbrow 2003; Hlusko 2004; Guatelli-Steinberg and Irish 2005; Bailey and Wood 2007; Skinner et al. 2008a, b), it would seem imprudent to attribute such variation to taxonomic heterogeneity in the

Sterkfontein assemblage. The variability in Sterkfontein premolar crown size is more intriguing and—perhaps in concert with that displayed by the maxillary second molar (Kimbel and White 1988; Calcagno et al. 1999)—may hint at taxonomic heterogeneity. However, this variability may also be related to temporal heterogeneity if the Sterkfontein Member 4 deposit represents a considerable time aggregate. Unfortunately, despite attempts to obtain absolute dates for the Sterkfontein Member 4 deposit, its precise geochronology remains maddeningly elusive. We simply do not know how much time was involved in its accumulation, although it need not be substantial to account for a single species whose level of variation in several morphometric features of the dentition appears to exceed that of the western lowland gorilla. Indeed, temporal heterogeneity and exaggerated sexual dimorphism have been cited in analyses of other fossil assemblages to conclude that they represent a single species (e.g., Kelley and Xu 1991; Richmond and Jungers 1995; Lockwood et al. 1996).

As such, and under the caveat that only mandibular postcanine dental traits were examined here, the results of the present study would not necessarily seem to contradict arguments that a single, polymorphic species, *A. africanus*, is represented in the Sterkfontein Member 4 deposits.

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Chapter 9
Australopithecus sediba from Malapa, South Africa

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Abstract First discovered in August of 2008, the site of Malapa, South Africa revealed two relatively complete partial skeletons that we assigned to a new species, *Australopithecus sediba*. Additional individuals have since been detected, and await excavation at the site. It appears that these hominins were washed into the cave through a deep vertical shaft, likely in a single depositional event resulting from a large storm inflow. Burial and cementation were rapid, occasioning the exceptional preservation of these skeletons. Uranium-lead and paleomagnetic dating combine to precisely constrain the age of the site to 1.977 ± 0.0015 Ma. Cranial and postcranial remains of *A. sediba* demonstrate numerous australopith-like features that denote a hominin at an australopith adaptive grade, prompting its inclusion in the genus *Australopithecus*. However, *A. sediba* also displays a series of characters that align it more closely with *Homo* than any other australopith species. We consider the evidence supporting the appearance of *Homo* prior to 1.977 Ma to be inconclusive, therefore we hypothesize that *A. sediba* from Malapa could be ancestral to *Homo*. Alternatively, if the existence of *Homo* prior to 1.977 Ma can be confirmed, this would not preclude a population of *A. sediba* that predated Malapa from occupying this role. Therefore we hypothesize that *A. sediba* indeed represents the ancestor of the genus *Homo*.

> "Every fossil that might potentially be intermediate is always classified as either *Homo* or *Australopithecus*. None is ever classified as an intermediate…. The most perfect intermediate you could possibly imagine would *still* find itself shoehorned into either *Homo* or *Australopithecus*. In fact, it would probably be called *Homo* by half the palaeontologists and *Australopithecus* by the other half. And unfortunately, instead of getting together to agree that ambiguously intermediate fossils are exactly what we should *expect* on the evolution theory, the palaeontologists could probably be relied upon to give an entirely false impression by seeming almost to come to blows over their terminological disagreement."
>
> Richard Dawkins 2009, *The Greatest Show on Earth*

Keywords *Homo* • Skeletal morphology • Taxonomy

Introduction

The recently discovered site of Malapa (site U.W. 88; Zipfel and Berger 2010) represents an especially rich early hominin locality in Africa. It contains the partially articulated and associated skeletal remains of several individuals of the newly recognized species *Australopithecus sediba*, alongside an abundant, well-preserved fauna (Berger et al. 2010; Dirks et al. 2010). It appears that all of these skeletons were accumulated during a seemingly rapid, homogenous depositional event that occurred approximately 1.977 Ma (Dirks et al. 2010; Pickering et al. 2011a). The site of Malapa was first discovered by one of us (LRB) on August 8, 2008, during the course of a geospatial survey for new fossil-bearing cave deposits in the dolomitic region of the Cradle of Humankind World Heritage Area to the northwest of Johannesburg, South Africa (Fig. 9.1). The locality was recognized as a deroofed cave of at least 15 × 10 meters in an area where limited limestone mining had taken place, probably during the late nineteenth or early twentieth century. No scientific or official record of the site was found to exist at the time of discovery, and subsequent research has demonstrated that the site was unknown to science.

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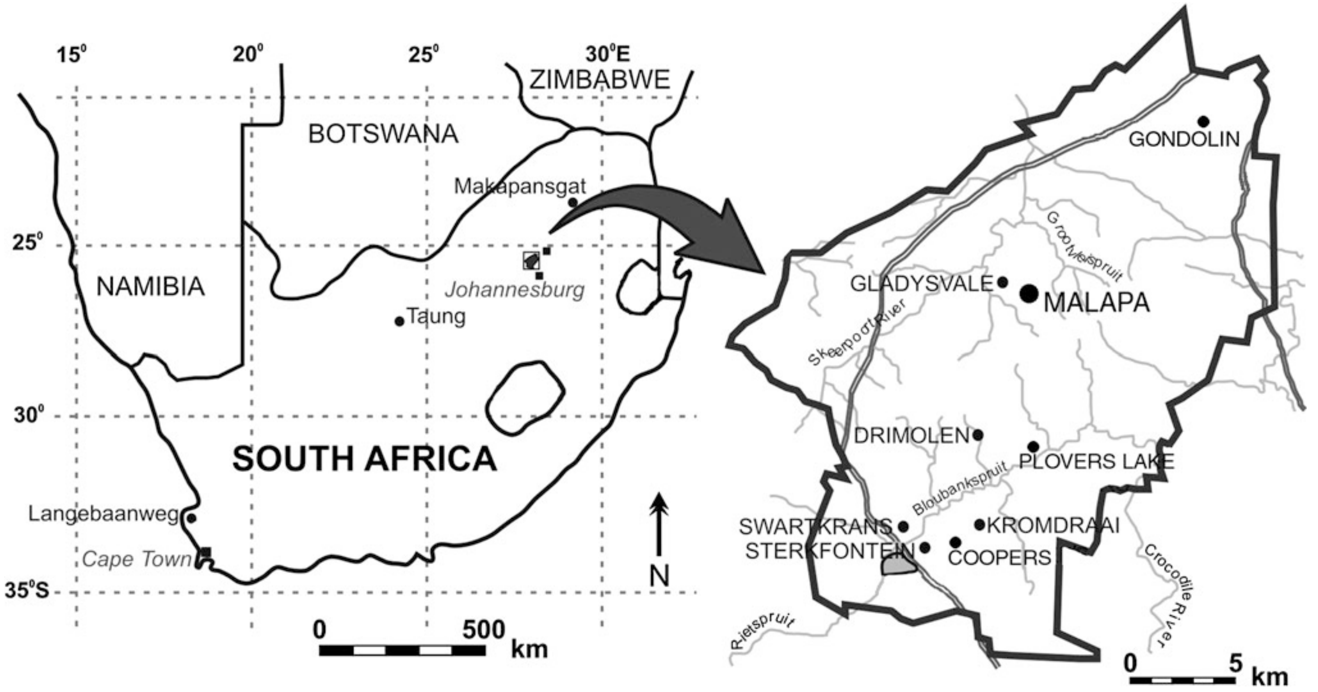

Fig. 9.1 Map of hominin-bearing fossil localities in the Cradle of Humankind World Heritage Area of South Africa. *Solid line* surrounding fossil sites on the right denotes the boundaries of the Cradle of Humankind. Modified from de Ruiter et al. (2009)

On the 15th of August 2008, upon our initial return to the site to investigate its fossil-bearing potential, the first hominin specimens were discovered by Matthew Berger. This discovery prompted considerable interest in the site, as the first specimen recognized, a hominin clavicle, was directly associated with a fragment of a mandible in a single block of ex situ calcified clastic sediment presumably displaced from the in situ locality by limestone miners. In the following weeks we came to recognize the rich potential of the site as more and more skeletal elements were encountered during the course of preparation of this single block, including both cranial and postcranial remains of a relatively complete juvenile individual (MH1, Fig. 9.2). Then, on September 4, 2008, on only the third visit to the site, a second, well-preserved adult partial skeleton and two associated maxillary teeth (MH2) were discovered by LRB in situ in the calcified clastic sediments of the mining pit. Removal of the slightly dislodged, but otherwise in situ block containing the adult hominin MH2 took place in late 2008, and preparation of the specimen revealed a partially articulated upper limb including most of the right scapula, the lateral half of the right clavicle, parts of the thorax, and lower limb elements. During the course of recovery of ex situ material from the site, the remaining parts of the right scapula and clavicle were found in a block that also contained the adult's mandible. Thus by early 2009 it had become clear that we were dealing with at least two relatively complete partial skeletons. These skeletons showed little damage other than a moderate amount of breakage that was due primarily to a series of three or four mining blasts, a small amount of taphonomic damage likely incurred in a massive debris flow as the skeletons were transported to their final resting place, and perhaps some perimortem trauma to a small number of elements of the upper body of MH1. In February of 2009, a block containing the diaphysis of the humerus of MH1 was found by LRB, and during the course of preparation of this specimen, we uncovered a well-preserved partial cranium and several other postcranial elements. This discovery allowed us to reassemble a significant part of the head and body of the juvenile MH1, and continued preparation of the adult MH2 skeleton revealed it to be significantly intact as well. Additional parts of the juvenile cranium and skeleton were discovered in the course of cleaning operations of the surface of the Malapa deposit, allowing us to confidently control the provenience of both specimens within the site.

In this paper we discuss the geological setting from which the hominins were recovered that demonstrates their homogeneity in time and space, outline the characteristics that define *A. sediba*, and discuss the potential taxonomic and phylogenetic implications of this new hominin taxon.

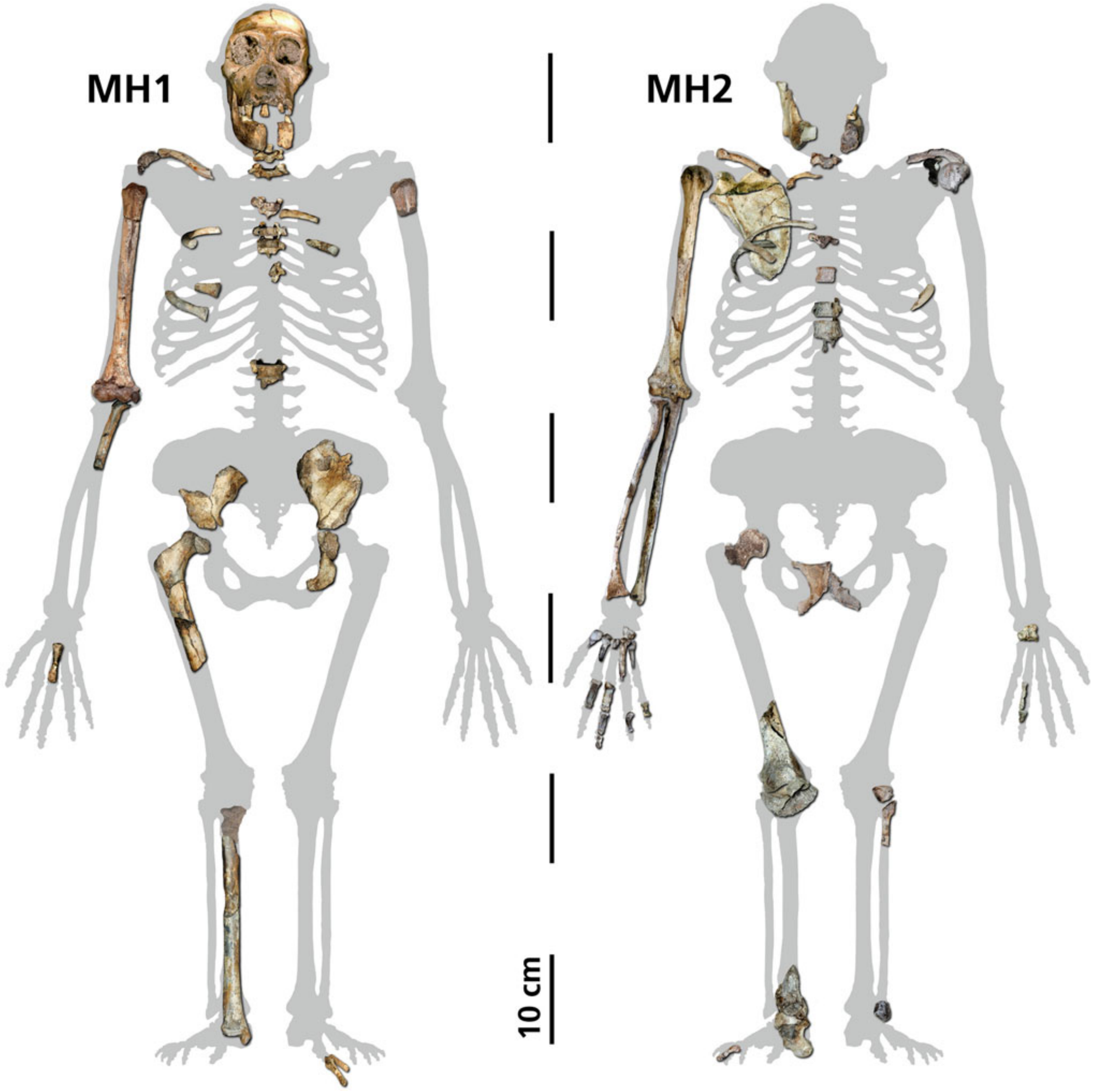

Fig. 9.2 Associated skeletal elements of MH1 (*left*) and MH2 (*right*) in approximate anatomical position. Note that since this image was produced, we have recognized that the right tibia pictured here is from a separate individual, MH4. Picture reprinted with permission of Peter Schmid

Geology and Dating of the Site

Work at Malapa has benefited greatly from geologists and geochronologists having been involved at the site from the very beginning. Dirks et al. (2010) and Pickering et al. (2011a) describe the geology of the area and the site, and provide a more detailed chronological context that we summarize here. The site of Malapa resides at the north end of a series of north–south trending caves housed in a late Archaean dolomite of the Lyttleton Formation of the Malmani Subgroup of the Chuniespoort Group. This is the same formation that houses a number of other fossil-bearing caves, including the site of Gladysvale, which is located only 2 km to the west of Malapa (Berger et al. 1993). The calcified clastic sediments that make up the majority of the Malapa deposit are comprised of five distinct sedimentary facies interspersed with sheets of flowstone. All of the sedimentary facies were deposited by water action or mass flow, and show little evidence of post-depositional compaction. Intrusions in the calcified clastic sediment housing the hominins (Facies D) indicate that the event that transported the only partially decomposed and still partially articulated hominin carcasses to their final resting place occurred as a single depositional episode, perhaps during a single large storm inflow, and that transport was over a very short distance. Cementation of these debris flow sediments was rapid, and as of yet there is no definitive indication of mammalian carnivore damage to any of the specimens. These factors contribute to the high quality of preservation of the Malapa fossils. At present, we interpret these geological data to mean that the hominins and other fauna associated with them somehow entered a natural death trap, likely through the opening of a vertical shaft some several meters above the cave floor. Cosmogenic dating of the surrounding land surface, which allows us to calculate erosion rates, indicates that the cave floor resided approximately 30–50 m below the land surface at the time of deposition. The hominins and other animals were most likely killed by a fall, and their rotting carcasses might have been a factor in attracting the several large carnivores that have also been found in the same sediments. We can only speculate as to why the hominins and other fauna approached the cave in the first place, though at least two possible explanations present themselves. Either they were unaware of its existence, and fell in by accident, or more likely they were attracted to the cave by water or some other resource that was to be had in the vicinity of the cave opening, or within the cave itself, and fell in while attempting to access this resource.

Dating the South African fossil-bearing cave deposits has in the past been notoriously difficult, though recent breakthroughs in the application of a variety of dating techniques have shown tremendous promise. In particular, advances in the use of U–Pb dating have allowed very precisely constrained dates to be recorded for speleothems and flowstones associated with the fossils from sites such as Sterkfontein, Coopers, Swartkrans, and Malapa (Walker et al. 2006; de Ruiter et al. 2009; Dirks et al. 2010; Pickering and Kramers 2010; Pickering et al. 2011b). Examining the fauna associated with the Malapa hominins, taxa such as *Equus* and *Tragelaphus* cf. *strepsiceros* first appear ca. 2.33 Ma in Africa (Brown et al. 1985; Bernor and Armour-Chelu 1999; Berger et al. 2002) providing a maximum age bracket for Malapa, while the presence of *Megantereon whitei*, with its last appearance datum at 1.5 Ma (Lewis and Werdelin 2007), provides a minimum age bracket. Immediately below the adult hominin skeleton is a flowstone seam that provided samples suitable for U–Pb dating. Samples were sent to two separate labs for analysis, which returned independent dates of 2.024 ± 0.062 Ma (Bern) and 2.026 ± 0.021 Ma (Melbourne). These dates are effectively identical within error, and further refine the maximum age estimate for the hominins, whose remains in some places actually contact this flowstone. A normal polarity event is recorded near the base of this flowstone that correlates with the Huckleberry Ridge Subchron [2.05–2.03 Ma (Lanphere et al. 2002)]. Higher up in the same flowstone we detected a reversed polarity event that correlates with the Matuyama Chron (2.03–1.95 Ma). We initially used the transition from the reversed polarity Matuyama Chron to the normal polarity Olduvai Chron at 1.95 Ma (Ogg and Smith 2004) to constrain the age of the Malapa fossils to 1.95–1.78 Ma, since the hominin-bearing sediment (Facies D) records a normal polarity (Dirks et al. 2010). However, subsequent stratigraphic research revealed an additional datable flowstone above the hominin skeletons, with a U–Pb date of ca. 2.048 ± 0.140 Ma (Pickering et al. 2011a); this date appears anomalously older than the U–Pb dates for the flowstone underlying the hominins, though taking the error margins into account results in a not-incompatible range of 2.188–1.908 Ma. Combining the minimum potential U–Pb age of 1.908 Ma with the reversed polarity detected in this new flowstone demonstrates that the flowstone must have formed before the onset of the Olduvai Normal event at 1.95 Ma (i.e. within the Matuyama reversal). Given that the hominin-bearing sediments underlying this reversed polarity flowstone record a normal polarity, these sediments must have been deposited during the short-lived pre-Olduvai normal polarity excursion that is dated to 1.977 ± 0.0015 Ma (Channell et al. 2002). The 3000 year time span reflected in this pre-Olduvai event provides us with an especially precise age estimate for the Malapa fossils, resulting in an age estimate undreamed of in a South African fossil cave.

The Fossil Hominin Sample from Malapa

To date, we have recovered in excess of 200 numbered hominin specimens from Malapa, largely originating from the holotype and paratype skeletons MH1 and MH2. And, while our initial report included only these specimens, we have since recognized an infant (MH3) and another adult individual (MH4) in ex situ blocks of calcified clastic sediment. Continued exploration of in situ cave sediments has revealed traces of possibly more individuals, though this remains to be confirmed. This remarkable hominin assemblage is rendered all the more striking when we note that we have not yet begun excavations, as infrastructure development is still currently underway. The singular exception to this is the removal of the in situ block containing the right upper limb skeleton of MH2, which had been detached from the adjacent matrix by miner's blasting, otherwise we have not disturbed the in situ deposits. Apart from limited blasting by limestone miners at the turn of the last century, the site is in almost pristine condition.

At present, while the MH1 type specimen is the only individual that preserves a cranium, the skeleton of MH2 is more complete, though recovery of additional remains of both individuals from blocks of calcified clastic sediment continues at a substantial pace. As noted in our original descriptions, MH1 preserves much of the cranium, minus the cranial base and much of the right side of the cranial vault (Fig. 9.3). The right half of the mandible is preserved from close to the mandibular symphysis to the complete ascending ramus with condyle, and we have recently recovered portions of the left half of the mandible. All of the maxillary premolars and molars are present, with the third molars still forming in the crypt. The maxillary left lateral incisor is in place, while the isolated right central incisor and canine have been recovered. The right mandibular molars are preserved, including the 3rd molar in the crypt, along with the left canine in a small fragment of the anterior mandible. Postcranially, MH1 preserves portions of the axial skeleton, pectoral girdle, upper limb, pelvic girdle, and lower limb. Some, but not all, secondary growth centers in the humerus, ulna, radius, os coxa, and femur were unfused at the time of death. Combined with the state of eruption and attrition of the dental remains, we estimate that MH1 was at a developmental stage equivalent to a human child of 12–13 years, making it roughly comparable in ontogenetic age to the type specimen of *Homo habilis* (OH7) and the Nariokotome *Homo erectus* skeleton (KNM-WT 15000). The development of the supraorbital torus and glabellar prominence, pronouncement of the canine juga, eversion of the gonial angle of the mandible, relatively large and rugose muscle scars of the postcranial skeleton, and relatively narrow sciatic notch of the pelvis all support the contention that MH1 was a male individual, even in the absence of comparisons with MH2.

MH2 is represented by a relatively complete but fragmented mandible, the damage being more extensive on the left side. Three isolated maxillary teeth and significant portions of the axial skeleton, pectoral girdle, upper limb, pelvic girdle, and lower limb are preserved. All of the teeth of MH2 are relatively worn, while the epiphyseal lines of all observable long bones are completely fused and obliterated, indicating this individual was fully adult at the time of death. Compared to MH1, the mandibular ramus is smaller in height, and the gonial angle less everted (the gonial region in MH2 is damaged and displaced, and reconstruction of this area would minimize the artificial eversion that is presently evident in the specimen). The ramus of MH1 is slightly narrower than MH2, though it is likely that continued growth of this juvenile individual would alter this. Since our initial description of this skeleton, an undistorted partial pelvis of MH2 has been recovered, but unfortunately the specimen lacks the ischium, precluding metric evaluation of sciatic notch morphology as an aid to sex diagnosis. Notwithstanding, features of the cranial remains, as well as

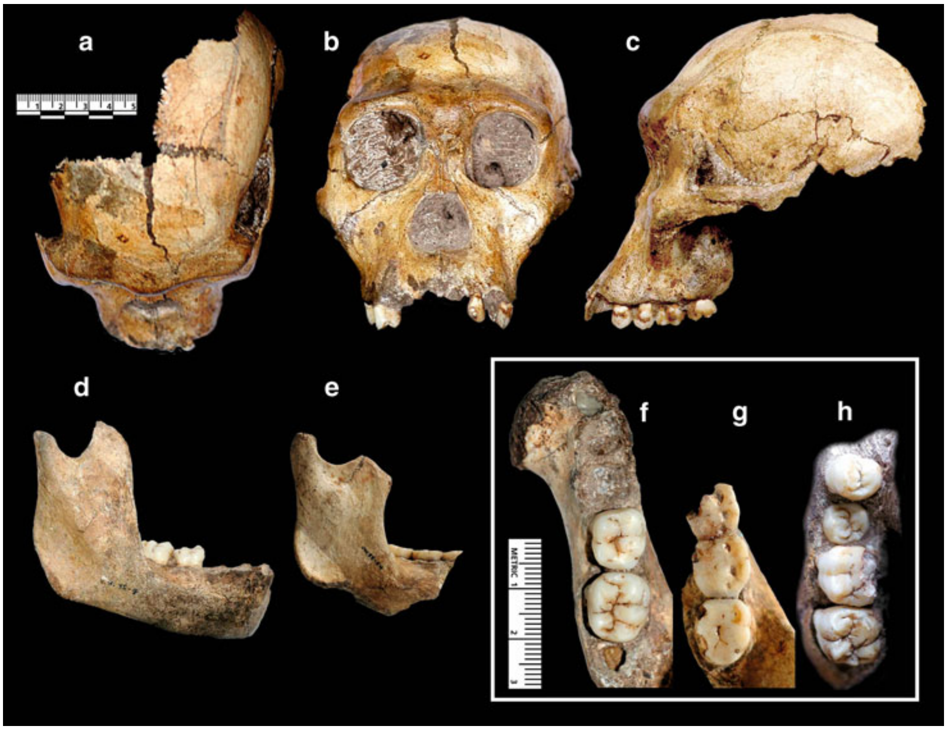

Fig. 9.3 Craniodental elements of *A. sediba*: **a** UW 88-50 superior aspect; **b** UW 88-50 frontal aspect; **c** UW 88-50 left lateral aspect; **d** UW 88-8 right lateral aspect; **e** UW 88-54 right lateral aspect; **f** UW 88-8 occlusal aspect; **g** UW 88-54 occlusal aspect; **h** UW 88-50 occlusal aspect. Picture reprinted with permission of Peter Schmid

Table 9.1 Dental metrics of *A. sediba* from Malapa

	MH1								MH2			
	Maxillary				Mandibular				Maxillary		Mandibular	
	Left		Right		Left		Right		Right		Right	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
I1			10.1	6.9							4.4	5.6
I2	7.7	5.1									5.1	6.6
C			9.0	8.8	8.0	8.5					7.1	7.4
P3	9.0	11.2	7.7[a]	10.8							7.8	9.3
P4	9.2	11.4	10.6[a]	13.3							8.4	9.7
M1	12.9	12.0	11.3[a]	11.0			12.5	11.6			11.8	11.1
M2	12.9	13.7	12.5	13.3			14.4	12.9			13.1	12.2
M3	13.3	14.1	13.1	13.6			14.9	13.8	11.3	12.9	14.2	12.7

[a] The right P3 is not erupted, while the left is; this possibly pathological condition is likely influencing the dental metrics of the right premolars and probably the right first molar

the fact that the pubic body of the os coxa is mediolaterally broad and square shaped, and the muscle markings of the other postcranial remains are typically weakly to moderately rugose in comparison to MH1, lead us to suggest that MH2 was a female.

Data on dental dimensions of *A. sediba* are presented in Berger et al. (2010), and we summarize these here (Table 9.1). Apart from the maxillary incisors, the teeth of *A. sediba* are relatively small, generally plotting at the lower end or outside the range of tooth sizes for *Australopithecus africanus*, and within the ranges of specimens assigned to early *Homo*, including African *H. erectus*. The canine teeth of both individuals in particular are small. Only a single specimen of *A. africanus*, TM 1512, has a maxillary canine that is smaller than MH1, while the mandibular canine of MH1 is smaller than any *A. africanus* specimen. The molars of MH2 are smaller than those of MH1, falling below the size range of *A. africanus*. In fact, the molars of MH1 are 9.0 % (M_1), 8.6 % (M_2) and 8.8 % (M_3) larger than those of MH2, indicating minimal size dimorphism between the two in the postcanine dentition. Conversely, the femoral head of MH1 is approximately 9.1 % smaller than that of MH2, though it is likely that additional appositional growth in MH1 would have decreased this size difference. On the other hand, the distal humerus of MH1, which has a fused epiphysis, is slightly larger than MH2's distal humerus. These small levels of dimorphism appear similar to that seen in modern humans. But, unlike definitive representatives of the genus *Homo*, the molars of *A. sediba* increase in size from M1 to M3, as is seen in *A. africanus* and other australopiths. Also, the cusps of the premolars and molars of *A. sediba* are centrally arranged, unlike the marginal arrangement of specimens attributed to early *Homo*. The overall pattern that emerges is that the teeth of *A. sediba* are similar in absolute size to specimens attributed to early *Homo*, while the post-canine dentition shows a cuspal arrangement and posterior molar size increase that is more similar to *A. africanus*.

Australopithecus sediba

In the early days of our investigation, prior to the cranium of MH1 being fully exposed, our craniodental studies were restricted to the mandibular remains of both individuals and the attendant maxillary teeth of MH2 when attempting to determine the taxonomic affinity of these finds. We were initially struck by the similarities between these mandibles and other specimens attributed to early *Homo*. Thus, our initial working hypothesis was that the skeletons we had recovered from Malapa likely represented some form of early *Homo*. This perception was strengthened by several derived characters we noted in the pelvis of MH1, three pieces of which had been recovered during late 2008. However, as our analysis proceeded over the following months, it became apparent that although there were derived features in both the cranial and pelvic remains, the overall body plan appeared to be that of a hominin at an australopith adaptive grade (or occupying an australopith adaptive plateau, sensu White et al. 2009). Once the cranium had been sufficiently prepared from the matrix, detailed comparisons between it and other hominin crania from both East and South Africa reinforced our appraisal of the predominantly australopith nature of these individuals.

The cranial capacity of MH1 was established through a variety of actual and virtual methods at a surprisingly small 420 cc, even though our assessment of its ontogenetic development indicated this juvenile would have completed some 97 % of its brain growth by the time of death. More recently, virtual reconstruction of the endocast of MH1 revealed a brain with an australopith-like convolutional pattern (Carlson et al. 2011). In contrast, the posterior positioning of the olfactory lobes and the breadth of the orbitofrontal region of the brain appears more derived than that seen in other relatively complete specimens of *A. africanus*, foreshadowing the condition found in later *Homo*. This suggests that brain reorganization was decoupled from the brain expansion that marks later specimens of *Homo*.

On present evidence, the species *A. sediba* is not marked by any autapomorphies, though it can be distinguished from other hominin taxa by a unique constellation of characters outlined in Berger et al. (2010) (Table 9.2). It is worth highlighting the more notable differences. *A. sediba* can be differentiated from *Australopithecus afarensis* in the relatively weak development of the cranial crests in the former, and the relatively pronounced postorbital constriction in the latter. In *A. afarensis* a prominent supraorbital bar appears, though a supratoral sulcus is absent, while in *A. sediba* a weak supraorbital torus and supratoral sulcus are evident. *A. afarensis* shows considerable subnasal prognathism and procumbent incisors, while *A. sediba* shows limited prognathism and more vertically oriented incisors. The large, high, flaring zygomatics of *A. afarensis* result in a facial profile that is tapered superiorly and inferiorly, while in *A. sediba* the zygomatics are smaller, lower, and less flaring, resulting in a facial profile that is tapered inferiorly, but squared superiorly. In addition, the mandibular symphysis in *A. afarensis* is weakly inclined and receding, with a well-developed post-incisive planum, while in *A. sediba* the mandibular symphysis is nearly vertical, as is the weakly developed and steeply inclined post-incisive planum. Although fewer remains of *A. anamensis* have been recovered, what is preserved is distinctly more similar to *A. afarensis* than to *A. sediba*, in particular in mandibular morphology. *Australopithecus garhi*, *Australopithecus aethiopicus*, *Australopithecus boisei*, and *Australopithecus robustus* all reveal pronounced cranial cresting patterns and megadont post-canine teeth not witnessed in *A. sediba*. In addition, the derived facial morphologies of the three "robust" taxa are incompatible with *A. sediba*, thus *A. sediba* is readily distinguishable (see Rak 1983). In particular, the highly derived facial morphology of *A. robustus* is not seen in *A. sediba*, therefore we can certainly rule out *A. robustus* as a possible conspecific South African form.

The closest morphological comparison to *A. sediba* within the australopiths is *A. africanus*, as the two share numerous similarities in the cranium, face, palate, mandible, and teeth (Table 9.2; see also Table 9.1 of Berger et al. 2010). Nonetheless, they can be differentiated in that *A. africanus* is marked by a relatively tapered cranial vault, which in *A. sediba* is more squared with distinctly vertically oriented parietals. The temporal lines in *A. africanus* tend to be relatively closely spaced, even meeting as a small sagittal crest in Stw 505, while in *A. sediba* they are notably widely spaced. *A. africanus* lacks a true supraorbital torus, while *A. sediba* displays a weak torus and shallow but distinct supratoral sulcus. The lateral orbital margins of *A. africanus* are rather unique in that they face predominately anteriorly and show a distinct angular indentation that is unknown in any other australopith (Rak 1983), including *A. sediba* with its laterally facing, gently concave lateral orbital margins. In addition, the frontal process of the zygomatic is expanded both medially and laterally in its contribution to the lateral orbital margin in *A. africanus*, while in *A. sediba* it is only medially expanded, and only the medial aspect of the process contributes to the lateral orbital margin. *A. africanus* shares with *A. afarensis* the large, flaring zygomatics and tapered upper facial profile, as opposed to the smaller, less flared zygomatics of *A. sediba* that results in its squared upper facial profile. *A. sediba* is marked by canine juga and fossae that do not conform to the pattern of canine pillars and maxillary furrows described by Rak (1983) for most specimens of *A. africanus*. The mandibular symphysis of *A. sediba* is slightly more vertical than that of *A. africanus*, and with a weakly developed and steeply inclined post-incisive planum that differs from the stout, weakly inclined post-incisive shelf seen in the latter. The mandibular corpus of *A. sediba* is also considerably more gracile than *A. africanus*, with a distinct subalveolar fossa that is weakly apparent to absent in *A. africanus*.

Given the derived appearance of *A. sediba* relative to *A. africanus*, which makes it appear quite *Homo*-like in morphology, some have questioned its position within the genus *Australopithecus*, preferring instead to place it within the genus *Homo* (Balter 2010; Cherry 2010). However, there are several characters that we contend precludes placing *sediba* in *Homo*. The cranial capacity of MH1 has been estimated at 420 cc, and to include this cranium in the genus *Homo* would require another revision of the definition of *Homo* in order to accommodate such a small brain (e.g., Leakey et al. 1964). Additional morphological features link select specimens of the *A. africanus* hypodigm with *A. sediba*. For instance, although *A. sediba* possesses a weak supraorbital torus that is not seen in *A. africanus*, the glabellar region of the former is especially pronounced, appearing most similar to Sts 71. The premaxillary suture is still evident at the superior extent of the nasal aperture in *A. sediba*, a feature Clarke (2008) considers indicative of australopiths. Although *A. sediba* lacks the anterior pillars of *A. africanus*, it nonetheless displays a well-developed canine jugum with an associated canine fossa that appears most similar to that of Sts 52 (a specimen that does not display anterior pillars), and

Table 9.2 List of craniodental characters distinguishing species of *Australopithecus* and *Homo*. This list is extracted from the larger table in Berger et al. (2010)

	A. aethiopicus	*A. boisei*	*A. robustus*	*A. garhi*	*A. afarensis*	*A. africanus*	*A. sediba*	*H. habilis*	*H. rudolfensis*	*H. erectus*
Cranial capacity	Small	Small	Small	Small	Small	Small	Small	Intermediate	Large	Large
Orientation of parietals	Tapered	Tapered	Tapered	Tapered	Tapered	Tapered	Vertical	Variable	Vertical	Vertical
Position of temporal lines on parietals	Crest	Crest	Crest	Crest	Crest	Variable	Wide	Variable	Wide	Wide
Postorbital constriction	Marked	Marked	Marked	Moderate	Marked	Moderate	Slight	Moderate	Moderate	Slight
Supraorbital expression	Bar	Bar	Bar	Intermediate	Bar	Intermediate	Torus	Torus	Intermediate	Torus
Glabellar region forms as prominent block	No	Yes	Yes	No	No	Variable	Yes	No	Variable	No
Canine juga prominence/ anterior pillars	Weak	Weak	Pillars	Prominent	Prominent	Variable	Prominent	Variable	Weak	Weak
Patency of premaxillary suture	Obliterated	Obliterated	Occasional	?	Obliterated	Occasional	Trace	Obliterated	Obliterated	Obliterated
Eversion of superior nasal aperture margin	Slight	Variable	None	?	?	None	Slight	Slight	Slight	Slight
Subnasal projection	Marked	Moderate	Moderate	Marked	Marked	Variable	Weak	Variable	Weak	Weak
Canine fossa	Absent	Absent	Absent	Present	Present	Present	Present	Present	Absent	Absent
Incisor procumbency	Vertical	Vertical	Vertical	Procumbent	Procumbent	Variable	Vertical	Variable	Vertical	Vertical
Anterior nasal spine relative to nasal aperture	Posterior	Posterior	Posterior	?	Absent	Anterior	Anterior	Anterior	?	Anterior
Expansion of frontal process of zygomatic bone	Medial and lateral	Medial and lateral	Medial and lateral	?	Medial and lateral	Medial and lateral	Medial	Medial	Medial	Medial
Angular indentation of lateral orbital margin	?	Curved	Curved	?	?	Indented	Curved	Curved	Curved	Curved
Lateral flaring of zygomatic arches	Marked	Marked	Marked	?	Marked	Marked	Slight	Slight	Slight	Slight
Outline of superior facial mask	Tapered	Tapered	Tapered	?	Tapered	Tapered	Squared	Squared	Squared	Squared
Zygomaticoalveolar crest/malar notch	Straight	Straight	Straight	?	Straight	Straight	Straight	Notch	Notch	Notch
Height of masseter origin	High	High	High	Low	Low	High	High	Low	Low	Low
Derived facial morphology of robust australopiths	Present	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent

(continued)

Table 9.2 (continued)

	A. aethiopicus	*A. boisei*	*A. robustus*	*A. garhi*	*A. afarensis*	*A. africanus*	*A. sediba*	*H. habilis*	*H. rudolfensis*	*H. erectus*
Orientation of mandibular symphysis	Vertical	Vertical	Vertical	?	Receding	Receding	Vertical	Vertical	Vertical	Vertical
Post-incisive planum of mandible	Prominent	Prominent	Prominent	?	Prominent	Prominent	Weak	Prominent	Weak	Weak
Mandibular corpus cross-sectional area at M1	Large	Large	Large	?	Small	Small	Small	Small	Variable	Small
Maxillary I1 - MMR development, lingual face	?	Moderate	Moderate	?	Moderate	Moderate	Moderate	Weak	Weak	Weak
Median lingual ridge of mandibular canine	?	Weak	Weak	?	Prominent	Prominent	Weak	Weak	Weak	Weak
Post-canine megadonty	Present	Present	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent
Arrangement of molar cusp apices	Central	Central	Central	Marginal	Marginal	Central	Central	Marginal	Marginal	Marginal

unlike specimens generally assigned to early *Homo*. Although there is a small anterior attachment of the nasal septum (or anterior nasal spine, see McCollum et al. 1993) in *A. sediba*, it is neither as pronounced nor as projecting as that of most fossil specimens attributed to early *Homo*. Likewise the morphology of the margins of the nasal aperture and the orientation of the nasal bones indicates that *A. sediba* was not possessed of a *Homo*-like projecting nose, and accordingly does not appear to evince the derived thermoregulatory features found in the faces of most members of the genus *Homo* (Dean 1988; Franciscus and Trinkaus 1988). Despite the fact that the zygomatics of *A. sediba* are not as flaring as in other australopith specimens, the zygomaticoalveolar crest is long, straight, and steeply inclined as in *A. africanus*, resulting in a relatively high origin for masseter that differs from the malar notch typically seen in early *Homo*. And dentally, the upper central incisors of *A. sediba* show a moderately developed mesial marginal ridge on the lingual face, and the cuspal apices are centrally positioned, both features aligning *A. sediba* with the australopiths and not *Homo* (Grine 1989; Strait et al. 1997).

As in the craniodental remains, the postcranium of *A. sediba* evinces a mosaic of features that appear transitional between australopiths and later *Homo* in its unique combination of primitive and derived traits. The inference that *A. sediba* was at an australopith adaptive grade was based on such features as small body size, a relatively long forelimb with a high brachial index, upper limb joint dimensions that are large relative to those of the lower limb, a relatively primitive calcaneous, and what appeared at the time to be a fairly conical-shaped thorax (this latter inference was based on the relative dimensions of a complete first rib and mid-thoracic rib from MH2; subsequent discoveries and analysis are, however, causing us to revisit this interpretation). Thus the overall postcranial *bauplan* is australopith-like. MH1 and MH2 are comparable in size to the smaller, presumably female, individuals known from *A. afarensis* and *A. africanus*: estimated body masses (based on femoral head superoinferior diameter, and using the mean of the all hominoid and *H. sapiens* prediction equations from McHenry 1992) are about 30.5 and 37.4 kg for MH1 and MH2, respectively (cf. female mass estimates for other australopiths in McHenry 1992). In most aspects of the postcranial skeleton, *A. sediba* is similar to the smaller-bodied representatives of *A. afarensis*, and to *A. africanus* generally, in having features that might be interpreted as reflecting a significant arboreal component to its locomotor repertoire (Stern and Susman 1983; McHenry and Berger 1998; Stern 2000). These include arms that are long relative to body size, a high brachial index, large upper limb joint surfaces relative to those of the lower limb, relative pronouncement of some upper limb entheses, and a highly mobile knee.

The hand of *A. sediba* reveals a suite of australopith-like characters, including a strong flexor apparatus that indicates a probable arboreal component (Kivell et al. 2011). At the same time, the relatively long thumb and short fingers of *A. sediba* are notably *Homo*-like, and possibly indicate a precision grip capable of stone tool production. Similarly, the ankle and foot of *A. sediba* reveal a mosaic of australopith-like and *Homo*-like features, suggesting these hominins practiced a unique form of bipedalism that still included arboreal locomotion (Zipfel et al. 2011). In particular, the gracile calcaneal body and robust medial malleolus find their closest comparison with australopiths, while the talocrural joint appears mostly *Homo*-like in both form and function. And, the partial pelves of both MH1 and MH2 share features with australopiths such as a large biacetabular diameter, small sacral and coxal joints, and long pubic rami (Kibii et al. 2011). Conversely, the vertically oriented and sigmoid-shaped iliac blades, greater robusticity of the iliac body, sinusoidal anterior iliac borders, shortened ischia, and more superiorly oriented pubic rami are all characters shared with *Homo*. This mosaic of pelvic features combines with the small cranial capacity of *A. sediba* to suggest that the birthing of large-brained babies was not the principal force driving the evolution of the pelvis ca. 1.977 Ma.

The preliminary picture appears to be one of a postcranial skeleton that is symplesiomorphic with other australopiths in most characters of the upper and lower limbs. This contrasts with the relatively derived features seen in the pelvis of *A. sediba* (Berger et al. 2010; Kibii et al. 2011), which when combined with the observation of a *Homo*-like pattern of humeral/femoral load sharing (based on the structural properties of the diaphyses of these elements), suggests that the Malapa hominins may have differed in important ways from other australopiths in their locomotor kinematics. Elucidation of these differences must await further detailed analysis of the fossil material.

We were thus confronted with a hominin that retained a significant number of primitive characters in the cranium, face, arms, thorax, and feet, with perhaps the most notable among these being the low estimated adult cranial capacity of MH1. In conjunction with these, the spate of derived features in the cranial, dentognathic, and pelvic remains make these skeletons appear more derived toward *Homo* than any other australopith taxon on record. While we are fully cognizant that by the guidelines of phylogenetic systematics, the synapomorphies shared between the Malapa hominins and later *Homo* suggest placement of the new species into the genus *Homo*, we find ourselves in philosophical agreement with the arguments of Wood and Collard (1999) that an exclusively cladistic approach is insufficient (see also Trinkaus 1990, for a critical discussion of the use of cladistics in paleoanthropology). Rather, in line with Wood and Collard (1999), we consider a genus to be a monophylum whose members occupy a common adaptive grade. Detailed analysis of both craniodental and postcranial remains demonstrates that the Malapa fossils are not yet at a *Homo* adaptive grade (see below). We also agree with Wood and Collard (1999) that *habilis* and *rudolfensis* are not yet at the adaptive grade of *Homo*, and therefore suspect that they might indeed belong in the genus *Australopithecus*. However, such a systematic revision of the hominins is beyond the scope of this paper, therefore in this paper we refer to these latter two species as being in *Homo*, while noting that a more comprehensive systematic and phylogenetic analysis is presently underway.

Considering the conditions that Wood and Collard (1999, p. 70) cite as necessary for attribution of a fossil taxon to *Homo*, the Malapa fossils clearly fail two of their six criteria (both body mass and body proportions should be more similar to humans than australopiths) and quite probably fail on a third (should show obligate bipedalism *with limited climbing ability*). The status of the Malapa hominins on a fourth criterion (should show extended ontogenetic development) is currently unknown, though craniodental indicators currently appear inconsistent with a human pattern. The fifth criterion (teeth and jaws similar in relative size to humans) appears to position the Malapa hominins within *Homo*, though we would note that the small teeth from Malapa retain an australopith-like cuspal arrangement. The remaining criterion (should be more closely related to humans than to australopiths) is the essence of our argument, and here too we think that the Malapa fossils do not belong in the genus *Homo*, since they appear more closely related to *A. africanus* than to *H. sapiens*.

The Status of Stw 53

Another hominin specimen from South Africa, Stw 53, has a bearing on this discussion. Derived from the “Stw 53 Infill” (renamed Member 5A) and dating to either 2.6–2.0 Ma (Kuman and Clarke 2000) or perhaps less than 2.0 Ma (Herries et al. 2009, 2013; Pickering and Kramers 2010), the specimen was initially described as probably belonging to early *Homo* (Hughes and Tobias 1977), and soon came to be widely accepted as such (Cronin et al. 1981; Wood 1987, 1992). Eventually it was firmly attributed to *H. habilis* (Curnoe and Tobias 2006), though one of these authors shortly thereafter designated Stw 53 as the type specimen of a new species, “*H. gautengensis*” (Curnoe 2010). However, the attribution of Stw 53 to *Homo* has been challenged (Kuman and Clarke 2000; Clarke 2008, 2013; Berger et al. 2010). In particular, Stw 53 possesses a number of characters in the cranium and face that most closely align it with

A. africanus. These include closely spaced temporal lines, marked post-orbital constriction, a weakly developed supraorbital torus, narrow and non-projecting nasal bones, anterior pillars, marked nasoalveolar prognathism, medial and lateral expansion of the frontal process of the zygomatic bone, and laterally flared zygomatics (Clarke 2008; Berger et al. 2010). The derived craniodental morphology of *A. sediba* raises further doubt regarding the attribution of Stw 53 to early *Homo*, as Stw 53 looks more *A. africanus*-like relative to MH1, while MH1 looks more *Homo*-like relative to Stw 53. If Stw 53 really is an advanced representative of *A. africanus*, as it indeed appears to be, then there is little reason to consider it to represent a discrete species of early *Homo*. Without Stw 53, the diagnosis of the taxon "*H. gautengensis*" does not discriminate the remaining hypodigm from other previously named taxa, and there is little reason to consider it a valid species.

The assignment of Stw 53 to *A. africanus* has important ramifications for other specimens that were assigned to *Homo* based on their similarity to Stw 53. Most notably, OH 62 was referred to *H. habilis* based in large part on its resemblance to Stw 53 (Johanson et al. 1987). Following on this, KNM-ER 3735 was also tentatively referred to *H. habilis*, in part because of its likeness to OH 62 (Leakey et al. 1989). As a result, we must be cautious regarding our current perceptions of the postcranium of *H. habilis*, since the only skeletal remains that can be directly associated with *H. habilis* are the manual remains attributed to the type specimen OH 7 (Leakey et al. 1964). The foot skeleton OH 8 and the leg bones OH 35 have also been put forth as representing *H. habilis* (Susman and Stern 1982), and have even been argued to belong to the type specimen OH 7 (Susman 2008), although sufficient doubts exist (DeSilva et al. 2010) as to warrant caution in accepting this attribution (though see Susman et al. 2011). The postcranium of *A. sediba* appears more *Homo*-like than that of either OH 62 or KNM-ER 3735 (Berger et al. 2010), which supports the inference that these latter specimens might sample a late-surviving, non-robust australopith. In addition to these specimens, the assignment of A.L. 666-1 to *H. habilis* was likewise based, in part, on a favorable comparison with Stw 53 and OH 62 (Kimbel et al. 1997), thus those characters that aligned A.L. 666-1, Stw 53, and OH 62 might not be as diagnostic of early *Homo* as was initially thought.

The Taxonomic and Phylogenetic Status of *Australopithecus sediba*

Recent efforts with U–Pb dating at Sterkfontein have resulted in revised age estimates for *A. africanus* material from this site, the largest sample available for this taxon. Pickering and Kramers (2010) have produced a minimum age estimate of ca. 2.0 Ma for the top of Member 4 of Sterkfontein, possibly representing the latest appearance of this taxon in the fossil record. However, if Stw 53 is better placed in *A. africanus* (Clarke 2008; Berger et al. 2010), and if the Stw 53 Infill is actually dated to younger than 2.0 Ma (Herries et al. 2009, 2013; Pickering et al. 2011a, b), then the last appearance of this taxon could overlap with *A. sediba* at 1.977 Ma. If so, then *A. africanus* and *A. sediba* would not represent a simple anagenetic lineage. Although the samples of *A. africanus* from Taung and Makapansgat are imprecisely dated, they are generally considered to fall within the broad time span of 2.4–2.8 Ma (Delson 1984; Kimbel 1995; Vrba 1995; White 1995). Consequently, the age of *A. africanus* can be broadly constrained to somewhere between 2.8 and 2.0 (or less) Ma, though as White (1995) has noted, these first and last appearance datums are of relatively low fidelity, and we cannot be certain of the actual dates for the origin or extinction of *A. africanus*. As a result, the exact relative time-frames for both *A. africanus* and *A. sediba* are currently poorly understood.

Based on current literature, a probable age of 1.977 ± 0.0015 Ma might be considered inconsistent with the contention that *A. sediba* represents a candidate ancestor for the genus *Homo*. We note that a small number of fossils dated in excess of 1.977 Ma have been referred to the genus *Homo* (Howell et al. 1987; Hill et al. 1992; Schrenk et al. 1993; Kimbel et al. 1996, 1997; Suwa et al. 1996; Prat et al. 2005), while fossils of a broadly equivalent age to *A. sediba* have been assigned to *H. erectus* (Wood 1991; Gabunia and Vekua 1995). We contend, however, that the evidence for early *Homo* prior to 1.977 Ma is not unequivocal. Beyond a few isolated teeth, which can be difficult to diagnose taxonomically (Howell et al. 1987; Suwa et al. 1996; Pickering et al. 2011a), only three relatively poorly preserved and isolated craniodental specimens older than 1.977 Ma have been attributed to early *Homo*: A.L. 666-1 (Kimbel et al. 1997), KNM-BC 1 (Hill et al. 1992), and UR 501 (Schrenk et al. 1993). Questions regarding the taxonomic assignment of these fossils, as well as the provenience and dates of each of these specimens can and have been raised, thus a definitive presence of *Homo* prior to1.977 Ma has not been established (see also Kimbel 1995, 2009; White 1995; Pickering et al. 2011a). Along these lines, it also bears noting that an isolated *os coxa*, KNM-ER 3228, which is undeniably *Homo*-like in its overall morphology, was recovered from 1.95 Ma deposits at Koobi Fora (Rose 1984). While the KNM-ER 3228 and Malapa *ossa coxae* both share many derived *Homo*-like features, the Koobi Fora specimen appears to signal the establishment of larger-bodied, *H. erectus*-like (at least in terms of their postcranial morphology) hominins in East Africa that are roughly contemporaneous with the hominins from Malapa.

Notwithstanding, even if both the dates and the taxonomic assignment of the few fragmentary craniofacial surface finds stand, and even if the fossil hip bone from Koobi Fora signals the contemporaneous presence of hominins with more *Homo*-like body plans, it does not preclude *A. sediba* from being ancestral to the genus *Homo*. In this latter situation it is clear that the Malapa hominins themselves would be too young to be ancestral to the earliest fossils attributed to the genus *Homo*, but it is probable that the species *A. sediba* is not too young. We hypothesize that the fossils recovered from Malapa sample a population that in turn samples a species that almost certainly existed for some period both earlier and later in time (see Wood 2010, for an informative discussion of first and last appearance datums of hominin species). Although at present we have no fossil evidence to support such a notion, the reality is that Malapa represents a single point in a biological continuum, and the species *A. sediba* should not be considered exclusively endemic to Malapa, nor to a single moment in time that occurred approximately 1.977 Ma. We therefore propose that even if the dates and attributions of these three purported early *Homo* specimens stand (A.L. 666-1, KNM-BC 1, UR 501), the possibility remains that an ancestral population of *A. sediba* existed prior to the appearance of the earliest *Homo*. Given the mosaic of features seen in *A. sediba* that are shared by both *Australopithecus* and early *Homo*, and which are found in specimens in a sound temporal setting and of exceptional quality of preservation and completeness from Malapa, we contend that *A. sediba* presently represents the best candidate for the immediate ancestor of the genus *Homo*.

Conclusions

In our initial publication we suggested that *A. sediba* was derived from *A. africanus* via a cladogenetic event (Berger et al. 2010). It is possible that the two represent an anagenetic lineage, though as we point out above, a younger age estimate for Stw 53, and its recognition as a probable *A. africanus*, would argue against such a notion. Additional support for a cladogenetic interpretation comes from the constellation of *Homo*-like characters in *A. sediba*, alongside its *Australopithecus*-like traits, which push it outside the range of variability seen in the entirety of the *A. africanus* sample from the geographically disparate sites of Taung, Sterkfontein, and Makapansgat. Even though *A. sediba* is morphologically closest to *A. africanus*, the derived appearance of aspects of the cranium and postcranium outlined above prevent inclusion of MH1 and MH2 within the *A. africanus* hypodigm. It is important to note that the *A. africanus* sample is already recognized for its extremely high levels of morphological diversity, possibly even sampling more than one species (Lockwood and Tobias 2002; Clarke 2008). Given that *A. sediba* exceeds the total known morphological diversity of the *A. africanus* sample, yet is both temporally and geographically closest to the site of Sterkfontein, from which the largest and most diverse sample of *A. africanus* comes, we see this as strong evidence for its unique specific status. As a result, our present interpretation is that although there are features shared between *A. africanus* and *A. sediba*, there are nonetheless sufficient differences to warrant a specific separation between them.

Clearly more research into the tempo and mode of later Pliocene australopith evolution is needed. However, present fossil samples from across Africa allow us to hypothesize as to the phylogenetic position of *A. sediba*. On present evidence, *A. sediba* appears derived from *A. africanus*, probably via cladogenesis. In turn, *A. sediba* shares more derived characters with specimens assigned to early *Homo* than any other candidate ancestor, including *A. afarensis*, *A. garhi*, or *A. africanus*. In the initial announcement of *A. sediba* (Berger et al. 2010), we proposed four possible hypotheses regarding the phylogenetic position of *A. sediba*: (1) *A. sediba* is ancestral to *H. habilis*; (2) *A. sediba* is ancestral to *Homo rudolfensis*; (3) *A. sediba* is ancestral to *H. erectus*; and (4) *A. sediba* is a sister group to the ancestor of *Homo*. In an accompanying cladistic analysis, the most parsimonious cladogram placed *A. sediba* as a stem taxon for the *Homo* clade comprised of *H. habilis*, *H. rudolfensis*, *H. erectus*, and SK 847 as an OTU (Berger et al. 2010, supporting online material). Although caution must be employed when performing a cladistic analysis on possibly interdependent characters of uncertain taxonomic valence, our cladogram was consistent with our interpretations based on gross morphology and cranial and dental metrics. We are presently continuing our analysis of the phylogenetic status of *A. sediba* along numerous avenues of research, and although it is unlikely that our interpretations will meet with universal acceptance, we do look forward to continuing to expand our understanding of the genus *Australopithecus* and the debate regarding the origin of the genus *Homo*.

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Part III
Biogeography

The articles in this part address issues concerning the biogeography of *Australopithecus*. What are the phylogenetic relationships among species in different parts of Africa, and what does that tell us about the processes that led to speciation. Can we use details of morphology to calibrate dispersal events in the history of the genus?

In Chap. 10, "The Adaptive Radiation of *Australopithecus*" Robert Foley examines the distribution of *Australopithecus* species in time and space to see if this radiation of early hominins meets criteria used to identify an adaptive radiation in other organisms. In general, the pattern of diversification in *Australopithecus* does not seem to qualify as an adaptive radiation. Rather, diversity of *Australopithecus* seems to be a product of dispersal events rather than selection for morphological adaptations to different habitats. He also suggests that *Australopithecus* seems to be depauperate in the number of species one might expect based on comparisons with later aspects of hominin evolution.

In Chap. 11, "Whence *Australopithecus africanus*? Comparing the skulls of South African and East African *Australopithecus*", the late Charles Lockwood examines the relationship between *A. africanus* from South Africa and the *Australopithecus anamensis*–*Australopithecus afarensis* lineage from Eastern Africa for clues to the origin of *A. africanus* and the likely timing of that cladogenic event. He finds that *A. africanus* most likely evolved from early *A. afarensis* such as the population from Laetoli, rather than from *A. anamensis* or later *A. afarensis* as recovered from Hadar. He then evaluates and compares four biogeographic scenarios for the evolution of *Paranthropus* and *Homo* from an ancestor similar to *A. africanus*. In two of these, Eastern Africa is the center of origin for later taxa, with subsequent dispersal to South Africa. Other scenarios involve a "piston" process with more movement of taxa between the two regions.

In Chap. 12, "Biogeographical Implications of Early Hominid Phylogeny" David Strait examines dispersal events in hominin evolution by mapping the geogeography of hominin species onto the most parsimonious cladogram of hominin evolution. The most parsimonious explanation of the distribution of taxa involves four dispersals. All but one—an initial dispersal from Central to Eastern Africa by the ancestor of all hominins except *Sahelanthropus*—involve dispersal from East Africa to South Africa. The southward dispersing taxa are the ancestors of *A. africanus*, *Paranthropus robustus*, and *Homo habilis*. These dispersals generally accord with the direction of dispersals of other mammals at the same time. His analysis indicates that most major adaptive changes in hominin evolution, including enlargement of the brain and development of a robust chewing apparatus, took place in East Africa. The origin of bipedalism is less easy to place geographically.

The Editors

Chapter 10
Comparative Evolutionary Models and the "Australopith Radiations"

Robert A. Foley

Abstract This paper makes a case for the more formal use of evolutionary models in trying to understand human evolution. As the fossil record for hominin evolution has accumulated, and the level of diversity recognized has increased, we have moved to viewing the evolutionary history of the lineage as a series of adaptive radiations, rather than as a process of continuous, within lineage, change. The australopithecines would be seen to represent one such radiation, diversifying phylogenetically and expanding geographically. It is assumed that this is a response to a combination of the evolution of bipedalism and the expansion of more open habitats. Such interpretations have been largely inductive, and little attention has been paid to the way in which processes such as adaptive radiations and dispersals have been analyzed more widely in evolutionary biology. In this paper the australopithecine radiation is examined in the context of a number of models that have been developed to identify adaptive radiations. The results suggest that while there is some evidence for adaptational directionality to the group, in other ways australopithecine evolution falls short of the criteria for an adaptive radiation. As an alternative, australopithecine diversity is looked at in the context of dispersal models and the distribution in Africa. Finally, as it is clear that such model-based approaches are very sensitive to scale, the pattern of early hominin evolution is compared to two events at different scales—the evolution of modern humans, and the diversity of the chimpanzee clade.

Keywords Anagenesis • Australopithecine diversity • *Australopithecus* • Cladogensis • Dispersal models • Evolutionary theory • Geographical models

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Introduction

Paleoanthropology is a strongly empirical discipline. To some extent this is an inevitable consequence of being a field largely dependent upon the chance events of the history of discovery. If evolution is a tinkerer, as Jacob (1977) has called it, then palaeontology is the tinkerer's apprentice—looking at the new parts of the fossil record as they come in, and trying to work out where they can be strapped on to the existing structure.

Although there are some exceptions (Vrba 1985; Foley 1987, 1991; Stanley 1992; Conroy 2002; Hunt 2003), the empirical evidence for human evolution has seldom been put up against formal models derived from evolutionary theory. Many might say that it would be a worthless exercise, as the history is what it is, and the history of any lineage, especially one as peculiar as our own, will simply reflect itself. This may be the case, and the pattern of human evolution may not fit any particular model, but there are a number of responses to this critique that are possible. One is that differences between the expectations of a model and what is observed are as informative as a good fit, for they make us ask questions about why the conditions of evolution should be different. Another is that models can help us to see where the gaps in our knowledge lie, or what might be critical data, and so direct future research. Most important, though, is that if we are to do more than describe the pattern of our evolutionary history, we need to have a means of accessing the processes involved.

There are two problems with exploring the australopithecine radiations—one is the word radiation, and one the word australopithecine. "Radiation" can be used casually, but it can also be a formal event—thus when is a radiation a radiation? To put this another way, what sort of evolutionary event, or events, comprise the evolution of the australopithecines. This question can be explored theoretically by placing the australopithecines into a comparative

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Vertebrate Paleobiology and Paleoanthropology, DOI: 10.1007/978-94-007-5919-0_10,

framework—or expectations—and try to determine which one of these may best fit what we observe. The two primary contexts are firstly, the concept of adaptive radiation, and secondly, the evolutionary process of dispersal. As will emerge, the applicability of any model is highly influenced by scale, and I shall examine this by focusing on two more empirical frameworks—recent human evolution and chimpanzee genetic diversity. However, it is first necessary to consider how best to define the term australopithecine.

The Australopiths

"*Australopithecus*" is a problem because there is no clear consensus as to what should be included in this group. Broadly speaking there are three defensible positions on this:

1. *Australopithecus* comprises all the non-*Homo* materials and is simply the early parts of hominin evolution, characterised largely by the absence of the features that define *Homo*, and the presence of those that distinguish it from the African apes.
2. *Australopithecus* comprises all the non-*Homo* material, excluding those earliest hominins that lack indisputable evidence for bipedalism (*Sahelanthropus, Ororrin, Ardipithecus*)—i.e., this would be what was historically referred to as the "robust" and "gracile" australopithecines.
3. *Australopithecus* is a narrow genus, differentiated from *Homo*, *Paranthropus, Kenyanthropus* and the earliest hominins (*Sahelanthropus*, *Ardipithecus*, and *Ororrin*) by a set of apomorphies largely related to the shape of the cranium and dental characteristics. This may or may not, according to various authors (Wood and Collard 1999), include *Australopithecus habilis* and *Australopithecus rudolfensis*, normally placed into *Homo*. A more extreme view would be that *Australopithecus* refers solely to the type species, *Australopithecus africanus*, and *Australopithecus afarensis* is placed in *Praeanthropus africanus* (Strait and Grine 2004).

Each position has some support, and deciding between them is a question of how clearly monophyly can be established and taxonomic preference within that. On the one hand, it could be argued that a small lineage such as the hominins, in a broader comparative perspective, cannot really consist of seven genera, and therefore lumping all the smaller brained hominins into a single genus is, from a primatological perspective, the best solution. On the other hand, the earliest hominins are extremely poorly known, very diverse, and lack many of the traits that have traditionally been associated with *Australopithecus* (White et al. 2009, and related papers). Of these, perhaps the most significant is a greater degree of bipedal adaptation than that found in extant apes, yet associated with no marked cranial expansion. In between, it can be argued that the dental specialisations of the robust australopithecines are sufficiently distinct to justify a generic separation on the basis of adaptive difference.

Here the *Australopithecus* radiation is used as a working hypothesis for a monophyletic lineage comprising *Australopithecus anamensis, A. afarensis, Australopithecus bahrelghazali, A. africanus,* and *A. garhi*, i.e., the less extreme version of option 3 above. To this group one would also add the recently described *A. sediba* (Berger et al. 2010; de Ruiter et al. 2013). The justification for this is that, from an evolutionary ecological perspective, this scale of evolutionary event may be amenable to analysis in ways that would be lost if a broader definition were adopted (i.e., sliding together multiple events and trends). The aim here is not to define either the lineage or its place in hominin evolution more broadly, but to place it into the context of evolutionary models and processes. According to Strait and Grine's (2004) cladistic analysis, this group would be monophyletic, although technically it should also include a stem clade that would later give rise to *Paranthropus* or robust *Australopithecus* and possibly early *Homo*. Where necessary for the purposes of analysis these stem lineages are used as such.

Figure 10.1 shows the chronological and geographical distribution in the fossil record. Although there are uncertainties and variable resolutions for all of these, the most controversial part of this is, ironically, the type australopith, *A. africanus*. Not only are the dates of this still debated, ranging from a FAD of 4.0+ Ma (Partridge et al. 2003) to considerably less than 3.0 or even 2.0 Ma (Berger et al. 2002), but it is also far from clear whether or not there is more than one taxon represented in Sterkfontein (Grine 2013; Clarke 2013). A relatively conservative approach is adopted to this problem.

Anagenesis and Cladogenesis

It is implicit in this paper that *Australopithecus* evolution involves diversification. This is not, however, a universally held view. White (2003) has consistently been a proponent of minimal taxonomic diversity among hominins, and Kimbel et al. (2006) have proposed such a pattern for *A. anamensis* and *A. afarensis*. However, most recent researchers have tended to accept at least some level of diversity (Fleagle 1999), with either full cladogensis or some level of geographically-based diversity (Foley 1999; Strait and Wood 1999; see Strait 2013) (Fig. 10.2).

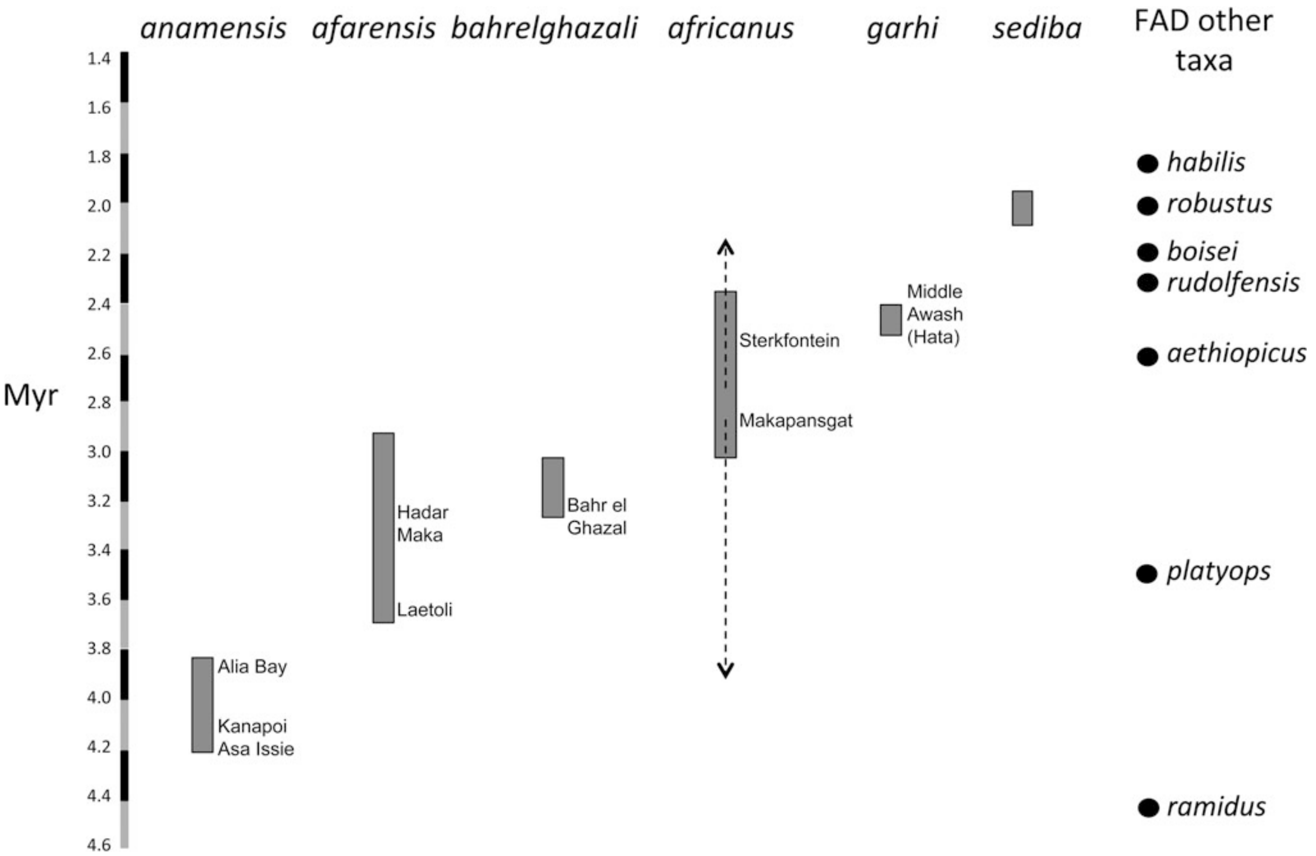


Fig. 10.1 Chronological distribution of the australopith taxa; the column on the *right* shows the first appearance points (FAD) of other hominin taxa that overlap chronologically. Scale in millions of years

To some extent differences between cladogensis and anagenesis is a matter of process and scale. While anagenesis may be a fair description of a pattern seen from afar, it does not reflect an evolutionary process (Eldredge and Cracraft 1980). When we refer to species A evolving into species B, at a micro level this will be still be a process of cladogenesis. When a new species evolves, it will do so by the greater survivorship of some of its populations, relative to others. As this happens there will be declining reticulation among these populations, and it is this declining reticulation that comprises speciation. As can be seen from Fig. 10.3, there are three possible outcomes. However, in each case, some form of cladogenesis will have taken place; either the evolution of the daughter species and the extinction of the ancestral phenotype; or the evolution of the daughter species and the survival of the ancestral form (as a relict species, perhaps), or, perhaps, the evolution of two daughter species, and the extinction of the ancestral one. Although there are variable evolutionary outcomes, nonetheless, they are all forms of cladogenesis, with branching (declining reticulation) at the sub-specific level, leading to two species (one of which may become extinct).

For this reason, although we may observe a situation where at one time there is species A, and subsequently species B, nonetheless this is the result of cladogenesis, with one lineage becoming extinct. Although this may seem like splitting hairs, and that *A. anamensis* really does evolve into *A. afarensis*, it is important to understand the process by which it operates. One important implication of this is that it is perfectly possible for *A. anamensis* to "evolve into" *A. afarensis*, and yet still to exist. In the same vein, the co-existence of *H. erectus* and *H. habilis* does not necessarily prevent the latter being the ancestor of the former (Spoor et al. 2007).

Is There an Australopith Radiation?

The description of hominin evolution as a series of radiations has become relatively common in recent years (Foley 2002). However, exactly what is meant by an adaptive radiation, and how does one assess whether one has occurred?

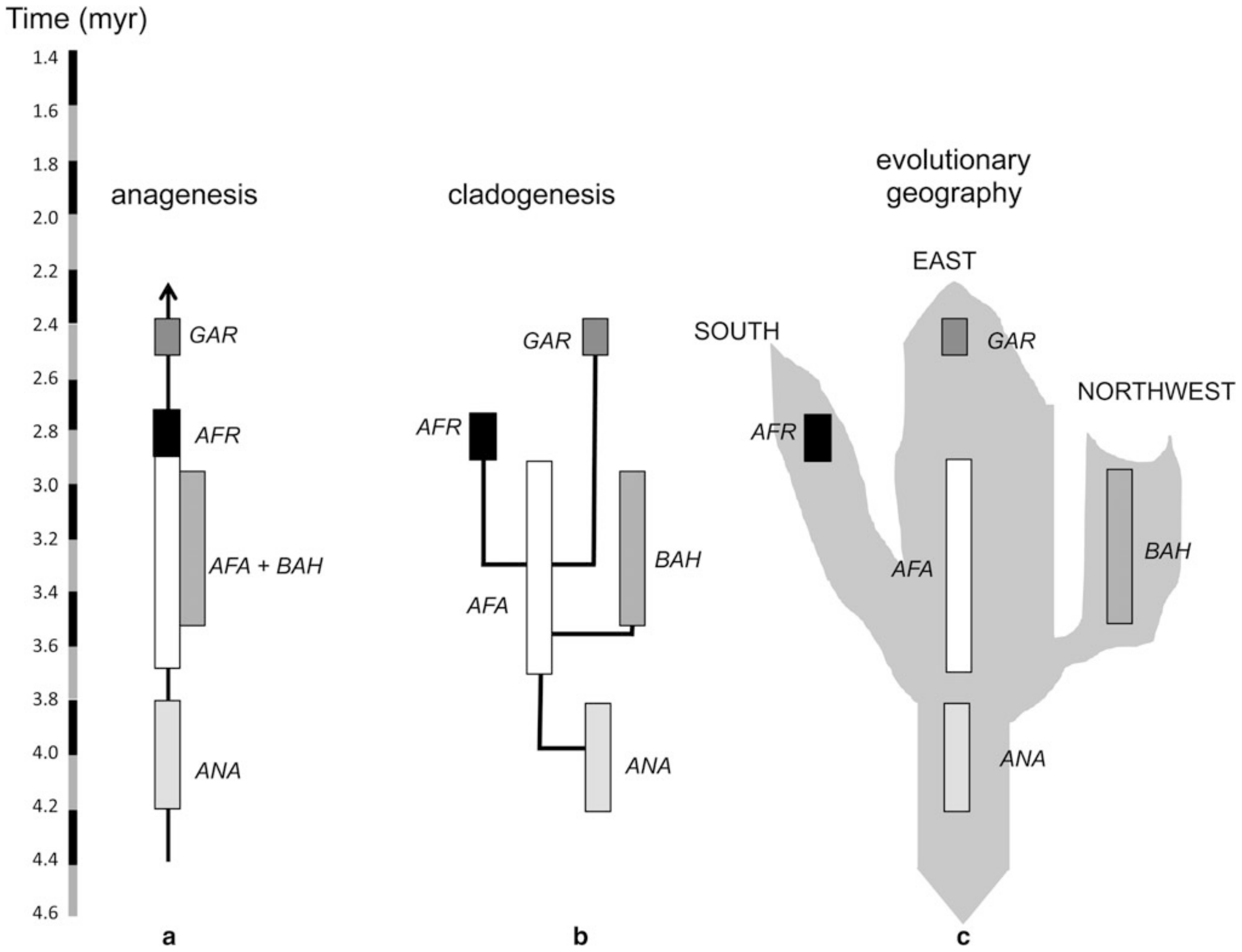


Fig. 10.2 Three views of *Australopithecus* evolution **a** anagenesis; **b** cladogenesis; **c** evolutionary geography. See text for discussion

At one level radiations in evolution are simply shorthand for any form of diversification, and thus all evolution is in some way or other, a radiation. However, there are more formal definitions. According to Schluter (2000), an adaptive radiation is "the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage. It involves the differentiation of a single ancestor into an array of species that inhabit a variety of environments and that differ in the morphological and physiological traits used to exploit those environments. The process includes both speciation and phenotypic adaptation to divergent environments."

The question is, what is the signal that an adaptive radiation has taken place? Schluter provides four criteria by which we can test whether or not we are dealing with an adaptive radiation:

1. Common ancestry of the component species;
2. Phenotype-environment correlation among the component species;
3. Evidence that there is a trait-utility—i.e., that the features of the component species provide environmentally specific fitness advantages;
4. Rapid speciation.

Placing the australopiths against these criteria is no simple matter. The monophyly is a largely circular argument, as one can use the accepted level of monophyly to determine the component species, rather than the other way around. In the case of the taxa under consideration here, it would probably make no sense to exclude the megadont clades, as all analyses suggest they are derived from an *Australopithecus* species (sensu stricto). However, it is probably also the case that *Homo* should be included as well. Criteria 2 and 3 can be taken together, as the second is essentially an attempt to explain in fitness terms the correlation found under criterion 2. For the australopiths, we know that there are a number of phenotypic differences between the taxa. One approach would be to list the various

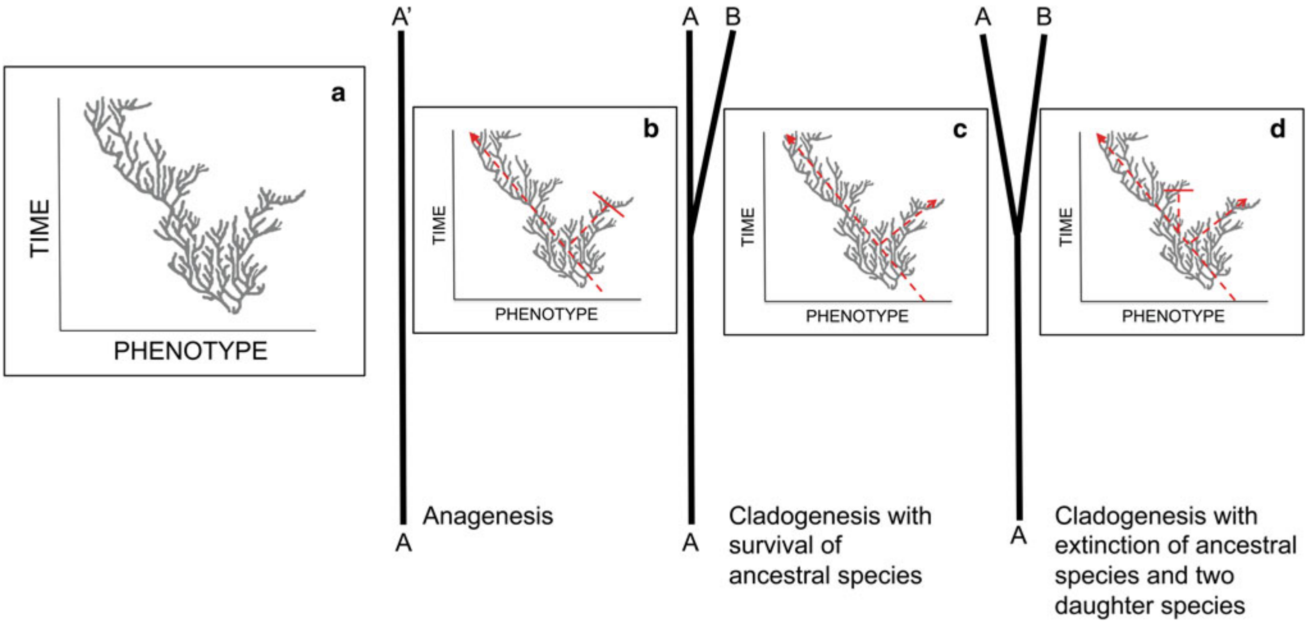


Fig. 10.3 Evolution as cladogenesis. **a** shows how as the phenotype changes or evolves, it is characterised by a process of divergence from the ancestral form, and so is a form of cladogenesis as reticulation declines between populations. In **b–d** different outcomes that can occur are shown—where ancestral "species" becomes extinct, and so in effect a form of anagenesis has occurred (**b**); where ancestral 'species' survives alongside daughter species (**c**); and where cladogenesis occurs and the two daughter phenotypes are different from the ancestral form, which becomes extinct (**d**)

phenotypic traits of the component species (tooth size, body size, brain size, pattern of locomotion, etc.), and then try to correlate these with the known environments. Apart from the problem of the patchy fossil data (what is the EQ of *A. bahrelghazali*?), there is also the problem that the environmental reconstructions of the various taxa overlap considerably—for all the component species, there is general acceptance that the habitats involved a fair degree of tree cover, with patches of bushland and more open grassland (Reed 1997; Behrensmeyer and Reed 2013). Without more precise quantification and better environmental resolution of these, it would be hard to detect a correlation, let alone demonstrate a fitness measure.

In the light of these methodological difficulties, another approach is to consider the question of what is the alternative hypothesis to adaptive divergence. The observation that we are trying to explain is divergence of a number of lineages from a single one. Two mechanisms can be proposed—one is natural selection and adaptation, which underlies the concept of an adaptive radiation. If this is the mechanism, then there should be an environment-phenotype correlation. The other mechanism would be neutral change, or rather the range of non-adaptive processes which can lead to evolutionary change—drift, founder effect, vicariance, and sexual selection. The expected outcome under this set of mechanisms would be a lack of phenotype-environment correlation. The predictions of each model are shown in Table 10.1.

However, prior to considering these predictions it is necessary to consider whether criterion 4, a necessary precondition, holds. An adaptive radiation is generally considered to be where the ancestral lineage diversifies

Table 10.1 Predictions of distribution of traits under an adaptive radiation model and a neutral divergence model

Prediction	Adaptive radiation model	Neutral diversification model
Relationship between key derived functional traits and the environment	Strong correlation	Weaker correlation
Level of homoplasy	High—due to similar selective pressures in relation to the conditions promoting the radiation	Low—chance effects greater than selection, reducing convergence
Within species variance in key adaptive traits	Low—due to strong selection during speciation for key local adaptive traits	High—reduced effect of local selective processes
Between species variance in key adaptive traits	High—adaptive differences to local conditions promoting inter-population and then species variation	Low—less differentiation in traits between species

relatively quickly, apparently responding to new environmental conditions or the selective benefits of a new adaptation. If that is the case, then the phenotypic differences, and their environmental correlates would indeed be strong evidence for an adaptive radiation. However, if there is not a burst of speciation, but rather a gradual appearance of new species, then it would be difficult to untangle what would, in effect, be evolutionary trends in adaptation, rather than an adaptive radiation.

To explore this possibility, Fig. 10.4 looks at the pattern of "taxon accumulation" across hominin evolution. In the top graph is shown the relative number of *Australopithecus* species which have appeared, plotted against time. The slope of the line will show bursts of speciation. An essential problem here is that the number of taxa are very few (5), and so an alternative is to look at all hominins (excluding the Late Miocene-Early Pliocene ones, which are too poorly known). This is shown in the bottom graph. As can be seen there is a rather continuous pattern of accumulation. The most striking upward trend is between 2.5 and 2.0 Ma, accounted for by the paranthropines (a real adaptive radiation?), and the appearance of early *Homo*.

The absence of a strong signal of rapid speciation among the australopiths might suggest that what is occurring is time transgressive. That, in combination with the absence of sufficient evidence to explore fitness and phenotype-environment relationships, in the context of Schluter's model of adaptive radiations, provides some insights, but it is far from conclusive. On the whole there is not, in relation to Schluter's model, a strong adaptive radiation signal among the australopiths. However, we should bear in mind that an adaptive radiation is itself an analytical abstraction; we are not really looking for an event that is or is not an adaptive radiation, but rather, where, on a continuum from simple cumulative divergence, to a full blown explosion of diversification, do the australopiths (and other hominins) fit? While the data tend to indicate an answer closer to the former than the latter, this conclusion is strongly influenced by the selected taxonomic scale—an issue to which I shall return at the end of this paper.

Missing Australopiths and Adaptive Asymmetry

Part of the problem with testing Schluter's model lies in the fact that the taxonomic scale is relatively small, and it is likely that errors in dating and sampling could have a significant influence on the results. An alternative is to look for another signal of adaptive radiation. Some time ago, Guyer and Slowinski (1993) suggested that the topologies of phylogenies can provide evidence for adaptive radiations.

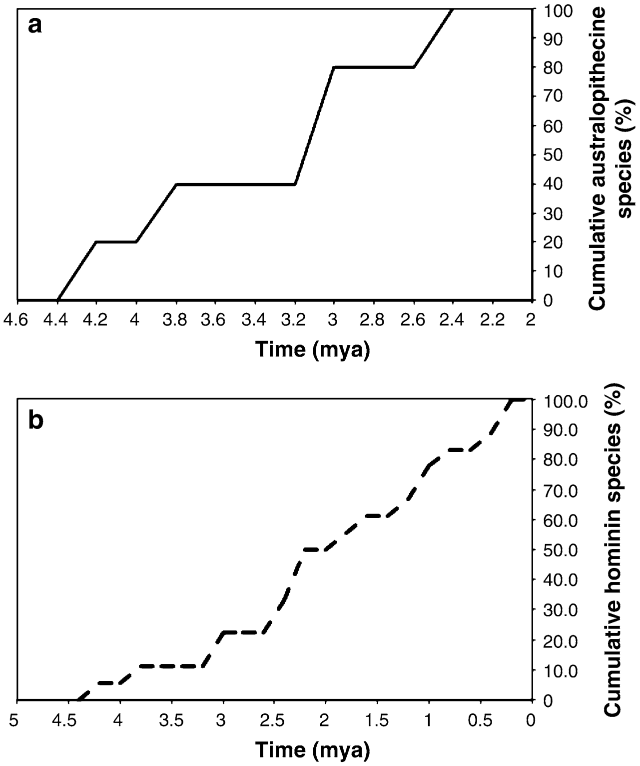


Fig. 10.4 Relative accumulation of new taxon in hominin evolution. The *horizontal* axis is time in millions of years, and the *vertical* one shows the percent of the total number of hominin species which have appeared. **a** Australopiths; **b** all post 4.3 Mya hominins

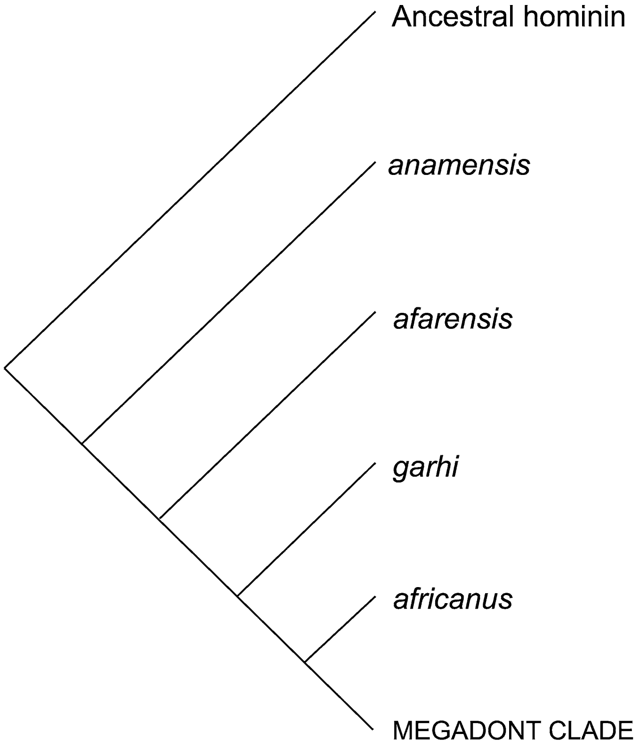
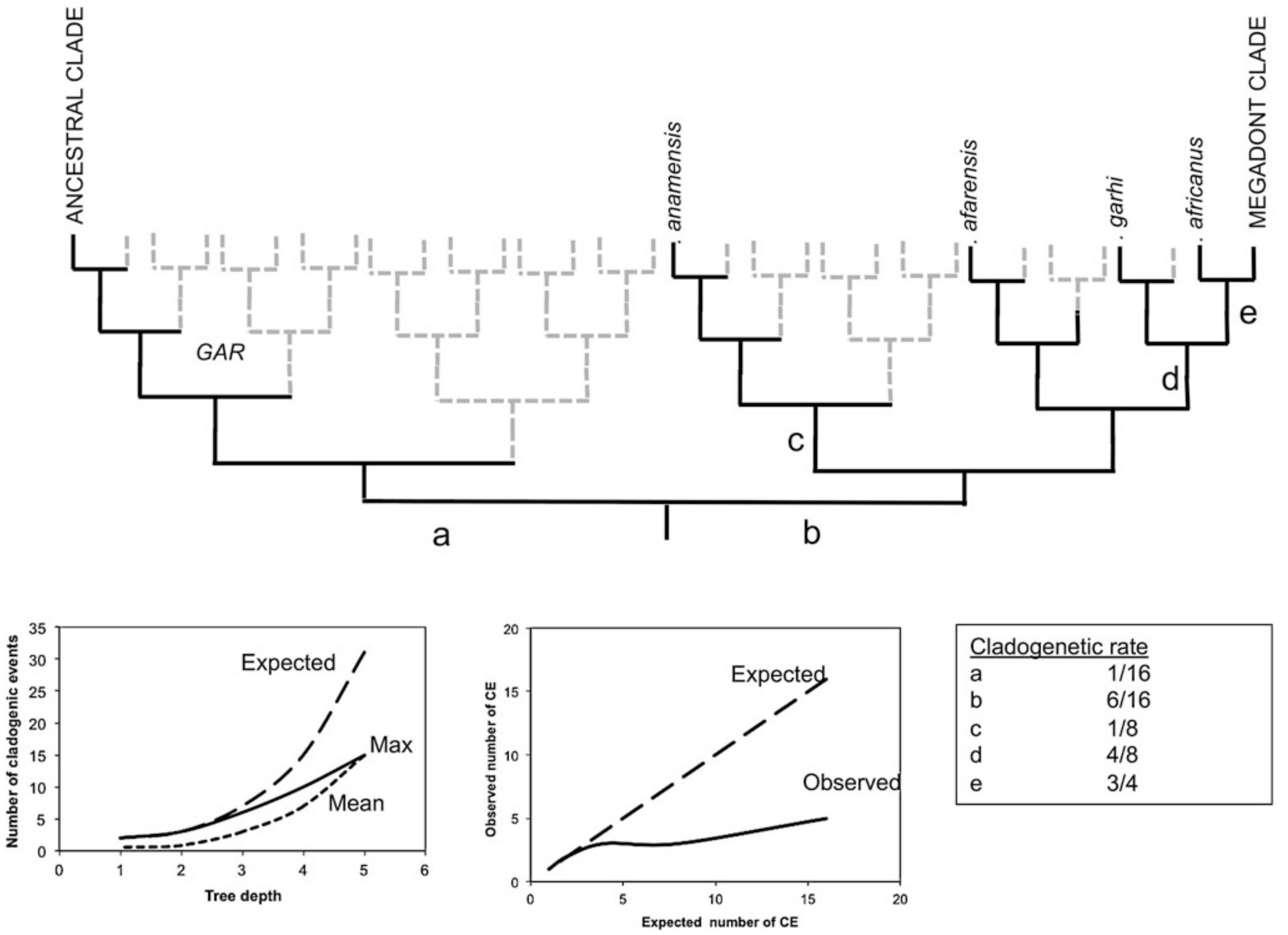


Fig. 10.5 Cladogram of australopith taxa used in text Strait and Grine (2004)



Cladogenetic rate	
a	1/16
b	6/16
c	1/8
d	4/8
e	3/4

Fig. 10.6 Deviations from the perfect tree. The *top left panel* shows the Equal Rates Markov chain Model for australopiths (known taxa in *black*, "missing taxa" in *dashed lines*). The table at the *bottom right* shows the relative deviation of the *Australopithecus* fossil record from the model. The graph on the *bottom left* shows the deviation from expected in relation to the depth of the tree, and the graph to the *right* compares observed and expected clades. Right hand table shows the cladogenetic rate for sub clades (letters refer to those in main figure).

Since the publication of their paper there has been considerable progress in this field, and also a multiplication of models (Harcourt-Brown et al. 2001; Bokma 2003; Pineli 2003).

Depending upon scale and taxonomic inclusiveness, the phylogeny of the australopiths is one for which there is broad consensus in general terms, but disagreements about some of the branching sequences. Strait (2013) shows one version, with the entire clade history of hominins until the beginning of the Pleistocene. For the purposes of the analysis here, focusing on the australopiths in a relatively narrow sense, a simplified tree is sufficient to make a theoretical rather than a phylogenetic point (Fig. 10.5). The early hominin phylogenetic tree is a highly odd one—it is strongly asymmetrical. Figure 10.6 illustrates this by showing the same taxa but placed on to an Equal Rate Markov Chain Model tree (with and without the tree pruned (clades shown with dashed line)). What we can see is that diversification is only apparent on one side of the tree, or, expressed alternatively, there may be a high rate of extinction and low persistence on the other side. Guyer and Slowinski, and subsequently many others, have argued that the degree of asymmetry is a signal of adaptation. Put the other way round, under conditions of neutrality, one can expect Markov Chain processes to occur, and therefore the more asymmetrical the tree, the greater the evidence for adaptation, and thus adaptive radiations.

There are a number of ways of measuring asymmetry. These are mathematically relatively simple, but there are issues relating to analytical artifacts that arise from such things as the taxonomic level. It has also been pointed out that paleontological trees tend to be even more asymmetrical than neontological trees. While this may be expected to be a function of the poor fossil record, it has also been shown that it arises because of the way in which paleontological trees sample across time (Harcourt-Brown et al. 2001).

I have estimated the deviation from that expected under an ERM model (Fig. 10.6) by calculating the ratio of expected to observed clades for different parts of the tree. As can be seen, it is considerable. While this indicates that there are many more taxa out there for us to find, it can perhaps better be interpreted as evidence for adaptive trends, and in the emerging diversity, some trend also towards an adaptive radiation, rather than neutral drift, in the pattern of *Australopithecus* evolution.

A Dispersal Model

Given that there is only a weak signal for an adaptive radiation, we should perhaps ask whether there is a better model for explaining the observed pattern of australopith evolution. In a previous publication we (Lahr and Foley 1994, 1998) set up a general model of dispersal-based evolution, derived from Tchernov's (1992) geographical perception of the evolution of a lineage. Put simply, the history of a lineage can be described as a series of changes in geographical distribution, from a narrow point of origin, through range expansion(s), to contraction into refugia, and finally, a localised point of extinction. We have used this model extensively to understand the evolution of later *Homo*, but it has also been applied to the Pliocene hominins more generally (Foley 1999). There it was argued that the phylogeny of the early hominins across the Plio-Pleistocene within Africa matched the geographical context, and that the diversity could best be explained in terms of a series of dispersals.

This evolutionary geographical model, adapted for some more recent discoveries, still broadly holds. Rather than develop that element here (but see Strait 2013), instead I want to explore how we might use geographical models to generate new hypotheses. When we think about the geography of African hominins, we are strongly directed towards a simple East versus South perspective, with arrows linking the two (e.g. Lockwood 2013). There is a tendency to add directionality to this, largely from East to South, as this is consistent with chronology, mammalian patterns, and ecological principles (Turner and Wood 1993; Strait and Wood 1999). However, sub-Saharan Africa (and indeed northern Africa too; it should be remembered that the Sahara is by no means a fixed geographical feature) is actually made up of a series of lake basins, river networks, and watersheds. As Kingdon (1984, 1989, 2003) has shown, the evolutionary diversity of mammals is strongly related to these basins, and to the ways in which they respond to climatic change, forming refugia and basins of isolation. Furthermore, their shifts and changes, tectonic or climatic, can form the basis for connectivity as well.

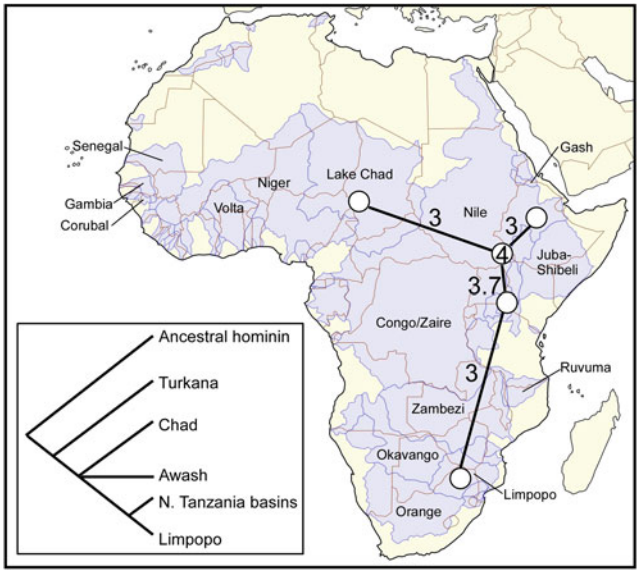


Fig. 10.7 The basins of Africa. The *white circles* indicate basins with australopith fossils. The *connecting lines* indicate possible routes of connection, with dates in millions of years. The *inset* cladogram shows a "basin-based" cladogram for early hominins

Figure 10.7 shows the basins of sub-Saharan Africa with *Australopithecus* localities superimposed. The first striking thing about these is that there are basins intermediate between those in which hominins are found which would have to be crossed; key ones would be the Nile and the Zambezi, and the Okavango and Rovuma might also be relevant. We can think of our extinct hominins not as species, but more neutrally as paleodemes (Howell 1999), structured by their geography, and the basin structure of Africa can provide the appropriate framework. Links between those basins are created by dispersals and range expansions; differences by subsequent isolation and refugia. Our fossil record is likely to consist of a series of snapshots in that process, repeated over many millennia.

Also superimposed on to the map of the basins are some potential links between the australopiths, with FADs as indicators of a chronology. These links do not replicate the consensus trees, but basins could perhaps be used to generate testable hypotheses, independent of the generally accepted taxa (inset, Fig. 10.7). Further resolution can be added to this by considering distances, numbers of intermediate basins, and paleoenvironmental reconstructions[1]—especially as these basins have changed and developed

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[1] Figure 10.7 also shows the eastern coastal forest zone, which should more accurately display river systems as well. Kingdon (2003) has suggested that these were crucial to the evolution of bipedal hominins, and played a key role in subsequent diversification, with the river valleys into the interior producing isolation, adaptation, and considerable convergence. They should clearly be considered as both a dispersal route, and as set of north–south barriers in some zones.

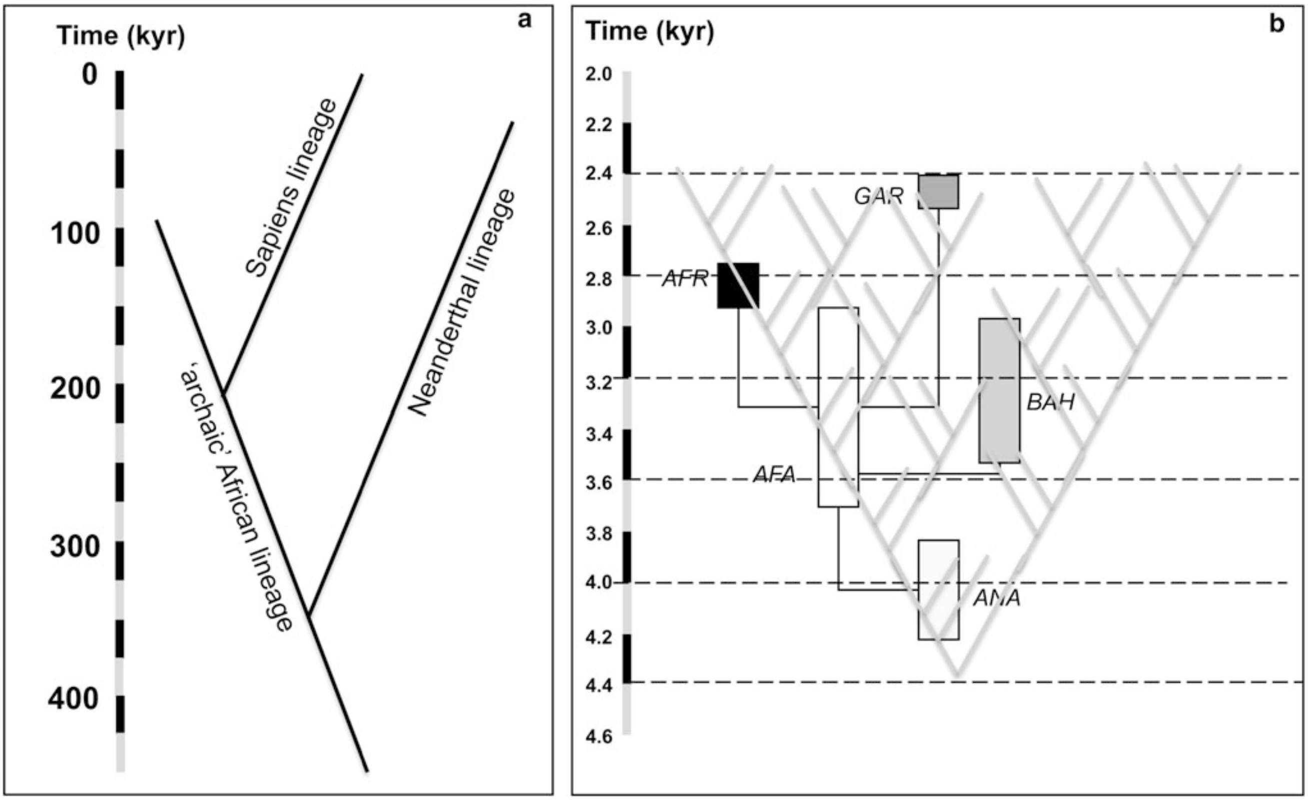

Fig. 10.8 Comparison of evolutionary scale. **a** Shows the evolution of *Homo* over the last 400 kyr. **b** Shows the phylogeny of the australopiths superimposed onto the scale of later *Homo* evolution. Australopith evolutionary scale equates to at least four "later *Homo* events"

considerably over the course of the Pliocene and Pleistocene (e.g., Zambezi, Nile, Congo).

Emerging Problems: Scale

In the models and discussions presented so far one issue that has recurrently been implicit is that of scale. Most of the models and tests that are carried out in the field comparatively consider much larger radiations (vertebrates, birds, cichlids, etc.), where often hundreds of species are involved. The australopiths, and even the hominins as a whole, are a relatively small clade, and so stochastic effects could influence the results rather more than would be the case with large radiations. One example is the analysis of rates of speciation shown above. These are low, and yet it is probably the case that were we to carry out this type of analysis across the whole of the catarrhines, and at a larger chronological scale, bursts of speciation would be more apparent. It is reasonable to ask, therefore, what scale of evolutionary event is represented by the australopiths. To answer this question two comparisons can be made—with the evolution of later *Homo*, and the diversification of *Pan*.

The evolution of later *Homo* is probably the best known diversification event in mammalian evolution, with evidence from genetics, archaeology and fossils. Although this is often characterised as an area of great controversy, in fact we know with considerable precision what happened. Broadly speaking, we can say that over a period of about 450 kyr, hominins diverged into two major lineages, a Eurasian one and an African one (Fig. 10.8a). The Eurasian one evolves into Neanderthals, almost certainly, on the basis of genetic evidence, involving a demographic bottleneck. The African one is diverse, geographically widespread, and also diverges (and presumably speciates), with an ancestral "archaic" population (what we would refer to as *H. helmei* (Lahr and Foley 1998) with a small bottlenecked population evolving into modern humans, and subsequently undergoing a series of major dispersals. The issue here is not the exact phylogenetic details, let alone the question of gene flow, but simply that these two events provide us with a well-documented comparative scale which we can use to examine the australopiths. Essentially we can think of four to five hundred thousand years as a "modern human evolutionary unit" where there is a major continental scale divergence and a geographically smaller divergence within Africa. Figure 10.8b shows the later

Homo "events" superimposed on the *Australopithecus* record, using an equal rate Markov Chain model (ERM). As can be seen, the *Australopithecus* record is, by comparison, rather course-grained. The entire evolutionary history of the australopiths covers four units of later *Homo* evolutionary events. In terms of scale of process, or perhaps more accurately, number of events, the Pliocene is likely to have been much more complex than the models we generally use would imply. This is not to say that there should be another twenty or thirty species to be found, but that, at the demic, sub-species, and lineage divergence level, there are likely to have been far more events.

This comparison has the advantage of making us focus on how the microevolutionary processes which underly a more macroevolutioanry pattern can help us explore greater complexity. However, it could be argued, of course, that this is not an appropriate comparison. The reasons for this would include the view that culture-bearing modern humans are completely different, that the scale of climatic variability in the later Pleistocene is higher, or that *Homo* is a global species, whereas the australopiths are confined to a part of Africa. All of these may or may not be true. An alternative comparative framework can therefore be sought in the genus *Pan.* At one level we could simply say that there are three species in *Pan*, and four sub-species, over a period of five or more million years. However, emerging genetic evidence makes it clear that this is an oversimplification. Current estimates would place the divergence of *Pan paniscus* and *Pan troglodytes* at about 800 ka, somewhat younger than previous calculations. The divergence of the most distant of the chimpanzee taxa, *Pan verus* and *P. troglodytes*, is thought to have occurred about 420 ka (Fischer et al. 2004; Won and Hey 2005), and the formation of the other subspecies, somewhat younger. In other words, the current species and sub-species of *Pan* are all relatively recent in the context of the origin of the clade. The observed diversity, in terms of species and sub-species, represents only one fifth of the period since the divergence with the hominins. It is not possible to simply draw these clades back through time; instead we would have to think of a series of (semi?) replacement events, with the *Pan* diversity constantly shifting, albeit with relatively little speciation. The useful insight that can perhaps be used to throw light on the australopiths is that there may be a whole series of dispersals in which, depending on conditions, either previous diversity was erased, or re-organised, and that species are a crude instrument for measuring this.

One way of looking at the diversity of *Pan* as a model for hominin evolution is that it would lead to a rather more conservative view of diversity than the later *Homo* model, albeit still a complex one. However, there is another element to which it is worth drawing attention. While there is no evidence for gene flow between *P. paniscus* and *P. troglodytes*, there is within *P. troglodytes*. According to Won and Hey (2005), this flow is primarily from west to east, suggesting a recurrent directionality that will produce a level of sub-species asymmetry. Eastern chimpanzees will accumulate traits of their own, but also absorb novelties from the west. This might be a factor in differential levels of variation, conservatism, and apomorphies among australopiths, where instead we are likely to be looking at north–south/south–north patterns.[2] We tend to think of dispersals as events with directions, but these results show that gene flow can also have strong biogeographical directionality.

Discussion

This paper started by accepting the challenge of exploring the idea that there was an australopith radiation. This led to a consideration of one or two of the formal models that have been developed more broadly to determine whether evolutionary patterns are adaptive radiations. While there is a clear signal in the tree asymmetry of the australopiths, other signals were more ambivalent. The primary theoretical conclusion was that if our question relates to the patterns and processes of divergence, then there is a continuum from simple dispersal driven divergence to explosive speciation. *Australopithecus* species, and probably all hominins, are likely to be closer to the former than the latter, but nonetheless, are moderately speciose.

An alternative approach was to consider the australopith diversity as a product of dispersal under an evolutionary geography model. This showed that there is broad congruence between geographical patterns and the australopith (and robust australopith) probable dispersals. In order to develop this approach it was proposed that biogeographic basins could be used as a framework for phylogenetic analysis, and developing new hypotheses that were not necessarily based on current species designations.

Some general conclusions about the australopith radiations are:

1. Dispersals are the driving force in diversification following the evolution of "a new trick" (bipedalism?) and/or changes in environment.
2. Adaptively driven diversification of the phenotype following dispersal will be dependent upon the level of environmental variation and the degree of specialisation of the lineage (this is similar to Vrba's 1992, effect hypothesis which explained, for example, why impala speciated at a much slower rate than alcelaphines under

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[2] Interestingly enough, among gorillas the gene flow appears to be stronger from east to west (Thalmann et al. 2007).

similar conditions). For the austalopithecines it is likely that there was a broad similarity of habitat, and a lack of extreme specialisation as large bodied primates.
3. The outcome was a moderate level of speciation and diversification, of which we are picking up only a small proportion under the basin model proposed.
4. Adaptive radiations where there are very high levels of speciation tend to be associated with high levels of sexual selection (e.g., among passerine birds high rates of spceciation are associated with levels of plumage colouration (cf. cercopithecines)), and perhaps we can infer this is not the case for early hominins.
5. The scale of the australopith "radiation" is perhaps rather limited, but when the more general comparative models derived from larger studies are grounded against either recent hominins or African apes, we should perhaps still expect considerably more diversity to occur, although within limited phenotypic ranges.

This paper has explored the ausralopithecines in the light of various general evolutionary models. Many might say that we are better off being strictly empirical. However, all empirical studies are bounded by theories and models, and it is better to make them explicit rather than leave them unspoken. More importantly, unless we know what to expect in evolutionary history, it is very difficult to understand what it is we have observed (see Ezard et al. 2011, for a demonstration of this in relation to mammalian evolution more generally). There are, across the evolutionary field, many powerful models which can be used to investigate patterns of human evolution. But perhaps my strongest argument in favour of more theory in paleoanthropology is a completely different and surprising one. Although we all complain about the problems of the fossil record, hominin evolution is a remarkably well-studied and data rich field. The pattern of human evolution can be used to test and develop general models in evolutionary biology.

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Chapter 11
Whence *Australopithecus africanus*? Comparing the Skulls of South African and East African *Australopithecus*

Charles Lockwood

Abstract There is longstanding debate on the position of *Australopithecus africanus* in hominin phylogeny, possibly due to the phenetic gap that exists between *A. africanus* and *A. afarensis*. The fact that *A. africanus* is phenetically similar to *Paranthropus* and *Homo* allows it to endure as similar to each in cladistics analyses without resolving its exact phylogenetic position. This fact permits the development of a variety of both evolutionary and biogeographic models to explain the conundrum of *A. africanus*. This taxon likely arose from a population derived from somewhere in the middle of the *A. anamensis* to *A. afarensis* lineage that was subsequently isolated in South Africa. There are a variety of anatomical features that support this view. The variation through time in *A. africanus* is somewhat unexpected in that the Makapansgat sample is more *Paranthropus*-like than those from Sterkfontein, which, as a whole, are more *Homo*-like. Many of the relationships among these taxa are dependent on the biogeographical models that can be constructed from the limited data that we possess, but there are two basic ways to think about this: (1) eastern Africa was the center of evolution and ensuing distribution, with movement always to the south and with southern populations becoming extinct, or (2) a "piston" type model, which encompasses character displacement among sympatric species as they occur throughout back and forth movement across the continent through time. Each of these fits into evolutionary models in different ways, the former fits better with cladistic analyses and the latter is more stratophenetic. In the end, despite the fact that there are many fossil specimens of *A. africanus*, its phylogenetic position remains unresolved.

Keywords Biogeography • Comparative anatomy • Phylogeny • Stratophenetics

Introduction

If we take the current dates and distributions of early hominin species at face value, then at least one biogeographic event is perfectly clear: at some point prior to 3 million years ago (Ma), an ancestor of *Australopithecus africanus* dispersed (or spread) to southern Africa. *Australopithecus africanus* either evolved directly from the dispersing population (through a process of rapid allopatric or peripatric speciation), or was descended from an isolated population that had long been in residence in southern Africa. The likelihood of these possibilities depends to a great deal on the dates and affinities of fossils associated with the "Little Foot" skeleton from Sterkfontein Member 2. Similarly, further analysis of *Kenyanthropus* will affect how we interpret the potential east African source populations for *A. africanus*. Because these issues are currently at least partially unresolved, this paper focuses on two questions: (1) how much morphological change took place at the origin of *A. africanus*? and (2) is there evidence for a particular segment of the *A. anamensis–afarensis* lineage being the origin of *A. africanus*-like hominins in southern Africa? These questions lead naturally to a consideration of whether these comparisons serve to test broader hypotheses of biogeography among early hominin taxa.

How Much Change?

Most phylogenetic analyses of early hominin taxa agree that *A. afarensis* is the sister group to a clade containing at least *Homo*, *Paranthropus robustus*, *P. boisei*, *P. aethiopicus*, and *A. africanus* (Johanson and White 1979; White et al. 1981; Kimbel et al. 1984; Skelton et al. 1986; Chamberlain and Wood 1987; Wood 1988, 1991, 1992; Skelton and McHenry 1992; Liberman et al. 1996; Strait et al. 1997; Strait and Grine 2004; Kimbel et al. 2004; Strait 2013) (Table 11.1). Depending on when they were published,

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Table 11.1 Apomorphies and synapomorphies of early hominins as recorded by Strait et al. (1997)

Synapomorphies of the *A. africanus* + *Homo* + “robust” clade:
- 5. Nasoalveolar clivus straight in coronal plane
- 13. Index of palate protrusion is variably prognathic and mesognathic
- 16. Cranial capacity increased to state 1 (approximately 500 cm^3)
- 21. Partial compound T/N crest
- 22. Asterionic notch either variable or absent
- 33. Postglenoid process size and position intermediate
- 34. Tympanic crest with vertical plate
- 40. Nuchal plane weakly inclined
- 47. Hollowing above and behind mental foramen variable
- 52. Prominence of median lingual ridge of mandibular canine is variable
- 58. Well developed P3 metaconid is frequent

Synapomorphies of the *Homo* + “robust” clade:
- 38. Petrous orientation coronal
- 42. Foramen magnum roughly horizontal
- 45. Vertically oriented mandibular symphysis
- 46. Mental foramen opens laterally
- 47. No hollowing above and behind mental foramen
- 51. Canines very reduced
- 52. Weak median lingual ridge of mandibular canine

Apomorphies of *A. afarensis*:
- 14. Masseteric tubercle at or anterior to sellion (parallel with “robust” clade)
- 18. O–M sinus frequently present (parallel with *A. robustus* + *A. boisei* clade)

Apomorphies of *A. africanus*:
- 1. Projection of nasal bones variable
- 4. Anterior pillars variable (parallel with *H. habilis*).
- 12. Palate deep anteriorly (shelved; parallel with *A. boisei* and *H. rudolfensis* + *H. ergaster* + *H. sapiens* clade)
- 21. Compound T/N crest absent (parallel with *H. rudolfensis* + *H. ergaster* + *H. sapiens* clade)

Apomorphies of *P. aethiopicus*:
- 13. Index of palate protrusion prognathic (reversal)
- 16. Cranial capacity reduced to state 0 (less than 500 cm^3; reversal)
- 21. Compound T/N crest extensive (reversal)
- 22. Asterionic notch present (reversal)
- 30. Flat cranial base (reversal)
- 32. Shallow mandibular fossa (reversal)

Apomorphies of *P. robustus*:
- 4. Anterior pillars present
- 27. Reduced pneumatization of temporal squama (parallel with Homo clade)
- 37. Eustacian process present and prominent (reversal)

Apomorphies of *P. boisei*:
- 12. Palate deep anteriorly (parallel with *A. africanus* and the *H. rudolfensis* + *H. ergaster* + *H. sapiens* clade)
- 32. Deep mandibular fossa (parallel with *H. sapiens*)
- 34. Tympanic crest with inclined plate
- 53. Premolar crown area increased to state 5 (largest)

Apomorphies of *H. habilis*:
- 4. Anterior pillars variable (parallel with *A. africanus*)
- 7. Variable entrance to nasal cavity
- 35. M–L position of external auditory meatus variable
- 41. Foramen magnum variably at or anterior to bi-tympanic line.

Apomorphies of *H. rudolfensis*:
- 6. Nasoalveolar contour does not protrude beyond bicanine line (parallel with “robust” clade)
- 11. Intermediate projection of zygomatic bone relative to piriform aperture
- 44. Mandibular cross-sectional area at M1 variable
- 47. Variable hollowing above and behind mental foramen (reversal)

different analyses have included other taxa in this clade (such as *A. garhi* and/or *Kenyanthropus*). Disagreement has focused on the relationships among these taxa, and *A. africanus* in particular has not found a permanent home on any branch of the tree. Precisely because of the oft-cited disagreements among phylogenies, it is striking that the position of *A. afarensis* outside of the “*africanus* et al.” clade has not changed since it was discovered.

This general consistency among phylogenetic results says as much about *A. africanus* as it does about *A. afarensis*, because it illustrates the phenetic gap that exists between the two taxa. Recent comparisons of skull anatomy underscore the differences in anatomy (Fig. 11.1; Lockwood and Tobias 1999; Kimbel et al. 2004). *A. africanus* is phenetically similar to both *Homo* and *Paranthropus*, and this mixed bag of similarities has the cladistic effect of keeping *A. africanus* close to each of those genera, without resolving exactly where in history it fits. Comprehensive lists of characters can be found in the phylogenetic analyses of Strait and colleagues (see Strait and Grine 2004) and Kimbel et al. (2004). To give some examples, *A. africanus* has a divided supraorbital region (like *Homo*), several features associated with a more rounded braincase (*Homo*), universally bicuspid lower P3s (both *Homo* and *Paranthropus*), midfacial morphology including an anterior pillar and anteriorly placed zygomatic process (*Paranthropus*), and temporal bone anatomy including a moderately deep mandibular fossa and a “petrous crest” along the lower edge of the tympanic, among other features (similar to *Homo*). Figure 11.2, which summarizes the temporal bone anatomy, is a succinct illustration

Fig. 11.1 From *left* to *right*, crania of *Australopithecus afarensis*, *A. africanus*, and *H. rudolfensis*

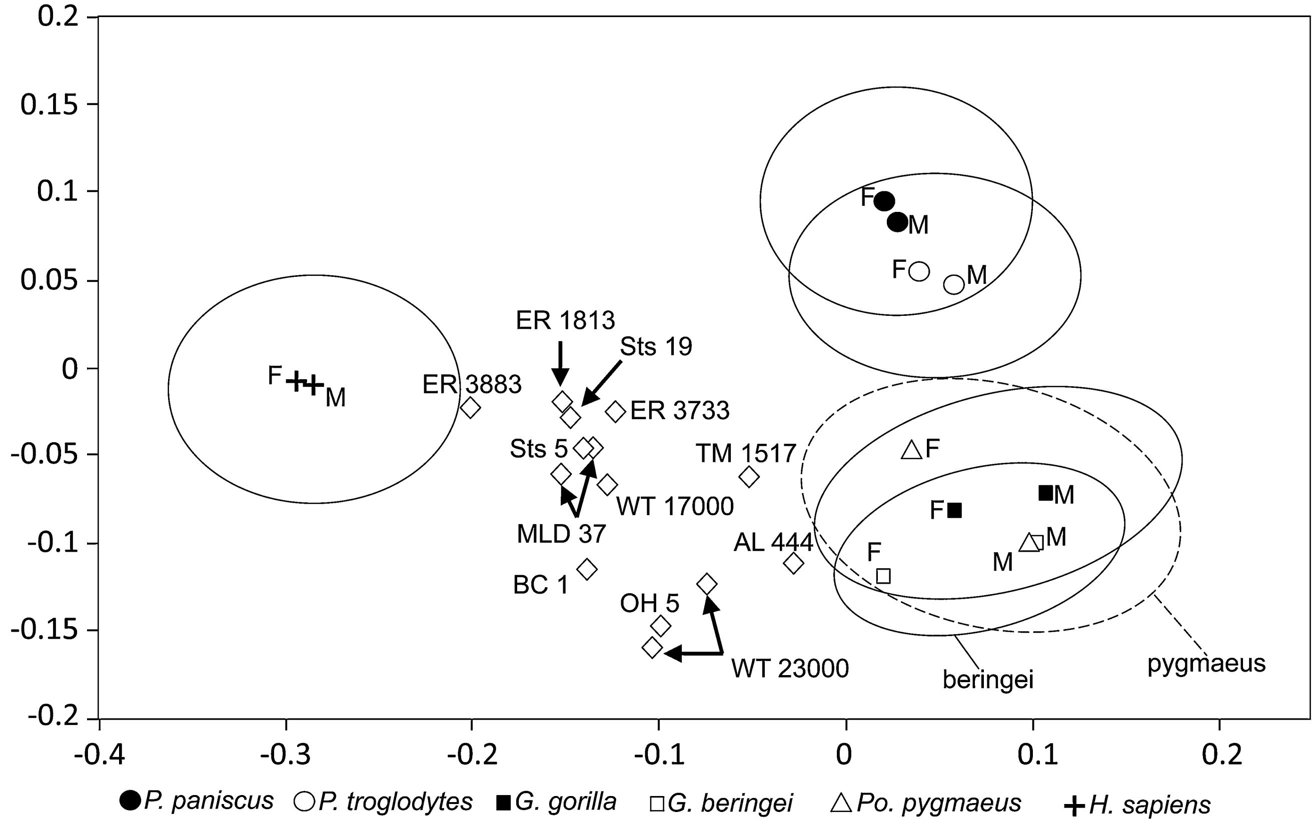

Fig. 11.2 First two principal components (PC1 = x-axis, PC2 = y-axis) from a geometric morphometric analysis of 14 3D landmarks representing fossil hominin temporal bone anatomy. Specimens of *A. africanus* (Sts 5, Sts 19, MLD 37/38) are much more similar to specimens of *Homo* (KNM-ER 1813, KNM-ER 3733) than are other *Australopithecus* species

of how phenetically similar *A. africanus* is to *Homo*. *Australopithecus africanus* also lacks some key characters shared by *Homo* and *Paranthropus*, such as the more coronally oriented petrous axis. But however one chooses to look at it, there was a substantial shift in skull morphology between *afarensis*-like and *africanus*-like species. For the time being, this is a difference between eastern and southern African forms, respectively, although *Kenyanthropus* does bridge the morphological gap to some extent.

How did this change come about? Until the record is more resolved, interpretations depend on one's a priori views of macroevolution. If one expects punctuated change associated with a founder effect, then *A. africanus* originated as a small population, cut off from its eastern African relatives and rapidly became something different. If one prefers gradual evolution of large populations, associated with adaptationist explanations, then the implication is that *A. africanus* was in southern Africa for a long time, and it was adapted over the long-term to an environment that was different from habitats in eastern Africa. Again, the Little Foot material will prove crucial in this regard. Does it show that *A. africanus* was already "*A. africanus*" immediately upon arrival in southern Africa? Or is Little Foot basically eastern African in appearance, suggesting that *A. africanus* evolved over a longer period or through a more complex process?

Picking Apart the Eastern African "Lineage"

Australopithecus afarensis is largely defined by fossils dated to between 3.0 and 3.4 Ma. Possible dates for Makapansgat *A. africanus* prior to 3 Ma make it unlikely that any of the well-known *A. afarensis* material is among the populations that were ancestral (even in the broad sense) to *A. africanus*. We probably have to look to Laetoli-era *A. afarensis* or its predecessors in *A. anamensis* to find the time of migrants heading south.

Kimbel et al. (2006) treated the *A. anamensis-afarensis* sequence as four site-samples, for the purpose of evaluating its status as a lineage. From early to late, they are Kanapoi, Allia Bay, Laetoli, and Hadar. Hadar could be divided into "early Hadar" and "late Hadar" to make the site samples more similar in the amounts of time they represent (see Kimbel et al. Fig. 11.3). It is possible to exclude certain samples of *A. afarensis* from the ancestry of *A. africanus* if the latter lacks derived features present in late *A. afarensis* samples but retains primitive traits present in earlier *A. afarensis* samples. This is not easy to do at present, because Kanapoi, Allia Bay, and Laetoli samples are mostly comprised of teeth and jaws. However, there are some clues.

In two features of the maxillary canine, *A. africanus* retains a primitive condition similar to Laetoli specimens, but differs from Hadar samples. The crown shape index is similar to Laetoli insofar as the canines in *A. africanus* are relatively longer mesiodistally than are those from Hadar. Also, maxillary canines of *A. africanus* are symmetric in profile, like those at Laetoli and in earlier samples, while Hadar maxillary canines tend to be asymmetric with higher shoulders mesially. Some specimens of *Homo*, such as OH 16 and KNM-ER 1590 also have symmetric upper canines, though they are different in other respects from *A. africanus*.

Canines thus suggest that *A. africanus* is unlikely to be derived from Hadar-like populations. Other features are more confusing, however. In the position of the maxillary incisors relative to the nasal aperture, the Garusi maxilla from Laetoli has an appearance more similar to *A. africanus*, *Kenyanthropus* and later hominins than to Hadar specimens. The lateral incisors are between the parasagittal planes defined by the lateral boundaries of the nasal aperture (i.e., underneath the nose), rather than sitting lateral to them as at Hadar. Also, in the shape of the lower lateral incisors, *A. africanus* retains mesiodistally expanded incisors, similar to *A. anamensis*, not like Laetoli or Hadar.

Finally, there are a variety of characters in which *A. africanus* shares synapomorphies with later hominins, such as uniformly bicuspid lower P_3s that are oriented perpendicular to the tooth row. These are among the features that support a position of *A. africanus* higher up the tree than *A. afarensis* at Hadar.

While there is no perfect way to tie samples together to evolve these character distributions without homoplasy, the distribution of features hints that *A. africanus* stemmed from the middle part of the *A. afarensis*–*A. anamensis* lineage. The evidence is admittedly thin, but even without getting into details, it seems clear that an *earlier* origin of *A. africanus*—from populations similar to *A. anamensis*—would invoke more homoplasy than an origin of *A. africanus* from populations similar to Laetoli and Hadar specimens. We can take as a working hypothesis that there was genetic continuity between eastern and southern African *Australopithecus* at approximately 3.4–3.5 Ma. Something happened soon after this to isolate the southern African populations, which evolved into *A. africanus*-like forms by the time they are sampled at Makapansgat. It is the "something" that is interesting. Very likely the same process that cut the populations off—habitat fragmentation—was the one that led to selection for a different array of morphologies associated with mastication as well as with brain size and shape.

A cooling event probably disrupted hominin habitats between 3.2 and 3.5 Ma (see Bonnefille et al. 2004; Vrba 2007). The timing of this climatic change provides a testable hypothesis to explain the origin of *A. africanus*. When fossils from South Africa are securely dated to periods before this event, they will either resemble eastern African populations, substantiating a local climate-based explanation of *A. africanus* origins, or they will already resemble *A. africanus*, rejecting at least the 3.2–3.5 Ma version of a climate-driven hypothesis.

The Fate of *A. africanus*

While Makapansgat gives us a relatively secure date for the earliest known *A. africanus* remains, Sterkfontein is important with respect to two issues: (1) the longevity of the *A. africanus* lineage in southern Africa, and (2) the

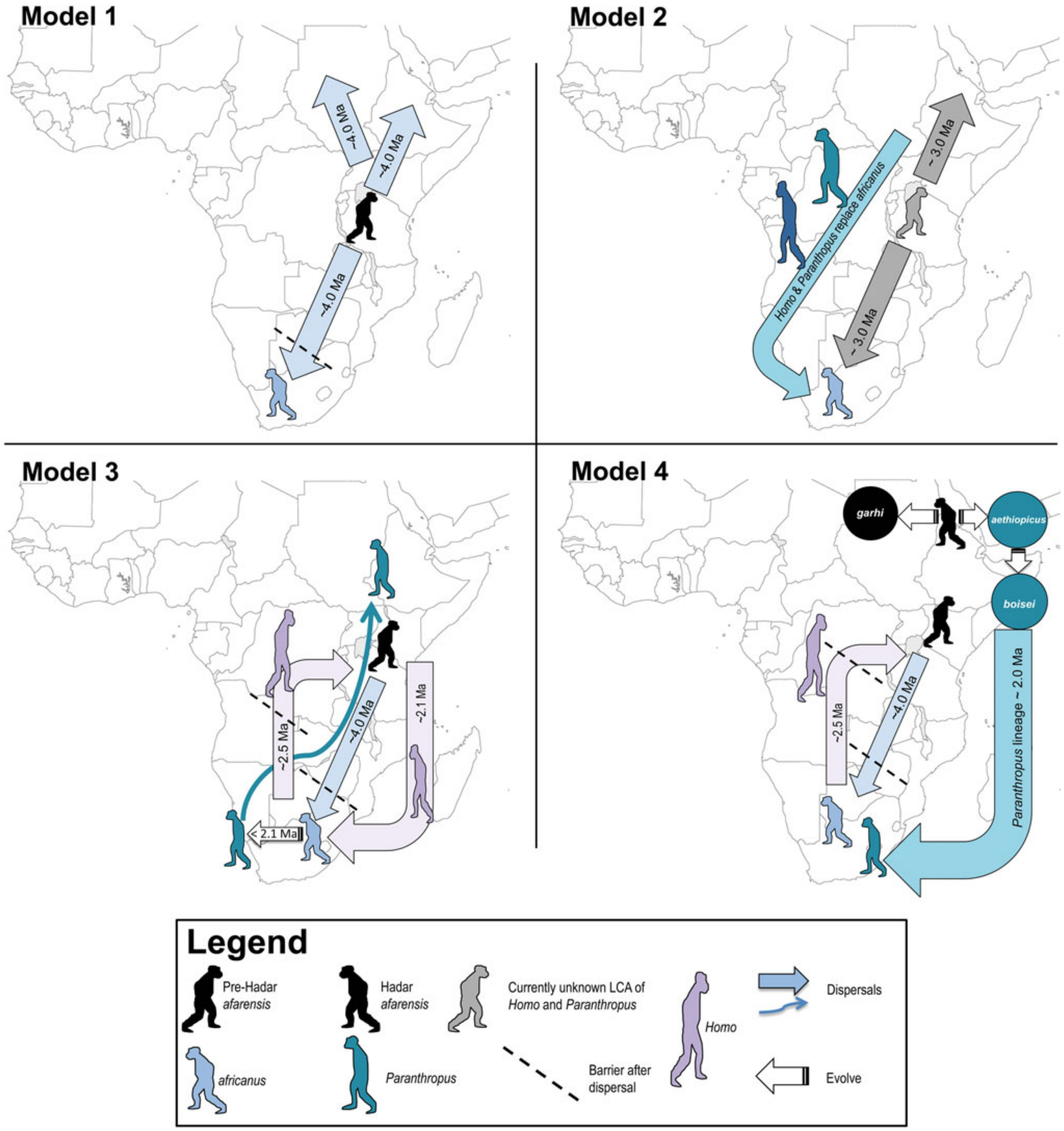

Fig. 11.3 Depiction of the four models of hominin biogeography. Models 1 and 2 suggest that east Africa was the center of distribution; Models 3 and 4 depict the "piston" requiring character displacement in each region

relationship of *A. africanus* to the origin of *Homo* at 2.3–2.5 Ma. Establishing a "long chronology" of *A. africanus* in southern Africa, as suggested by the 2.1 Ma date possibly associated with Sts 5, would be the first well-documented hominin lineage in that region. Implications of dates for the origin of *Homo* are less clear. Even at present, it appears that *Homo* originated prior to the extinction of *A. africanus*. This allows to reject a scenario of anagenetic transformation of *A. africanus* into a species such as *H. habilis*, although the hypothesis cannot yet be completely rejected. Overlap in time between *A. africanus* and *H. habilis* could be interpreted as ruling out the ancestral status of the former. However, it seems to me that overlap in time between these taxa is exactly what is expected if early *Homo* populations are derived from some *A. africanus* populations. This would not be anagenetic evolution, but instead a cladogenetic event resulting from the isolation of *A. africanus* populations from each other. This model is detailed below along with alternatives.

One unusual feature of the *A. africanus* lineage is that variation through time is apparent, but it is not in the expected direction. The Makapansgat hominins, though few in number, are enough to illustrate a tendency towards characteristics of *Paranthropus* species. However, this does not mean the Sterkfontein Member 4 sample is uniformly more generalized than the Makapansgat sample. Some specimens show derived characters of *Homo*, and the sample as a whole is more similar to *Homo* than is the Makapansgat sample.

What Can Be Known?

A question for any scenario of biogeography, or other aspects of human evolution that require accurate first appearance dates, is how reliable the fossil record is in terms of diversity and representation of ranges (e.g., White 1988). There are certainly some unreliably empty regions, in which the absence of fossils does not mean absence of hominins. South Africa prior to 3.0 Ma, and western Africa at any point during the Pliocene, are obvious examples. The absence of hominins at Langebaanweg at 5.2 Ma (Roberts et al. 2011) is the only sign that hominins appeared in eastern Africa prior to southern Africa, but by itself it is weak evidence. If western Africa played a central role in hominin origins or hominin radiations through the Pliocene, it is likely we will never know the whole story or have accurate dates for key events. In an extreme view, construction of detailed biogeographic scenarios or tests of the link between global or regional climate change and events in human evolution are essentially a waste of time, given the limitations of the fossil record.

A more optimistic view derives from the modern distribution of fauna, which suggests that habitats and mammalian communities are more similar across western and eastern Africa than they are to southern Africa. Broadly similar latitude, rainfall, and vegetation underlie an east–west corridor of faunal interchange. Southern Africa is more provincial in its fauna, and that was the case through the Plio-Pleistocene as well (Reed and Lockwood 2001). Among modern mammals, it is rare to find a genus in western Africa that is not also found in eastern Africa. Among primates, many genera are found on both sides of the continent, including *Pan, Gorilla, Papio, Cercopithecus, Cercocebus, Lophocebus, Cercopithecus, Colobus* and *Piliocolobus*. In contrast, there are a number of anthropoid genera whose ranges do not extend to South Africa, underscoring the greater provinciality of southern African fauna. I would argue, therefore, that the division between eastern and southern Africa gives us a reasonable picture of hominin diversity, and—more tentatively—that major events which occurred in western African hominin populations would soon make themselves apparent in eastern Africa. Given this assumption, therefore, it is possible to pose several alternative and, hopefully, testable models to explain the biogeographic relationships between eastern and southern African hominins.

There and Back Again: Models of Early Hominin Biogeography Pertaining to *A. africanus*

Four models are presented. The first two identify eastern Africa as the center from which early hominins originate. In the latter two models, hominin species arise as a consequence of populations dispersing back and forth between eastern and southern Africa (Fig. 11.3).

Model 1: Australopithecus africanus originates from pre-Hadar *A. afarensis* populations dispersing to the south that are subsequently cut off from eastern African populations, leading to speciation. *Paranthropus* and *Homo* likewise originate from eastern African populations that are *A. afarensis*-like. In this scenario, *A. africanus* does not give rise to descendants but evolves a number of derived traits in parallel with *Homo* and *Paranthropus.*

Model 2: Just after 3 Ma, *A. africanus* evolves in eastern Africa and subsequently spreads throughout eastern and southern Africa. The species remains static in southern Africa, but between 2.0 and 2.5 Ma eastern African populations transform into a currently unknown form representing the last common ancestor of *Paranthropus* and *Homo*. Both descendant groups later spread to southern Africa where they replace *A. africanus*. This scenario is relatively parsimonious in terms of character transformations, except for reversals that must have occurred in *P. aethiopicus*.

Model 3: Australopithecus africanus originates from populations of *A. afarensis* dispersing to the south and then being cut off. At approximately 2.5 Ma, *A. africanus* populations spread north and evolve into *Homo* when they, too, become isolated from their parent population. *Australopithecus garhi* and *P. aethiopicus* evolve in eastern Africa and subsequently go extinct. When *Homo* populations disperse to the south, remnant populations of *A. africanus* in southern Africa evolve into *P. robustus*. *Paranthropus robustus* populations spread back to the north and ultimately evolve into *P. boisei*. In this model, *A. africanus* is ancestral to both *Paranthropus* and *Homo* (in a manner analogous to how *H. heidelbergensis* is likely to be ancestral to both Neanderthals and modern humans). The model entails the parallel evolution of certain robust craniodental traits in *P. aethiopicus* and the *P. robustus* + *P. boisei* clade, and it posits that some populations of *P. robustus* predated the first appearance of *P. boisei*.

Model 4: Australopithecus africanus originates from populations of *A. afarensis* that become isolated as they disperse to the south. At roughly 2.5 Ma, populations of *A. africanus* disperse to the north and evolve into *Homo* as they become isolated. *Australopithecus garhi* and *P. aethiopicus* evolve in eastern Africa and *P. aethiopicus* changes rapidly into *P. boisei* in response to competition with *Homo*. The *P. aethiopicus/P. boisei* lineage disperses to the south at approximately 2.0 Ma, and isolated populations evolve into *P. robustus*. In this case, *A. africanus* is the sister taxon of *Homo*. Late Hadar populations and *A. garhi* are the sister taxa of *Paranthropus*. *Australopithecus anamensis* and Laetoli are the sister taxa of the Hadar + *A. africanus* + *Paranthropus* + *Homo* clade.

In connecting the record of *Australopithecus* fossils to the origin of *Homo*, the question of what happened is much simpler than the question of where. With the biogeography of *Australopithecus*, we at least have the convenience of (apparently) regionally specific species. *Homo habilis*, on the other hand (and in the broad or narrow sense), is found at sites in both eastern and southern Africa. Samples are not sufficiently large in southern Africa to be certain of the affinities of these populations, but the similarity of Stw 53 (Sterkfontein) to specimens at Olduvai Gorge is striking. Whether one calls them "*Homo*" or not, they appear to represent one species living across a broad region. Given the lack of representative sites in western Africa to tell us otherwise, we have to entertain the likelihood that *Homo* was occupying areas across much of sub-Saharan Africa.

In any case, there are two principal ways to think of the biogeographic connections between eastern and southern Africa up to the origin of *Homo*. One is that eastern Africa was the center of distribution: the region where a combination of anagenetic and cladogenetic evolution was generating the main sequence of changes in human evolution. From this center, populations would spread south periodically, and peripatric speciation would result. Strait and Wood (1999) provided a good illustration of this model and alternatives. If the flow was always from north to south, the implication is that southern African species usually went extinct. From the anatomical perspective, there is some intuitive appeal to this model—repeated occupation of the southern tip of Africa, with local evolution followed by extinction, may have produced the repeated appearance of a variety of characteristics. Thus these scenarios (Model 1, Model 2) provide an explanation for some of the extensive seen homoplasy in hominin evolution (e.g., Kimbel et al. 1988).

An alternative scenario is a "piston" model, with a greater degree of back and forth movement, and a significant role for character displacement between sympatric species (Model 3, Model 4). When the ecological door to the south was open, populations spread there. When it closed, allopatric speciation resulted. When it opened again, range-expanding hominins would come across other hominins, and competition would drive the behavior of the species apart, as it does in other animals when species are sympatric in some parts of their range.

For *A. africanus*, this model can explain the substantial transformation that *A. africanus* had already made towards a *Homo*-like skull anatomy. *Australopithecus africanus* originated during a period (prior to 3.0 Ma) when southern Africa was faunally isolated from eastern Africa. When habitats became contiguous between regions again (sometime between 2.5 and 3.0 Ma), northward dispersal produced contact and overlap between *A. africanus* and late *A. afarensis* (or *A. garhi*, or other *Australopithecus*). Character (i.e., ecological) displacement may have elicited the evolution of *Homo*-like features in *A. africanus* populations that had spread north. Again, returning to what we know of anatomy, this model has the intuitive appeal of explaining the complex but brief period of experimentation and diversification in eastern Africa circa 2.5 Ma (as represented by *A. garhi* and *P. aethiopicus*, soon followed by specimens of *Homo*). Character displacement would not have been deterministic, but instead produced a variety of local, ephemeral outcomes.

The two scenarios—"north to south" and "piston"—differ in other ways as well. North to south fits with a strict cladistic interpretation and the consistent prediction that the *Homo/Paranthropus* common ancestor was most parsimoniously "like" *A. africanus* but not *A. africanus* itself (see discussions of character evolution in Strait and Grine 2004; Kimbel et al. 2004). It requires the existence of at least one unknown form, which could have existed outside our small window of sites. The piston model is more stratophenetic in approach and assumes that the fossil record has at least captured the main taxa, if not all of the details.

Summary

A comparison of eastern and southern African *Australopithecus* at 3 Ma demonstrates that substantial cranial diversity was apparent at that time (assuming that the *A. africanus* sites are as old as they appear to be). Details of *A. africanus* anatomy may point towards the Laetoli/early Hadar period as the time when a dispersal event occurred or genetic continuity between eastern and southern Africa ended. The nature and timing of a cooling event between 3.2 and 3.5 Ma sets up a testable hypothesis to explain why southern and eastern African habitats were disconnected, and why *A. africanus* evolved the characteristics it did. How *A. africanus* fits into biogeographic scenarios has a downstream effect on other taxa. Even if it was not the direct ancestor to *Homo*, the transition to *A. africanus* anatomy was a significant one in understanding the context for the origins of *Homo* and *Paranthropus*, as many authors have recognized before. Ironically, although *A. africanus* is relatively well known in the hominin fossil record, a major challenge yet facing paleoanthropologists is to resolve its phylogenetic and biogeographic relationships.

Addendum

The present chapter was unfinished at the time of the author's tragic death. It was discovered before this volume was sent to press, and has been edited by John Fleagle and David Strait, and the abstract and accompanying Figs. 11.2 and 11.3 were provided by Kaye Reed. The manuscript was originally prepared as an essay to be discussed at the TBI *Australopithecus* symposium, and thus its language was, in places, somewhat informal. The style and formatting has therefore been adjusted and references have been added but, fundamentally, the ideas expressed within are those of Charles (Charlie) Lockwood. That there will be no new ideas forthcoming from him is a loss that will be dearly felt.

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Chapter 12

The Biogeographic Implications of Early Hominin Phylogeny

David S. Strait

Abstract The biogeographic implications of early hominin phylogeny were investigated using cladistic analysis. Geography was treated as a cladistic character with three states (eastern, southern and central Africa). The geography character was plotted onto a cladogram derived from a recent study of early hominin phylogeny, and each change in character state was interpreted as a dispersal event. Results indicate that hominins dispersed at least four times between African regions, and that most hominin speciation events took place in eastern Africa. Many adaptively significant morphologies also evolved in eastern Africa, although the possibility exists that bipedalism originated in central Africa.

Keywords *Ardipithecus* • *Australopithecus* • Biogeography • Cladistics • Dispersal • Hominins • *Homo* • *Orrorin* • *Paranthropus* • Parsimony • Phylogeny • *Praeanthropus* • *Sahelanthropus*

Introduction

Biogeography cannot be fully understood without an appreciation of phylogeny. Phylogeny refers to pattern of evolutionary history, and that pattern is, in turn, inextricably linked to biogeographic patterns. For example, if an ancestor in one region gives rise to a descendant in another region, then some type of biogeographic event (i.e., dispersal or vicariance) must have taken place. Thus, phylogenetic patterns constrain the types of biogeographic patterns that can be observed (e.g., Nelson and Platnick 1981; Myers and Giller 1988; Humphries 1992). Often, the most interesting biogeographic questions concern processes rather than patterns (e.g., can a given dispersal event be explained by changes in vegetation related to climate change?), but those process questions cannot be posed properly until biogeographic patterns are established. Thus, phylogeny plays a paramount role in investigations of biogeography. This study interprets early hominin biogeography within the framework of phylogenetic analysis.

Although several hypotheses concerning early hominin biogeography have been proposed (Foley 1987, 1994, 1999; Schrenk et al. 1993, 2007; Turner and Wood 1993; Bromage et al. 1995b; Suwa et al. 1996), only one study has previously examined this topic from an explicitly phylogenetic perspective (Strait and Wood 1999). That study treated geography as a cladistic character in which different regions were considered distinct character states. By doing so, it was possible to examine the character evolution of the geography trait in the same way as one examines the evolution of a morphological trait; parsimony was used to plot the geography character onto multiple phylogenies (Delson 1986; Walker et al. 1986; Grine 1988; Wood 1991, 1992; Skelton and McHenry 1992; Strait et al. 1997), with each recorded character state change representing a dispersal event. The logic underlying this protocol is merely that the simplest and best biogeographic reconstruction is the one that requires the fewest number of dispersals. Strait and Wood (1999) observed that all of the phylogenies implied between four and seven dispersal events between southern, eastern and south-central Africa, and that hominins typically (although not universally) dispersed in the same direction as contemporaneous mammals (see Turner and Wood 1993). Recently, several new hominin species have been discovered (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) that were not included in Strait and Wood's (1999) analysis, and a revised hominin phylogeny incorporating most of these species has been proposed (Strait and Grine 2004). This study revisits the matter of hominin biogeography while adding a consideration of how hominin dispersal patterns may relate to patterns of morphological

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evolution. In doing so, this study attempts to elucidate possible adaptive explanations for hominin biogeographic patterns.

Materials and Methods

Following Strait and Wood (1999), geography is treated as a cladistic character. Characters in hominin phylogenetic analyses typically take the form of descriptions of distinct aspects of skeletal anatomy in which two or more discernable "forms" or states can be recognized. The geography character employed here is directly analogous to a morphological character, except that whereas morphological traits are usually used as tools to reconstruct phylogeny, the geography character will not be used in this fashion. Rather, the geography character will be plotted onto a cladogram previously derived from an analysis of morphological characters (see below). In the geography character, three geographic regions are recognized, each one of which is assigned their own character state. The regions and states are: (0) central Africa west of the Rift Valley, (1) eastern Africa in the vicinity of the Rift Valley, and (2) southern Africa south of the Rift Valley. Note that this is a simplification of the states recognized by Strait and Wood (1999), who considered the Rift Valley sites in Ethiopia, Tanzania, and Kenya to be separate from those in Malawi. Treating Malawi as a separate character state in this fashion adds considerably to the complexity of the geography character, and requires the assumption that dispersals from, for example, the Turkana Basin to Malawi are equivalent (in terms of difficulties facing the dispersing fauna) as dispersals from South Africa to Malawi. However, the sites from Malawi exhibit an essentially eastern African fauna, notwithstanding the presence of some southern African taxa (Bromage et al. 1995a), which would seem to argue against such equivalence. Consequently, all of the Rift Valley sites are conflated here into a single region. Ultimately, this is a fairly coarse representation of geography that allows an assessment only of dispersal events between major African regions. In theory, one could examine geography on a much finer scale (e.g., by defining geographic regions on the basis of sedimentary basins), but doing so would require knowledge about hominin phylogenetic relationships that cannot currently be obtained (e.g., the relationships between *Paranthropus boisei* populations in Olduvai Gorge, Koobi Fora, and Konso).

Parsimony is used to examine the evolution of the geography character with respect to a phylogenetic hypothesis. The phylogeny employed here (Fig. 12.1) is based on Strait and Grine's analysis of 109 characters that have traditionally been of interest in studies of hominin systematics (2004: Analysis 5). Strait and Grine (2004) found three equally parsimonious trees that differed only with respect to the phylogenetic positions of *Kenyanthropus platyops* and *Homo rudolfensis. Kenyanthropus* was either the sister taxon of *Paranthropus,* or the sister taxon of a clade that includes *Homo* and *Paranthropus. Homo rudolfensis* was either the sister taxon of all other *Homo* species, or the sister taxon of a *H. ergaster* + *H. sapiens* clade. These alternative branching arrangements were each considered separately in the biogeographic analysis, but for simplicity are depicted on the tree as unresolved polychotomies, meaning that nodes from which more than two branches arise reflect uncertainty rather than, for example, a true three-way split. Strait and Grine's tree has been modified to include *Orrorin tugenensis* and *Ardipithecus kadabba.* These taxa were not included in the original analysis because their fossils preserve so few of the relevant morphological characters. However, they are biogeographically relevant because they represent the first appearance of hominins in eastern Africa. Thus, for heuristic purposes, their phylogenetic relationships are depicted here as an unresolved polychotomy at the base of the hominin clade. Finally, because *H. habilis* is known from both southern and eastern Africa, this species is assigned two operational taxonomic units (OTUs), one for each region. This allows an assessment of both the region in which the species first evolves (eastern or southern Africa) and the direction in which it disperses to reach the other region (northward or southward).

Obviously, the cladogram derived by Strait and Grine (2004) is not the only plausible hypothesis of hominin phylogeny (a topic about which paleoanthropologists tend to debate rather vigorously). Indeed, recent descriptions of *Ardipithecus ramidus* indicate that the postcranial skeleton of this species is remarkably primitive-appearing (Lovejoy et al. 2009a–c), and highlights the potential limitations of phylogenies based largely or solely on morphological traits derived from the skull (as was the cladogram of Strait and Grine 2004). Clearly, biogeographic patterns depend critically on phylogenetic patterns, so it might appear as if analyses of biogeography would be compromised by disagreements about phylogeny. This is true to a point, but as it happens, not all disagreements about hominin phylogeny are biogeographically significant. In some cases, alternative cladistic branching patterns have no effect on biogeographic patterns. Accordingly, following presentation of the biogeographic pattern implied by the Strait and Grine (2004) cladogram, the biogeographic significance of alternative phylogenies is discussed.

The geography character was considered to be unordered, meaning that hominins could disperse between any two regions in a single cladistic step. Each state change in the geography character corresponds to a dispersal event. The timing of that event can be estimated by considering

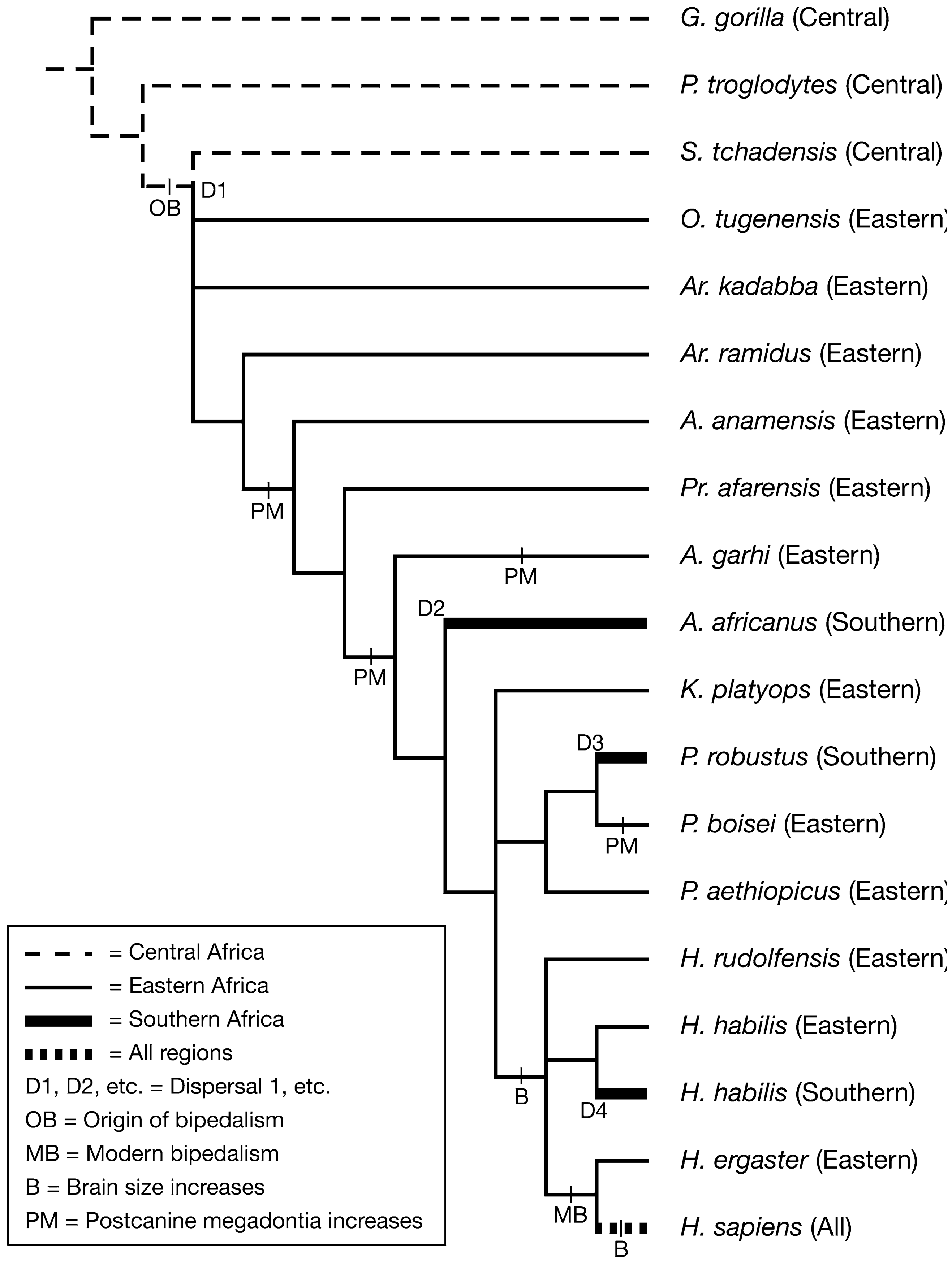

Fig. 12.1 Phylogeny and biogeography of early hominins. Phylogeny modified after Strait and Grine (2004). Regional distributions of taxa and branches are indicated by differences in *dashing* and *line thickness*. Dispersals take place when *dashing* and *line thickness* change along branches. Major evolutionary events are also indicated along branches

Table 12.1 Unambiguous morphological state changes[a] associated with dispersal events

Dispersal #	Associated character state changes
1	No unambiguous state changes[a]
2	Variable projection of nasal bones above frontomaxillary suture
	Variable presence of anterior pillars
	Compound temporonuchal crest absent, even in presumptive males
	Variable orientation of the anterior face of the zygomatic bone
	Variable patency of premaxillary suture in adults in frontal view
	Variable expression of molar cingulum
3	Anterior pillars present
	Reduced pneumatization of temporal squama
	Postglenoid process small and fused to tympanic
	Eustachian process of tympanic present and prominent
	Supraorbital contour arched
	Distal trigonid crest on dP_4 reaches protoconid apex
	Mandibular corpus depth variable along tooth row
4	No unambiguous state changes[a]

[a] Some state changes required by a given phylogeny might be ambiguous because there may be equally parsimonious ways of reconstructing character evolution in the tree, or because certain phylogenetic relationships are unresolved

the first appearance dates of the taxa in the relevant clade. The unambiguous morphological changes associated with each dispersal event are recorded, as are the geographic locations associated with major adaptive and evolutionary events such as the origin of bipedalism, the evolution of postcanine megadontia, increases in brain size, and the origins of the *Paranthropus* and *Homo* clades. Note that these methods differ from those of formal cladistic biogeography (e.g., Platnick and Nelson 1978; Rosen 1978; Wiley 1980, 1981; Humphries 1992), which examines the area distributions of two or more distantly related sets of taxa (e.g., bovids and suids), each with known phylogenies, to infer whether vicariance may have influenced the evolutionary and biogeographic histories of these groups in similar ways. These methods cannot yet be applied here because the cladistic relationships of many non-hominin mammalian groups require further study.

Results

Four dispersals are implied by the Strait and Grine (2004) phylogeny (Fig. 12.1). The derived morphological changes associated with these dispersal events are presented in Table 12.1. An additional hominin dispersal not depicted in the phylogeny is also described, as are the regional settings in which major evolutionary events occurred.

Dispersals

Dispersal 1: The last common ancestor of the clade including all hominins except *Sahelanthropus* disperses from central Africa to eastern Africa at or before 6.0 Ma

The cladogram employed here implies that the hominin clade originated in central Africa. This may not necessarily be true (see below), but if it is, then a dispersal of hominins from central to eastern Africa is implied. The exact nature of this dispersal event is complicated by the fact that the phylogenetic relationships of *Orrorin* and *Ar. kadabba* are debated (Senut et al. 2001; Haile-Selassie et al. 2004) and have yet to be subjected to cladistic analysis. Given this uncertainty, the simplest biogeographic pattern is one in which there was a single dispersal event. The timing of the dispersal is set by the age of the sediments overlying the Kabarnet Trachytes in the Lukeino Formation, from which *Orrorin* is known (Pickford and Senut 2001; see also Deino et al. 2002). The morphological changes associated with this dispersal event are uncertain (Table 12.1).

Dispersal 2: *Australopithecus africanus*, or its immediate ancestor, disperses from eastern to southern Africa at or before ~3.0 Ma

The timing of this event corresponds to the age of Makapansgat Member 3, which Herries (2013; see also McFadden and Brock 1984; Cooke 1997) suggests is likely between 3.03 and 2.58 Ma (although a slightly older age is possible). Although it had been thought that australopiths (not necessarily *A. africanus*) from the Silberberg Grotto in Sterkfontein Member 2 were older than those from Makapansgat (Clarke and Tobias 1995; Clarke 1998, 2013), a recent U-Pb analysis indicates that these specimens may be substantially younger (Walker et al. 2006). Other potentially older hominins from Sterkfontein include those from the Jacovec Cavern, which may be as old as 4.0 Ma (Partridge et al. 2003). However, the taxonomic affinities of these specimens are unclear, and the date has yet to be independently confirmed. Note that the clade defined by *A. africanus, Kenyanthropus, Paranthropus*, and *Homo* must be at least 3.5 Ma based on the age of hominins attributed to *Kenyanthropus* from the Nachukui Formation (Leakey et al. 2001). The ancestor of this clade lived in eastern Africa and may have substantially predated the time at which the *A. africanus* lineage dispersed to southern Africa. Six derived morphological state changes are associated with this dispersal, and most are potentially associated with the design of the feeding apparatus.

Dispersal 3: *Paranthropus robustus*, or its immediate ancestor, disperses from eastern to southern Africa at or before 1.8 Ma

The timing of this event corresponds to the age of Swartkrans Member 1 and Kromdrai Member B East (Brain 1993; Vrba 1995). The date might be somewhat earlier depending on the age of Drimolen (Keyser et al. 2000). Seven derived morphological state changes are associated with this dispersal, but most are difficult to interpret in terms of adaptation. One feature, the anterior pillar, is generally thought to be an adaptation for withstanding masticatory loads on the premolar (Rak 1983).

Dispersal 4: *Homo habilis* disperses from eastern to southern Africa at or before 1.8 Ma

The timing of this event corresponds to the age of Swartkrans Member 1 and Sterkfontein Member 5 (Brain 1993; Vrba 1995). It is possible that *H. habilis* appeared in southern Africa somewhat earlier if the putative early *Homo* specimen Sts 19 derives from Sterkfontein Member 4 (Vrba 1995) and belongs to *H. habilis*. However, both the stratigraphic provenance and taxonomic affinities of this specimen are debatable (e.g., Kimbel and Rak 1993; Ahern 1998). There are no unambiguous morphological changes associated with this dispersal event.

Dispersal of *Australopithecus bahrelghazali*

This dispersal is not depicted on Fig. 12.1 because the phylogenetic relationships of *A. bahrelghazali* are unknown. However, unless this species is the sister taxon of *Sahelanthropus* or derives from a very basal branch of the hominin tree, then either this species or its ancestor must have dispersed from eastern to central Africa at or before approximately 3.0–3.5 Ma (Brunet et al. 1996). Nothing is known about morphological changes that might be associated with this dispersal. Note that if ultimately it is shown that *A. bahrelghazali* in fact represents a central African population of *A. afarensis*, then the same dispersal would be implied.

Major Evolutionary Events

Many of the key evolutionary events in early human evolution appear to have taken place within regions rather than as a result of dispersals between regions (Fig. 12.1). According to the phylogeny examined here, bipedalism originates in central Africa and becomes fully modern in eastern Africa. Postcanine megadontia increases in stages in eastern Africa. Other major events, like increases in brain size and the appearance of the *Paranthropus* and *Homo* clades likewise take place in eastern Africa.

Discussion

Biogeographic Implications of Alternative Phylogenies

The biogeographic patterns described here are direct consequences of the phylogenetic hypothesis on which they are based. Thus, it is possible that alternative phylogenies may imply alternative biogeographic results. However, dispersals 2, 3, and 4 are implied in several hypotheses of early hominin phylogeny (Wood 1991, 1992; Skelton and McHenry 1992; Strait et al. 1997; Strait and Grine 2004; Kimbel et al. 2004). These three southerly-directed dispersals would occur in any phylogeny except those in which *A. africanus* is the sister taxon or direct ancestor of either *P. robustus* or *H. habilis* (e.g., Walker et al. 1986). Similarly, a northward dispersal from southern to eastern Africa does not occur in any phylogeny except those in which *A. africanus* is the sister taxon or ancestor of *H. habilis* (e.g., Schrenk et al. 2007). In contrast, Dispersal 1 is more sensitive to alterations in phylogeny. Any fully resolved phylogeny in which *S. tchadensis* is not the basal member of the hominin clade (i.e., if either *Orrorin* or *Ardipithecus* diverged before *Sahelanthropus*) would imply either two dispersals from central to eastern Africa, or a dispersal from central to eastern followed by a subsequent dispersal from eastern to central. In either case, both dispersals would necessarily occur prior to the first appearance date of *Sahelanthropus*. Of course, two dispersals would not be required if *Sahelanthropus* was not a hominin (e.g., Wolpoff et al. 2006). Moreover, the direction of Dispersal 1 is tied to the geographic distribution of the outgroup taxa, *Pan* and *Gorilla,* which are both coded here as being found in central Africa. Certainly, it is possible that the basal members of the *Pan* and *Gorilla* clades once broadly occupied eastern Africa (see below), in which one could imagine a scenario in which hominins originated in eastern Africa prior to 7.0 Ma and subsequently dispersed to central Africa.

A further complication derives from the fact that the hominin status of at least some of the taxa (*Sahelanthropus, Ardipithecus*) that might collectively be called the "pre-australopiths" can now legitimately be questioned on the basis of the remarkably primitive-appearing postcranial skeleton of *Ardipithecus ramidus* (Lovejoy et al. 2009a–c). This species lacks nearly all of the postcranial traits traditionally associated with bipedalism, and possesses only a few putative craniodental synapomorphies with hominins. Although it is possible that this species is a hominin, it is not unreasonable to consider the alternative that it may not be. Because *Sahelanthropus* also shares only a few derived craniodental traits with hominins but its postcranial morphology is as yet unknown, one perhaps ought to be cautious about considering it a hominin. A very early hominin dispersal between central and eastern Africa might not be necessary if *Sahelanthropus* is not a hominin.

Adaptive Scenarios Explaining Biogeographic Patterns

The adaptive significance of early hominin dispersals depends in part on the dispersal patterns of contemporaneous mammals (Vrba 1992). For example, if hominins disperse between two regions as part of a wave of mammalian dispersals (i.e., many species dispersing in the same direction at the same time), then the hominin dispersal can be interpreted as a potentially passive response to environmental changes affecting many taxa. However, if hominins are dispersing in the direction opposite that of contemporaneous mammals, then presumably the hominins have adaptations allowing them to overcome the prevailing mammalian trend (Strait and Wood 1999). Vrba (1992) predicts that only species with eurytopic (ecologically generalized) adaptations can depart from these trends.

Turner and Wood (1993) used data on the first appearance dates of mammalian taxa to identify three waves of mammalian dispersal between eastern and southern Africa. One wave moves from eastern to southern Africa prior to 3.0 Ma, and includes species of *Canis, Diceros*, and *Metridiochoerus*. A second wave moves northward from southern to eastern Africa between 2.7 and 2.0 Ma and includes *Cercopithecoides*, *Connochaetes*, *Parmularius*, *Tragelaphus*, and *Antidorcas*. The final wave moves, again, from eastern to southern Africa between 1.8 and 1.5 Ma and includes *Theropithecus*, *Nyctereutes*, *Equus*, *Metridiochoerus*, *Kobus*, and *Hippotragus*. Thus, the waves alternate direction from southward, to northward, to southward again, and may conform to continental trends in temperature and aridity (Vrba 1992; Schrenk et al. 2007). These dispersal patterns were not based on phylogenetic analysis, so they are unlikely to represent a full picture of dispersals in Plio-Pleistocene African mammals (i.e., because cladistic branching patterns might reveal dispersals that might not have been inferred on the basis of first appearance dates alone, especially given the incompleteness of the fossil record). Moreover, the patterns found by Turner and Wood (1993) may now be out of date following nearly two decades of paleontological fieldwork in Africa. Clearly, it would be worthwhile to comprehensively update their findings. However, their study is adequate for providing a preliminary context in which to interpret hominin dispersals (e.g., Bromage et al. 1995a, b; Strait and Wood 1999). All of the hominin dispersals between eastern and southern Africa identified here (dispersals 2, 3, and 4) are consistent with the mammalian trends found by Turner and Wood (1993) in that they are southerly directed and take place at approximately 3.0 and 1.8 Ma. Thus, hominins appear to be dispersing in concert with contemporaneous mammals. An implication is that hominins, like other mammals, may be tracking the shifting distributions of vegetational zones (e.g., Vrba 1992).

In theory, patterns of character evolution ought to provide insights into the adaptive significance of biogeographic events because certain character state changes will have evolved along the same branches of a cladogram in which a dispersal event would have occurred. However, the morphological changes associated with hominin dispersals appear to be adaptively subtle (Table 12.1). Nothing can be said with certainty concerning the morphological changes accompanying the initial dispersal of hominins into eastern Africa (Dispersal 1). The morphological changes associated with the appearance of *A. africanus* in southern Africa are conceivably associated with feeding biomechanics (Dispersal 2), but it is noteworthy that many of them represent variable character states. This is consistent with prior observations that the fossils typically attributed to this species are quite variable (Clarke 1988; Kimbel and White 1988; Lockwood 1999; Lockwood and Tobias 2002; but see Moggi-Cecchi et al. 2006). Indeed, some workers view this variability as evidence that more than one australopith species may be present in Sterkfontein Member 4 (Clarke 1988, 2013; see also Lockwood and Tobias 2002). Regardless of the details of taxonomy, the question remains as to why the variability exists. It is difficult to evaluate whether or not the variability is a biologically meaningful characteristic of *A. africanus* populations, or whether taphonomic factors are at play. One way to begin to address this question would be to assess whether contemporaneous southern African mammals also exhibit high levels of intraspecific variability relative to modern taxa and their eastern African fossil counterparts.

The dispersal of *P. robustus* or its ancestor to southern Africa is not associated with morphological changes that can be easily interpreted from an adaptive standpoint. Some characters (particularly the anterior pillar) may be related to feeding biomechanics, but many of the traits may be adaptively neutral. Presumably, these features accumulated as the southern African "robust" australopiths became increasingly isolated from their eastern African congeners. Likewise, the dispersal of *H. habilis* to southern Africa does not appear to be associated with a profound adaptive shift in the dispersing population. The main difference in the dispersals of these two taxa is that whereas the "robust" australopiths speciated as a result of the dispersal, *H. habilis* merely experienced a range expansion. Of course, if the southern African early *Homo* specimens are considered a distinct species (as implied by Grine et al. 1993, 1996), then both dispersals would have resulted in speciation.

Certain results point to the central role that eastern Africa plays in human evolution. First, once hominins reach eastern Africa, all subsequent dispersals originate from that region. Southern African hominins are apparently derived from eastern African ancestors and represent a periphery of the early hominin range. Second, nearly all of the major evolutionary events highlighted here took place in eastern Africa. It is likely, therefore, that any evolutionary scenario explaining these changes requires a more precise understanding of variation in local habitats in eastern Africa. A substantial caveat, of course, is the fact that the majority of early hominin species are known from eastern Africa. This may reflect reality, or it may be a sampling artifact owing to the fact that the conditions for fossil preservation and discovery are exceptionally good in the Rift Valley. Regardless, the preponderance of eastern African species in the cladistic data set influences profoundly the biogeographic patterns derived from the resulting cladogram. Of course, the potential over-representation of eastern African species is not merely a problem of cladistic biogeography; all biogeographic analyses are working with the same basic data set, so the possibility of sampling bias affects all biogeographic reconstructions. The patterns found here reflect data that are currently available. Ultimately, this issue can only be resolved by the discovery of more fossil sites in southern and central Africa, so until then the results obtained here should be considered provisional.

The only major evolutionary event considered here to have taken place outside of eastern Africa is the origin of bipedalism (and, thus, the origin of hominins). Although dependent on the inference that *Sahelanthropus* was bipedal (see above), the current phylogeny indicates that this event took place in central Africa (see also Brunet et al. 2002), which is entirely logical considering the geographical distribution of extant *Pan* and *Gorilla*. Although fossil evidence of *Pan* in eastern Africa exists (McBrearty and Jablonski 2005), it is sparse and substantially postdates the inferred time of the last common ancestor of hominins. Of more relevance may be the recent discovery of possible members of the African ape and human clade (*Chororapithecus*, *Nakalipithecus*) in Miocene deposits in eastern Africa (Kunimatsu et al. 2007; Suwa et al. 2007). These species could conceivably affect the character transformation of the geography character in such a way as to locate the origin of bipedalism outside of central Africa (or, at least, make the location in which this behavior evolved equivocal). However, these species are known from few and fragmentary fossils, and their phylogenetic relationships are not known with confidence. Regardless, an implication of the current study is that hypotheses purporting to explain the origin of bipedalism should incorporate information about central African paleoenvironments. Of course, future fossil discoveries and ensuing functional and phylogenetic analyses may necessitate a re-evaluation of where bipedalism first appears, but central Africa is a reasonable working hypothesis at present.

Future Directions

The biogeographic patterns and scenarios described here can be tested in a number of ways. More fossil localities can be discovered in central and southern (or even western) Africa. As importantly, more fossil sites can be discovered in the areas between eastern, southern and central Africa. There is no reason to expect that hominins did not once live in these places. On the basis of those discoveries, certain of the biogeographic patterns found here may be corroborated, while others may require revision. That is the normal process of science (i.e., new data are used to test existing hypotheses). In addition to the discovery of new fossil sites, our understanding of hominin biogeography would be improved by a better understanding of phylogeny within various orders of Plio-Pleistocene mammals. This would allow a more complete assessment of mammalian biogeography, which would provide the context in which to interpret hominins. At present, Turner and Wood's (1993) observations about mammalian dispersals are based only on first appearance dates, and thus are likely to be only a sketch of the total mammalian biogeographic pattern. Finally, attention must be paid to assessing small-scale environmental variation within regions. A "landscape" approach to excavation in combination with advanced methods of paleoecological reconstruction (e.g., isotopic analysis) would likely provide valuable insights in this regard (e.g., Potts et al. 1999; Sikes et al. 1999; Blumenschine et al. 2003; Faith and Behrensmeyer 2006). In other words, the analysis presented here concerns biogeography on a broad regional scale, but it would be worthwhile to consider biogeography in terms of local habitats or sedimentary basins.

Conclusion

Over 30 years ago, Tattersall and Eldredge (1977) noted that phylogeny reconstruction should logically precede the description of evolutionary scenarios. Although paleoanthropologists are fond of disagreeing about phylogeny, they should not lose sight of the fact that phylogeny has consequences. Indeed, it is precisely because of these consequences that debates about phylogeny have meaning. One such consequence is that phylogenetic patterns imply biogeographic patterns. To accept a phylogenetic hypothesis is in many cases logically equivalent to accepting a biogeographic hypothesis. Conversely, rejecting a biogeographic hypothesis may by necessity require rejecting a phylogenetic hypothesis. Phylogeny may not, by itself, provide a complete picture of biogeography, but, clearly, biogeography cannot be understood without phylogeny.

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Part IV
Paleobiology

The articles in this section address aspects of the behavior of *Australopithecus* and how this can be reconstructed from the bones and teeth that make up the fossil record. The six articles focus on three specific aspects of the biology of early hominins-sexual dimorphism, diet, and locomotion.

In Chap. 13, "Sexual Size Dimorphism in *Australopithecus*: current understanding and new directions," Adam Gordon reviews the factors, including both sexual selection and natural selection, which seem to affect levels of sexual dimorphism among extant primates. He also reviews the strengths and weaknesses of various methods that have been used to reconstruct patterns of sexual size dimorphism in fossil primates, specifically fossil hominins. In reviewing the literature on body size dimorphism in early hominins, he suggests that *Australopithecus afarensis* probably had slightly more size dimorphism than chimpanzees or bonobos, and *Australopithecus africanus* had slightly less dimorphism. The sample for *Australopithecus anamensis* is too small to estimate dimorphism, and *Australopithecus sediba* seems to have very little size dimorphism. He suggests that dimorphism in *Australopithecus* is probably the result of natural selection rather than sexual selection. He notes that dimorphism in *Ardipithecus ramidus* is also difficult to assess.

In Chap. 14, "Molar Microwear, Diet and Adaptation in a Purported Hominin Species Lineage from the Pliocene of East Africa", Frederick Grine, Peter Ungar, Mark Teaford, and Sireen El-Zaatari examine associations between molar microwear, environmental change, and time in fossils of *A. anamensis* and *A. afarensis* that have been identified as possibly forming a continuous ancestor-descendant lineage. It is widely accepted that during the time period from which the fossils were drawn (4.12–3.18 Ma) African climates were becoming dryer and closed wooded habitats were giving rise to more open habitats, and it has been argued that there are morphological changes in the dental morphology between *A. anamensis* and *A. afarensis* indicative of dietary change. However, in their analyses, Grine et al. find no evidence of a correlation between the incidence of several microwear features and either time, or reconstructed habitats for the fossil samples, or any indication of microwear indicative of a diet composed of hard items. Rather, all of the fossil molars of *A. anamensis* and *A. afarensis* teeth fall within the range of microwear patterns found in *Gorilla gorilla*. The microwear patterns on the fossils are similar to those found in gorillas and geladas rather than hard object feeders. This suggests that *Australopithecus* may have been able to selectively maintain a consistent diet of soft foods despite environmental changes and that the dental and gnathic features indicative of a hard diet reflect an ability to masticate hard, brittle "fallback" foods only seasonally or in difficult times.

In Chap. 15, "Some Ruminations on Australopith Diets", Matt Sponheimer reviews the accumulated and often conflicting data on the diet of early hominins from studies of both microwear and isotopes. Studies of microwear often place early hominins with the range of extant apes, but isotope studies often show greater use of plants relying on the C_4 pathways, usually plants adapted to open grasslands. The concept of " fallback" foods does not seem to resolve the discrepancies.

In Chap. 16, “Locomotion and Limb Use in *Australopithecus*”, Carol Ward reviews the evidence for locomotor adaptations in the skeleton of *Australopithecus*, as best known from *A. afarensis*. She argues that all *Australopithecus* species were adept bipeds with a gait like that of modern humans and this included a curved spine, straight lower limb elements, and a fully adducted hallux. It is not possible to determine if purported adaptations for climbing in the upper extremity are the result of natural selection for arboreal behavior or the result of neutral selection that retains primitive features. The basic locomotor adaptations of *Australopithecus* remained the same for approximately 3 million years. There are some differences in limb proportions and other features among species.

In Chap. 17, “Shoulder Function in Early Hominid Evolution”, Susan Larson reviews the morphological features that characterize the shoulders of apes and modern humans and evaluates the limited fossil evidence regarding this region for species of *Australopithecus*. She notes that many details of shoulder morphology appear to show developmental plasticity as a result of function. Clavicular remains of *Australopithecus* are limited and previous analyses are often confusing, but it seems likely that early hominins had a relatively short clavicle and a scapula placed high on the thorax. Scapular fossils are equally limited, but all suggest that *Australopithecus* had a scapula with a cranially oriented glenoid fossa as in extant apes. Details of the muscle attachments on the tubercles of the humerus of *Australopithecus* are more similar to living apes than to modern humans; the intertubercular groove and shape of the head are intermediate between apes and humans; and humeral torsion is low as in Asian apes in contrast with the high humeral torsion found in African apes and modern humans. Overall, the shoulder morphology of *Australopithecus* is neither like that of African apes nor modern humans, but suggests an adaptation that is the result of selection for arboreal locomotion and posture.

In Chap. 18, “Age and Sex Differences in the Locomotor Skeleton of *Australopithecus*”, the late Elizabeth Harmon reviews the many, often interacting, factors that influence the ontogenetic development of bony morphology. These include genetics, hormones, body size, and behavior. Distinguishing the relative influence of each on particular aspects of the bony skeleton is difficult, but it seems that overall scapula shape is largely under genetic control and changes little during postnatal ontogeny, whereas phalangeal curvature and the bicondylar angle of the femur respond to behavioral changes during postnatal life. The ontogeny of *Australopithecus* was almost certainly short as in chimpanzees rather than extended as in modern humans. The limited fossil remains of juvenile *Australopithecus* (mostly *A. afarensis*) indicate that *Australopithecus* certainly practiced both bipedalism and some grasping with both hands and feet throughout life.

The Editors

Chapter 13

Sexual Size Dimorphism in *Australopithecus*: Current Understanding and New Directions

Adam D. Gordon

Abstract Sexual size dimorphism in extant and extinct species has often been viewed as a proxy for sexual selection, and by extension, mating system. As a result, various measures of relative size variation have been calculated for australopiths (particularly *Australopithecus afarensis*) as a means to infer mating system and social structure in these extinct hominins. Such analyses are confounded by several factors, including (1) different levels of sexual dimorphism may be present within one species when comparing different systems such as canine size, postcranial size, and body mass; (2) evidence suggests that sexual size dimorphism responds not only to sexual selection acting on both male and female size, but also to natural selection acting differentially on the sexes; and (3) measures of relative size variation within skeletal and/or dental samples of unknown sex are not direct measures of size dimorphism, but rather estimates which are subject to both known and unknown sources of error. This chapter addresses concerns and possibilities for future analyses that relate to these confounding effects, and goes on to present the current understanding of size dimorphism within *Australopithecus*. Specific methodologies for measuring relative size variation within fossil taxa are discussed, particularly newer techniques which incorporate information from across multiple skeletal elements. Finally, the biological and phylogenetic significance of different possible levels of dimorphism within *Ardipithecus ramidus* and various species of *Australopithecus* is discussed in the context of extracting information on selection pressures beyond simple reconstruction of mating systems and social structure.

Keywords Size dimorphism • *Australopithecus* • Sexual selection • Skeletal variation

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Sexual dimorphism, the presence of typical, distinctive differences between males and females of the same species, manifests in animals in a number of ways. These include sex-specific differences in the size (or presence) of particular portions of the body (e.g., canines, tail feathers, antlers) or the body as a whole, the shape of anatomical regions (e.g., pelvic shape, cranial crests), and coloration. Here I address sexual *size* dimorphism, as this has been the main focus of dimorphism research in *Australopithecus*, primarily due to the theoretical and empirical support for a relationship between size dimorphism and behavior in living primates. For example, the degree of size dimorphism within *Australopithecus* and the presence or absence of temporal trends in size dimorphism in later hominin evolution has played a key role in discussions of various broad scenarios for the evolution of human behavior from the Early Pliocene to the present (e.g., Lovejoy 1981, 2009; McHenry 1994, 1996).

Sexual Selection and Sexual Dimorphism

Sexual dimorphism in body size is associated with a number of behavioral features in living primates. For example, in two hominoid genera which show pronounced mass dimorphism, *Pongo* and *Gorilla*, sex differences in locomotor behavior are apparent in degree and type of arboreal locomotion (Galdikas and Teleki 1981; Sugardjito and van Hooff 1986; Remis 1995; Doran 1997) presumably due to males' greater mass and the lack of adequate arboreal support. There are also sex differences in some primate diets that appear to be related to size dimorphism (Clutton-Brock 1977; Demment 1983). However, dietary and locomotor sex differences within primates appear to be the result of dimorphism rather than the cause (Clutton-Brock and Harvey 1977), whereas sexual selection theory suggests that sexual dimorphism results from specific types of mating/social behavior.

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The basic explanation for the evolution of sexual dimorphism as suggested by Darwin (1871), and still understood today to be essentially correct, is that dimorphism results from competition for mating opportunities, choice of mates based on particular characteristics, or some combination of the two. More specifically, sexual selection (and thus sexual dimorphism) results from situations which set up reproductive skew such that one sex has greater variability in its reproductive output than the other. For example, if all healthy adult females in a population produce roughly the same number of viable offspring over their reproductive lifespans while some males produce many offspring and others produce few or none, sexual selection will result. Those heritable characteristics that distinguish the males that father the most offspring from those that do not will be preferentially passed on to the next generation. Thus characteristics that allow males to win contests with other males for mating opportunities (male–male competition) or that make them more attractive to estrous females (female choice) will become emphasized in descendant males. Within primates, these characteristics have typically been recognized to be body size and weapon size (i.e., canines in the case of non-human primates), although we also know that reproductive competition among males need not necessarily involve face-to-face conflict. For example, it may occur as sperm competition (Harcourt 1997; Anderson and Dixson 2002) or via alternative mating strategies such as those used by "unflanged" adult male orangutans (Utami et al. 2002). Likewise, female mate choice is not limited to precopulatory choice, but can also involve postcopulatory and even postfertilization mechanisms (Paul 2002), and in some cases males also exhibit mate choice, with high ranking males mating preferentially with those females most likely to be experiencing conceptive cycles (e.g., Alberts et al. 2006).

Decades of research in non-human anthropoid primates has shown that high levels of canine size and body mass dimorphism are usually associated with social structures that produce high intensity competition between males for mating opportunities (e.g., Clutton-Brock et al. 1977; Gaulin and Sailer 1984; Clutton-Brock 1985; Rodman and Mitani 1987; Kay et al. 1988; Ely and Kurland 1989; Greenfield 1992; Plavcan and van Schaik 1992, 1997b; Ford 1994; Martin et al. 1994; Mitani et al. 1996; Lindenfors and Tullberg 1998; Plavcan 1999, 2001, 2004; Barton 2000; Gordon 2004, 2006a; Thorén et al. 2006), and new research is beginning to show that female choice can reinforce or dampen these relationships (Plavcan 2004; Maestripieri and Roney 2005). Within the extant hominoids, high dimorphism is found in gorillas, which live in uni- or multi-male groups with multiple females, and in orangutans, in which one male's territory typically overlaps with that of multiple females; in both cases high male–male competition is expected. Somewhat less dimorphism is present in chimpanzees and bonobos, which live in multi-male, multi-female groups in which male–male competition can occur, but where it is presumably more difficult to monopolize access to estrous females. Very little dimorphism is found in gibbons and siamangs, which typically form pair-bonds in which one adult male and one adult female will jointly defend a territory, although "monogamous" gibbons are known to engage in extra-pair copulations (Reichard 1995; Jiang et al. 1999), and an increasing number of hylobatid social groups with more than one adult male are being reported (e.g., Brockelman et al. 1998; Fuentes 2000; Sommer and Reichard 2000; Lappan 2007).

The other extant hominoid, *Homo sapiens*, presents at least two complications for this relatively simple picture: (1) modern human social structure and mating patterns are incredibly varied and defy easy categorization (e.g., Flinn and Low 1986; Marlowe 2003), and (2) canine size, one of the obvious targets of sexual selection in non-human primates, has undergone dramatic decrease in both sexes throughout hominin evolution (Washburn 1971; Plavcan and van Schaik 1997a) as well as a shape reorganization in early hominins associated with the reduction and eventual loss of the canine-premolar honing complex (Lockwood et al. 2000; Kimbel et al. 2006; White et al. 2006). These changes jointly act to reduce the effectiveness of canines as weapons and greatly decrease the likelihood that canines are targets of sexual selection in modern humans or earlier hominins.

Natural Selection and Sexual Dimorphism

As important as the role of sexual selection is in generating and maintaining sexual size dimorphism, it is unlikely to be the only force acting on size dimorphism. Among the studies mentioned above, the model with the greatest explanatory power for the relationship between sexual selection and body mass dimorphism within anthropoids is that described by Plavcan (2004) with $r^2 = 0.549$ for a sample of 85 species. While some of the 45% of variation in dimorphism that is unaccounted for is undoubtedly due to an imperfect fit between the proxy for sexual selection (competition levels) and sexual selection itself, and some variation is probably due to noise in the body mass signal, there is likely to be a large portion of the variation in dimorphism that is associated with other forces.

For example, natural selection can also affect dimorphism, and this has implications for the interpretation of size dimorphism in the fossil record. First, there are indirect effects of natural selection on sexual dimorphism. For example, predation risk appears to be correlated with minimum group size in many primates (e.g., Stanford 2002; Lehmann et al. 2007), and it has been shown that predation risk also affects group sex-ratios (Hill and Lee 1998), which in turn affects reproductive skew and sexual selection intensity. Resource seasonality may also drive changes in group size and breeding seasonality, thus affecting sexual selection and sexual dimorphism (Plavcan et al. 2005b). Second, natural selection may also directly affect sexual dimorphism by differential response of male and female adult size to resource availability. In a study of the ontogeny of sexual size dimorphism in primates, Leigh (1992) found that although sexual selection is the primary driver of dimorphism, female growth rates and duration respond to natural selection, which in turn has an effect on adult dimorphism. Several other studies have shown that growth rates are negatively correlated with ecological risk (i.e., resource availability and seasonality) in primates (sifakas, Ravosa et al. 1993; baboons, Altmann and Alberts 1987; and African apes, Leigh and Shea 1996). In particular, variation in female growth rates between African ape species appears to be due primarily to differences in resource stress (where resource stress is diet-dependent), with species living in habitats with greater resource stress (e.g., *Pan troglodytes*) showing depressed female growth rates relative to species in lower stress habitats (e.g., *G. gorilla*) (Leigh and Shea 1996). Assuming growth durations remain constant (which may not be true), if female growth rates are more responsive to ecological pressures than male growth rates, natural selection in the form of ecological stress may depress female adult body size relative to that of adult males, increasing sexual size dimorphism. Thus interpreting the meaning of size dimorphism in *Australopithecus* is not as simple as inferring high levels of male competition from high levels of dimorphism, since ecological effects may also contribute to dimorphism. This is not a trivial concern, since many models for the evolution of bipedalism invoke a role for increased aridity and reduction of forests; i.e., ecological stress. The flip side of the coin is that dimorphism potentially offers a window into not only the social behavior of extinct taxa, but also the ecological pressures that they experienced.

In order to tease apart the effects of natural selection and sexual selection on sexual size dimorphism, it is necessary to investigate the mechanisms through which ecological stress has a differential effect on male and female body size. Resource pressure probably has a stronger effect on females than males because of the energetic costs associated with reproduction and lactation (Ralls 1976; Emlen and Oring 1977; Wrangham 1980; van Schaik 1989; Isbell 1991; Mitchell et al. 1991; van Hooff and van Schaik 1992; Isbell and Pruetz 1998; Boinski et al. 2002). Because larger females have absolutely greater metabolic costs than those of smaller females, healthy small females should be able to develop an energetic surplus for reproduction quicker than larger females during periods of resource scarcity. Larger females will thus reproduce less frequently than smaller females in times of scarcity because of the required greater investment of internal reserves, and thus greater risk, on the part of larger females, hence a decrease in expectation of future offspring (Pianka and Parker 1975; Pianka 1976).

Empirical evidence from Darwin's finches supports these predictions, showing that smaller females breed more often than larger females in variable environments (Downhower 1976). Similarly, a long term study of red deer showed that size dimorphism was negatively correlated with forage quality due to decreased female size, and thus increased dimorphism, when forage quality was low (Post et al. 1999); smaller females were also more likely to breed earlier than larger females and to have more offspring over their reproductive lifespan than larger females (Post and Stenseth 1999). Beehner et al. (2006) found that female baboons in Amboseli were significantly less likely to cycle and significantly less likely to conceive than expected following periods of drought or extreme heat; they argued that this is related to female body condition, and that when females have adequate body reserves, they cycle and conceive. Although Beehner and colleagues did not look at the effect of body size, it follows that healthy smaller females with their lower absolute metabolic needs would be likely to build up the necessary reserves allowing them to cycle and conceive more frequently than larger females during periods of extended resource stress.

Research on the role of resource stress in the evolution of sexual size dimorphism in non-human primates suggests that it can be an important selective force. For example, the application of a quantitative genetics model to identify the forces driving differences in sexual dimorphism among four populations of *Cercocebus pygerythrus*, the African green monkey, showed that these differences are primarily due to negative selection on female body size in more dimorphic populations, counter to the predictions of sexual selection theory; in addition, dimorphism is negatively correlated with food availability, consistent with a differential sex response to resource stress (Gordon 2006a). A comparative analysis looking at the direct effects of resource seasonality on mass and cranial size dimorphism within primates found that increased dimorphism is occasionally associated with increased seasonality, although not consistently so across all taxa (Plavcan et al. 2005b). In addition, a comparative study of the evolution of mass dimorphism across living primates demonstrated that differences in dimorphism between distantly related species are generally due to the effects of sexual selection, but that differences between congeners are as likely to be due to selection (presumably natural) acting on female size as they are to be responding to sexual selection acting on males (Gordon 2006b). Thus there is the potential for any primate species (including fossil hominins) to record an ecological signal in their size dimorphism that is at least partially independent of social behavior.

Evaluating the Relative Effects of Sexual and Natural Selection on Sexual Dimorphism in Living Primates

One possible way of identifying how strong a selective force resource pressure is for primate size dimorphism, and thus how much care should be taken in inferring particular social behaviors for australopiths based on their dimorphism alone, is to consider the relationship between mass dimorphism and canine size dimorphism in living primates. Although canine size dimorphism is probably not a good indicator of competition levels in hominins because of the change in canine shape and size early in hominin evolution, it has been shown to be an excellent indicator in living nonhuman primates (Plavcan and van Schaik 1992, 1997a; Plavcan 2000, 2004), and perhaps more responsive to sexual selection than body mass dimorphism (Plavcan 2000; Thorén et al. 2006). In addition, as Plavcan et al. (2005a) have noted, canine size is less likely than body mass to be directly affected by resource pressure. Therefore canine size might be expected to reflect a strong competition signal, while mass dimorphism could be expected to record a mix of competition and resource pressure signals. By comparing mass dimorphism to canine size dimorphism, the importance of ecological factors in driving differences in mass dimorphism could be evaluated by considering the amount of covariance between the two types of dimorphism. In addition, the relative importance of resource stress on particular populations or species could be determined by analyzing the residuals from regressions of mass dimorphism on canine size dimorphism (Fig. 13.1).

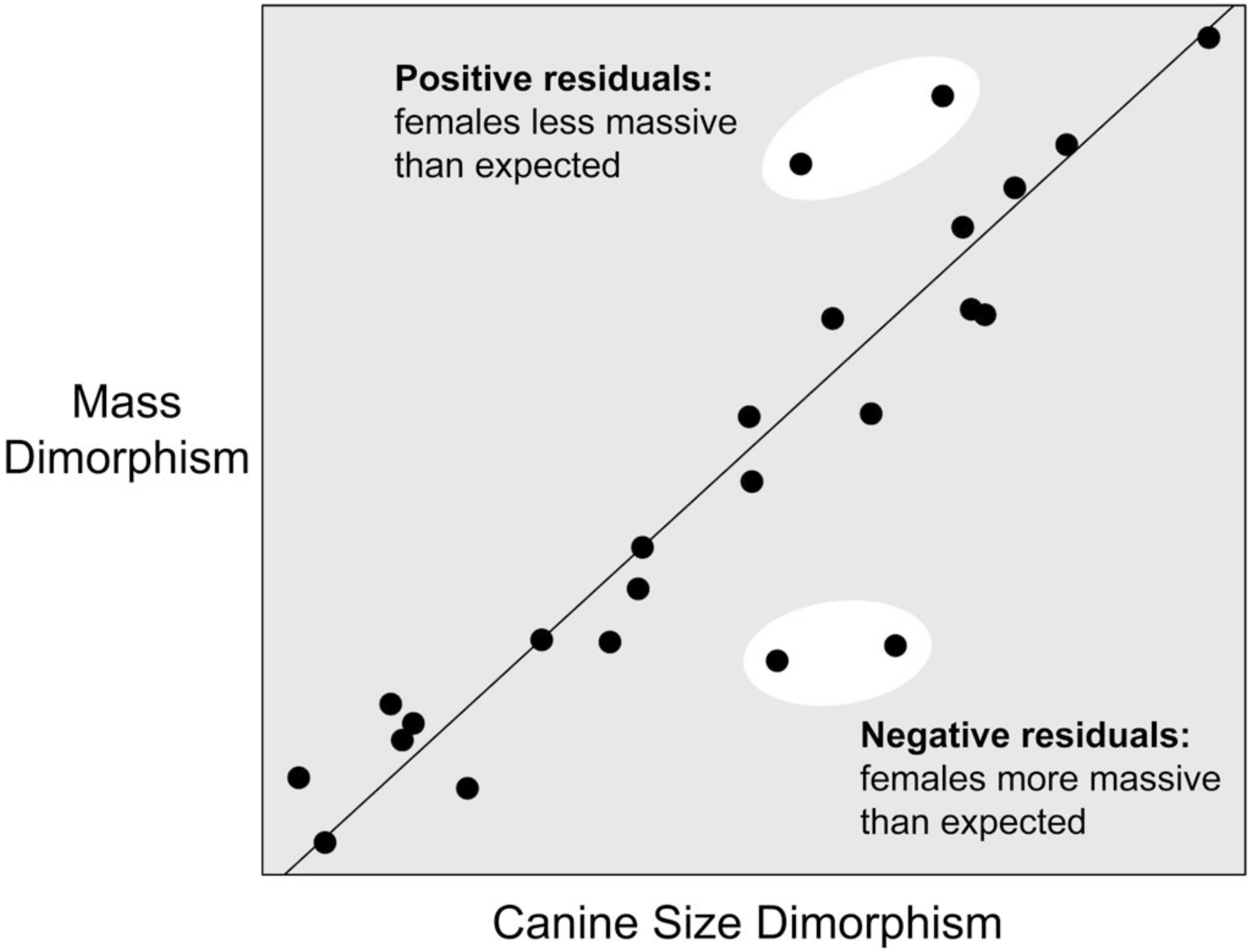

Fig. 13.1 Hypothetical comparison of mass dimorphism and canine size dimorphism in living primates. Data points may represent species or populations. Line may represent hypothetical scaling relationship (e.g., isometry) or empirically-derived scaling relationship. If deviations from the overall trend are driven by the response of female mass to ecological factors, then those data points which have pronounced positive residuals indicate that mass dimorphism is unexpectedly high in those populations or species because females are less massive than expected; the reverse is true for pronounced negative residuals. The individual contribution of male and female mass differences to these deviations can be evaluated in more detail by regressing mass against canine size separately for each sex and then comparing the plots and residuals

Of course, there are potential complications to be considered. For example, food distribution may play a large role in determining whether small females gain a selective advantage during periods of resource stress. If resources are uniformly distributed (e.g., leaves, bark), larger females may not have a competitive advantage over smaller females in procuring resources, and thus small size will be at a selective advantage due to the advantage in reproductive frequency enjoyed by smaller females. However, if resources are clumped (e.g., fruit outside of masting events), larger females may be able to competitively exclude small females from feeding patches, thus countering the smaller females' advantage of lower absolute metabolic requirements (Plavcan et al. 2005b). In such a case the implications for directional selection on female body size are unclear. Further research into fallback foods among living primates during periods of resource stress may help identify whether resources are more likely to be distributed uniformly or in clumps at such times. For example, where chimpanzees and lowland gorillas are sympatric, they tend to have similar diets during the wet season, but during periods of food scarcity gorillas rely more on ubiquitously-distributed vegetative foods such as pith and bark while chimpanzees maintain a more patchily-distributed fruit-dominated diet (Wrangham 1977; Sugiyama and Koman 1987; Tutin et al. 1997; Rogers et al. 2004; Yamagiwa and Basabose 2006). Given that these are both large-bodied ape species living in the same habitat, ecological (or paleoecological) variables alone are not enough to predict the likely distribution of fallback foods for a given species; dietary information (or dietary reconstructions in the case of fossil hominins) must also be considered.

Another complicating factor is that canines are not only used by males for competition over mating opportunities; they are also used by females for competition over resources (Plavcan 2004). Thus if resources are distributed in such a way that some females can competitively exclude others, selection may favor larger canines in females and thus reduced canine dimorphism, potentially without a decrease in female body size and thus no change in mass dimorphism. When mass dimorphism is plotted against canine dimorphism, this scenario would be indistinguishable from stable canine dimorphism and increased mass dimorphism, since in both cases the population under consideration will have a positive residual. Comparisons between populations of the same species or subspecies where mass and canine size are examined separately for each sex may be able to identify which variables are changing, in which direction, and in which sex.

More broadly, comparative studies can investigate these relationships by determining whether female mass responds more to ecological differences than male mass and whether mass dimorphism is significantly correlated with ecological variables. Recent work in wild lemurs has shown that within brown lemurs and sifakas, female body size differs more than male body size between closely-related populations and subspecies that live in different ecological zones in Madagascar (Johnson et al. 2005; Lehman et al. 2005; Lewis and Kappeler 2005). Madagascar potentially provides a particularly useful test case because ecological conditions vary widely across the island and lemurs do not appear to respond to sexual selection with changes in mass dimorphism, leaving natural selection as a more likely candidate for producing changes in dimorphism. A complicating ecological factor should be noted, however: anthropogenically disturbed habitats (at forest edges, as opposed to cropland) may actually reduce resource stress if they provide a new food resource (e.g., guava); recent research on fecal cortisol levels comparing lemur populations in undisturbed and disturbed habitats indicates that stress levels are often reduced in disturbed habitats (Tecot 2008, 2013). Ecological variables must be selected with care to reflect actual resource stress.

Sexual Dimorphism in Extinct Taxa

Of course, before one can begin interpreting the biological significance of sexual dimorphism within the hominin fossil record, one must have a reliable assessment of the degree of dimorphism present within a fossil sample. A major problem in studying sexual dimorphism in extinct taxa is that it is practically impossible to definitively identify the sex of every specimen in a fossil hypodigm. Since sexual size dimorphism is typically measured as a ratio of mean male size to mean female size or the log of that ratio (Smith 1999), sexual dimorphism cannot usually be measured in the fossil record. Instead, relative size variation of the fossil sample is compared to that of extant taxa. Many different techniques exist for measuring relative size variation, including the max/min ratio (e.g., Richmond and Jungers 1995), mean method ratio (e.g., Simons et al. 1999), method of moments (e.g., Josephson et al. 1996), coefficient of variation (e.g., Leutenegger and Shell 1987; Lockwood et al. 1996), assigned resampling method (e.g., Lee 2001), and the binomial dimorphism index (e.g., Reno et al. 2003). Each of these techniques is susceptible to error under various conditions, although simulation studies and studies of actual primate data have shown max/min ratios to be particularly poor estimators while mean method ratios are relatively good estimators (Plavcan 1994; Rehg and Leigh 1999; Kościński and Pietraszewski 2004). Although many of these techniques express relative size variation in a ratio form, it is important to remember that these are not measures of sexual dimorphism and are not directly comparable to sexual dimorphism ratios for living taxa. These measures tend to be highly correlated with actual dimorphism, but the correlation is typically not completely linear, and taxa with low dimorphism almost always have values of relative size variation that are higher than expected due to size overlap in the sexes (Plavcan 1994; Gordon et al. 2008).

A second problem is the question of what sort of size should be measured. As mentioned above, the two types of sexual dimorphism in size that have been shown to be related to competition levels in living primates are canine size and body mass dimorphism. Canine size dimorphism may or may not provide useful information because of the reduction of canine size throughout the hominin lineage (Plavcan and van Schaik 1997a; Plavcan 2000) and a change in canine shape away from that of a useful weapon (Lockwood et al. 2000; Kimbel et al. 2006). Body mass cannot be measured directly in the fossil record, and although it can be estimated, estimates vary widely depending on the measurement used and the taxon selected to provide the regression model (e.g., body mass estimates for A.L. 288-1 ranging from 25 to 41 kg; Jungers 1988a, 1990a; McHenry 1988, 1992; Hartwig-Scherer 1993; Porter 1995). In addition, body mass estimates are accompanied by prediction errors that are usually so large that estimates are useless for significance tests (Smith 1996). So although some studies have used mass estimates to provide a general sense of the level of mass dimorphism we might expect to see in fossil taxa (e.g., McHenry 1991, 1992, 1996; Plavcan 2000), most research in recent years has focused on comparative studies of relative size variation in various skeletal measurements (e.g., mandibular, craniofacial, femoral, humeral, etc.). These studies incorporate an implicit assumption that the degree of relative size variation present in extinct and extant taxa for a particular skeletal region is proportional to the level of mass dimorphism present in those same taxa—an assumption which may or may not be true.

Studies of Sexual Dimorphism/Relative Size Variation in *Australopithecus*

Studies of relative size variation in australopith canines suggests that canine dimorphism in *Australopithecus afarensis* and *A. africanus* is most similar to that of monogamous and polyandrous primates (Plavcan 2000). It has been suggested that there might be higher canine size dimorphism in *A. anamensis* (Ward et al. 2001, 2010) although the presence of apparently higher dimorphism in *A. anamensis* than *A. afarensis* is only present in the mandibular canine, and only in tooth root areas, not crown dimensions (Plavcan et al. 2009). It is unclear whether this difference is significant with respect to sexual selection pressures, as it has been shown that the best canine indicator of competition levels is canine height dimorphism, not canine area dimorphism (Plavcan and van Schaik 1997a; Plavcan 2000). Furthermore, with the well-documented reduction of canine size and relative canine size throughout time in *Australopithecus* (and *Homo*), it has been suggested that canines were similarly less important in male–male contests, and thus high levels of male competition would not be expected to produce high degrees of canine dimorphism (Plavcan and van Schaik 1997a). Thus it is not clear that a hominin species and a non-hominin primate species which were subjected to the same degree of male–male competition would exhibit the same amount of canine size dimorphism, and thus the results of such analyses are difficult to interpret.

A more promising area of research for behavior reconstruction is the study of body size dimorphism. Due to the sparse nature of the hypodigms of most *Australopithecus* species and the comparatively rich hypodigm of *A. afarensis*, the statistical study of body size dimorphism in *Australopithecus* has primarily focused on *A. afarensis*. Although the presence of large postcranial elements combined with the broad size range of cranial material in *A. anamensis* (Ward et al. 2001) suggests high levels of body size dimorphism, no single postcranial element is well enough represented in this species for existing techniques to distinguish between high, gorilla-like levels of dimorphism and low, chimpanzee- and human-like levels of dimorphism in any particular element. The newly-described species *Australopithecus sediba* includes two partial skeletons presumed to be an adult female and a juvenile male; comparison between these specimens suggests a low level of dimorphism, although the juvenile clearly has not completed growth and of course this a comparison of only two individuals (Berger et al. 2010; de Ruiter et al. 2013). The size range of postcranial elements preserved for *A. africanus* indicates at least a moderate level of dimorphism (McHenry and Berger 1998), and some proximal femoral measurements show significantly greater dimorphism in *A. africanus* than in modern humans, but most do not (Harmon 2009). Craniofacial dimorphism in *A. africanus* appears to be intermediate between high gorilla-like dimorphism and low human- and chimp-like dimorphism (Lockwood 1999), but craniofacial dimorphism is of unknown utility in reconstructing social structure and/or competition levels. The reason for this is that comparative studies linking behavior to dimorphism in living primates have been on body mass dimorphism (Clutton-Brock et al. 1977; Leutenegger and Kelly 1977; Gaulin and Sailer 1984; Cheverud et al. 1985; Kappeler 1990, 1991; Leigh 1992, 1995; Ford 1994; Martin et al. 1994; Leigh and Shea 1995; Mitani et al. 1996; Plavcan and van Schaik 1997a, b; Smith and Cheverud 2002; Gordon 2004, 2006b; Plavcan 2004) or canine size dimorphism (Leutenegger and Kelly 1977; Kay et al. 1988; Greenfield 1992; Plavcan and van Schaik 1992,

Table 13.1 Summary of primary mating systems and levels of dimorphism within some extant hominoids and two australopith taxa with large postcranial hypodigms[a]

Species	Mating system	Canine dimorphism	Mass dimorphism	Postcranial dimorphism
Gorilla gorilla	Polygyny	High	High	High
Pongo pygmaeus	Polygny (noyau)	High	High	High
Pan troglodytes	Polygynandry	Moderate	**Moderate**	**Low**
Homo sapiens	Serial monogamy?	Low	**Low**	**Moderate**
Hylobates lar	Monogamy	Low	Very low	Very low
Australopithecus afarensis	?	Low	?	High?
Australopithecus africanus	?	Low	?	Moderate?

[a] Levels of dimorphism tend to be higher in species which exhibit more male–male competition for mating opportunities. However, this pattern is reversed within postcranial dimorphism between chimpanzees and modern humans (in bold)

1997a; Plavcan et al. 1995; Plavcan 2004), not craniofacial dimorphism. Furthermore, the relationship between craniofacial dimorphism and body mass dimorphism is highly variable between taxa (Plavcan 2003).

Numerous studies have performed statistical comparisons of skeletal size dimorphism in *A. afarensis* and living hominoids (e.g., Kimbel and White 1988; McHenry 1991, 1996; Richmond and Jungers 1995; Lague and Jungers 1996; Lockwood et al. 1996; Lague 2002; Reno et al. 2003, 2005, 2010; Plavcan et al. 2005a; Harmon 2006; Gordon et al. 2008). Most recent research has found relatively high levels of dimorphism in *A. afarensis*, similar to that seen in orangutans and gorillas, although Reno et al. (2003, 2005, 2010) found that dimorphism in *A. afarensis* could not be differentiated from that of chimpanzees or modern humans (to be discussed in more detail below). All published single-element studies of actual postcranial dimorphism (as opposed to dimorphism in estimated mass or estimated femoral head size) produce an observed level of *A. afarensis* dimorphism that exceeds that of all living hominoids, although the difference in dimorphism between *A. afarensis* and the extant taxon is not usually significant for gorillas and orangutans (Richmond and Jungers 1995; Lockwood et al. 1996; Harmon 2006). Interestingly, these postcranial studies are also distinct in that they construct an overall measure of size for each specimen from multiple measurements using a geometric mean, and thus incorporate more information than univariate analyses. Unfortunately, such measures of overall size cannot be calculated when one or more measurements are missing for a given specimen.

Also, as with craniofacial dimorphism, to date no studies have analyzed the relationship between postcranial dimorphism and social behavior in living primates. While studies linking body size dimorphism to social behavior generally show that higher levels of dimorphism are associated with mating systems where greater competition between males is expected (Table 13.1), all such studies to date have examined body mass, not postcranial size. This is a particular problem within the hominids (African apes and humans), because chimpanzees are more mass dimorphic than humans, while humans are more postcranially dimorphic than chimpanzees (Gordon et al. 2008; Table 13.1). Notably, researchers who argue for a human-like mating system for *A. afarensis* because their analyses show no significant difference between dimorphism in *A. afarensis* and modern humans (Reno et al. 2003, 2010) have downplayed the fact that those same analyses also show no significant difference between *A. afarensis* and chimpanzees, and thus the dimorphism signal could just as easily be used to argue for a chimpanzee-like mating system in *A. afarensis*.

Improving Measures of Relative Size Variation in *Australopithecus*

So what can be done to improve these measures of relative size variation in fossil hominins, particularly in relation to the variable which is likely to be the target of sexual selection; i.e., mass dimorphism? Two areas of research are called for: (1) developing new techniques which can include more of the information present in fossil specimens for any particular taxon, and (2) generating a better understanding of the relationship between mass dimorphism and skeletal dimorphism, including both craniofacial and postcranial dimorphism. These topics are explored in more detail below.

New Techniques for Improving Hypodigm Representation

A source of frustration in the study of size variation in *Australopithecus* is that the hypodigms of both *A. afarensis* and *A. africanus* include relatively large numbers of elements, yet for any given element or set of measurements, the sample size available within each species is usually quite small. Ideally, analyses could be developed which combine information from all specimens in a species hypodigm, regardless of which elements are present for a given individual. The major hurdle for such analyses is how to handle the missing data problem. In the past several years, two different types of multivariate approaches have been developed to address this issue. The first uses relationships between measurements in a single fossil specimen to estimate the missing data for other fossils, then compares relative size variation in the resulting data set to that in comparative taxa (i.e., template methods). The second uses Monte Carlo resampling techniques to compare sets of measurements from a fossil taxon to sets of measurements from extant comparative taxa in which the extant specimens are sampled in such a manner that they are missing the same measurements as the fossil specimens (i.e., resampled geometric mean methods). These two types of methods are described more fully below.

Template Methods

These methods first attracted wide attention with Reno et al.'s (2003) analysis of size dimorphism in *A. afarensis*. The basic concept is that if a single specimen preserves many different skeletal elements (e.g., A.L. 288-1), that specimen can be used as a template in which the relationship between the size of various elements is used to predict the size of missing elements for other specimens. For example, the ratio between femoral head size and humeral head size in the template specimen can be used to estimate femoral head size for isolated proximal humeri, the ratio between femoral head size and radial head size in the template specimen can be used to estimate femoral head size for isolated proximal radii, etc. As a result, any specimens that contain elements present in the template specimen can be included in the data set. Researchers can then use their favorite measure of relative size variation (e.g., mean method ratio, binomial dimorphism index, coefficient of variation, etc.) and compare the result against similarly-constructed datasets for extant comparative taxa of interest. Thus template methods are multivariate in the sense that multiple types of measurements are used to estimate one representative measure of size, although univariate methods are used to compare relative size variation between fossil and extant taxa.

One problem with template methods is that as currently applied, the size of absent elements is predicted using the ratio between element sizes (Reno et al. 2003, 2010). Using a ratio implicitly assumes that the two elements in question scale isometrically with each other in *A. afarensis*, an assumption which may or may not be correct. For example, although articular surface areas generally scale isometrically with body mass (and thus each other) in non-human hominoids, many articular surface areas scale allometrically with mass and each other in humans, a difference which is likely related to differences in distribution of loads between quadrupedalism and bipedalism (Jungers 1988b, 1990b). Without several relatively complete specimens of *A. afarensis* it is not possible to determine scaling relationships between elements, but it is certainly possible (and likely) that human-like deviations from isometric scaling occur in the australopith skeleton. Deviations from isometry have serious consequences for ratio-based estimates. As Fig. 13.2a shows, using a ratio when the actual scaling relationship is not isometric can seriously under- or over-estimate size, particularly when the template specimen is known to be one of the smallest individuals in the species.

A second problem with template methods is that they do not account for "biological error;" that is, few if any individual specimens will plot directly on scaling lines. Size estimates are affected by biological error in both the template specimen and the estimated specimen. For example, suppose that the relationship between two variables is exactly isometric. Even in this situation, the template specimen will most likely sit above or below the line (i.e., have a non-zero residual from the scaling line). When ratios between the observed sizes in the template specimen are used to estimate size for another specimen, this biological error is multiplied, resulting in an under- or over-estimate of size (Fig. 13.2b). In addition, even if the template specimen happens to sit exactly on the actual scaling line, the real measure of size in the other specimen is likely to also incorporate some biological error, and thus differ from the predicted value.

A third related problem with template methods is that, to date, they have not incorporated prediction intervals for the estimated measurements. As noted earlier, prediction intervals for fossil measurements are often so large as to render predictions practically useless in a statistical sense (Smith 1996). Prediction intervals can be calculated for measurements estimated using templates. The template method is actually a regression technique: predicting an unknown femoral head size using the ratio of femoral head diameter to some other measurement in A.L. 288-1 is mathematically equivalent to using a regression of femoral head size against the predictor variable, where the regression is constrained to the origin (solid diagonal lines in Fig. 13.2) and has a sample size of one (A.L. 288-1 in this case). The number of degrees of freedom in such a regression are zero ($n-1$), and thus 95% prediction intervals for the estimated femoral head measurement include negative and positive infinity.

A fourth problem relates to the susceptibility of template methods to error due to including multiple measurements from the same individual (Plavcan et al. 2005a; Scott and Stroik 2006; however, see Reno et al. 2005). For example, if two or more "unassociated" elements that are used to predict separate measures of femoral head size actually

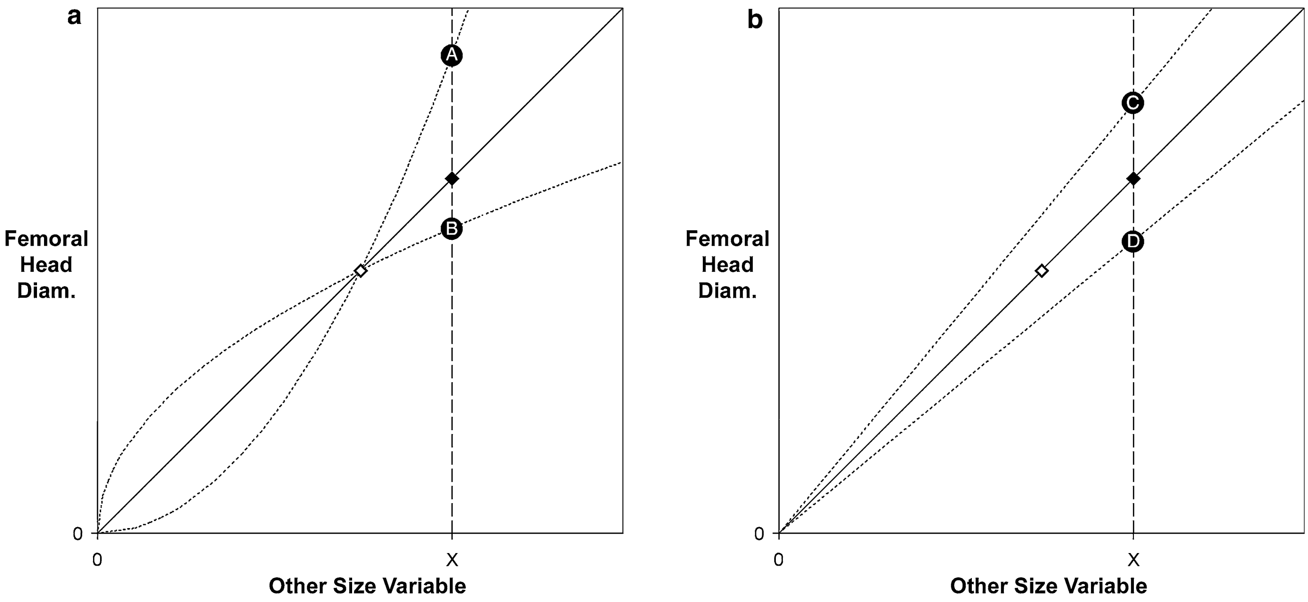

Fig. 13.2 Examples of possible estimation error though use of a template method ratio. Errors can be due to (**a**) allometric scaling and/or (**b**) biological error. Both plots show femoral head diameter (FHD) plotted against another variable for the template specimen in raw (non-logged) data space (*open diamond*), the measured value for the other variable in a second specimen (*x* and *vertical dashed line*), and the estimated value of FHD for the second specimen (*closed diamond*), which is based on the ratio of FHD to the other dimension in the template specimen (*solid line*). Examples show a small template specimen as in the case of A.L. 288-1 in Reno et al. (2003). If FHD scales positively allometrically with respect to the other variable, then the template ratio will underestimate the actual value of FHD in the second specimen (compare the *closed diamond* with **A**). Likewise, negative allometry means that the template ratio will overestimate the actual value of FHD (**B**). Even if both variables scale isometrically with each other, biological error (variation of individual specimens about the regression line) can result in estimation error. If the template specimen plots below the actual scaling line, the template ratio will underestimate the true scaling slope (in raw data space; for logged data, this is equivalent to underestimating the intercept) and will underestimate the actual value of FHD in the second specimen (compare the *closed diamond* with **C**). Similarly, if the template specimen plots above the actual scaling line, the template ratio will overestimate the actual value of FHD in the second specimen (**D**)

belong to one individual, then that single individual is overrepresented in the fossil sample and will affect the observed size variation in the sample. This is particularly a problem in studies of size dimorphism in *A. afarensis*, which typically include specimens from A.L. 333, because there is a high probability that multiple elements from the A.L. 333 site come from fewer individuals than there are elements, perhaps as few as five individuals (Plavcan et al. 2005a).

Despite all of these issues, or perhaps because of them, template methods initiated a renewed interest in studies of dimorphism in australopiths, particularly in developing techniques for incorporating multiple specimens with missing data into a single analysis. It should be noted that Henry McHenry had already developed such a technique 12 years earlier: in his analysis of body size dimorphism in *A. afarensis*, he generated estimates of body mass for fossil specimens representing various skeletal elements based on body mass regressions for extant taxa (McHenry 1991). While McHenry's work might be criticized on the grounds that the reference samples for his regression equations may not be appropriate (given the lack of australopiths of known body mass), that study did not assume that all measurements scaled isometrically with each other, nor did it base predicted values on regressions with a sample size of one.

Resampled Geometric Mean Methods

These methods are more traditionally multivariate than template methods and address some of the problems of template methods. Conceptually they are much like the previously described geometric mean methods (e.g., Richmond and Jungers 1995; Lockwood et al. 1996; Harmon 2006) except that modifications have been made to accommodate missing data. For example, it can be shown mathematically that the ratio of mean male size to mean female size for the geometric mean of several variables is equivalent to the geometric mean of those ratios calculated individually for each variable (see the appendix in Gordon et al. 2008). For example, consider the gorilla data presented in Table 13.2. The same measure of sexual size dimorphism, a ratio of 1.26, is found regardless of whether

Table 13.2 Example showing mathematical equivalence of ratio of GMs and GM of ratios. Measurements are in mm; ratios are unitless[a]

Sex	HUMHEAD	ELBOW$^{0.5}$	RADTV	FEMHEAD	FEMSHAFT$^{0.5}$	DISTFEM$^{0.5}$	PROXTIB$^{0.5}$	DISTTIB$^{0.5}$	GM
F	45.6	34.9	21.1	37.5	29.6	44.7	49.0	24.2	34.4
F	49.3	35.4	26.4	40.0	28.0	48.6	53.2	25.1	36.8
F	47.2	37.9	27.1	40.6	27.0	50.3	56.0	27.1	37.7
F	51.6	38.7	26.7	40.9	31.3	50.3	55.1	27.5	38.9
F	50.7	37.7	28.9	43.6	31.0	52.2	58.9	29.0	40.1
M	54.4	43.1	29.2	47.7	33.9	57.1	67.3	29.5	43.4
M	62.1	46.3	32.1	48.5	37.3	58.5	64.8	34.3	46.5
M	63.0	46.0	36.6	50.6	36.5	62.1	69.4	30.7	47.5
M	65.1	46.5	35.0	52.1	40.0	62.9	71.4	31.0	48.5
M	64.3	49.3	36.6	54.1	39.9	64.9	74.4	34.4	50.4
SD	*1.26*	*1.25*	*1.30*	*1.25*	*1.28*	*1.24*	*1.28*	*1.20*	***1.26***

[a] Reproduced from Gordon et al. (2008). Values are provided for ten adult gorillas for each of eight linear postcranial measurements. Male:female ratios are calculated for each linear measurement and GMs of all measurements are calculated for each individual. Multivariate dimorphism for this data set can be calculated as either the ratio of average male GM divided by average female GM, or as the geometric mean of the male:female ratios for each linear measurement. In either case the result is the same, the ratio of 1.26 shown in bold italics. Note that in all cases sex-specific means are calculated as geometric means, not arithmetic means; however, ratios of sex-specific arithmetic means are identical to the ratios of sex-specific geometric means shown here at three significant digits

Table 13.3 Example of *A. afarensis* specimens and postcranial measurements used to calculate overall measure of postcranial size dimorphism. Measurements in mm[a]

Specimen	HUMHEAD	ELBOW$^{0.5}$	RADTV	FEMHEAD	FEMSHAFT$^{0.5}$	DISTFEM$^{0.5}$	PROXTIB$^{0.5}$	DISTTIB$^{0.5}$
A.L. 288-1	27.3	20.5	15.0	28.6	20.9	–	40.3	18.2
A.L. 128-1/129-1	–	–	–	–	21.6	37.5	39.9	–
A.L. 137-48a	–	22.9	–	–	–	–	–	–
A.L. 211-1	–	–	–	–	28.2	–	–	–
A.L. 322-1	–	22.9	–	–	–	–	–	–
A.L. 333-3	–	–	–	40.2	31.3	–	–	–
A.L. 333-4	–	–	–	–	–	45.6	–	–
A.L. 333-6	–	–	–	–	–	–	–	21.7
A.L. 333-7	–	–	–	–	–	–	–	24.8
A.L. 333-42	–	–	–	–	–	–	50.6	–
A.L. 333-95	–	–	–	–	29.1	–	–	–
A.L. 333-96	–	–	–	–	–	–	–	21.0
A.L. 333-107	35.1	–	–	–	–	–	–	–
A.L. 333w-40	–	–	–	–	30.8	–	–	–
A.L. 333w-56	–	–	–	–	–	45.0	–	–
A.L. 333x-14	–	–	22.2	–	–	–	–	–
A.L. 333x-26	–	–	–	–	–	–	52.3	–
MMR:	1.29	1.12	1.48	1.41	1.40	1.21	1.28	1.19

[a] Reproduced from Gordon et al. (2008). Fossil measurements taken from McHenry (1992) and McHenry and Berger (1998). Mean method ratio (MMR) calculated for each measurement. Overall measure of MMR is the geometric mean of these eight values: 1.29

dimorphism is calculated for the overall size variable (the geometric mean of all measurements) or if it is calculated as the geometric mean of dimorphism in each measurement. This property means that geometric mean methods can be applied in cases of missing data. Consider the *A. afarensis* data presented in Table 13.3: although it is impossible for a measure of overall size to be calculated for any one specimen using the geometric mean, a measure of overall relative size variation can be calculated for the sample as a whole by calculating the geometric mean of the ratios for each variable. This value can then be compared to values from extant comparative samples that have been generated in the same way; i.e., subsamples of equal size as the fossil sample are selected, data is removed from the comparative

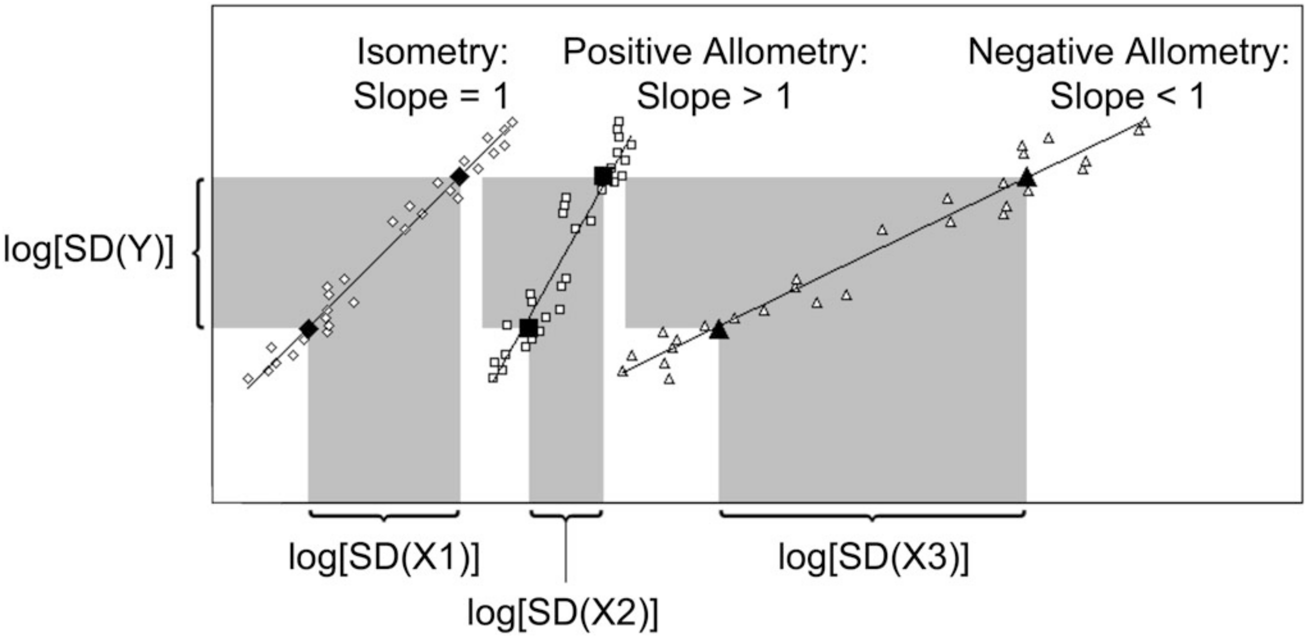

Fig. 13.3 Relationship between scaling and size dimorphism for pairs of variables (hypothetical data). Reproduced from Gordon et al. (2008). When plotted in log space, the log of sexual dimorphism (SD) is the difference between the mean of male values and the mean of female values. For example, the length of the bracket along the Y-axis is equal to the log of the male:female ratio for variable Y, where the *bracket* indicates the distance between the sex-specific means (shown as *closed symbols*). When two variables of the same dimensionality (i.e., linear, area, or volume measurements) scale isometrically with each other they will have highly similar SD values (compare the length of the *brackets* for Y and X1); these SD values would be identical if there were no variation about the regression line. When there is positive allometry for the scaling of Y on X, the X variable will have a lower SD value than Y (compare *brackets* for Y and X2), while the reverse is true for negative allometry (compare *brackets* for Y and X3). Note that the slope of the scaling relationship can be estimated by the slope of a line passing through the female and male means, which is equivalent to log(SD(Y))/log(SD(X))

sample so that fossil and extant comparative samples are missing the same number and types of measurements, and then overall relative size variation is calculated for the resulting comparative sample (Gordon et al. 2008).

Resampled geometric mean methods enjoy several advantages over template methods. First, specimens can be included which do not have elements present in a template specimen (e.g., the three specimens with distal femur measurements in Table 13.3, a measurement not available for A.L. 288-1). Second, no measurements are estimated; only values which are measured directly are included. Third, because relative size variation is calculated independently for each variable, only antimeres can result in multiple representation for single individuals for a given variable. Representation of single individuals by multiple elements is not a drawback but a goal in geometric mean methods, and empirical tests have shown that results change very little if supposed unassociated elements are actually drawn from a single individual (Gordon et al. 2008). Fourth, because of the manner in which multiple variables are used to calculate the final measure of relative size dimorphism, fossil sample sizes are generally large enough to calculate distributions of relative size variation for fossil taxa as well as comparative taxa, whereas all previous analyses (including previous geometric mean analyses) compared distributions for comparative taxa to the single observed value for a fossil sample. Thus resampled geometric mean methods can potentially provide a much more conservative yet more accurate test for significant difference between fossil and extant samples in relative size variation.

One problem that template methods and resampled geometric mean methods share, although to a lesser extent in the latter, is that of the assumption of isometric scaling between variables. As Fig. 13.3 illustrates, the ratio between size dimorphism as measured for two variables within a single sample is directly proportional to the scaling relationship between those two variables. Thus when all variables scale isometrically with each other, all variables are expected to show the same level of dimorphism and thus a geometric mean of those dimorphism levels will be an accurate representation of the overall level of dimorphism in all of the included variables. However, if positive or negative allometry exists between some of the included variables, then the observed level of dimorphism will be expected to differ between variables. In that case comparisons between taxa would only be valid if all taxa included in the analysis shared the same scaling patterns for all variables.

Gordon et al. (2008) circumvented this problem by only including variables that did not differ significantly from isometry in their scaling with the other variables in the analysis as measured within each of the extant species. (Notably, they found that *A. afarensis* exhibited gorilla-like levels of size dimorphism in agreement with most other recent studies, whereas Reno et al. (2003, 2010), who did not demonstrate that their variables scaled isometrically with each other, did not.) However, this problem can also be addressed by using a weighted geometric mean, where the weights are the scaling relationships between each variable and an overall standard. This standard could be one of the variables in the analysis or another variable such as body mass. Multiple sets of weightings could be generated for the fossil geometric means based on the scaling relationships of each of the comparative taxa, with interpretation taking particular notice of the results using the most conservative set of weights.

Improving Understanding of the Relationship Between Mass Dimorphism and Skeletal Dimorphism

This leads into the second area of research, which is the investigation of the relationship between different types of dimorphism. As previous researchers have noted, skeletal dimorphism is not equivalent to body mass dimorphism (e.g., Plavcan 2003; Plavcan et al. 2005a; Harmon 2006; Gordon et al. 2008). Because sexual selection probably targets body mass rather than skeletal size, it is important to understand how the two are related. For example, sexual dimorphism for most postcranial measurements is higher in modern humans than in chimpanzees, but the reverse is true for body mass (Richmond and Jungers 1995; Gordon et al. 2008). However, little work has been done to investigate these relationships. Preliminary research suggests that dimorphism in postcranial measurements may be more variable intraspecifically than is dimorphism in craniofacial measurements among living primates (Plavcan and Gordon 2007), but much more work remains to be done in this area. In particular, the scaling of body mass with measurements used in fossil analyses needs to be identified for those taxa that are typically used in comparative studies, and ideally these should be identified for a broad range of primates and evaluated in the context of variation in positional behavior.

Applying New Methods to Other Species

Aside from the benefit of being able to better evaluate relative size variation in *A. afarensis*, these new techniques also open up the possibility of applying rigorous statistical approaches to analyzing size dimorphism in other australopiths. For example, recent studies of size and shape variation in *A. afarensis* and *A. africanus* suggest that postcranial size dimorphism is probably greater in *A. afarensis* than in *A. africanus* (Cunningham 2005; Green et al. 2007; Harmon 2009), but this comparison has yet to be directly tested. Fortunately, the hypodigm of *A. africanus* is now large enough to apply the new methods described above. Furthermore, the postcranial hypodigm of *A. afarensis* continues to expand, which will improve estimates of skeletal dimorphism and increase the power of statistical tests. For example, the new postcranial specimen KSD-VP-1/1 from Woranso-Mille, Ethiopia, falls somewhere in the range from mid-sized male to among the largest males of *A. afarensis* (Haile-Selassie et al. 2010). Thus estimates of postcranial dimorphism in *A. afarensis* will likely either go up or stay the same while standard error of the estimates will go down, making it more likely that significant difference in dimorphism will be found between *A. afarensis* and taxa with lower apparent levels of dimorphism. Finally, although *A. anamensis* is lacking in postcrania, it is possible that techniques could be developed which incorporate the relationship between craniofacial dimorphism and body mass dimorphism, taking into account that the connection between male competition and cranial size dimorphism may not be particularly tight. Such techniques may ultimately allow us to make comparisons not only between single fossil species and extant taxa, but among fossil taxa as well.

Dimorphism in *Ardipithecus ramidus*

With the long-anticipated publication of the analysis of *Ar. ramidus* in a special issue of *Science* in 2009, it is interesting to consider how dimorphism in this taxon relates to the overall patterns seen in *Australopithecus*. Unfortunately, no direct analysis of postcranial size dimorphism in *Ar. ramidus* has been published to date, but there are arguments made within the special issue of *Science* that body size dimorphism was probably low (Lovejoy 2009; Suwa et al. 2009b). Evaluating this assertion and its implications for evolutionary pressures acting on hominin dimorphism requires consideration of the sex assessment of the specimen ARA-VP-6/500 as well as the phylogenetic placement of *Ar. ramidus*.

Ardi or Artie? Sex Assessment in ARA-VP-6/500

Sex assessment in ARA-VP-6/500 relies on the following argument: the canine of ARA-VP-6/500 is among the smallest in the hypodigm of *Ar. ramidus*, while the postcranial elements are among the largest. Therefore, either sex is a possibility, but according to Suwa et al. (2009b) ARA-VP-6/500 must be female because the probability of sampling a male canine that is as small as that of ARA-VP-6/500 is very low.

The rank-based sampling procedure of Suwa et al. (2009b) for assessing the probability of a male canine being as small as that of ARA-VP-6/500 relies upon the assumption that there is a moderately high level of variability in canine size in *Ar. ramidus* that is due to significant size difference between the sexes. However, as they themselves note, canine size variation in *Ar. ramidus* is very low. As shown in their Fig. 1e, f (Suwa et al. 2009b), the variability of upper canine metrics in *Ar. ramidus* is less than that seen in modern humans, *A. anamensis*, and *A. afarensis*, all of which are considerably less variable than *Pan troglodytes* and *P. paniscus*. As shown in that same figure, there is substantial overlap in male and female metrics in modern humans (although not in *Pan*), a taxon more variable in size than *Ar. ramidus*. As such, there is a reasonable probability that a male *Ar. ramidus* can have a canine as small as ARA-VP-6/500. The point here is that low canine size variation on the order of that seen in *Ar. ramidus* indicates that no strong statement regarding attribution to either sex can be made for *any* specimen on the basis of canine size alone.

Furthermore, the assumption in Suwa et al. (2009b) and the accompanying papers is that because canine size variation is low, body size variation must also be low. However, as discussed above, the hominins as a clade demonstrate a decoupling of canine and body size variation with low canine size variation in *A. afarensis* and later hominins, but substantial postcranial size variation. Regardless of whether or not *Ar. ramidus* is a hominin, that same decoupling may be present in this taxon. Unfortunately, these papers do not present any analysis of size variation in the postcranium. However, two possibilities are considered below.

Low canine size variation, high postcranial size variation: If this is the case, the large size of the postcranium of ARA-VP-6/500 in conjunction with high postcranial size variation such as that seen in *A. afarensis*, *G. gorilla*, and *P. pygmaeus* could be interpreted as strong evidence that ARA-VP-6/500 is male; i.e., Artie, not Ardi.

Low canine size variation, low postcranial size variation: If this case is true, the large postcranium of ARA-VP-6/500 tells us just as much as its small canine, i.e., not much. In the presence of low size variation, no confident assessment of sex can be made.

The implications of these scenarios are clear: depending on how variable postcranial size is in *Ar. ramidus*, it may be possible to make a strong argument for ARA-VP-6/500 being male, but regardless of how much size variability exists in the postcrania, one cannot make a strong argument for ARA-VP-6/500 being female on the basis of size variation in the canine and postcrania alone. Suwa et al. (2009a) argue that the supraorbital torus in the cranium of ARA-VP-6/500 is thin relative to chimpanzees, thus confirming that this specimen is female. However, the lack of comparison to supraorbital torus thickness in conspecifics makes this assertion dubious. They also note that ARA-VP-6/500 possessed a small compound temporal/nuchal crest, but suggest that since such a crest appears in both male and female chimpanzees, it should not be taken as an indicator that the individual was male (Suwa et al. 2009a). In any event, the case for ARA-VP-6/500 being female is weak. This is important because the argument for low body size dimorphism in *Ar. ramidus* is based entirely on the assumption that ARA-VP-6/500 is a female with some of the largest postcranial elements in the hypodigm (Lovejoy 2009; Suwa et al. 2009a).

Canine Size, Canine Dimorphism, and Body Size Dimorphism: Implications for Understanding Evolutionary Pressures on Large-Bodied Hominoids in the Early Pliocene

When considering canine size, canine size variation, body size variation, and phylogenetic placement of *Ar. ramidus*, there is good evidence that the canines are relatively small compared to extant African apes, and that there is low size variation within the canines (Suwa et al. 2009b). As noted earlier, there have not yet been any rigorous assessments of body size variation in *Ar. ramidus*, and there is some question regarding whether this species is a member of Hominini (e.g., Sarmiento 2010; Wood and Harrison 2011). Thus one could consider four possible scenarios given the data presented for *Ar. ramidus* so far, as shown in Table 13.4. Implications of each of these scenarios are considered in turn.

Scenario 1: **Hominin** *with relatively small canines, low canine size variation, and* **low** *body size variation*. In this case, *Ar. ramidus* would follow the hominin trend of reduced canine size and dimorphism, but would be unusual in that it had low body size dimorphism, contrary to the pattern seen in later fossil hominins, *Pan*, and *Gorilla*. Given the ubiquity of moderate to high body size dimorphism in fossil hominins and the African apes, this low dimorphism would most parsimoniously be interpreted as an autapomorphy of *Ar. ramidus*, implying that either a reversal occurs in later hominins if they are descended from an *Ar. ramidus*-like ancestor, or that *Ar. ramidus* represents a side branch diverging from the main trunk of later hominin evolution.

Scenario 2: **Hominin** *with relatively small canines, low canine size variation, and* **high** *body size variation*. Under

Table 13.4 Possible scenarios regarding dimorphism and phylogenetic placement of *Ar. ramidus*[a]

Scenario	Canine size	Canine size variation	Body size variation	Member of Hominini
1	Small	Low	Low	Yes
2	Small	Low	High	Yes
3	Small	Low	Low	No
4	Small	Low	High	No

[a] Canine size and measures of variation are relative to living African apes

this scenario, *Ar. ramidus* would indicate that the hominin pattern of decoupled canine and body size dimorphism was established at least 4.2 Ma, increasing the temporal gap between the decoupling of the various types of size dimorphism and the first appearance of stone tools.

Scenario 3: **Non-hominin** *with relatively small canines, low canine size variation, and* **low** *body size variation*. In this case, the existence of *Ar. ramidus* would indicate that there were at least two lineages of large-bodied hominoids with decreased canine size in the Early Pliocene (i.e., hominins and the *Ar. ramidus* lineage). Furthermore, inferred locomotor and postural differences between *Ar. ramidus* and hominins based on their postcranial morphology (Lovejoy et al. 2009a–c) would suggest that those multiple hominoid lineages were exploiting different niches in the changing landscape of East Africa at that time.

Scenario 4: **Non-hominin** *with relatively small canines, low canine size variation, and* **high** *body size variation*. Finally, this scenario would indicate that not only were there multiple East African ape lineages with decreased canine size exploiting different niches in the Early Pliocene, but also that the pattern of decoupled body size and canine size dimorphism occurred in at least two lineages at around the same time. This pattern would argue for some external forcing due to a region-wide selection pressure, presumably related to climatic variables of some sort. Furthermore, note that in this and the previous scenario, the reduction of canine size could not be considered a synapomorphy of hominins.

While all four of the scenarios outlined above are inherently interesting, and three of them represent large changes from earlier models of hominid and hominin evolution in the Pliocene (scenarios 1, 3, and 4), at present there is no way to choose between them. Although the phylogenetic placement of *Ar. ramidus* may be debated for many years to come, the eventual publication of more detailed analyses of postcranial dimorphism in this species will help narrow down the possibilities.

The Biological Significance of Sexual Dimorphism in *Australopithecus*

At the end of the day, what can we say about dimorphism in *Australopithecus*, and what can we infer from it? Most studies demonstrate strong statistical support for a moderate to high degree of skeletal size dimorphism in *A. afarensis*. Even assuming human-like scaling patterns for postcranial dimensions with body mass, *A. afarensis* almost certainly exhibited greater mass dimorphism than modern humans, and possibly more than chimpanzees and bonobos, although probably not as much as gorillas or orangutans. A slightly lower level of mass dimorphism is likely for *A. africanus*, while the levels of postcranial and mass dimorphism in *A. anamensis* are hard to evaluate at this point. That said, given the evidence supporting the role of resource stress in selecting against large female size and thus increasing dimorphism, combined with paleoecological reconstructions of high environmental variability at sites where the australopith material under consideration is found (e.g., Hadar between 3.4 and 2.9 Ma; Bonnefille et al. 2004), a significant portion of the dimorphism observed in *Australopithecus* species could potentially be due to ecological effects rather than sexual selection. How can we determine what role various selective factors played, and how may we use that knowledge in reconstructing behavior and ecology in fossil hominins?

One possibility relies on the relationship between growth rate variation and ecological stress in producing sexual size dimorphism. It is possible to develop techniques which assess the amount of size variation present at different developmental ages in fossil taxa and compare them to extant species in order to determine whether dimorphism is primarily due to duration differences (in which case relative variation in adult size would be expected to be high, but relative variation at all earlier age stages would be low), indicating a relatively small ecological component, or due to rate differences (in which case relative variation would be expected to steadily increase with developmental age), indicating a significant ecological component. For example, in a recent analysis of *Paranthropus robustus* facial material, Lockwood et al. (2007) compared dimorphism levels at different dental wear stages to demonstrate that facial dimorphism in this species appears to result from extended male growth relative to females. Such procedures are easiest with craniofacial and mandibular size, where developmental age can be inferred from dental eruption and wear, but they might also be developed for postcranial elements based on degree of epiphyseal fusion to identify patterns of size variation at younger developmental ages.

A second possibility is to evaluate australopith dimorphism in a phylogenetic comparative context. For example, Gordon (2004) used a phylogenetically independent contrasts approach to consider the relationship between evolutionary changes in female and male skeletal size in *Pan troglodytes troglodytes*, *P. troglodytes schweinfurthii*, *P. paniscus*, and *A. afarensis* (where female size in *A. afarensis* was represented by A.L. 288-1, and male size by a composite of A.L. 333-3, -x26, -42, -107, and -x14). In that study, differences in size dimorphism between subspecies of *P. troglodytes* were due to differences in female size, consistent with ecological differences between their habitats. Dimorphism differences between *P. troglodytes* and *P. paniscus* were due to differences in male size, consistent with expectations of greater sexual selection occurring in common chimpanzees than in bonobos. Finally, differences in dimorphism between *Pan* and *A. afarensis* were primarily due to differences in female size, suggesting that *A. afarensis* probably experienced similar levels of sexual selection as the genus *Pan*, but exhibited higher levels of dimorphism than *Pan*, perhaps due to the effect of natural selection on female body size in the form of ecological stress. Approaches like this can be adapted to include larger sample sizes, remove assumptions of presumed sex, analyze other species, etc. Ultimately, such approaches may allow us to infer much more than just analogous social structures, and permit us to build new human evolutionary models where paleoecological signals from the environment can be compared against ecological signals preserved in fossil hominin dimorphism.

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Chapter 14
Molar Microwear, Diet and Adaptation in a Purported Hominin Species Lineage from the Pliocene of East Africa

Frederick E. Grine, Peter S. Ungar, Mark F. Teaford, and Sireen El-Zaatari

Abstract Craniodental morphologies of early hominins have been widely perceived as having evolved to effectively process the generally harder food items that would have accompanied the expansion of drier, more open habitats from the Late Miocene into the Early Pliocene. In particular, it has been argued that *Australopithecus anamensis* may have been the first hominin to exhibit dentognathic adaptations for processing hard-food objects. The morphology of its presumptive descendant, *Australopithecus afarensis*, is viewed as having been further enhanced to deal with such items. Molar microwear fabrics in extant mammals vary with diet and, more particularly, the physical properties of the items consumed. Previous studies of molar microwear in these early hominin taxa suggest that while both may have been morphologically equipped to process a hard, brittle diet, neither appears to have necessarily preferred such items. We examined molar microwear in this purported species lineage for fossils from eleven temporal horizons spanning roughly 940 kyr (4.12–3.18 Ma). Six broad paleoecological categories were recognized for these horizons, and were ranked on the basis of floral cover and composition. With the sole exception of wear striation breadth, which is marginally correlated with habitat, microwear variables are not significantly associated with temporal or paleoecological rank. Occlusal striae tend to be narrower in individuals from more closed habitats, perhaps attesting to the importance of exogenous grit in the formation of microwear in some environments. Thus, the mechanical properties of masticated foods do not appear to have altered in the purported *Au. anamensis* - *Au. afarensis* lineage through time or in response to different paleoecological circumstances. The microwear fabrics and textures of *Au. anamensis* and *Au. afarensis* overlap extensively those of the mountain gorilla (*Gorilla beringei*) and gelada baboon (*Theropithecus gelada*). Most importantly, they differ notably from species such as the brown capuchin (*Cebus apella*) and grey-cheeked mangabey (*Lophocebus albigena*) that consume hard objects. Explanatory scenarios that describe *Au. anamensis* and *Au. afarensis* as part of an evolutionary trajectory involving a more heavily masticated diet with an increased reliance on hard, brittle items may need to be reconsidered. However, fallback foods that were consumed during relatively short, albeit critical periods may have exerted sufficient selective pressure to explain the evolution of the comparatively robust trophic apparatus of this lineage.

Keywords *Australopithecus afarensis* • *Australopithecus anamensis* • Molar microwear • Diet • Geochronology • Paleoecology • Kanapoi • Allia Bay • Laetolil Beds • Woranso-Mille • Hadar Formation

Introduction

Because diet is central to a species' ecology and behavior, it is understandable that considerable effort has gone into elucidating the dietary proclivities of our extinct hominin relatives. Dental microwear preserves non-genetic signals related to an individual's diet, and there is a demonstrable relationship between occlusal wear fabrics and/or textures and the properties of food items that are consumed (Walker et al. 1978; Scott et al. 2005). As a result, occlusal

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microwear is capable of distinguishing among broad dietary categories when there are correspondent differences in the fracture properties of their constituent items (Teaford and Walker 1984; Teaford 1985, 1986, 1988a; Daegling and Grine 1999). Further, microwear fabrics can be used to identify sometimes subtle differences and short-term (e.g., seasonal) variations in diet (Teaford and Oyen 1989; Teaford and Robinson 1989; Teaford and Glander 1991, 1996).

Notwithstanding the well-known constraints of microwear, such as those relating to the so-called "Last Supper Effect" (Grine 1986), and the potential for taphonomic artifacts to pose problems (Teaford 1988b; King et al. 1999), it can provide important information relating to the diets of extinct individuals because it holds evidence of the physical properties of those items consumed (Teaford and Walker 1984; Grine 1986; Ungar 2002; El-Zaatari et al. 2005; Scott et al. 2005; Grine et al. 2006a, b; Schubert et al. 2006). Thus, one important question that microwear has the potential to address is that of changes in a species' diet over time or in response to different environmental or ecological conditions.

A number of hominin taxa are evident from deposits in Africa that span the Late Miocene to Middle Pliocene, a period that witnessed both global climatic and significant regional environmental change (Shackelton 1995; Cerling et al. 1997; Denton 1999; Foley 1999). Discussions of these taxa often invoke scenarios of adaptive morphological response to changing environments (Ward et al. 1999, 2001; Teaford and Ungar 2000; Walker 2002; Haile-Selassie et al. 2004; Macho et al. 2005). Environmentally mediated dietary adaptation has been central to arguments pertaining to hypothetical ancestor–descendant relationships in presumptive hominin lineages, and in particular between *Ardipithecus ramidus* and *Australopithecus anamensis* (Ward et al. 1999; White 2002; Haile-Selassie et al. 2004) and between *Au. anamensis* and *Australopithecus afarensis* (Kimbel et al. 2006; Haile-Selassie 2010; Haile-Selassie et al. 2010; Ward et al. 2010).

Just as an ancestor–descendant relationship between *Ar. ramidus* and *Au. anamensis* has been surmised (Ward et al. 1999; White 2002; Haile-Selassie et al. 2004), so too it has been hypothesized that *Au. anamensis* was the direct phyletic ancestor of *Au. afarensis* (Kimbel et al. 2006; Haile-Selassie 2010; Haile-Selassie et al. 2010; Ward et al. 2010). While both purported relationships are conjectural, the latter is at least consistent with the results of numerical cladistic studies that have postulated *Au. anamensis* to be the sister taxon to *Au. afarensis* and all subsequent hominins (Strait et al. 1997; Kimbel et al. 2004; Strait and Grine 2004). Although no cladistic analysis to date has identified these two species as members of a unique clade, at the very least, *Au. anamensis* does not possess any known autapomorphies that would preclude it as a potential ancestor for *Au. afarensis*.

In their description of *Au. anamensis*, Leakey et al. (1995) noted similarities between the specimens from Kanapoi and those from Laetoli—especially between the Kanapoi (KNM-KP 29283) and Laetoli (Garusi 1) maxillae—noting that while *Au. anamensis* can be "readily distinguished" from the younger Hadar sample, it has "closer affinities" with the older Laetoli fossils. Support for this proposed phyletic relationship has been presented by Ward et al. (2010) and Haile-Selassie et al. (2010) in the form of dental morphology of new Kanapoi specimens and of temporally intermediate fossils from Woranso-Mille. Indeed, in an echo of Wolpoff's (1999) argument that the Kanapoi and Allia Bay fossils simply extend the geochronological range of *Au. afarensis* Haile-Selassie et al. (2010; Haile-Selassie 2010) have taken the mandibular premolar morphology as evidence that *Au. afarensis* and *Au. anamensis* "do not appear to represent distinct taxa." On the other hand, Ward et al. (2010) identify *Au. anamensis* "not just as a more primitive version of *Au. afarensis*, but as a dynamic member of an evolving lineage leading to *Au. afarensis*."

Ward et al. (2010) also conjectured that in the presumptive *Au. anamensis*-*Au. afarensis* lineage, "significant changes appear to occur particularly in the anterior dentition, but also in jaw structure and molar form, suggesting selection for altered diet and/or food processing." In particular, they observe that dietary change involving anterior dental use is suggested by the less intense wear to the incisors and canines relative to the molars in *Au. afarensis*. Moreover, it has been suggested that *Au. anamensis* was possibly the first hominin to have been adapted to the harder foods that would have accompanied the Pliocene expansion of drier, more open habitats (Ward et al. 1999, 2001; Teaford and Ungar 2000; Walker 2002; Macho et al. 2005). *Australopithecus afarensis* is held to have had an "enhanced masticatory apparatus" compared to earlier hominins (White et al. 2000, p. 66), with "nuts, seeds and hard fruits [possibly having] been an important component" of its diet (Wood and Richmond 2000, p. 29). Indeed, it has even been surmised that *Au. anamensis* and *Au. afarensis* represent "the initial functional steps that would eventually culminate in the far more derived, specialized masticatory apparatus of later hominid species, particularly *Au. boisei*" (White et al. 2000, p. 65).

Molar microwear in *Au. anamensis* and *Au. afarensis* has been examined individually by us (Grine et al. 2006a, b) and their microwear textures also have been documented (Ungar et al. 2010). However, no analysis has been undertaken of possible temporal- or habitat-related changes in wear fabrics in the sense that these two taxa may represent a

Table 14.1 *Australopithecus anamensis* and *Au. afarensis* specimens preserving occlusal microwear included in this study

Site/formation	Specimen	Jaw	Molar
Hadar Formation	A.L. 128-23	Mandible	M1
	A.L. 145-35	Mandible	M2
	A.L. 188-1	Mandible	M2
	A.L. 200-1	Maxilla	M1
	A.L. 225-8	Mandible	M3
	A.L. 288-1	Mandible	M1
	A.L. 333-74	Mandible	M1
	A.L. 333w-1	Mandible	M2
	A.L. 333w-12	Mandible	M1
	A.L. 333w-57	Mandible	M2
	A.L. 333w-59	Mandible	M3
	A.L. 333w-60	Mandible	M2
	A.L. 366-1	Mandible	M3
	A.L. 400-1	Mandible	M2
	A.L. 486-1	Maxilla	M1
	A.L. 487-1	Mandible	M3
Laetolil Beds	LH 4	Mandible	M2
	LH 15	Mandible	M3 1
	LH 8/22	Maxilla	M1
Allia Bay	KNM-ER 35236	Maxilla	M2
Kanapoi	KNM-KP 29287	Mandible	M1
	KNM-KP 34725	Mandible	M1

Table 14.2 Geochronological ages (ranks) and paleoecological categories of *Au. anamensis* and *Au. afarensis* specimens that preserve occlusal microwear

Specimen	Age (Ma)	Paleohabitat category
A.L. 288-1 A.L. 487-1	3.18	Wet/dry grassland
A.L. 188-1 A.L. 333-74 A.L. 333w-1 A.L. 333w-12 A.L. 333w-57 A.L. 333w-59 A.L. 333w-60 A.L. 366-1 A.L. 486-1	3.20	Dry grassland
A.L. 400-1	3.30	Woodland
A.L. 128-23 A.L. 145-35 A.L. 225-8	3.35	Forest
A.L. 200-1	3.37	Wet grassland
LH 15	3.41	Wooded grassland
LH 8/22	3.51	Wooded grassland
LH 4	3.58	Wooded grassland
KNM-ER 35236	3.95	Wooded grassland
KNM-KP 29287	4.07	Wooded grassland
KNM-KP 34725	4.12	Wooded grassland

phyletic lineage. In light of the evidence that has been espoused in support of an ancestor–descendant relationship between *Au. anamensis* and *Au. afarensis*, we here examine molar microwear to determine whether there is evidence for postulated dietary change through time in this purported lineage.

Materials and Methods

The hypodigms of *Au. anamensis* and *Au. afarensis* have been reviewed by Grine et al. (2006a, b). Specimens of the former that preserve microwear signatures are known from Kanapoi and Allia Bay, Kenya; fossils of the latter that exhibit microwear have been recovered from the Laetolil Beds, Tanzania, and the Hadar Formation, Ethiopia (Table 14.1). These specimens can be partitioned into eleven temporal categories on the basis of their stratigraphic relationships to radiometrically dated horizons (Table 14.2).

Paleoenvironmental reconstructions have been proffered for all localities from which the molars that preserve microwear derive. Depending upon the information available, these reconstructions are usually rather broad, and sometimes conflicting, but most envision a mosaic of habitats associated with at least seasonally well-watered, fluvial or lacustrine environments (Grine et al. 2006a, b). Nevertheless, following Grine et al. (2006a), it is possible to categorize them into one of six rather broad categories on the basis of floral cover and/or composition (Table 14.2).

The occlusal microwear data employed here are those recorded by Grine et al. (2006a, b). All measurements were taken from scanning electron micrographs using Microware 4.02 (Ungar 1995), with independent digitization and subsequent averaging to reduce measurement error (Grine et al. 2002). Data pertaining to six variables were collected for each image: feature number, percentage incidence of pitting (with pits being defined as features with a length to breadth ratio $\leq$4:1), striation breadth, striation vector (a measure of directional dependence, or striation anisotropy), pit breadth, and pit length.

The statistical analyses focused on assessing molar microwear variation within the *Au. anamensis* - *Au. afarensis* sample relative to time and paleohabitat. Three microwear variables—pit percentage, striation breadth, and pit breadth—have been shown to be especially useful for distinguishing among living species with different diets (Walker and Teaford 1989; Rafferty et al. 2002; El-Zaatari et al. 2005). These variables were therefore compared against geochronological and paleoecological ranks using the non-parametric Spearman's rho and Kendall's Tau statistics.

Results

The microwear data obtained for the individual fossil hominin specimens are recorded in Table 14.3. The statistics pertaining to these variables for the two species samples, and the combined lineage sample are provided in Table 14.4.

Comparison of these data by temporal rank (Table 14.5) reveals that time per se is not correlated with any microwear variable. This is perhaps to be expected, since there is no distinct trend for environments to change through time in a consistent manner towards either more closed or open conditions. Thus, for example, Spearman's rho (−0.494; p = 0.38) and Kendall's Tau (−0.317; p = 0.37) statistics reveal no correlation between the ecological and temporal ranks employed here. There is, of course, no reason to expect time *per se* to impact microwear in the absence of sustained directional change in environmental conditions unless one postulates an alteration in dietary habits without concomitant change in the ecological setting.

With the exception of striation breadth, microwear features show no correlation with paleoecological rank (Table 14.5). This is evident when the Laetoli specimens are treated as individuals from three temporal horizons and the two Kanapoi specimens as individuals from two temporal horizons with wooded grassland habitats (Table 14.5; 11 temporal ranks). It also holds if the values for the three Lateoli specimens are averaged, and the values for the two Kanapoi are averaged, thus yielding eight temporal ranks so

Table 14.3 Microwear variables recorded for *Au. anamensis* and *Au. afarensis* specimens

Specimen	Feature number	Pit breadth (μm)		Striation breadth (μm)		Pitting (%)
		Mean	SD	Mean	SD	
A.L. 128-23	168	2.48	1.63	0.94	0.87	17.7
A.L. 145-35	237	2.03	1.01	0.91	0.54	22.5
A.L. 188-1	175	2.06	0.84	1.12	0.82	42.0
A.L. 200-1	110	3.90	2.60	1.59	1.09	22.9
A.L. 225-8	109	4.20	2.20	1.45	1.09	25.3
A.L. 288-1	127	2.57	1.71	1.33	0.81	35.4
A.L. 333-74	109	3.74	1.73	1.83	1.43	41.3
A.L. 333w-1	317	2.38	1.08	1.15	0.71	27.3
A.L. 333w-12	256	2.75	1.35	1.19	0.69	28.4
A.L. 333w-57	104	3.06	1.49	1.28	0.67	14.6
A.L. 333w-59	297	2.44	1.12	1.16	0.61	34.2
A.L. 333w-60	247	2.42	1.34	1.11	0.49	31.4
AL 366-1	69	3.13	1.50	1.08	0.50	41.2
AL 400-1	120	2.77	1.58	1.15	0.74	45.1
AL 486-1	84	3.85	2.37	1.69	1.43	37.4
AL 487-1	83	3.90	2.54	1.41	0.95	25.9
LH 4	111	3.05	1.92	1.57	1.02	19.6
LH 15	113	4.43	3.32	1.27	0.74	29.3
LH 8/22	89	2.75	1.25	1.26	0.82	23.3
KNM-ER 35236	133	2.81	1.27	1.27	0.40	40.0
KNM-KP 29287	186	2.78	1.80	1.13	0.70	31.9
KNM-KP 34725	184	3.74	3.10	1.21	0.95	35.9

Table 14.4 *Australopithecus anamensis* and *Au. afarensis* sample averages for occlusal microwear variables

	n	Pit breadth (μm)		Striation breadth (μm)		Pitting (%)	
		Mean	SD	Mean	SD	Mean	SD
Au. afarensis	19	2.99	0.71	1.26	0.24	29.23	8.90
Au. anamensis	3	3.11	2.21	1.20	0.79	35.93	4.05
Lineage sample	22	3.06	0.71	1.28	0.23	30.57	8.61

Table 14.5 Tests for correlation of microwear variables with temporal and paleoecological ranks

	Spearman's rho	p-value	Kendall's Tau	p-value
Temporal rank (11 ranks)				
Pit breadth	0.0364	0.915	0.1018	0.938
Striation breadth	0.2414	0.474	0.2202	0.346
Pitting incidence	−0.0636	0.852	−0.0545	0.815
Paleoecological rank (with 11 temporal ranks)				
Pit breadth	−0.3123	0.350	−0.2130	0.361
Striation breadth	−0.7452	0.009	−0.6025	0.010
Pitting incidence	−0.0099	0.977	0.0007	0.995
Paleoecological rank (with 8 temporal ranks)				
Pit breadth	−0.2684	0.520	−0.1889	0.513
Striation breadth	−0.7486	0.033	−0.6158	0.033
Pitting incidence	0.0243	0.954	0.0377	0.896

as to eliminate the preponderance of wooded bushland habitats in the comparisons. This is a surprising finding, since habitat is expected to impact the types and availability of different plant foods.

There is a tendency for microwear striae to be somewhat narrower in individuals that derive from more closed environments. Thus, four of the six samples from wooded grassland environments and both samples from woodland and forested environments tend to evince narrower wear striations than those from wet and dry grasslands.

Representative occlusal microwear fabrics of *Au. anamensis* and *Au. afarensis* as imaged by high-magnification SEM are illustrated in Fig. 14.1. As noted above, microwear pitting incidence and scratch breadth tend to distinguish among extant primates that have different diets and/or consume items with different physical properties different dietary. These two variables in *Au. anamensis* and *Au. afarensis* are compared with homologous data recorded for extant primate taxa in Fig. 14.2. Not only are the *Au. afarensis* sample means for striation breadth and pitting incidence almost identical to those of *Gorilla beringei*, their ranges also overlap extensively. The *Au. anamensis* microwear signature is wholly encompassed by that of *Au. afarensis*, and it too overlaps that of *Gorilla*. Significantly, the microwear signatures of hard object feeders such as *Lophocebus albigena* (the grey-cheeked mangabey) and *Cebus apella* (the brown capuchin) are clearly differentiated from *Au. anamensis* and *Au. afarensis*.

Suwa et al. (2009) reported that their examination of microwear on eight molars from Hadar confirm the results of Grine et al. (2006a) for *Au. afarensis* with regard to the absence of distinct pitting.

Rather than the expected trend towards the consumption of harder objects in *Au. anamensis* and *Au. afarensis*, it appears that these individuals tended to eat foods that produced microwear fabrics closer to those ingested by mountain gorillas than by extant hard object consumers.

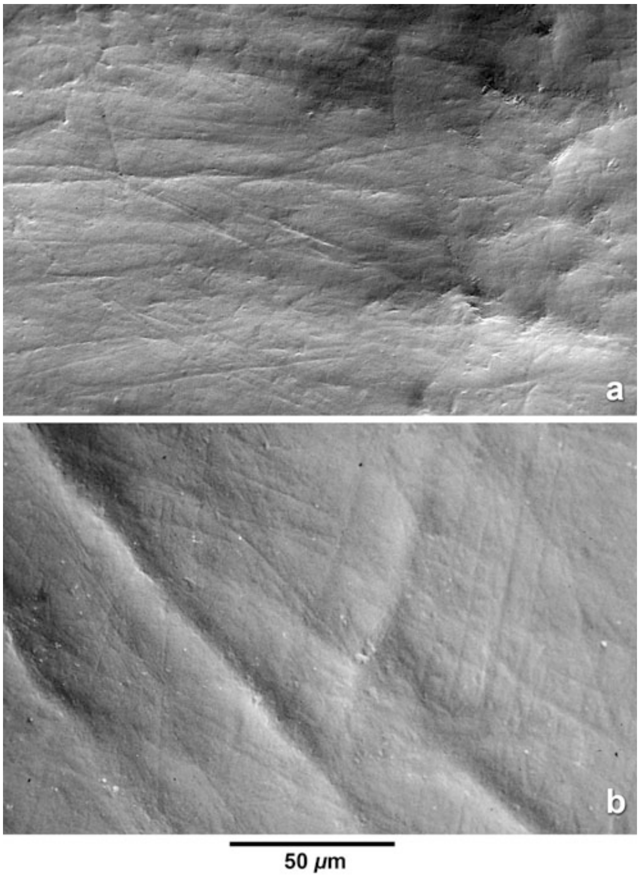


Fig. 14.1 Scanning electron micrographs of occlusal microwear preserved on *Australopithecus anamensis* (**a**) and *Australopithecus afarensis* (**b**) molars from Kanapoi (KNM-KP 29287) and Hadar (AL 200-1a) respectively. Note the similarity in the wear fabrics, which are dominated by heterogeneously orientated, rather fine scratches and small pits

Examination of microwear textures in *Au. anamensis* and *Au. afarensis* by confocal microscopy has yielded concordant results (Ungar et al. 2010). In particular, the wear textures of

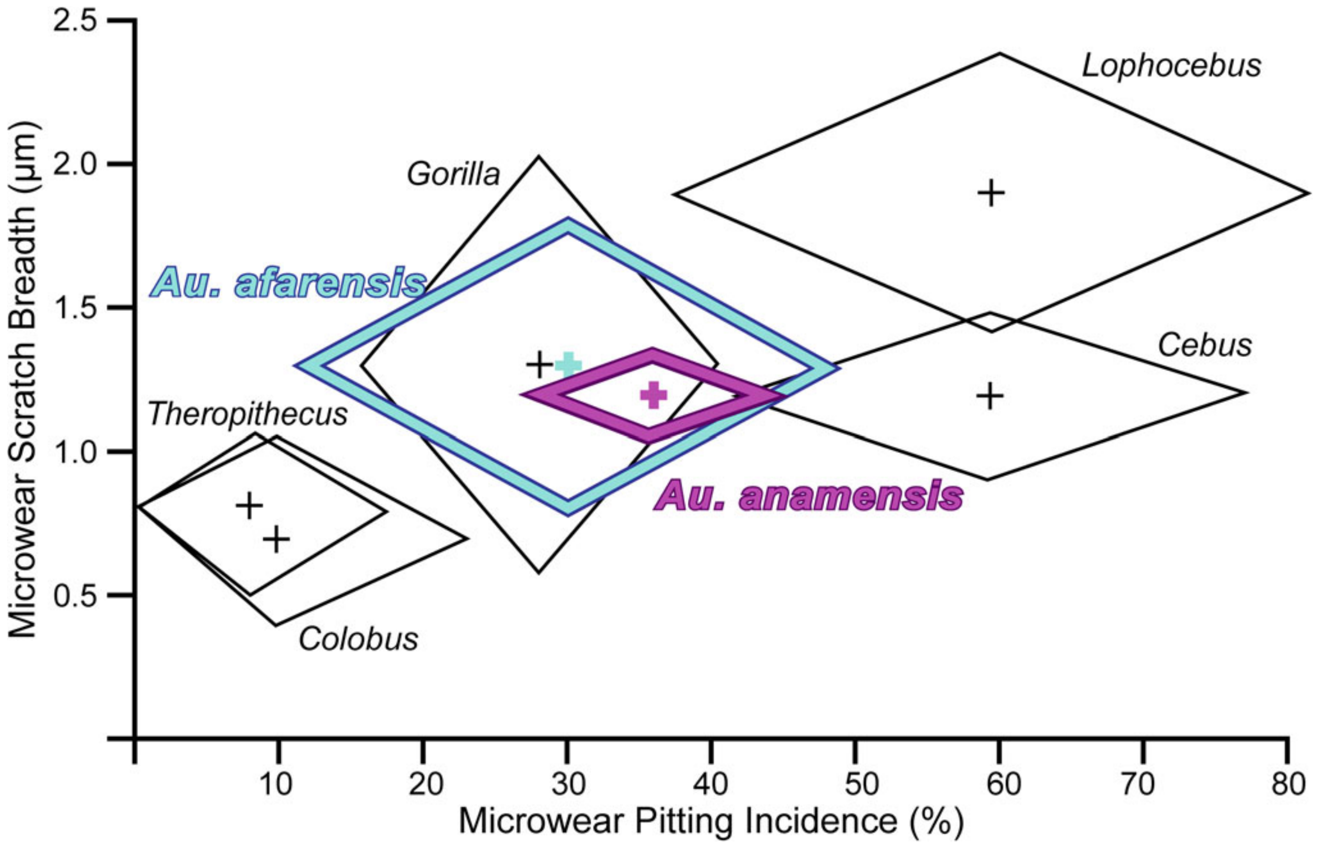


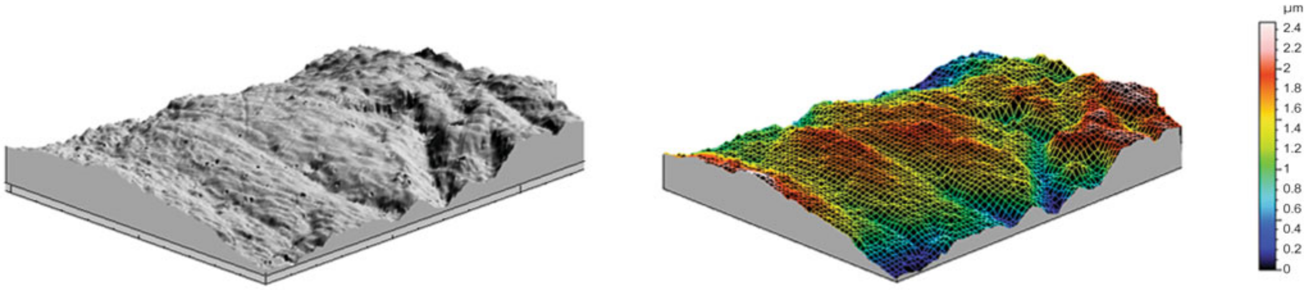
Fig. 14.2 Comparison of species means and "fiducial" envelopes for microwear scratch breadth and pitting incidence for *Au. anamensis*, *Au. afarensis* and several extant primate species. Sample means are indicated by crosses; the diamonds represent ±2 SD of the means for these variables. Note that *Gorilla* and *Pan* occupy an intermediate position between *Lophocebus* and *Cebus* on one hand, and *Theropithecus* and *Colobus* on the other. The sample statistics upon which this figure is based are provided in Grine et al. (2006a, Table 7)

these two species samples cannot be differentiated from one another (Fig. 14.3). However, Ungar et al. (2010) considered the gelada baboon rather than the mountain gorilla as the closest extant primate analogue for the wear textures exhibited by the fossils (Fig. 14.4). Whether or not the 22 specimens of *Au. anamensis* and *Au. afarensis* that preserve microwear suggest *Gorilla* or *Theropithecus* as the best modern analogue for dietary preference, the point of importance is that there is no microwear evidence for the mastication of hard, brittle items such as those found in the diets of taxa such as *L. albigena* and *C. apella*.

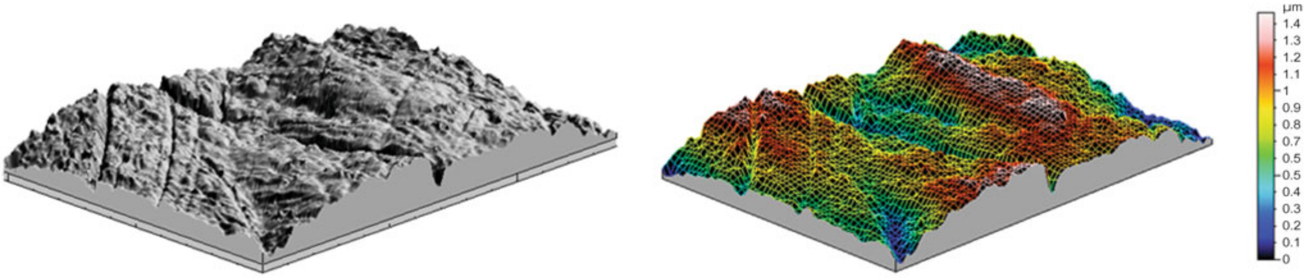
Discussion

The microwear fabrics and textures exhibited by specimens of *Au. anamensis* and *Au. afarensis* are very similar to each other. Microwear variables that are sensitive to dietary differences in extant mammals do not appear to vary in terms of the temporal scale or paleoenvironmental changes associated with this presumptive lineage.

The only possible exception pertains to wear striation breadth, which shows a marginally significant association with habitat, whereby striae tend to be somewhat narrower in individuals that derive from more closed environments. However, given the small sample sizes, this observation should be considered tentative at best. If it does hold, it might indicate the relative importance of exogenous grit in the formation of microwear in some environments (Teaford and Glander 1991, 1996; Ungar 1994; Ungar et al. 1995; Daegling and Grine1999; Nysrom et al. 2004). In this case, more closed habitats might be expected to have smaller particles of exogenous grit assuming the potential for larger wind-borne abrasives in more open environments. At the same time, however, more well-watered areas (e.g., closed settings) tend to have more small soil particles (i.e., more clays) in their A horizons than more open settings (Jury and Horton 2004), and the phytoliths of monocots and dicots tend to differ substantially in size (Piperno 2006). This could then implicate the types of food eaten or grit, since topsoils in vegetated areas often have large quantities of phytoliths.



Australopithecus anamensis



Australopithecus afarensis

Fig. 14.3 Comparison of representative microwear textures of *Au. anamensis* (KNM-KP 29287) and *Au. afarensis* (AL 333w-60). The 3D axiomatic representations each reflect a projected surface of 102 µm × 139 µm. Images on the *left* are photosimulations based on point clouds with 0.18 µm spacing, and those on the *right* depict elevations by *color* as indicated in the scales

Significantly, the microwear fabrics and textures of *Au. anamensis* and *Au. afarensis* are clearly distinguishable from those of extant primates (e.g., *L. albigena* and *C. apella*) that consume hard foods, but they overlap extensively those of *G. beringei* and *T. gelada*. Given expectations to the contrary, it is perhaps surprising that the occlusal microwear data recorded here suggest that the mountain gorilla and/or gelada baboon constitutes perhaps the best modern analogues for dietary preference in *Au. anamensis* and *Au. afarensis*. Indeed, if there is any change between species averages—an observation that is vitiated by the small sample for *Au. anamensis*—it suggests a shift from a pattern closer to that of *Pan troglodytes* in *Au. anamensis* to that closer to *G. beringei* in *Au. afarensis*.

Australopithecus anamensis and *Au. afarensis* undoubtedly possessed a trophic apparatus capable of processing a wide range of foods (Ward et al. 1999, 2001; Teaford and Ungar 2000; White et al. 2000; Wood and Richmond 2000; Walker 2002; White 2002; Haile-Selassie et al. 2004; Macho et al. 2005), including hard, brittle items. However, their molar microwear fabrics suggest that they didn't always do so, even in the face of different habitats (or, at least those individuals we have been able to sample do not appear to have done so during the periods in which their microwear fabrics were being formed). As observed by Grine et al. (2006a) and Kimbel and Delezene (2009), the consistency of dental microwear in *Au. afarensis* molars across time and space may mean either that this species was able to track its preferred dietary resources in the face of alterations in habitat and environment, or that environmentally induced shifts in diet did not involve changes in the mechanical properties or abrasiveness of the foods typically consumed.

The ability to track preferred foods such as fleshy fruits in very different habitats has been documented for chimpanzees (Moore 1996; Sponheimer et al. 2006). That individuals of extinct hominin taxa may have tracked preferred food sources in the face of altered habitats would be consistent with Sussman's (1987) notion of "species-specific dietary adaptations," where members of a species that inhabit different environments eat foods with similar fracture properties as availability permits.

Current paleoclimatic evidence indicates that the Late Miocene-Early Pliocene witnessed an increase in the *amplitude* of climatic variation (deMenocal and Bloemendal 1995; deMenocal 2004). Potts (1998a, b) has argued that adaptive conditions were "highly inconsistent" on both the global and local scale during this time, and that hominin evolution is, therefore, best understood in terms of adaptation through selection by this climatic variability.

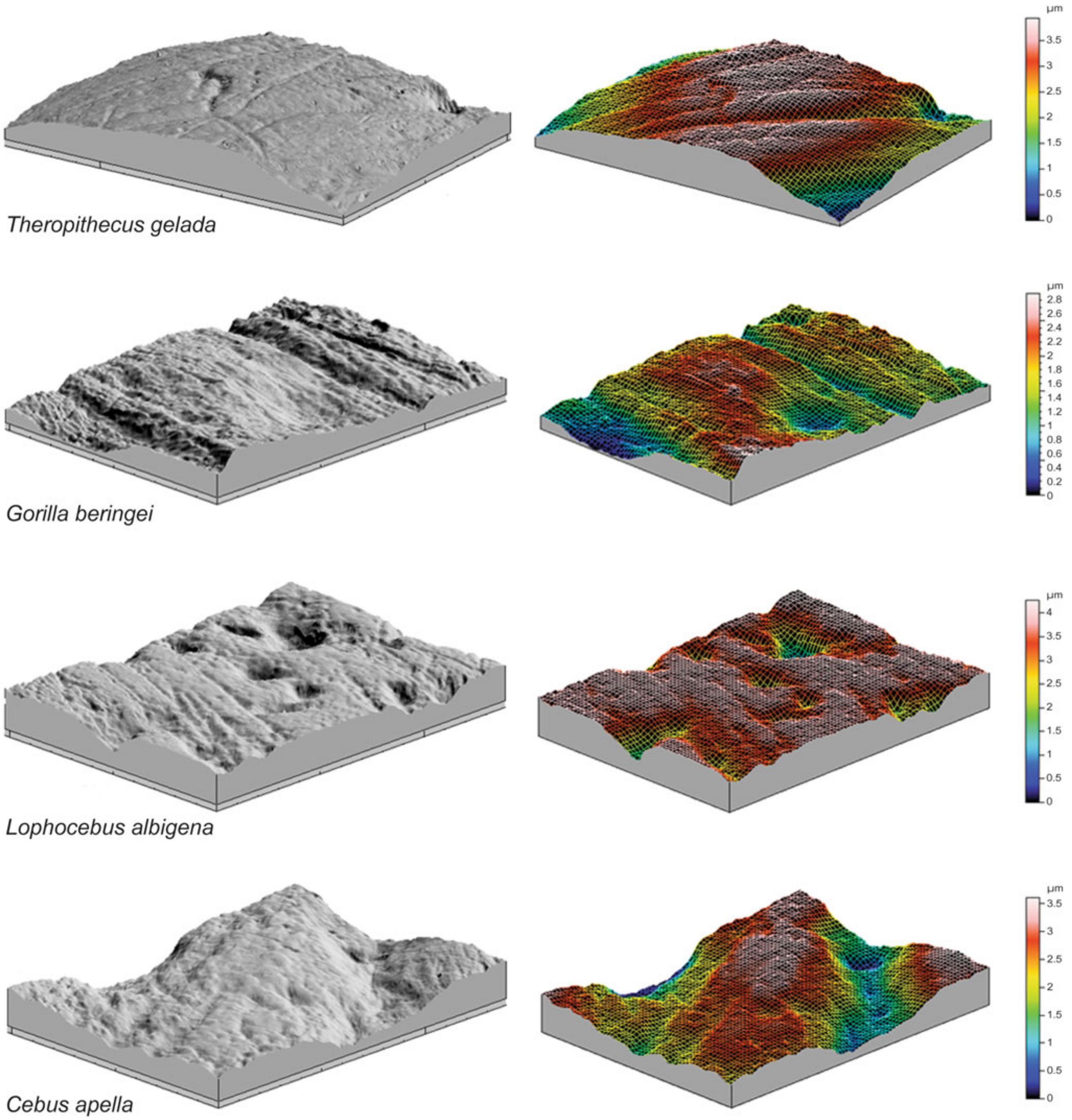


Fig. 14.4 Microwear texture fabrics of *Theropithecus gelada*, *G. beringei*, *L. albigena* and *C. apella*. The 3D axiomatic representations each reflect a projected surface of 102 µm × 139 µm. Images on the left are photosimulations based on point clouds with 0.18 µm spacing, and those on the right depict elevations by *color* as indicated in the scales

It is possible that hypogeous tubers, bulbs and roots, such as ingested by an eclectic and opportunistic feeder like the chacma baboon, may have constituted part of the dietary repertoire of these fossil species, especially as potential fall-back foods in times of seasonally mitigated stress (Teaford and Ungar 2000; Laden and Wrangham 2005). While the range of mechanical properties for such foods could be quite large (Dominy et al. 2008), some could indeed be characterized as either hard and brittle, or soft and tough. Indeed, differences in the mechanical properties of fallback foods may represent a significant selective factor in the differentiation of trophic morphologies (e.g., enamel thickness) of sympatric cercopithecines such as *Cercopithecus ascanius* and *L. albigena* (Lambert et al. 2004).

Thus, just as living primates have been observed to rely on less-preferred "fallback" foods during periods of seasonal stress, it is possible that individuals of *Au. anamensis* and *Au. afarensis* might also have consumed hard, brittle items seasonally (Picq 1990; Teaford and Ungar 2000; Ungar and Teaford 2001; Ungar 2004). If that were the case, it may simply be an artifact of inadequate sampling that few (if any) of the individuals examined by us were sampled from such conditions. Thus, with 22 individuals sampled over a temporal span of c. 940 kyr (i.e., sampling an individual on average every 42,700 years) it is possible that we would not have sampled many (if any) from periods of seasonal stress. Such an explanation would at least be consistent with the dentognathic morphologies of these species.

From another perspective, if the microwear data suggest dietary similarity in *Au. anamensis*, *Au. afarensis* and *G. beringei*, does this necessarily imply that these early hominins subsisted on a diet of tough or ductile items (such as leaves and stems) that are difficult to fracture? Morphological attributes of their dentitions would seem to suggest otherwise. Specifically, *Au. anamensis* and *Au. afarensis* molars exhibit comparatively little occlusal relief (Ungar 2004). It is therefore doubtful that they could have processed foods similar to those eaten by gorillas with the same efficacy. Thus, it is improbable that the diets of *Au. anamensis* and *Au. afarensis* were the same as that of the mountain gorilla, despite the similarities of their microwear signatures. The same might be concluded with regard to their texture similarities with *T. gelada*.

Considered together, the morphology and microwear of *Au. anamensis* and *Au. afarensis* molars suggest that these species likely ate less mechanically challenging, weaker foods that were abrasive but required little effort to chew. It is perhaps significant that this pattern appears to have remained little changed in this presumed lineage, especially in view of the arguments that have been proffered to explain the evolutionary "trajectory" involving their dentognathic morphologies.

Just as dietary stenotopy almost certainly has been overemphasized as an explanation for the morphological peculiarities of *Paranthropus* (Wood and Strait 2004), so too would it appear that explanatory scenarios describing *Au. anamensis* and *Au. afarensis* as part of an evolutionary trajectory involving a more heavily masticated diet of hard, brittle items need to be reconsidered.

The most productive approach to the elucidation of paleodiet is through the consilience of genetic (morphological) information and non-genetic (microwear and stable light isotope chemistry) data. While a given microwear pattern or isotopic signature may be associated with more than one diet, trophic morphology may effectively limit the range of foods that can be processed efficiently. Such an integrated approach—linking microwear, isotopic and ecomorphological evidence—has been applied in an elegant analysis of fossil bovids from the South African Pliocene site of Makapansgat (Schubert et al. 2006). We believe that the time has come for such an approach be taken with the Pliocene hominin fossil record.

Conclusions

Trophic features of *Au. anamensis* and *Au. afarensis*, such as thickly enameled molars and relatively robust mandibles, have been widely perceived as having evolved to effectively process the generally harder food items that would have accompanied the expansion of drier, more open habitats in the Pliocene (Ward et al. 1999, 2001; Teaford and Ungar 2000; Walker 2002; Haile-Selassie et al. 2004). A number of workers have argued that *Au. anamensis* underwent a dietary shift to harder foods than were eaten by its presumptive ancestor (Ward et al. 1999, 2001; Teaford and Ungar 2000; Walker 2002; Macho et al. 2005). *Australopithecus anamensis* and *Au. afarensis* have been argued to constitute a lineage that displays further enhancement of these morphological adaptations (White et al. 2000).

With the possible exception of striation breadth, microwear variables that are sensitive to dietary differences in extant mammals show no correlation with either temporal or palaeoenvironmental changes associated with the presumptive *Au. anamensis* - *Au. afarensis* lineage. Striation breadth displays a marginally significant association with habitat, perhaps attesting to the importance of exogenous grit in the formation of microwear in some environments. Given expectations to the contrary, it is surprising that the occlusal microwear data suggest that gorillas (especially *G. beringei*) or gelada baboons constitute perhaps the best modern analogue for dietary preference in *Au. anamensis* and *Au. afarensis*. Most importantly, the microwear patterns in both fossil hominin taxa differ notably from those exhibited by living primates (e.g., *C. apella* and *L. albigena*) that consume hard objects.

While these fossil hominins may have had the trophic capability to process a fairly wide range of foods, including the hard, brittle items such as might be expected in the sorts of environments that they inhabited, those few individuals we have been able to sample do not appear to have masticated these sorts of items during the formation of their microwear.

The wear pattern exhibited by *Au. anamensis* is entirely encompassed by the that which defines *Au. afarensis*. Thus, while explanatory scenarios describing *Au. anamensis* as part of an evolutionary trajectory that includes *Au. afarensis* may ultimately be correct, the linkage of that trajectory to a more heavily masticated diet of hard, brittle items may need to be reconsidered. The most productive approach to the elucidation of paleodiet is through the integration of genetic (morphological) and non-genetic (microwear and isotope chemistry) information. The time has come for such an approach be taken with these particular hominin fossils.

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Chapter 15
Some Ruminations on Australopith Diets

Matt Sponheimer

Abstract There are few data regarding hominin diets prior to 3.6 Ma, and thus we have only vague notions about the role of diet in early human evolution. We do know that the australopith masticatory package (e.g., robust mandibles, thick enamel, megadont molars) is evident in an incipient state over 4 Ma, and that these features are consistent with a diet of hard and/or abrasive foods. Nonetheless, recent studies found great similarities in the dental microwear of *Australopithecus afarensis* and extant African apes, especially the gorilla, and no evidence for the consumption of hard foods. This may indicate that these hominins consumed diets qualitatively similar to those of gorillas and chimpanzees during much of the year, but then utilized harder and/or more abrasive fallback foods when preferred resources (probably fleshy fruits) were scarce (the "fallback hypothesis"). We might speculate by analogy that the earliest East African hominins had large home ranges when in savanna woodlands much like extant chimpanzees, as such environments make it necessary to range widely to obtain sufficient preferred "forest" resources. South African australopiths, in contrast, more regularly consumed significant quantities of hard foods and C_4 resources which would have enabled them to utilize savanna woodlands more efficiently. This might have led to reduced home ranges and increased population densities, which might have redounded to their locomotor adaptations. However, the idea that australopith diets largely differed from those of extant African apes in their fallback foods has significant weaknesses, and recent studies suggest the possibility that extant ape and East African australopith diets differed profoundly. Thus, formulation of competitors to the fallback hypothesis is warranted.

Keywords *Australopithecus* • Carbon isotopes • Diet • Fallback hypothesis • *Paranthropus*

Introduction

The topic of early hominin diets is a thorny one. The ever-increasing evidence of early hominin taxonomic diversity (e.g., White et al. 1994; Leakey et al. 1995; Senut et al. 2001; Brunet et al. 2002) together with the burgeoning evidence of marked ecological distinctions between and within some hominin taxa (e.g., WoldeGabriel et al. 1994; Scott et al. 2005; Grine et al. 2006a; Levin et al. 2008; Reed 2008) underscore the likelihood that there is no simple and singular answer to the question "What did early hominins eat?" An even greater limitation is the simple lack of data available on hominin diets. There is virtually no direct (non-genetic) evidence of early hominin diets prior to 3.6 Ma, with the exception of dental microwear data for three molar teeth of *Australopithecus anamensis* (Grine et al. 2006b), which while important, are far from definitive. Thus, the first half of the probable hominin fossil record remains largely uninterrogated from a dietary standpoint. Another nettling problem is that currently available paleodietary tools have specific strengths and weaknesses, and actually address slightly different questions about diet (Grine et al. 2006a; Schubert et al. 2006; Sponheimer et al. 2007). As a result, if we are to meaningfully investigate hominin dietary behavior, we must do so using a number of complementary techniques. Yet, to date only two Pliocene and Early Pleistocene taxa have been reasonably well-studied using multiple independent techniques: *Australopithecus africanus* and *Paranthropus robustus* (e.g., Robinson 1954; Kay 1985; Lucas et al. 1985; Grine and Kay 1988; Sillen 1992; Lee-Thorp et al. 1994; Sponheimer and Lee-Thorp 1999, 2006; Scott et al. 2005).

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Nevertheless, I still feel that we know a fair bit about early hominin diets, and that our understanding will accrue rapidly in the coming years. In this paper I will present a partial review and synthesis of current data regarding the diets of Pliocene and Early Pleistocene hominins (excluding *Homo*), with a particular focus on research that has emerged in the past 15 years. I will also spend some time on recent and novel ideas, such as the primacy of fallback foods in engendering hominin dentognathic adaptations (Ungar 2004; Grine et al. 2006), and discuss the degree to which they are supported by various datasets. I will also move a bit beyond the data and speculate about the potential sequelae of our dietary reconstructions.

A Stroll Through Some Previous Research

Australopithecus

The australopiths differ from extant apes in both their locomotor and dietary adaptations (Fleagle 1998). Of particular significance here is the overall masticatory package that appears to emerge with *A. anamensis* (and possibly earlier) and reaches fruition with *Paranthropus boisei*, including the bony buttressing of the face, robust mandibles, thick enamel, and relatively large and flat teeth (e.g., Leakey 1959; Ward et al. 1999; Teaford et al. 2002; White et al. 2006). These features have generally been associated with the increased consumption of hard and/or abrasive foods (e.g., nuts, seeds, roots) as necessitated by a broad transition towards drier and more seasonal landscapes (Ward et al. 1999; Teaford et al. 2002; Macho et al. 2005; White et al. 2006). Despite this, non-genetic data, such as provided by dental microwear and stable carbon isotopic analyses, have not always readily distinguished australopiths from extant African apes. For example, early dental microwear studies of *A. africanus* molars demonstrated it had a very similar pitting percentage to that of chimpanzees, suggesting that it had a diet dominated by fleshy fruits and leaves (Grine 1986; Grine and Kay 1988). More recently, Grine et al. (2006, 2013) showed that the molar microwear patterns in *A. afarensis* fell entirely within the range of extant African apes, most especially eastern gorillas (*Gorilla gorilla beringei*). Particularly salient was the lack of variability in the *A. afarensis* sample, which is akin to what has been observed in extant hominoids, but in marked contrast to the South African australopith datasets (Scott et al. 2005). This suggests that, like chimpanzees, it did not change its diet from place to place, but rather focused narrowly on favored foods regardless of the environment (McGrew et al. 1988; Wrangham 2005; Schoeninger et al. 1999; Sponheimer et al. 2006a). Perhaps like chimpanzees, *A. afarensis* was an interloper in savanna woodland environments (see Reed 1998, on its habitat diversity), ignoring the vast majority of the edible vegetation in favor of ancestral "forest" resources? We will return to this conjecture a bit later in the paper.

In contrast, much evidence has accumulated over the last decade that *A. africanus* had a diet that differed quite significantly from those of extant apes. Stable carbon isotope analysis has shown this taxon to consume nearly 40 % C_4-based resources (these include the aboveground (e.g., seeds) or belowground (e.g., roots) parts of tropical grasses and some sedges) on average (Sponheimer and Lee-Thorp 1999; van der Merwe et al. 2003; Sponheimer et al. 2005) (Fig. 15.1). Equally important, the range of δ^{13}C values for *A. africanus* is so great that it nearly encompasses the range of *Papio* and *Theropithecus* (baboons with fundamentally different diets) combined (Lee-Thorp et al. 1994; Sponheimer et al. 2005). By comparison, chimpanzees are not known to consume any significant quantities of C_4 vegetation even in savanna environments, and show almost no carbon isotopic variability therein (Schoeninger et al. 1999; Sponheimer et al. 2006a). Overall, this might paint a picture of a hominin that probably preferred ripe fruits as do modern chimpanzees, but that also began to incorporate more hard and brittle foods (perhaps hard fruits, nuts, and/or underground storage organs) into its diet on at least a seasonal basis, and quite possibly more regularly (Ungar 2004; Laden and Wrangham 2005; Grine et al. 2006). I would further propose that while *A. africanus* and *Pan* might both have succeeded individually in any given savanna woodland habitat, they would have utilized the available resources very differently. I imagine that *A. africanus* would readily out-compete extant chimpanzees in such environments, as it would utilize a broad variety of resources ready to hand (including C_4-based resources and/or hard, brittle items), while *Pan* would have to increase its home range considerably to provide sufficient quantities of preferred "forest" foods, as it does in savanna environments today (McGrew et al. 1981; Moore 1996). This would further suggest increased population densities for *A. africanus* compared to hominids with more chimp-like dietary adaptations (that would presumably have much lower population densities and much larger day and home ranges), as well as a possible relaxation of selection pressure for an energetically-efficient gait.

Paranthropus

This genus has generally been characterized as a dietary specialist (see Wood and Strait 2004). Just what it specialized on has been the subject of considerable debate, but

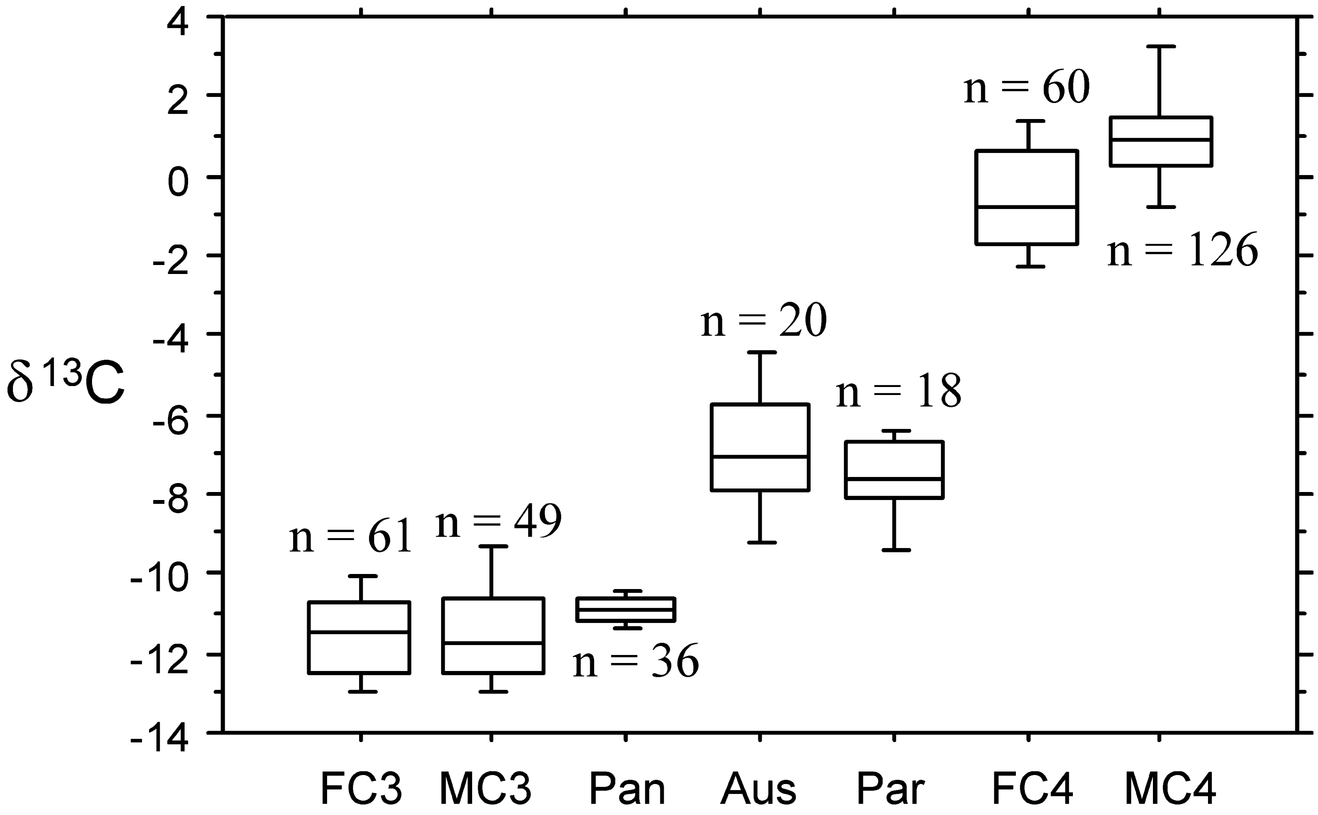

Fig. 15.1 δ^{13}C values of modern chimpanzees (Pan), *Australopithecus africanus* (Aus), and *Paranthropus robustus* (Par) juxtaposed with those of modern and fossil consumers of C_3 (MC3, FC3) and C_4 vegetation (MC4, FC4) in savanna environments. Note chimpanzee δ^{13}C values are consistent with nearly pure C_3 diets, even though many of the chimpanzee samples were from areas where C_4 resources abound. In contrast, most australopith δ^{13}C values are consistent with the consumption of various degrees of C_4 vegetation. The modern data have been adjusted to compensate for the fossil fuel effect (see Sponheimer et al. 2006a)

the focus has been on plant foods such as seeds (Jolly 1970), underground storage organs (Hatley and Kappelman 1980), or hard fruits (Kay 1985). Early dental microwear studies of this taxon were broadly consistent with a frugivorous diet (Walker 1981), albeit one rich in hard foods such as those consumed by some *Lophocebus* populations today (Grine and Kay 1988). Stable carbon isotope data are consistent with *P. robustus* being principally frugivorous, but also suggest that such a diet was supplemented with about 30 % C_4 foods on average (Lee-Thorp et al. 1994; Sponheimer et al. 2005) (Fig. 15.1). However, laser ablation was used to examine stable isotope ratios along the growth axes of *P. robustus'* teeth, and it demonstrated that while some C_4 foods were consumed year round, others were consumed largely seasonally or over interannual periods (Sponheimer et al. 2006b) (Fig. 15.2). Likewise, a new dental microwear study found greater variability in surface microwear complexity in *P. robustus* than in *A. africanus,* or presumably, *A. afarensis* (Scott et al. 2005)—thus, most recent evidence suggests *P. robustus* did not stick to its dietary last, but rather changed its diet (both in terms of mechanical properties and stable isotope compositions) as necessitated by prevailing conditions. Thus, both South African australopiths may have had very different diets, both in terms of composition and variability, than *A. afarensis.*

Intriguingly, however, new dental microwear and stable isotope data look quite different for the East African robusts. Ungar et al. (2008) found that seven *P. boisei* molars were dominated by fine striations and completely lacked the large pits that characterize the molar microwear of hard-object feeders such as *Cebus apella*. Moreover, surface fractal complexity (which tends to increase as does the consumption of hard foods) was shown to be lower in *P. boisei* than in either *P. robustus* or *A. africanus*, and similar to what is found in extant African apes. Nutcracker indeed! And importantly, there was very little variability in the *P. boisei* surface fractal complexity, whereas the variability in the *P. robustus* microwear was one of its most telling features. This was a completely unexpected result, and runs counter to most of our thinking about the diet of this taxon since its discovery in 1959 (Leakey 1959).

And more surprises continue to emerge with regard to the diet of this enigmatic taxon. Of particular note, van der Merwe et al. (2008) have reported the results from stable

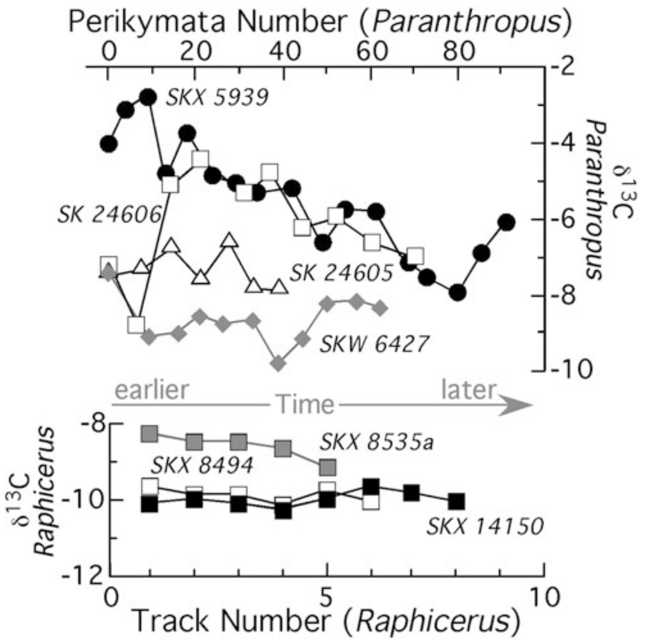

Fig. 15.2 δ^{13}C values for (**a**) *P. robustus* and (**b**) *Raphicerus* sp. obtained via laser ablation isotope ratio mass spectrometry (Sponheimer et al. 2006b). The δ^{13}C values of *Paranthropus* are highly variable, while there is little evidence for dietary change in the teeth of browsing steenbok

isotopic analyses of two *P. boisei* specimens, and shown them to have nearly identical stable isotope compositions indicating diets of up to 80 % C_4 foods (Fig. 15.3). This result is also inconsistent with much of what has been written about the diet of *P. boisei* over the last 50 years, with the notable exception of Jolly's (1970) seed-eating hypothesis. To put this in the proper perspective, note that the published mean δ^{13}C value for *P. boisei* (−0.9 ‰) is higher (more C_4) than the mean of seven published specimens of fossil *Theropithecus*, the grass eating baboon (−2.4 ‰) (Codron et al. 2005b; Fourie et al. 2008). Thus, these results are consistent with *P. boisei* having an adaptation for the consumption of C_4 grasses, C_4 sedges such as *Cyperus papyrus*, or some combination of these foods. Concomitantly, they are not consistent with these individuals having consumed more than 20–30 % fleshy fruits or nuts during crown formation. In short, these results are virtually irreconcilable with the idea of these individuals having eaten diets broadly similar to those of African apes.

Why the Australopith Masticatory Complex?

The overall masticatory package, including the large, thickly enameled molars and robust mandibular corpora, of australopiths appears to emphasize the importance of harder and/or more abrasive foods in their diets than are regularly consumed by extant African apes (Kay 1985; Grine 1986; Ward et al. 1999; White et al. 2006). This makes a great deal of sense given what is known about the evolution of African landscapes during the Pliocene (e.g., Vrba 1985; Cerling 1992; deMenocal 1995; Reed 1997; Feakins et al. 2005; Bobe 2006); it is also consistent with the dental microwear and isotopic records for the South African australopiths. Yet, if this is the case, why is there no evidence for the consumption of such foods in the dental microwear of *A. afarensis*, *A. anamensis*, or *P. boisei* (Grine et al. 2006a, b; Ungar et al. 2008)? One clue is most clearly evident in the data for the later australopith *P. robustus*. As discussed previously, both dental microwear and stable carbon isotope data suggest periods over which the diet of *P. robustus* differed in its mechanical properties and stable isotope composition from that of extant apes, yet also are consistent with the idea that its diet could have overlapped with that of *Pan* or *Gorilla* much of the time (Scott et al. 2005; Sponheimer et al. 2006a,b). One interpretation of these data holds that *P. robustus* and chimpanzee diets differed chiefly in their fallback foods, and that the dentognathic adaptations of the australopiths are for fallback, rather than preferred and/or predominant dietary resources (Ungar 2004; Laden and Wrangham 2005; Scott et al. 2005; Grine et al. 2006a, b; Ungar et al. 2008).

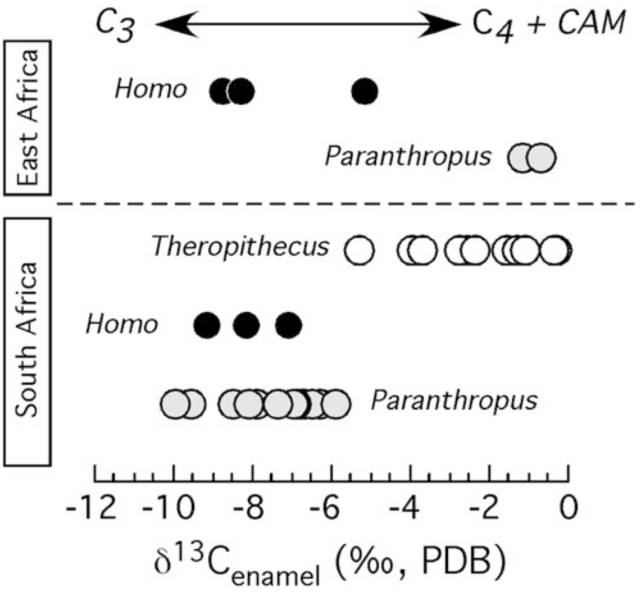

Fig. 15.3 δ^{13}C values of *Homo*, *Paranthropus*, and *Theropithecus* tooth enamel in South Africa and East Africa. Note the similarity in *Paranthropus* and *Homo* δ^{13}C values in South Africa, as well as their dissimilarity to the δ^{13}C values of the grass-eating baboon *Theropithecus*. In contrast, the East African data show a strong separation of *Homo* and *Paranthropus*, with the latter having higher δ^{13}C values than most specimens of *Theropithecus*, suggesting a diet of perhaps 70–80 % C_4 foods. The data are from Codron et al. (2005b), Sponheimer et al. (2005), Fourie et al. (2008), and van der Merwe et al. (2008)

This rather *outré* idea is solidly grounded in the broader ecological literature. Liem's paradox, which notes that animals often eat foods other than those for which they are specialized, speaks to this very issue (Robinson and Wilson 1998), and is in many ways unsurprising. For during times of plenty, one might consume abundant resources that prove little challenge to ones masticatory complex (such as ripe fleshy fruits); but during times of scarcity, one might be forced to consume less favored resources that are more challenging to the dentition (such as nuts and seeds). This phenomenon has been noted frequently in the primatological literature. For instance, Yamashita (1998) averred that the dental morphology of lemur species better indicates the hardest foods eaten than those consumed most frequently, and Lambert et al. (2004) found that despite large differences in the enamel thickness of *Lophocebus albigena* and *Cercopithecus ascanius*, their diets only differed in hardness during times of fruit scarcity. This is also evident in African apes, for when chimpanzees and gorillas are sympatric, they both tend to prefer fruits over herbaceous vegetation (Tutin and Fernandez 1985; Stanford and Nkurunungi 2003). During periods of scarcity, however, gorillas become much more reliant on terrestrial herbaceous vegetation, and this is reflected in the greater occlusal relief of their molars. Hence, it might be argued that differences in the dentition of gorillas and chimpanzees are largely a function of their fallback foods, and not a function of their preferred or even typical diets (Ungar 2004).

Thus, the idea that australopith mandibular robusticity, enamel thickness, and megadontia speak to changes in hominin fallback foods, has plenty of primatological backing. This is not to say, however, that the idea is without problems. To my mind, the most intractable of these is why did dental microwear reveal no evidence for the consumption of hard foods in any of the 29 East African australopith teeth analyzed (Grine et al. 2006a; Ungar et al. 2008)? *Praeanthropus*, *A. anamensis*, and *P. boisei* are all clearly megadont and possess a number of features consistent with the consumption of hard foods (McHenry and Coffing 2000; Teaford et al. 2002), but if they switched to harder and more brittle fallback foods than those consumed by extant African apes, why don't we see it? Of course, since the consumption of fallback foods is not a typical behavior it might not be readily observed. Yet, this has not stopped dental microwear from picking up such potentially atypical dietary behavior in a smaller sample of South African australopiths. Could this mean that the fallback foods of the East African taxa became increasingly incorporated into the diets of their southern counterparts, which were to some extent, perpetually falling back—and thus the enhanced visibility with dental microwear in the South? Given the temperature differences and unimodal rainfall patterns that would have greeted hominins as they forayed southward, and which probably led to longer lean periods, this idea is plausible. But ultimately, I do not find this or similar arguments overly compelling as they lack empirical validation at present. Hypothetically, it could also be argued that because dental microwear preserves dietary information about the period immediately preceding death (Grine 1986), and since the primate literature abounds with studies showing mortality to be very high during resource stress (Cheney et al. 1981; Hamilton 1985; Milton 1990; Gould et al. 1999; Richard et al. 2002; Nakagawa et al. 2003; Hanya et al. 2004; and see Young 1994, for mammal die-offs and nutritional stress), one might expect fallback foods to be at least marginally over-represented in the dental microwear record. But direct evidence for the consumption of fallback foods is completely lacking among the East African australopiths. Of course, this does not mean that the fallback hypothesis is incorrect, but it does suggest that some attempt at an alternate explanation for the masticatory package of many, if not all australopiths, is warranted. I will return to this topic at the conclusion of the paper.

Earlier Hominins

Given the preceding discussion of Pliocene to Early Pleistocene australopiths, can we surmise much about the diets of their Late Miocene and Early Pliocene antecedents? Perhaps the way to begin addressing this question is to briefly note what we know about the environments of these earliest potential hominins, as their habitats potentially constrain their dietaries. In recent years, much has been made of the abundance of woodland-loving taxa in association with the earliest potential hominins (e.g., WoldeGabriel et al. 1994; White et al. 2006). And while one might certainly argue the habitat preference or tolerance of any given fossil species (e.g., were the monkeys associated with *Ardipithecus ramidus* true forest forms?), there can be little question that the earliest hominins were not in treeless grassy plains as has sometimes been envisioned. Yet, I am also struck by the consistent appearance of taxa that might have been grazers and/or found in wooded grasslands associated with the earliest reputed hominins, such as the many hypsodont bovids associated with *Sahelanthropus tchadensis* (Vignaud et al. 2002), or the *Eurygnathohippus*, *Nyanzochoerus*, *Uranomys*, and *Tatera* associated with *Ar. ramidus*, to name only a few of many (WoldeGabriel et al. 1994; Louchart et al. 2009; White et al. 2009). Various datasets indicate that *Ardipithecus* was found in woodlands (Louchart et al. 2009; White et al. 2009; WoldeGabriel et al. 2009). However, the data are less directly informative about *Ardipithecus* habitat tolerances. For instance, while *Ardipithecus* is not reported from SAG-VP-1 + 3, the same could be said for nearly all woodland and grassland taxa. The carbon isotope data for *Ar. ramidus* do suggest that it consumed predominantly C_3 vegetation, even if it forayed into fairly open areas, much like the modern chimpanzee (White et al. 2009). Furthermore, carbon isotope compositions of herbivores associated with *Ardipithecus* at Gona are not what one expects in forest or even closed woodlands, and at face value would seem to indicate more open habitats than those experienced by *A. africanus* in South Africa (Levin et al. 2008; Sponheimer and Lee-Thorp 1999). This is not to say that Late Miocene and Early Pliocene hominins were inhabiting open environments, but only that the tendency of many to postulate "forested" environments for these hominins is a bit of a stretch. Certainly there is evidence for a habitat mosaic at most sites. Of course, we cannot yet tell where the hominins actually resided within such multifaceted landscapes. Did they stay close to the trees? Were they ecotone taxa, utilizing resources from both the closed and open portions of their habitats? Consequently, I feel that our current understanding of earliest hominin environments is insufficient to provide meaningful dietary constraints.

Fortunately, the microwear of *A. afarensis* and *A. anamensis* allows us to generate a few reasonable hypotheses about the diets, and even habitat preferences, of earlier hominins. In the past, it would have seemed reasonable to argue that the australopith dentognathic morphology indicated a continuing adaptation to hard/abrasive foods, at least some of which were based upon the C_4 photosynthetic pathway, such as grass roots and seeds or the underground storage organs of some sedges. This scenario would have been consistent with a variety of ecomorphological, dental microwear, and biogeochemical studies (e.g., Hatley and Kappelman 1980; Kay 1985; Grine 1986; Scott et al. 2005; Sponheimer and Lee-Thorp 2006). However, the fact that the earliest hominins studied to date show little dental microwear variability (so far as surface complexity goes) and do not fall outside the range of extant apes (Grine et al. 2006a, b), could indicate that they did not consume significant quantities of "savanna," or more properly, "non-forest" resources. Thus, *A. afarensis* and *A. anamensis* might not have utilized savanna woodland environments much more efficiently than do modern chimpanzees, making it even less likely that earlier taxa could do so.

Thus, one could reasonably argue that prior to 3 Ma hominins had not made an ecological leap that enabled them to utilize resources in the more open portions of the landscapes they inhabited. The recently published carbon isotope data for *Ardipithecus* point towards a chimpanzee-like reliance on C_3 foods (White et al. 2009). And like chimpanzees, they might have greatly increased their home ranges and decreased their population densities as preferred wooded habitats became increasingly fragmented and preferred "forest" resources became scarce (McGrew et al. 1981; Moore 1996). In contrast, the later southern australopiths, with their ability to process local savanna resources, might not have increased their home ranges, or decreased their population densities to the same extent in the face of environmental change. One might also surmise, as I did earlier, that selection for energetic-efficiency during travel might have been relaxed for the South African australopiths, even if they inhabited more open environments than their predecessors.

Admittedly, this is all rather speculative perforce as we have little direct evidence of the diets or ranging patterns of hominins prior to about 4 Ma. Yet, I think much follows naturally from an interpretation of the dental microwear that holds that *A. afarensis* and *A. anamensis* had diets similar to one or both extant African apes, except perhaps to some extent in fallback foods. Of course, if there were a reasonable alternative interpretation of the microwear data, much of the preceding edifice of speculation would fall.

Wild Surmises and Closing Thoughts

As discussed above, there is an apparent disjunction between the stories told by the craniodental morphology and dental microwear of the East African australopiths. The idea that this morphology is in fact an adaptation for hard/abrasive foods, but that such foods were only consumed sporadically, does a nice job solving this apparent discord. As discussed above, however, there are weaknesses in this explanation, most notably the complete lack of evidence for the consumption of these fallback foods in 29 specimens when their consumption might be expected to be relatively frequent near death. One way around this problem would be to invoke an extreme version of the fallback hypothesis wherein the fallback foods were not even consumed by some generations of australopiths, but only by those that experienced climatic extremes that induced tremendous selection pressure (and which left their indelible stamp on future generations). If this were the case, one might not expect to find traces of the consumption of hard fallback foods at all. Another possible solution could be that fossil preservation preferentially occurred during "times of plenty" when australopiths would have consumed preferred foods (Ungar et al. 2008), although there is no evidence that this is the case.

However, alternative explanations for the apparent disagreement between the morphological and microwear signals are certainly possible. And in fact, as the carbon isotope data for *P. boisei* have been further substantiated, another explanation is likely required (Cerling et al. 2011). Since *P. boisei* had a C_4 diet like that of *Theropithecus*, then it almost certainly indicates that it had a diet dominated by either grass products (e.g., seeds) and/or sedge products (e.g., underground storage organs). Given this, would it not follow that since *P. boisei* is the quintessence of the australopith masticatory package, that the package itself is an adaptation for such foods? In other words, is it possible that we have been misreading the morphology, or that the morphology is consistent with more than one type of dietary specialization, including one requiring a great deal of repetitive loading (as in Hylander 1988)?

Dental microwear studies might not support a grass-based diet for *P. boisei* and its close kin, as the microwear of grass-specialist *Theropithecus gelada* has even fewer pits and is even more dominated by scratches than the East African hominins (Teaford 1992; Daegling and Grine 1999). And *Papio*, which consumes grass and underground foods to some extent, has microwear that is highly-pitted and very different from that of the East African australapiths (although similar in some ways to that of *P. robustus*) (Daegling and Grine 1999). Intriguingly, however, the dental microwear pitting percentage of *T. brumpti* (Teaford 1992; Daegling and Grine 1999) is virtually identical to that of *A. afarensis* and *A. anamensis* (Grine et al. 2006a, b). But since *T. brumpti* is believed to have been more frugivorous than the extant gelada (Benefit and McCrossin 1990; Teaford 1992), this still does not support a grass-based diet. Nevertheless, I would be hesitant to remove grass products from the *P. boisei* dietary on these grounds alone, and eagerly await the results of ongoing comparative studies of *Theropithecus* microwear (Scott et al. 2009).

But what about sedges? Sedges were certainly abundant in many East African australopith habitats (e.g., Hay 1976; Bonnefille et al. 2004) and several researchers have suggested that they may have been important australopith foods (Hatley and Kappelman 1980; Verhaegen and Puech 2000; Conklin-Brittain et al. 2002; Wrangham 2005; van der Merwe et al. 2008). Unfortunately, dental microwear texture analysis has not been carried out on sedge consumers, so this hypothesis is not directly testable using microwear at present. Nevertheless, a crude study of the wear on *A. afarensis* cheek teeth led Verhaegen and Puech (2000) to conclude that these hominins often ate such aquatic plants. One potential blow to the sedge specialization hypothesis is that in environments roughly analogous to the ancient Sterkfontein Valley, the vast majority of sedges use C_3 photosynthesis, so that even if the South African australopiths ate sedges, they might have needed to eat significant quantities of other C_4 foods as well (Sponheimer et al. 2005).

Another potential food that could have led to the remarkable carbon isotope ratios evident in *P. boisei* is succulent vegetation using CAM photosynthesis such as *Euphorbia* sp. or the wild sisal plant “Oldupaai” (*Sansevieria ehrenbergii*). Although conceptually possible, this is difficult to imagine given the relative dearth of such foods (compared to grasses at least), their suspect nutritional quality, and the significant secondary (i.e., toxic) compound loads they harbor. Baboons eat such CAM plants although they are not preferred and are not consumed in quantities sufficient to produce the *P. boisei* δ^{13}C values (Rhine et al. 1989; Barton et al. 1993; Codron et al. 2005a).

Thus, it would seem we are left with a five-pipe problem, as none of our proposed diets square with all of the known facts. We clearly have much to learn about australopith diets and the functional significance of their distinctive craniodental morphology. Nevertheless, we have made great strides in the last few years, and while the resulting picture may not be clearer—and may be turbid by comparison to the picture a few years ago—it is certainly more accurate. Moreover, there can be little doubt that increased integration of the various paleodietary datasets will yield rich rewards. For instance, a clear priority should be to identify what, if any, “C_4” resource could produce the microwear evident on the East African australopith molars. This should be coupled with data on the distribution and nutritional quality of such resources, and the phylogenetic constraints on morphological adaptation for their consumption, at which point much richer interpretation of the datasets discussed herein will be possible. Of course, as someone whose research interests veer strongly toward the biogeochemical, it can be no surprise that I feel more carbon isotope data are needed for the East African australopiths, both across time and space. If the emergence of the australopith masticatory apparatus is shown to be broadly coincident with a marked increase in the consumption C_4 foods, the implications for our understanding of early hominin ecology, biology, and evolution will be profound and potentially transformative.

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Chapter 16
Postural and Locomotor Adaptations of *Australopithecus* Species

Carol V. Ward

Abstract This paper briefly reviews what is known about locomotor anatomy and behavior of *Australopithecus*. I argue that the evidence most strongly supports the hypothesis that *Australopithecus* species were fully upright, committed terrestrial bipeds that walked with a fundamentally human-like gait despite the fact that not all aspects of their morphology were identical to that of humans. Certainly, they retained some ape-like aspects of their morphology not seen in *Homo*. Whether selection was also acting to retain arboreal traits, and the extent to which they engaged in arboreal behaviors, is more difficult to test rigorously. Even if they did climb trees, it is apparent that selective pressures for doing so well were of considerably weaker than those on traveling bipedally. From what little fossil evidence is available, the various species of *Australopithecus* postcranial adaptations show only minor interspecific variation. Further research into determining the primitive condition on which selection acted to produce earliest hominins, plasticity of the skeleton, and on variation among *Australopithecus* species is needed to obtain a better understanding of the evolution of locomotor and postcranial anatomy in this genus.

Keywords Hominin • Postcranium • Bipedalism • Arboreality • Climbing • *Homo*

Introduction

Because the transition to upright bipedal locomotion appears to be the hallmark of the human lineage, understanding the nature of early hominin bipedality has been a focus of studies of australopith biology. Particularly for the best-known species, *Australopithecus afarensis*, most skeletal elements are known, and the morphology of australopith postcranial elements fairly well understood. Certainly far less is known about some species than others. Even with *A. afarensis* being so well known, however, there are debates over the significance of arboreality in their locomotor repertoires and for their reproductive success and about the kinematics of their gait. On top of this, it is not yet clear whether all species of *Australopithecus* shared a similar pattern of posture and locomotion, or if they varied in locomotor behavior or adaptation.

Here I review what is known about locomotor anatomy and behavior of *Australopithecus*, and consider what this means about their evolutionary history. In doing so, I consider the issues involved in the debate over whether australopiths retained adaptations to arboreality and/or climbed trees, and what sort of locomotor diversity is apparent among *Australopithecus* species. I discuss *Australopithecus afarensis* and in some cases *Australopithecus africanus* as baselines because they are well represented in the fossil record, and then compare the less completely known species to it. My goal is to outline the state of our understanding at the present time, and identify key issues to address with further analysis and when considering new fossil discoveries.

Evidence for Bipedality

There is no doubt that australopiths were bipedal when terrestrial (e.g., Lovejoy et al. 1973; Lovejoy 1975, 1978, 1988; Day and Wickens 1980; White 1980; Latimer 1983,

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1991; Stern and Susman 1983, 1991; Susman et al. 1984; Latimer et al. 1987; Latimer and Lovejoy 1989, 1990a, b; Crompton et al. 1998; Kramer 1999; excellent summaries of the evidence can be found in Aiello and Dean 1990; McHenry 1994; Stern 2000). Furthermore, australopiths can be considered committed bipeds, unlike the earlier *Ardipithecus ramidus* that was at most a facultative biped (Lovejoy 2005b, Lovejoy et al. 2009a, b; White et al. 2009). Not only do australopiths exhibit extensive and pervasive musculoskeletal modifications to accommodate the mechanical, kinetic, and kinematic consequences of habitual bipedality, they relinquished key adaptations for facilitating effective arboreal locomotion. Furthermore, the weight of the data suggests that they walked with a straight-limbed gait most similar to that of modern humans, rather than with bent hips and knees (but see Stern and Susman 1983; Susman et al. 1984; Schmitt et al. 1996, 1999; Stern 1999, 2000), despite some aspects of their morphology that are not fully modern human-like.

The upright posture of *Australopithecus* is evidenced by numerous skeletal indicators. The foramen magnum positioned and oriented anteriorly and the short anterior cranial base (e.g., Dart 1925; Kimbel and Johanson 1984, Kimbel et al. 1994; Kimbel and Delezene 2009). Furthermore, both species for which sufficient vertebral remains are known, *A. afarensis* and *A. africanus,* had sinusoidal vertebral curvatures that were as well developed as those of humans and allow the torso to balance over the hind limbs efficiently and effectively in bipedal posture (Robinson 1972; Ward and Latimer 1991, 2005a, b; Shapiro 1993; Sanders 1998; Whitcome et al. 2007; but see Sarmiento 1998). Most significant is the extensive lumbar posterior curvature, or lordosis, which is largely a consequence of differentially wedged vertebral bodies (Robinson 1972; Shapiro 1993; Sanders 1998; Whitcome et al. 2007; Ward et al. 2012) coupled with the presence of even one more functional lumbar segment than typical for extant humans (Robinson 1972; Rosenman et al. in preparation; but see Haüsler et al. 2002).

The australopith lumbar lordosis is not merely an epigenetic phenomenon such as the mild response seen in bipedally trained macaques (Hirasaki et al. 2004). Vertebral body wedging in *Australopithecus* is more pronounced and extensive in both the thoracic and lumbar regions, unlike in the monkeys in which it is only barely evident. Furthermore, *Australopithecus* lumbar vertebrae also exhibit synapomorphies with humans in the posterior elements that permit lordotic posture, and effectively transfer weight and maintain alignment of the vertebral column at the lumbosacral region. *Australopithecus* had zygapophyses that become mediolaterally more widely spaced towards the caudal end of the column, allowing the facets to imbricate and obtain lordotic posture (Latimer and Ward 1993; Ward and Latimer 2005a, b). Apes and other primates do not exhibit this increase. A sufficient interfacet distance increase is only possible with a relatively wide sacrum and posterior interiliac breadth, features characteristic of *Australopithecus* and *Homo* but not seen to such an extent in other primates (Lovejoy 2005a; Lovejoy et al. 2009a), and that contributes to the unique overall shape of the australopith-human pelvis. The zygapophyeal facet joints become more coronally oriented and larger at the caudal end of the vertebral column to resist anterior displacement of the vertebral column on the inclined sacrum, and provide sufficient articular surface contact area to resist and distribute anteroposteriorly-directed loads at this joint (Ward and Latimer 1991; Latimer and Ward 1993; Shapiro 1993; Sanders 1998; Stern 2000). This configuration is characteristic of all hominin lower lumbar vertebrae.

Further evidence for an upright torso is that australopith ribs were curved posteriorly and thoracic vertebral transverse processes dorsally angled, reflecting invagination of the vertebral column into the rib cage, effectively shifting the erector spinae and particularly iliocostalis muscles further dorsally from the vertebral bodies increasing their leverage for achieving and maintaining upright posture (Jellema et al. 1993; Ward et al. 2012; Haile-Selassie et al. 2010).

A vertical trunk with lumbar lordosis provides for efficient balance over the supporting limbs during bipedal posture, and so would have been positioned over straight lower limbs. These morphologies form a complex that allows energetically efficient balance over a single supporting limb when moving, or over two while standing. This same selective pressure applies to both an upright spine and extended lower limb, so it is difficult to imagine selection on one without the other. Clinically, straight (non-lordotic) spinal postures and anteriorly inclined trunk postures that accompany abnormally reduced lordosis (Saha et al. 2008) are associated with increased hip and knee flexion during gait for balance (e.g., Sarwahi et al. 2002). In the bipedally trained macaques, the trunk is more vertical than in normal monkeys and the limbs are also straighter (Hirasaki et al. 2004). But all monkeys, even the trained ones, have an anteriorly inclined trunk when bipedal, as do bipedal chimpanzees (Jenkins 1972). None of these animals has a fully upright trunk with spinal curvatures as in humans or *Australopithecus*.

Australopithecus and *Homo* ischia are inclined posteriorly, which provides hamstrings leverage in extended limb posture (McHenry 1975), and differ from the long, caudally-directed ischia of apes and *Ardipithecus* (Lovejoy et al. 2009a). Also, the distally flattened femoral condyles reflect habitual loading in extended postures, whereas in apes the condyles are almost uniformly rounded anteroposteriorly (Lovejoy 1975, 2005a, b; Tardieu 1986a, b; Tardieu and Trinkaus 1994). The distal flattening increases chondral contact area during knee extension, and also reflects a human-like extended limb posture (review in Lovejoy 1988). The slightly lower lateral lip of the patellar surface and slightly more rounded lateral femoral condyle in *Australopithecus* as compares to humans appears to be related to body size (Tardieu 1986a).

Australopithecus femora all have a pronounced bicondylar angle at the knee (Robinson 1972; Johanson et al. 1976; Tardieu and Trinkaus 1994; Duren and Ward 1995; Duren 1999) which positions the body's center of gravity over the knee and ankle during single limb support during extended posture only, providing more evidence against bent-knee gait. This angle only develops with the onset of bipedal locomotion, demonstrating that australopiths indeed walked bipedally (Tardieu and Preuschoft 1996; Tardieu and Trinkaus 1994; Shefelbine et al. 2002). Associated with this, the tibia of *Australopithecus* is also vertically oriented, lacking the valgus angle typical of apes and reflecting a knee that is positioned directly over the ankle during bipedal progression (Latimer et al. 1987; Ward et al. 1999).

Not only was the torso oriented vertically, the pelvis displays adaptations for maintaining a level pelvis during the single support phase of gait, with laterally flaring iliac blades. This abductor mechanism is unique to hominoid bipeds, and was clearly developed in *Australopithecus* species (see Lovejoy 1988).

The femoral neck of australopiths was ringed by thin cortical bone and expanded trabecular region, reflecting increased shock-absorption capacity and allowed by the hip abductors that neutralize bending of the neck (Lovejoy 1988, 2005a, b). The proximal and distal tibia both exhibit marked metaphyseal flaring adjacent to the joint surfaces, providing expanded cancellous bone volume for shock absorption during gait (see Lovejoy 1988). The expanded calcaneal tuberosity (Latimer and Lovejoy 1989) provides added cancellous bone area as well.

Computer modeling studies also support the energetic efficiency of straight, not bent, lower limb postures in *Australopithecus* (Crompton et al. 1998; Kramer 1999; Wang et al. 2003; Carey and Crompton 2005; Sellers et al. 2005).

The australopith hallux was adducted, as evidenced by the footprints at Laetoli, Tanzania (Leakey and Hay 1979; White and Suwa 1987). In addition, the first tarsometatarsal joint is distally positioned on the cuneiform. The attachment for the peroneus longus muscle on the calcaneus is large and would prohibit this hallucal adductor in apes from functioning to do the same in australopiths. Also, the proximal articular surface of the first metatarsal is not smooth, and so would not permit rotation at this joint (Latimer and Lovejoy 1990b).

The proximal metatarsals are dorsoplantarly deep and relatively flat, suggesting a lack of dorsiflexion at the tarsometatarsal joints and feet that were relatively stiff as compared with apes (Fig. 16.1) (DeSilva 2009; Ward et al. 2011). The distal ends of the metatarsals are distally and not plantarly oriented, and the proximal articular surfaces on the pedal phalanges are dorsally oriented, reflecting habitual dorsiflexion of toes during bipedal gait (Latimer and Lovejoy 1990a). The metatarsal heads also exhibit the dorsal doming characteristic of hominins and lacking apes that provides expanded articular surface in dorsiflexed postures (Latimer and Lovejoy 1989; DeSilva 2009; Lovejoy et al. 2009a, b; Ward et al. 2011). The presence of a large navicular tuberosity is not necessarily incompatible with the functional interpretations made by any of these morphologies, and so may not an indication of the presence of midtarsal mobility or lack of a longitudinal arch of the foot (but see Harcourt-Smith and Aiello 2004).

Thus, the pervasive adaptations to upright posture clearly indicate long-term directional selection for effective terrestrial bipedal travel. The questions surrounding australopith locomotion, however, are not about bipedality, but about the extent to which they were also at least partly arboreal.

Arboreality and Adaptation

Australopithecus also did not look exactly like *Homo* in its postcranial skeleton (excellent summary in Stern 2000). Some researches argue that *Australopithecus* retained significant adaptations to arboreality and thus was partly arboreal (e.g., Senut 1980; Stern and Susman 1981, 1983, 1991; Feldesman 1982; Jungers 1982, 1991; Jungers and Stern 1983; Schmid 1983; Rose 1984, 1991; Susman et al. 1984; Deloison 1985, 1991, 1992; Tardieu 1986a, b; Susman and Stern 1991; Duncan et al. 1994; Stern 2000), perhaps with a compromised form of bipedal progression stemming from these retained arboreal characters (Susman et al. 1984; Preuschoft and Witte 1991; Rak 1991; Susman and Demes 1994; Cartmill and Schmitt 1996; MacLatchy 1996; Ruff 1998; Schmitt et al. 1999; Stern 1999). Australopiths have higher intermembral and brachial indices, longer more curved fingers and toes, and a longer pisiform (Bush et al. 1982; Stern and Susman 1983; Susman et al. 1984), and perhaps a more cranially oriented glenoid fossa (Alemseged et al. 2006) albeit with a relatively low position of the shoulder (Ohman 1986). These features are likely to represent primitive retentions from what is almost certainly a more arboreal ancestor, and are features that would have made *Australopithecus* a slightly more able climber than *Homo*, though a dramatically less able climber than any ape. The question, then, is if this reduced level of arboreal capability was actively retained by stabilizing selection because this capacity was important for fitness, or if there simply had not been selection to alter it further.

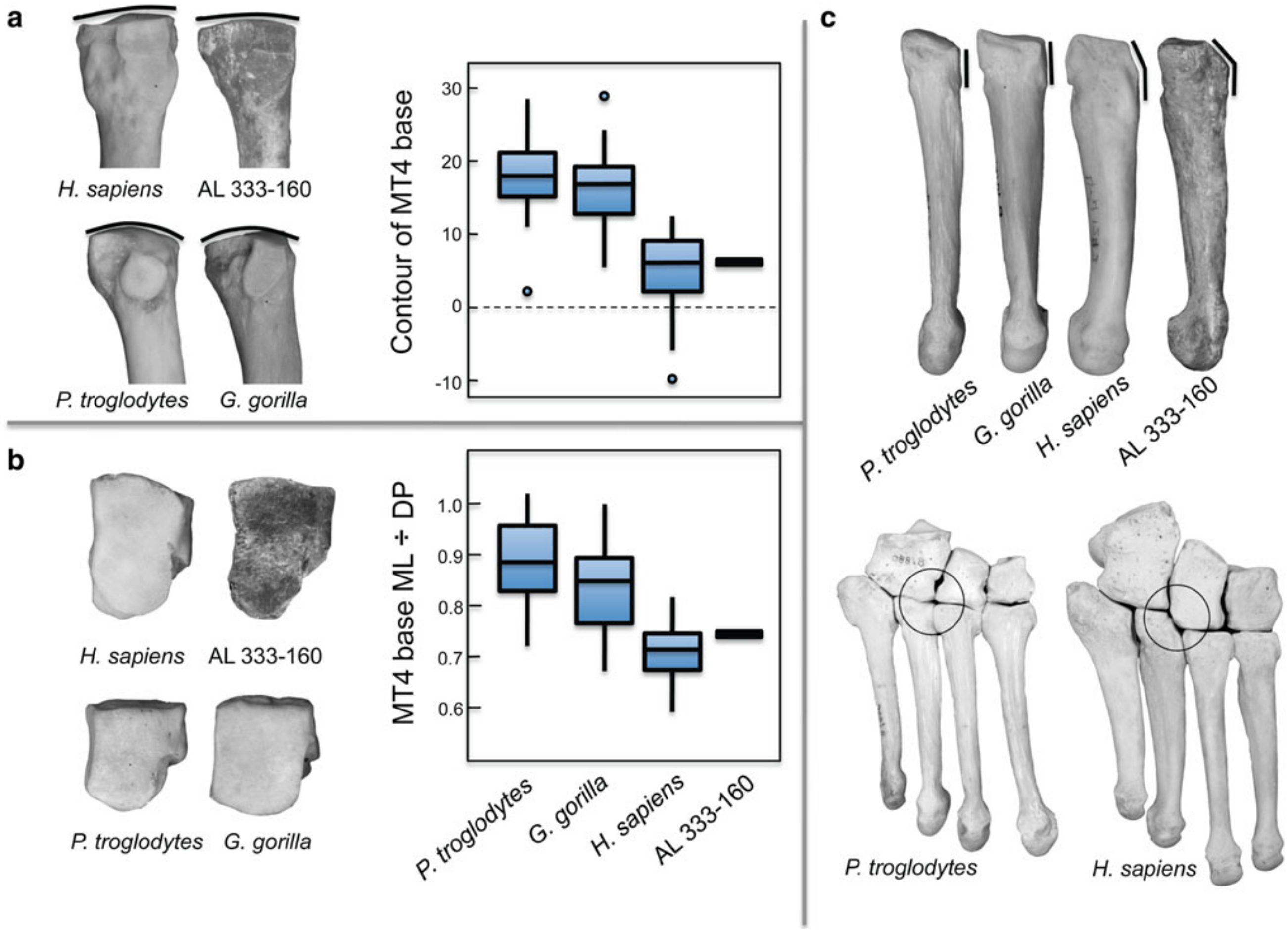

Fig. 16.1 **a** Proximal ends of left fourth metatarsals in medial view, showing the dorsoplantar contour of the distal end. The *box plot* shows measured curvature, measured as maximum distance of the proximal joint surface from a *line drawn* between dorsal and plantar articular margins, expressed as a ratio to dorsoplantar length. Data are from Berillon (2003). All hominins have relatively flat surfaces, rather than the convex profile of apes. **b** Proximal view of left fourth metatarsals, showing the dorsoplantarly expanded articular surface in hominins as compared with apes. The *box plot* of the ratio of dorsoplantar to mediolateral breadth shows the almost square proportion of apes, but the deep shape of the hominins. **c** *Above*, dorsal view of left fourth metatarsals, showing the articular facet for contact with the third metatarsal (*vertical line*) and the oblique articular facet for contact with the ectocuneiform in the hominins. *Below*, dorsal view of articulated cuboid, lateral, and medial cuneiforms and lateral metatarsals, showing the articular configuration of the lateral cuneiform with the third and fourth metatarsals. In apes, the cuneiform is directly medial to the cuboid and does not contact the fourth metatarsal. Both hominins have lateral cuneiform contact and an obliquely oriented facet on the fourth metatarsal for the cuneiform. Reprinted from Ward et al. (2011) with permission from *Science*

If we are interested in which behaviors shaped species, we need to reveal their adaptively significant behaviors. Since natural selection is the only force of evolution capable of producing long-term directional morphological change, derived morphologies are almost always the result of selection on behaviors enhanced by those morphologies (Weishampel 1995). Thus, derived traits are clearly the result of selection for bipedality, but primitive traits could be retained by stabilizing selection for a particular behavior, or simply have been selectively neutral (see also Brooks and McLennon 1991, 1992; Swofford and Maddison 1992). If a retained plesiomorphic trait compromises a derived function, we can infer that stabilizing selection retained it for an alternate function. If not, we are left with the inability to discriminate between the hypotheses that a trait was retained for a reason, or it was selectively neutral.

So while *Australopithecus* may have climbed trees, and indeed were slightly better suited to do so than are modern humans, we cannot be certain that the ability to do so was necessarily shaped by natural selection. Given the loss of characters that would have improved their arboreal abilities, such as a grasping big toe, it appears that even if australopiths spent some time in the trees, their activities there did not necessarily shape their skeletons. Therefore, in terms of reconstructing what behaviors selection acted on to produce their phenotypes, it is imperative to reconstruct what altered the reproductive success of individuals. For example, poorly designed joints would be potentially subject to degenerative or other painful conditions, limiting an individual's ability to be an effective biped and cope with this lifestyle. This would result in selection for improved joint design. In contrast, humans can climb trees to a limited extent as compared with chimpanzees, but selection has not favored individuals who were any better at doing so than are other individual humans. Thus, tree climbing in humans, or *Australopithecus*, is adaptively insignificant, or very minor significance, in terms of understanding morphology, even if climbing at even a limited ability is important for gathering food and/or avoiding predators. The apparent fact that selection drastically reduced arboreal competency in *Australopithecus* argues that even if climbing in the trees was important, it was not as important as being bipedal. They certainly could have climbed trees, and also almost certainly would have done so on occasion or even regularly, but would have not been nearly as good at it as any known living or fossil ape. Because tree climbing was almost certainly inherited from an even more arboreally well-adapted ancestor, it is difficult to ascertain the extent to which the traits that allow limited climbing abilities were still retained to the extent that they compromised any other functions, or whether they were simply just never selected against.

It is clear that bipedality was the adaptively most significant mode of locomotion in australopiths, because not only do they have these numerous apomorphies to allow effective bipedality, australopiths reduced their arboreal efficacy by sacrificing traits such as a high intermembral index, relatively long fingers and toes, and grasping feet as compared with the likely ancestral condition of apes and humans (Latimer and Lovejoy 1989; Latimer 1991; but see Harcourt-Smith and Aiello 2004). Without the ability to hold on well with the feet, it would be difficult to support weight on small branches to reach fruits or cross to other trees, especially when holding onto an infant which females would have had to do since the infants would not have feet that were nearly as effective at grasping as in all other primates. Even though the toes were longer than those of humans (Stern and Susman 1983; Susman et al. 1984), and even if the equivocal evidence for a somewhat more divergent big toe in *A. afarensis* and *A. africanus* did indicate marginally more divergence (Clarke and Tobias 1995; Harcourt-Smith and Aiello 2004), no australopith had nearly the grasping capability of any ape. To sacrifice substantive pedal grasping was to sacrifice ape-like arboreal abilities. So if australopiths did climb trees, they did not do it like living or fossil apes, nor were they nearly as facile in the trees.

It is also possible to ask whether *Australopithecus* individuals actually did climb trees in any substantial extent on a day-to-day basis or throughout their lives. Some features of *Australopithecus* are suggested to be ontogenetically plastic, and so indicate that they actually climbed trees more frequently than do humans, who lack the morphologies. Manual and pedal flexor muscle insertions of *Australopithecus* phalanges are large (Marzke 1983; Stern and Susman 1983; Susman et al. 1984), there appear to be larger sesamoid grooves on the metatarsal heads, and there is a large peroneal groove on the fibula and peroneal trochlea on the calcaneus (Latimer and Lovejoy 1989, 1990b), perhaps indicating strong finger and toe flexor muscles. However, all early hominins were generally more robust than modern humans, so a direct link between these features and arboreality cannot necessarily be made (Ruff et al. 1993, 1999; Coffing 1998). This in itself, however, would have made them more capable climbers even if they had not had any specific adaptations to doing so. The strongest case for ontogenetic evidence of climbing behavior has come from cross-sectional studies correlating general patterns of behavior with phalangeal curvature during ontogeny, and are interpreted to indicate climbing, at least by juvenile australopiths (Paciulli 1995; Richmond 1998, 2007). However, immature Hadar juvenile femoral epiphyseal surfaces resemble those of humans, lacking adaptations for stabilizing the epiphysis during arboreality (Tardieu and Preuschoft 1996; see also Duren 2001). Because plate morphology is developmentally plastic, this suggests that australopiths were not climbing extensively during growth (Tardieu and Preuschoft 1996; see also Duren 2001), and so this would seem to contradict the developmental evidence from the phalanges. More work needs to be done on skeletal plasticity and its relation to behavior to further evaluate potential evidence of specific individual behaviors in the *Australopithecus* skeleton.

Regardless of the amount of climbing *Australopithecus* individuals did, we still cannot be certain about the adaptive significance of climbing trees well, or in a better way than humans are capable of. The amount of time an organism spends engaged in a particular activity is not equivalent to the selective importance of that behavior. In terms of locomotor behaviors, primates spend most of their time sitting or lying down, or even walking slowly, as they groom and feed and rest, but these behaviors are not negatively potentially limited or impacted by their postcranial morphology, and so do not impose such stringent selective pressures as the ability to flee from predators or gather food, for example. What must be considered is not just how common or frequently performed a behavior is, but how morphology would affect or potentially limit or enhance that behavior in ways that would compromise fitness. Therefore, we can discuss whether australopiths climbed trees or not if we are interested in understanding their daily lives, but this is not necessarily the same as considering what they were adapted to do (see Ward 2002). If we could determine that *Australopithecus* species were engaging in frequent arboreal activities, it might hint that those activities were adaptively valuable in terms of reproductive success or not, but only provides hints about whether related morphologies enhanced or limited individual fitness.

At this point, the strongest evidence for retained selection for arboreal competence is probably the retention of some primitive traits for roughly 4 million years, possibly from *Orrorin tugenensis, Ardipithecus kedabba*, and *Sahelanthropus tchadensis* (see recent discussion in Richmond and Jungers 2008) through *Australopithecus*. Certainly, australopiths were not exactly like humans, but instead exhibit morphologies more like those of extant apes that probably represent primitive retentions and have been argued to indicate some continued reliance on arboreal locomotion. They almost certainly would have used trees for foraging, sleeping and/or avoiding predators. However, it does not appear that australopiths would have been as capable climbers as any Miocene ape or likely the last common ancestor of apes and humans, so the vector of morphological change (Simpson 1953; see also Latimer 1991; Weishampel 1995) leading to australopiths was towards anatomy that enhanced terrestrial bipedality and diminished arboreal competence (Latimer 1991). Subsequent postcranial changes seen in *Homo* may have been due to addition of novel behaviors, such as walking long distance, throwing or manipulating objects more proficiently, rather than abandoning the trees.

Variation Among *Australopithecus* Species

Postcranial variation among *Australopithecus* species is difficult to assess because there are relatively few species with many postcranial remains known. Only *A. afarensis* and *A. africanus* are well represented in the fossil record, with a few bones known for *Australopithecus robustus* (Robinson 1972; Susman 1988; see also Oakley et al. 1977), only one poorly preserved partial skeleton for *Australopithecus boisei* (Grausz et al. 1988), and a very small handful of fossils for *A. anamensis* (Leakey et al. 1995, 1998; White et al. 2006). The newly announced *Australopithecus sediba* (Berger et al. 2010; de Ruiter et al. 2013) is known from two partial skeletons and some other bones.

It appears that the general pattern of postcranial morphology exhibited within *Australopithecus* was essentially constant, and taxa vary little from one another (except perhaps in *A. sediba*; see below), although there may have been minor modifications of the basic pattern among these taxa (summaries in Aiello and Dean 1990). Broadly speaking, as far as we can tell so far there was an *Australopithecus* pattern of morphology that characterizes early hominins for over 2 million years and changed appreciably only with the advent of *Homo erectus* around 1.8 Ma.

The earliest *Australopithecus* species identified so far is *A. anamensis* (Leakey et al. 1995, 1998; Ward et al. 1999, 2001). The only postcranial remains described for *A. anamensis* so far are the proximal and distal thirds of a tibia, a distal humerus, a nearly complete radius, a capitate, and partial proximal manual phalanx. In almost all ways, *A. anamensis* postcrania resemble those of *A. afarensis*. The *A. anamensis* tibia displays a diaphysis that is oriented normal to the talocrural joint surface, rather than the varus angle found in apes; an adaptation to bipedal locomotion (Latimer et al. 1987; Ward et al. 1999). The humerus (Patterson and Howells 1967) is indistinguishable from that of *A. afarensis* (Feldesman 1982; Hill and Ward 1988; Lague and Jungers 1996; Ward et al. 2001; contra Senut and Tardieu 1985; Baker et al. 1998) as is the phalanx. The radius is similar morphologically to that of *A. afarensis* but belonged to a forearm that was longer than the longest one preserved for *A. afarensis* (Heinrich et al. 1993). This suggests that the forearms of *A. anamensis* were at least as long as those of *A. afarensis*, and almost assuredly longer for their body size than those of *Homo*. The capitate is poorly preserved, but the second metacarpal facet faced further laterally than in other hominins, and instead is more like that of great apes (Leakey et al. 1998). Thus, it appears that although bipedality may appear to have been established by *A. anamensis* based on the tibia, there may still have been changes over time in their skeletons. Only more fossils will provide an adequate test of this idea.

Australopithecus afarensis and *A. africanus* are similar postcranially in overall morphological pattern, although there are some comparatively minor differences (Häusler 2001; Green et al. 2007, and references therein). When they differ, *A. africanus* has slightly more *Homo*-like morphology than does *A. afarensis* in some features but not others. Although hands of the two species are strikingly similar morphologically, *A. africanus* appears to have more gracile metacarpal shafts and slightly straighter phalanges with less well-developed flexor ridges and presumably less well-developed long digital flexor muscles than does *A. afarensis* (Ricklan 1987). It also appears to have shorter, thicker terminal pollical phalanges, all of which may indicate a lesser reliance on powerful grasping and more on manual dexterity, although more work needs to be done on the significance of apparent differences (Bush et al. 1982; Ward et al. 2012).

The *A. africanus* pelvis appears to have had a slightly more anteroposteriorly expanded inlet with slightly more sagittally-oriented iliac blades and better-developed cranial angles of the sacrum (Schmid 1983; Stern and Susman 1983; Häusler 2001, and references therein; Lovejoy 2005a, b, and references therein). This suggests a different overall shape of the lower torso in the two species, but whether this would represent greater variation than found in a single species has yet to be determined. Häusler (2001) reports an indistinct iliofemoral ligament attachment on the pelvis *A. afarensis* compared with a distinct one in *A. africanus*, but given the prevalence of an intertrochanteric line on the femur in *A. afarensis*, there is no evidence that this ligament was less well developed in *A. afarensis* than *A. africanus*. Häusler (2001) also reports that the latissimus dorsi attachment site on the iliac crest is more medially restricted in *A. africanus* than *A. afarensis*, and suggests that this is more like modern humans, possibly suggesting less powerful upper limbs in the Sterkfontein hominins. However, given that this muscle has almost no bony attachment to the crest in humans, it is difficult to interpret these observations.

There are several other ways in which *Australopithecus africanus* has been interpreted to be more primitive and arboreal than *Australopithecus afarensis*, however. Its limb proportions may well be more ape-like (McHenry and Berger 1998; Green et al. 2007; but see Häusler 2001). These proportions were determined largely by comparing articular sizes and inferring lengths, which if so is suggested to imply more loading of the upper versus lower limb and perhaps a greater reliance on climbing (McHenry and Berger 1998). In addition, Clarke and Tobias (1995) argue that STW 573 had an abductable hallux. Observation of the original specimen reveals that this specimen does not differ in hallucal joint morphology and orientation from *A. afarensis* or from OH 8 (Leakey 1960, 1961), which is attributed to *Homo habilis* (Leakey et al. 1964).

If these taxa represent a single lineage, and *Australopithecus africanus* increased its specialization for arboreality or at least the extent of its arboreal behaviors (regardless of the evidence from the hand), this would be opposite the long-held idea that hominins became progressively more dedicated terrestrial bipeds over time. More work on comparative postcranial morphology is sorely needed to address this question.

The KNM-ER 1500 *Australopithecus boisei* skeleton (Grausz et al. 1988) is poorly preserved; it may have had roughly the same limb proportions as *A. afarensis*, but detailed comparative morphological analysis has not been done. No appreciable differences between *A. robustus* and other *Australopithecus* have been noted in the postcranial skeleton (summary in Aiello and Dean 1990). Postcrania from the Hata Member of the Bouri Formation in Ethiopia cannot be definitively attributed to *A. garhi*, the only hominin identified at the site (Asfaw et al. 1999). However, these fossils display a primitive, *A. afarensis*-like brachial index but with proportionately longer lower limb, suggesting selection for increased lower limb length if this hominin was a descendent of *A. afarensis*.

Australopithecus sediba appears to have had a postcranial skeleton most like that of other australopiths, but its pelvis differs and is described as being more like those attributed to *Homo* with a short, posteriorly expanded ilium with strong pillar (Berger et al. 2010; Kibii et al. 2011). It also appears to have a relatively low humerofemoral ratio, as in *Homo*. It had an unusual calcalcaneal heel process without the expanded tuberosity found in *Homo* and *Australopithecus* afarensis (Zipfel et al. 2011). It may have had a more *Homo*-like hand morphology as well (Kivell et al. 2011). Its morphology represents a combination of hominin features not known for other australopiths, but the significance of these morphologies for differences in gait or locomotor adaptation are currently unclear.

Thus, given the limited fossil evidence available at present, the overall pattern of postcranial anatomy exhibited by *A. afarensis* appears to persist for over 3 Myr, perhaps from 4 to ~1 Ma, suggesting that the basic locomotor adaptation of species in this genus remained stable, and not undergoing ongoing selection for improved terrestrial competence or any other major change, with the possible exception of *A. sediba*. Similarly, if the postcrania from the *A. garhi* site of Bouri Hata (Asfaw et al. 1999) and/or *A. sediba* (Berger et al. 2010) represent descendants of *A. afarensis*, lower limb elongation would have occurred within the genus. These observations are speculative, and meant only to point out possibilities. If they were eventually supported by further evidence, this might document selection against primitive traits within the genus *Australopithecus*.

Summary and Conclusions

The fossil evidence clearly reveals that the immediate ancestors of *Australopithecus* had undergone selection to be habitual terrestrial bipeds. This hypothesis is supported by derived skeletal modifications in the preserved parts of the *Australopithecus* skeleton. *Australopithecus* species all were fully upright and most likely would have walked with an extended limb posture not significantly different from that of modern humans.

No matter the ancestral condition reconstructed from extant and Miocene fossil apes, there was impressive rearrangement of bone and joint morphology and orientation evident in the *Australopithecus* skeleton that reveals that substantial loads were incurred while traveling bipedally. Extant chimpanzees are capable facultative bipeds, being able to travel short distances during food gathering episodes on two feet (Hunt 1994), but have not undergone selection to improve their bipedal abilities because doing so better than they are already capable does not seem to result in differential reproduction among individuals. In contrast, the *Australopithecus* skeleton is much more likely to have been shaped by selection for the ability to travel, rather than stand or shuffle, bipedally.

The hypothesis that arboreal competence continued to confer selective advantages for australopiths remains difficult to test. Given the strong directional signal away from arboreal competence towards bipedality, it is difficult to disprove the null hypothesis that these primitive traits were adaptively valuable. Climbing and walking are not fully incompatible. Being a competent biped does not mean relinquishing all traits that permit climbing, such as opposable thumbs, for example.

Although there are the occasional features that may differ among species, at present there is little fossil evidence for significant locomotor diversity within *Australopithecus*, unless the Bouri Hata fossils are indeed *A. garhi*. It is notable, as pointed out by Meave Leakey (personal communication), that variation among *Australopithecus* species is minor compared to that among congeneric species in other clades, such as colobine monkeys (see Jablonski and Leakey 2008). This suggests a very similar adaptation in all *Australopithecus* species.

In conclusion, *Australopithecus* species appear to show a remarkably similar pattern of postcranial morphology over a long period of time. They were primarily terrestrial bipeds, and while there may be indication that they did climb trees, it is apparent that selective pressures for doing so well were of considerably weaker than those on traveling bipedally. The best evidence of stabilizing selection on limited arboreal capabilities is in the long period of time the *Australopithecus* pattern persisted. Changes appearing in the *Homo erectus* skeleton may have been due to factors other than abandoning an arboreal niche, such as an increase in efficiency in walking longer distances or running, and/or selection for body size, throwing, tool use and transport, etc. Further research into determining the primitive condition on which selection acted to produce earliest hominins, plasticity of the skeleton, and on variation among *Australopithecus* species hold the greatest promise for a better understanding of the evolution of locomotor and postcranial anatomy in this genus.

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Chapter 17
Shoulder Morphology in Early Hominin Evolution

Susan G. Larson

Abstract Among the enduring debates about the earliest stages of human evolution is whether or not the early hominin upper limb continued to serve a locomotor function following the adoption of bipedal habits. While the morphology of the entire upper limb is relevant to this debate, the shoulder is a region of primate anatomy that past studies have shown strongly reflects the differing functional demands imposed by differences in locomotor modes and posture. This study, therefore, reviews what is currently known about the pectoral girdle and proximal humerus of early hominins. This morphology is compared to that of humans and extant apes to attempt to establish what the last common ancestor of the African ape/human clade might have looked like, and to determine to what degree early hominins depart from, or have retained that primitive condition. Available information regarding the functional interpretation of traits is also reviewed to help shed light on how the upper limb of early hominins was actually used. The results of this review indicate that the early hominin shoulder retained many features of the presumed ancestral condition. These include a dorsal scapula positioned high on the thorax, a well-developed supraspinatus muscle, a relatively short, oblique clavicle, and a low to modest degree of humeral torsion. While most of these features would have been compatible with a limb that either continued to serve a locomotor role or was completely freed from it, possession of modest humeral torsion seems counterproductive for a limb involved only in manipulation. Since this characteristic displays some developmental plasticity, maintenance of modest torsion implies continued functional importance. A persisting role in arboreal locomotion would seem the most likely selective force resisting the development of high humeral torsion as came to characterize later hominin evolution.

Keywords Clavicle • Scapula • Humerus • Humeral torsion • *Australopithecus*

Introduction

While there is widespread consensus that all known early hominins were habitual bipeds, there is enduring debate regarding whether or not early hominins continued to use their upper limbs to assist in climbing and moving in trees (see Ward 2002, 2013; Harmon, 2013). Since the morphology of early hominin upper limb elements consists of a mix of primitive and derived features, some researchers view the primitive features simply as phylogenetic "baggage" retained because of no selective force against them (e.g., Day 1978a; Lovejoy 1978, 1988; Ohman 1986; Latimer and Lovejoy 1989; Latimer 1991). However, others consider the persistence of primitive features as an indication of continuing function (e.g., Senut 1980; Feldesman 1982; Schmid 1983; Stern and Susman 1983, 1991; Susman et al. 1984; Rose 1991; Susman and Stern 1991; Stern 2000). The shoulder is a region of primate anatomy that past studies have shown strongly reflects the differing functional demands imposed by differences in locomotor modes and posture. Young (2008) has shown that diagnostic features of scapular shape are established early in primate ontogeny, with only relatively minor changes from infant to adult form, which supports the view that observed differences have been brought about by natural selection. Analysis of the origins and configuration of the pectoral girdle/shoulder of early hominins, therefore, may help resolve this debate.

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Pectoral Girdle/Shoulder Morphology

Since there is currently no fossil evidence to indicate what the shoulder of the last common ancestor of the African ape/human clade looked like, we must look to the morphology of extant apes to try and estimate what the primitive condition for hominins might have been, at the same time acknowledging that the extant apes have as long an evolutionary history as modern humans. Although the close phylogenetic relationship between hominins and the African apes makes the latter the most relevant comparative group, it is also useful to examine the morphological diversity among all extant apes to identify traits that are primitive for hominoids. The similarities and differences between modern human and extant ape upper limb morphology have been summarized elsewhere (Aiello and Dean 1990), and only the pectoral girdle and proximal humerus will be reviewed here.

Clavicle

All living apes as well as modern humans have a dorsally positioned scapula, which is functionally associated with an increased range of motion at the shoulder (Miller 1932; Le Gros Clark 1959; Erikson 1963; see Dempster 1965, for a description of shoulder range of motion as a composite of motion at the three component joints; for an contrary view, see Chan 2008). However, the scapula sits higher on the ribcage in apes than in humans, giving them a "shrugged-shoulder" appearance (Schultz 1956). Voisin (2006) reports that this difference in scapular position is reflected in differences in dorsal view clavicular curvature. While the familiar S-shape of the human clavicle in superior view is shared with some other primates including chimpanzees and gorillas, in dorsal view the human clavicle displays a unique single gradual inferior curvature that Voisin (2006) associates with the low position of the human scapula. Apes, with their high scapula position, have clavicles that in dorsal view display either two curves (African apes and orangutans) or a superior curve only (lesser apes). Among early hominins there are a number of fossil clavicular specimens known (Table 17.1), but most are only small segments. The most complete specimen is A.L. 333x-6/9 (Lovejoy et al. 1982) attributed to *Australopithecus afarensis*, which is mainly missing a portion of its sternal end (Fig. 17.1). A.L. 333x-6/9 does not appear to display the unique single dorsal view inferior curve of human clavicles that Voisin (2006) associates with a low scapula position in humans. The retained primitive curvature of the A.L. 333x-6/9 clavicle suggests that the last common ancestor of the African ape/human clade displayed a high dorsal scapular position, and this configuration was probably maintained in early hominins.

Although the fragmentary nature of most hominin clavicular specimens has precluded much detailed analysis, the size of the conoid tubercle has received some attention. Johanson et al. (1982) report that the tubercle is small for A.L. 288-1bz, and Lovejoy et al. (1982) indicate that that of A.L. 333X-6/9 is essentially just a roughed area. Similarly, Toussaint et al. (2003) report a poorly developed conoid tubercle for the clavicular fragment belonging to the StW 431 partial skeleton. However, Partridge et al. (2003) describe a pronounced conoid tubercle like those of chimpanzee clavicles for StW 606 from the Jacovec Cavern at Sterkfontein. They indicate that StW 606 is unlike modern humans and other hominin clavicles in this respect, including StW 431 and StW 582 from Member 4 at

Table 17.1 Early hominin pectoral girdle material

	Ardipithecus	*A. afarensis*	*A. africanus*	*Australopithecus* sp.	*A. sebiba*[1]	*Homo habilis*
Clavicle	STD-VP-2/893	A.L. 333x-6/9	StW 431	StW 606	UW88-1	OH 48
		A.L. 333-94	StW 582		UW88-38	KNM-ER 3735
		A.L. 288-lbz			UW88-94	
		A.L. 438-1v				
		L.H. 21P				
Scapula		A.L. 288-11	Sts 7		U88-56	KNM-ER 3735
		DIK-1-1	StW 366		UW88-103,104	
		KSD-VP-1/1g	StW 431		UW88-113	
Proximal humerus	ARA-VP-7/2	A.L. 288-1r	Sts 7	Omo 119-73-2718	UW88-57	
		A.L. 333-87	StW 328	KNM-ER 1473	UW88-101	
		A.L. 333-107	StW 517			
		KNM-BC 1745				

[1] The pectoral girdle material for *A. sediba* has not yet been described in detail

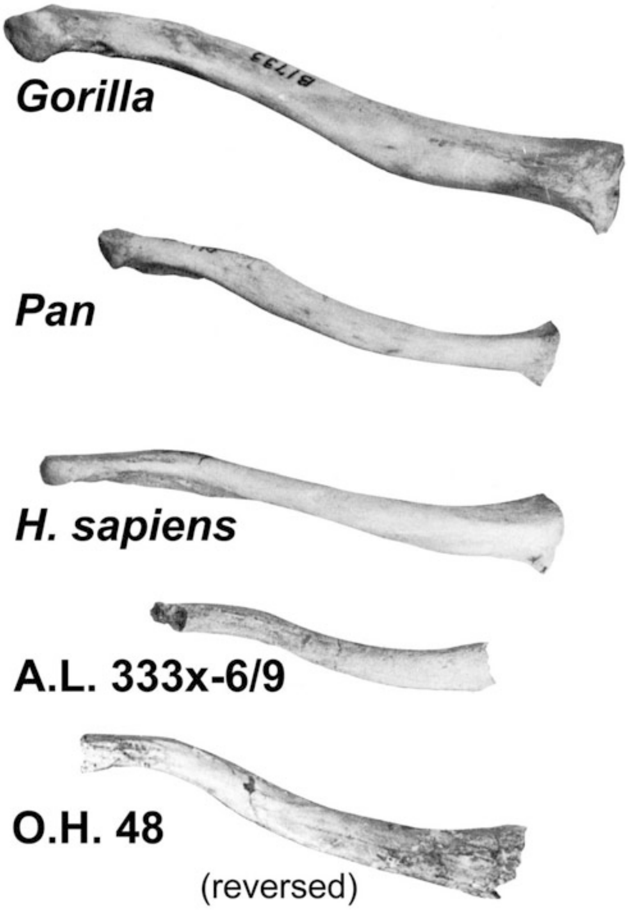

Fig. 17.1 Anterior views of right clavicles. Image has been modified from Ohman (1986) and is used with permission of the author

Sterkfontein. Finally, Haile-Selassie (2001) reports that the STD-VP-2/893 conoid tubercle is a mediolaterally elongate roughened surface comparable in overall robustness to A.L. 333X-6/9, but, paradoxically, indicates that it is absolutely more robust than in chimpanzees. In any event, there appears to be some diversity in conoid tubercle morphology among early hominins, the significance of which is unclear.

Clavicles of apes and humans are usually described as being relatively long compared to those of other primates, a supposed necessary correlate of a dorsal scapular position (Le Gros Clark 1959; Ciochon 1983; Andrews 1985; Martin 1986; Harrison 1987). However, since trunk length has commonly been used to express relative clavicular length (e.g., Napier and Napier 1967; Schultz 1968; Andrews and Groves 1976; Ciochon 1983), the relatively short trunks of apes and long trunks of monkeys and prosimians produce an inflated relative clavicular length in the former, and an underestimated length in the latter. Larson et al. (2007) have argued that humeral length is a more appropriate measure for the expression of relative clavicular length since it has a more conservative scaling relationship to body mass, particularly in African apes and humans (Jungers 1994). As shown in Fig. 17.2, a common isometric scaling relationship exists between clavicular and humeral length across all nonhuman primates, which suggests that this relation represents the primitive condition for primates. Most of the extant hominoids fall close to this line except orangutans, which fall well above it (see note added in proof). Modern humans also fall above the line as do later hominin fossils such as Neanderthals and early modern *Homo*. Unfortunately, a claviculohumeral ratio is not known for any early hominin, but early *Homo erectus* as represented by KNM-WT 15000, exhibits a relatively short clavicle similar to that of nonhuman primates. If this represents the retained primitive condition in *H. erectus*, this implies that the last common ancestor of hominids, and by inference early hominins, also displayed the primitive condition. Relative clavicular elongation then represents a derived condition characterizing later hominin evolution.

Scapula

It has long been recognized that apes, as well as humans, are distinguished from other primates by a scapula that is taller (craniocaudally) than it is broad (e.g., Ashton and Oxnard 1964; Ashton et al. 1971, 1976; Roberts 1974; Larson 1993). In a seminal study on scapular form in primates, Roberts (1974) attributes the distinctive shape of the ape scapular blade to a number of factors including its dorsal position on the thorax, which necessitates a reduction in scapular breadth to avoid impinging on the vertebral column, as well as to the need to accommodate larger areas of attachment for the muscles forming the rotator cuff to facilitate enhanced mobility at the shoulder as both prime movers and stabilizers. In particular, Roberts relates a large infraspinous fossa to the importance of climbing, and an enlarged supraspinous fossa to frequent forelimb elevation above the level of the shoulder. Although Roberts (1974) recognized that there is diversity in scapular shape among apes, a view recently emphasized by Young (2008), his broad categorizations regarding function offer limited insight into understanding this variation. Larson and Stern (1986, 1987) have examined the activity patterns of the rotator cuff muscles in chimpanzees, and emphasize the individual contribution each member makes to controlling humeral rotation. They report that while supraspinatus does play an essential role in the initiation of arm elevation, the other components of the cuff are also important in subtly altering humeral position depending on the direction of the motion. In addition, Larson and Stern (1986, 1987) note that certain behaviors elicit the recruitment of particular

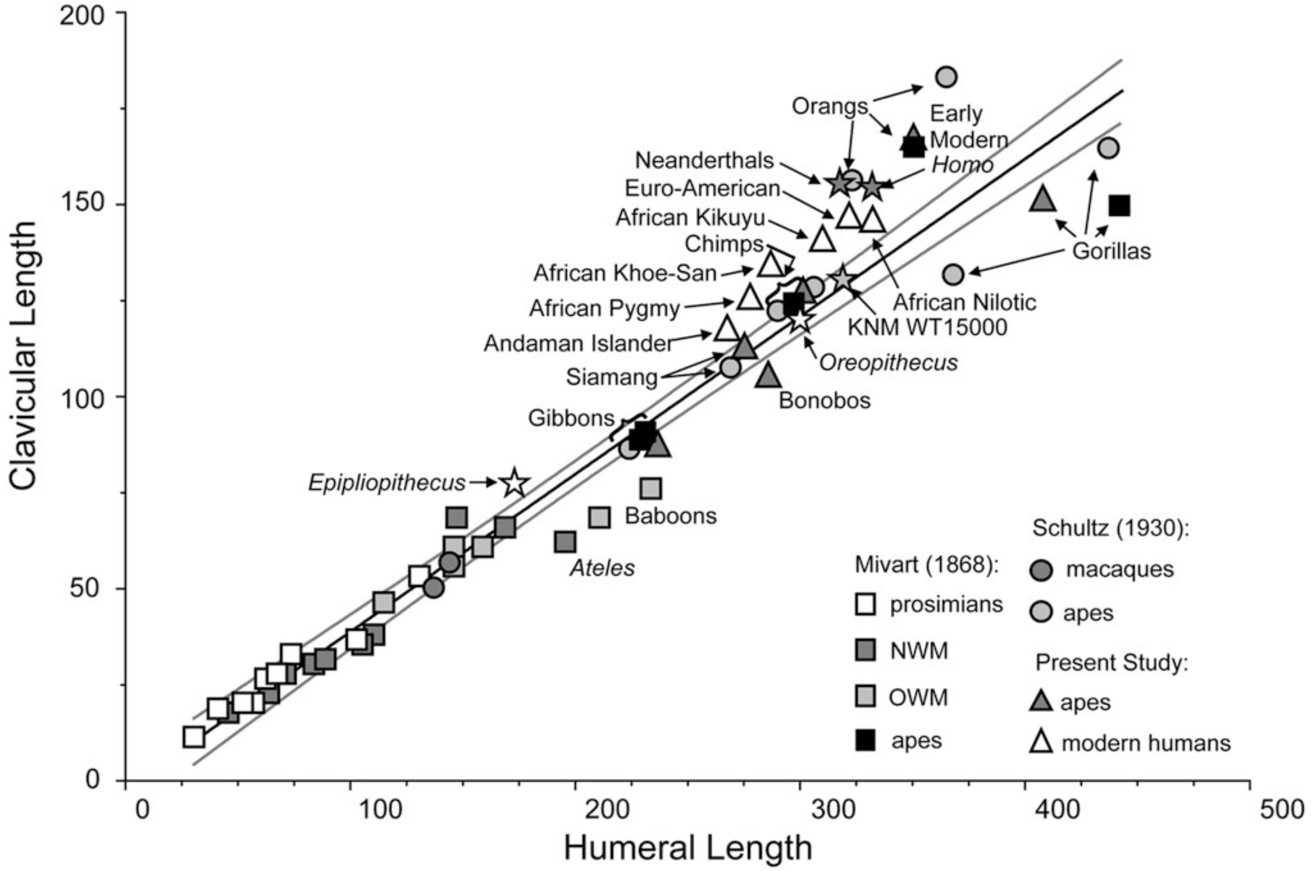

Fig. 17.2 Scatter plot of mean clavicular length against mean humeral length in nonhuman primates, modern human populations, and fossils. *Squares* indicate data derived from Mivart (1868); *circles* indicate data from Schultz (1930); *triangles* represent data provided by William Jungers (apes, Andaman Islanders, African pygmies, Euro-Americans), Chris Ruff (African Kikuyu and Nilotics), and Fred Grine and Louise Jacqui Friedling (African Khoe San). Fossils are represented by *stars*. Early modern *Homo* sample (*grey star*) includes: Abri Pataud 5 (Churchill 1994), Jebel Sahaba, Wadi Kubbaniya (Angel and Kelley 1986), Dolni Věstonice 13 and 15 (Sládek et al. 2000), and Skhul IV and V (McCown and Keith 1939). Neanderthal sample (*grey star*) includes: Kebara 2 (Churchill 1994), Shanidar 1 and 3, Régourdou 1, Tabūn C1, La Ferrassie 1 (Trinkaus 1983), and Neanderthal (McCown and Keith 1939). Value for KNM-WT 15000 (*grey star*) is from Larson et al. (2007). Clavicular and humeral lengths for *Epipliopithecus vindobonensis* (Ind. II) (*white star*) were measured on casts. An estimate of clavicular length for *Oreopithecus bambolii* (*white star*) was provided by Terry Harrison, and humeral length is from Harrison (1986). Values for the latter two taxa are included to offer an indication of relative clavicular length in a primitive catarrhine and a Miocene hominoid. Regression line (with 95 % confidence intervals) is for nonhuman extant primates only and has a correlation coefficient of 0.97. Since it passes through the origin, it indicates an isometric scaling relationship across primate species. Assuming that this linear relationship represents the primitive condition for primates, orangutans, later fossil hominins, and all modern human populations display relative clavicular elongation

members of the cuff over others. For example, subscapularis is minimally involved in most voluntary arm elevations or in suspensory or quadrupedal locomotion, but is intensively active during climbing. Infraspinatus typically acts in concert with supraspinatus, not only during forelimb elevation, but also during the support phase of quadrupedal locomotion to resist glenohumeral displacement. During forelimb suspension, however, supraspinatus is inactive while infraspinatus acts alone or with the help of teres minor to resist transarticular tensile stress.

Humans are distinguished from extant apes in having a somewhat small supraspinous fossa and a very large infraspinous fossa (Roberts 1974). Roberts (1974) links the reduced size of the supraspinatus to the habitually pendant posture of the human upper limb, and based on the roles of the cuff muscles in controlling humeral rotation, it is possible that the increased area of the scapular blade below the scapular spine in humans reflects a greater emphasis on lateral and medial rotatory motions during manipulatory behaviors in this posture.

The DIK-1-1 juvenile scapulae, attributed to *A. afarensis*, are the first specimens to reveal information on scapular shape and on the sizes of the scapular fossae in early hominins. According to Alemseged et al. (2006), the scapula is most similar to those of gorillas in overall shape, and the supraspinous fossa does not yet show the size decrease nor does the infraspinous fossa the size increase that characterize modern human scapulae. In their recent comparative ontogenetic study of scapular shape change among apes, humans and early hominins, Green and Alemseged (2012) confirm the overall apelike characteristics of the DIK-1-1 scapulae. They show that the relative lengths and breadths of its supraspinous and infraspinous fossae are more similar to those of comparable aged apes, particularly African apes, than they are to juvenile humans. Unfortunately, the relative sizes of the dorsal scapular fossae have yet to be documented in an adult early hominin so it is currently unknown if these proportions are maintained during ontogeny. However, based on comparisons of the DIK-1-1 scapulae to those of adult early hominins in other scapular characteristics, Green and Alemseged (2012) conclude that it is likely that the shoulder of *A. afarensis* followed an overall growth trajectory more like that of African apes than modern humans.

In addition to the larger overall size of the infraspinous fossa in apes compared to other anthropoids (Roberts 1974), hominoids also display a relatively wider interval between the base of the scapular spine and the axillary border at the neck of the scapula (Senut 1981; Larson 1995). Based on the observation that infraspinatus is the only member of the rotator cuff to be consistently involved in maintaining joint stability during suspensory postures in chimpanzees (Larson and Stern 1986), Larson (1995) argues that this feature is an accommodation to a straight line of action for infraspinatus during unimanual suspension. Humans, however, have the widest infraspinatus neck width of any primate, and Larson (1995) links the role of infraspinatus in helping to regulate the rotatory position of the pendant upper limb in humans with this and other modifications of the scapula, such as a horizontal scapular spine, which positions infraspinatus posterior to the shoulder joint to better perform this function. Larson (1995) measured relative infraspinatus neck width in the A.L. 288-11 *A. afarensis* scapular fragment, and reports that it overlaps with extant apes in this feature, and does not possess the uniquely wide interval of modern humans. However, juvenile apes, humans, and *A. afarensis*, as indicated by the DIK-1-1 scapulae, do not differ in this regard (Green and Alemseged 2012).

In addition to a tall scapula, the scapular spine in apes is typically oblique, although less so in orangutans, and the glenoid fossa faces cranially. These features, in particular a cranially facing glenoid, are associated with use of the upper limb by apes in overhead and suspensory postures. In humans, the scapular spine is nearly horizontal and the glenoid fossa faces laterally. All known early hominin scapulae including A.L. 288-11, (Johanson et al. 1982) and DIK-1-1 (Alemseged et al. 2006), and KSD-VP-1/1g (Haile-Selassie et al. 2010) attributed to *A. afarensis*, Sts 7 (Broom et al. 1950) attributed to *A. africanus*, and UW88-56 from the MH2 adult *A. sediba* partial skeleton (Berger et al. 2010) are similar to apes in having glenoid fossae that are directed more cranially than laterally as they are in humans (Fig. 17.3) (Oxnard 1968; Vrba 1979; Stern and Susman 1983; Alemseged et al. 2006; Haile-Selassie et al. 2010; Green and Alemseged2012); and all but KSD-VP-1/1g display ape-like oblique scapular spines (Fig. 17.4) (Haile-Selassie et al. 2010; Green and Alemseged 2012). Green and Alemseged (2012) show that in these characteristics, the juvenile DIK-1-1 scapulae are quite unlike those of comparable aged humans. They are similar to juvenile apes,which suggests that like apes early hominins maintained these characteristics throughout life. In humans, the scapular spine and glenoid fossa not only start out with different orientations than apes or early hominins, but also undergo different growth trajectories.

Fig. 17.3 Dorsal views of casts of fossil hominin scapulae Sts 7, A.L. 288-1l, and Stw 431

According to Roberts (1974), most quadrupedal primates have pear-shaped glenoid fossae compared to a more ovate fossa seen in humans and apes as well as some atelines. In addition, he reports that the fossa is more uniformly curved in hominoids, while many quadrupedal forms have an extended cranial lip that helps stabilize the joint (Roberts 1974; Whitehead and Larson 1994). These observations have been confirmed quantitatively by MacLatchy et al. (2000) who have demonstrated that the glenoid fossae of

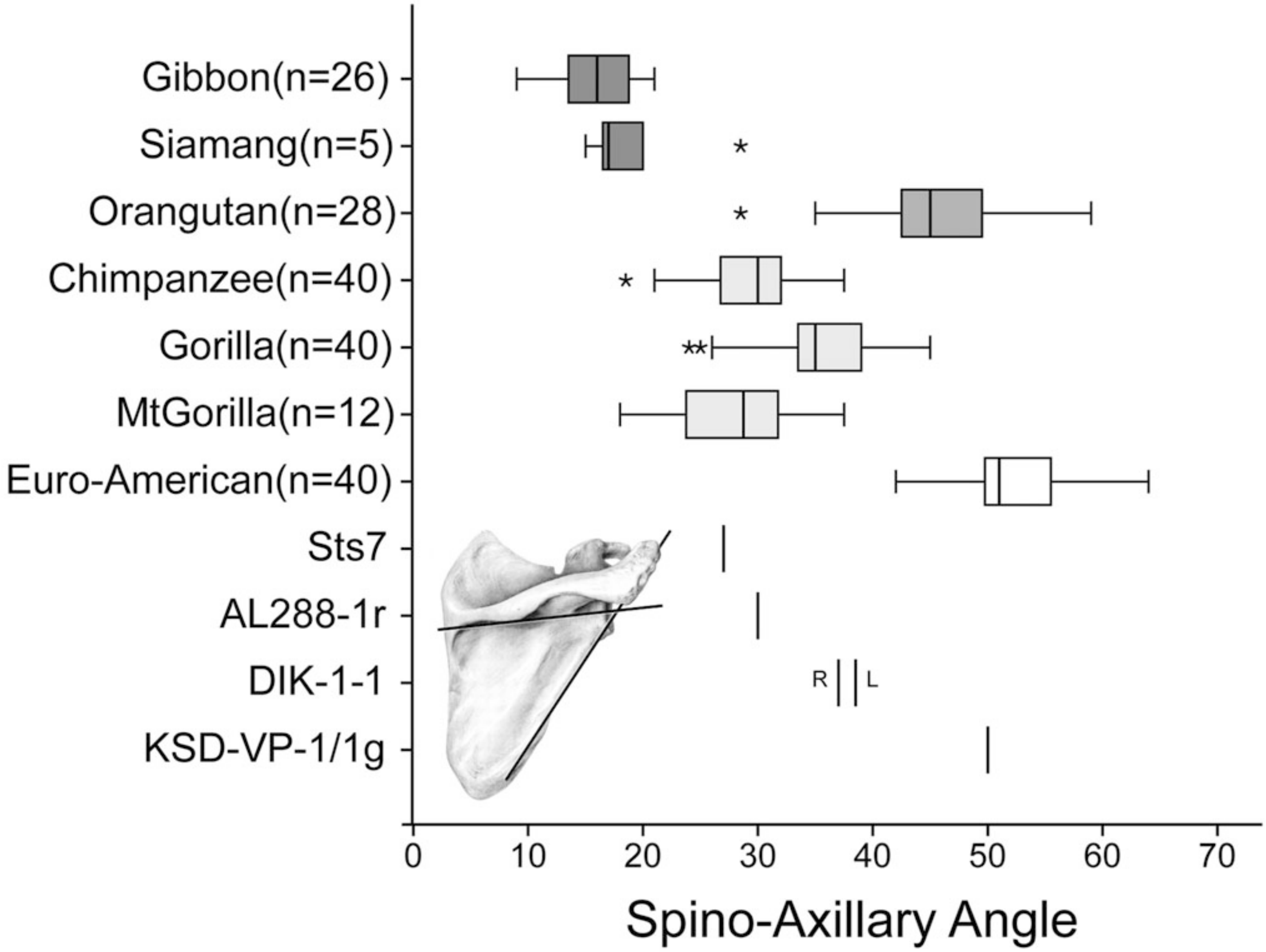

Fig. 17.4 Box and whisker plots for axillo-spinal angles for comparative samples and fossils. Comparative data for extant taxa are from Larson (1995). The values for DIK-1-1 are from Green and Alemseged (2012), and for KSD-VP-1/1g is from Haile-Selassie et al. (2010). Other early hominin angles were measured by the author. Most early hominins have oblique scapular spines similar to the African apes

apes and *Ateles* are significantly wider at the midpoint of their height than are those of other anthropoids, and that their glenoids are also more moderately curved along both their height and width. Humans share these characteristics of glenoid fossa shape with apes, and the glenoid fossa of A.L. 288-1l is described as being similarly ovate with gentle height and width curvatures (Johanson et al. 1982). The glenoid of Sts 7 appears to be more pear-shaped, but it is not possible to determine its actual shape since an area is missing along its dorsal margin (Vrba 1979). Although Alemseged et al. (2006) use the square root of glenoid fossa height multiplied by breath as a proxy for overall body size in their analysis of scapular form, they do not report the actual values. Nonetheless, though there is limited information available on early hominin glenoid fossa shape, the similarity between apes, A.L. 288-1l and modern humans suggests that early hominins retained the primitive condition for the shape of the glenoid fossa. It is interesting to note in passing that the glenoid fossae of Neanderthals are narrower than those of modern humans (Churchill and Trinkaus 1990), raising questions regarding the course of change in glenoid fossa shape in later hominin evolution.

A distinctive feature of ape scapulae is a prominent dorsolateral tubercle on the coracoid process, which is not seen in modern humans. Since the coracoclavicular ligaments attach at this tubercle, Vrba (1979) suggests that this configuration is related to the oblique orientation of the clavicle when the scapula is positioned high on the thorax. Noting that the coracoid of Sts 7 also displays a prominent dorsolateral tubercle that is placed somewhat more laterally than in modern humans, Vrba (1979) concludes that it is likely *A. africanus* also displayed a high scapular position. This agrees with the inference of a retained high scapular position in early hominins based on clavicular curvature.

Fig. 17.5 Anterior views of casts of early hominin proximal humeri. Both Omo 119-73-2718 and A.L. 288-1r are left humeri, while Sts 7 is a right humerus.

Humerus

Apes and humans are similar in having greater and lesser tubercles that are low compared to the level of the humeral head, and are distinct from most other anthropoids in displaying an obtuse angle between the supraspinatus and infraspinatus insertion facets on the greater tubercle (Larson 1995). In this regard, the A.L. 288-1r proximal humerus (Fig. 17.5) is similar to both African apes and humans (Larson 1995). However, the attachment sites for supraspinatus and infraspinatus on the greater tubercle of ape humeri are commonly separated by a ridge, whereas in humans these areas are more nearly continuous. The presence of such a ridge may be related to the attachment of a more powerful supraspinatus in apes. Robinson (1972) notes that the greater tubercle of Sts 7 displays a prominent ridge separating the attachment facets for supraspinatus and infraspinatus similar to apes. Although the area of attachment for supraspinatus is not complete in A.L. 288-1r, there is a ridge that would have separated it from the clearly

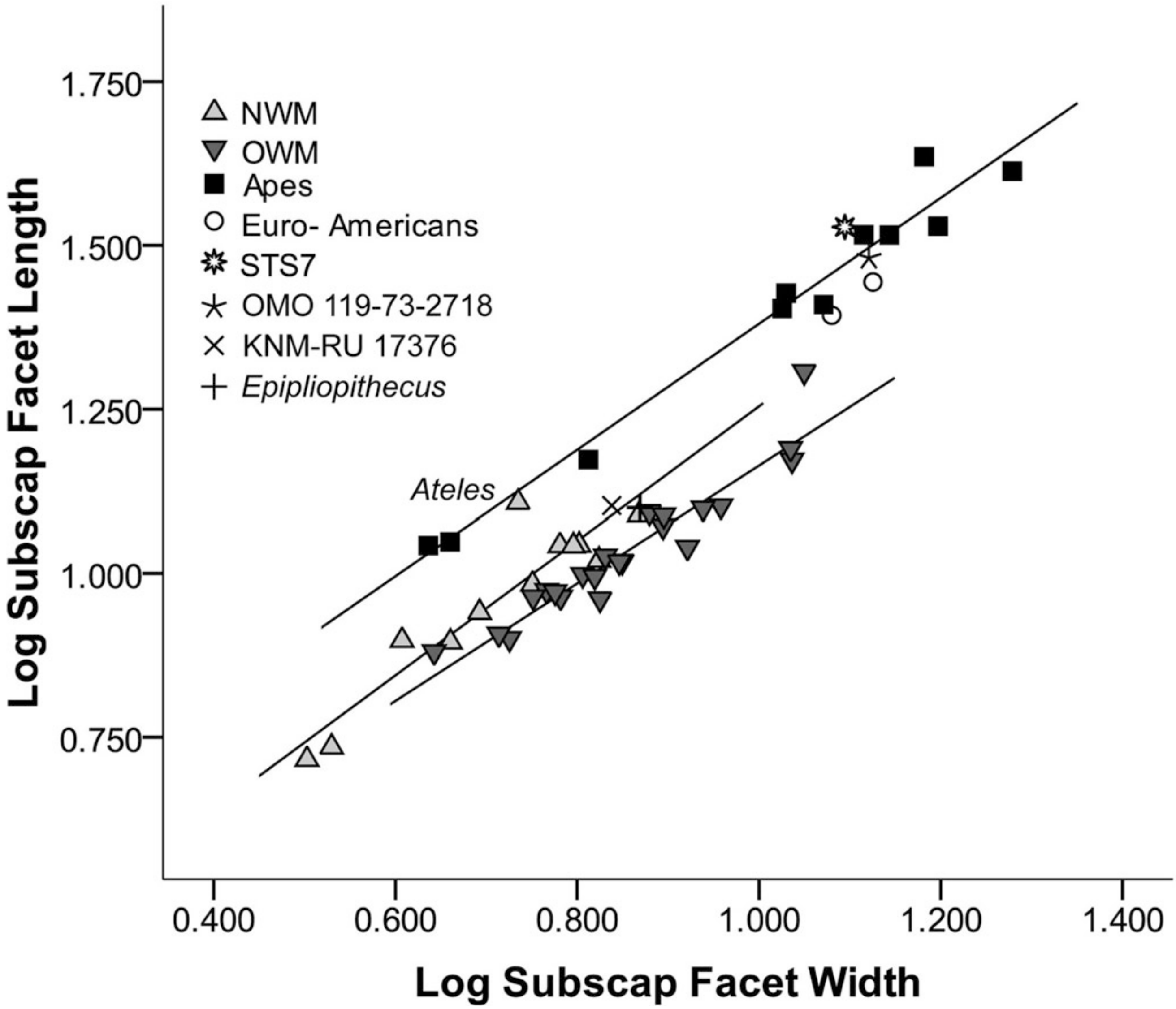

Fig. 17.6 Mean shape of the subscapularis insertion facet in primates (sexes separate). Data is reproduced from Larson (1995). Slopes of *lines* for apes (*black squares*), NWM (*light grey triangles*) and OWM (*inverted dark grey triangles*) are not significantly different and all approximate isometry. However, the ape *line* is shifted above those for monkeys indicating that apes have significantly longer subscapularis insertions facets indicating more versatility within subscapularis to control the position of the humeral head of a mobile shoulder joint. Sts 7 and OMO 119-73-2718 are similar to the extant apes, but only Sts 7 is significantly different from modern humans (*open circles*), who fall slightly below the *line* for apes. Subscapularis insertion facet shape was measured on casts of *Epipliopithecus vindobonensis* (Ind. II) and KNM-RU 17376 as indicators of the condition in primitive catarrhines. [Gebo et al. (1988) attributed KNM-RU 17376 to *Dendropithecus macinnesi* or *Proconsul heseloni*, but more recently Harrision (2002) referred it to *Nyanzapithecus*]

defined ovoid depression for the attachment of infraspinatus (Johanson et al. 1982). Lovejoy et al. (1982) describe a similar separation of the facets for attachment of the dorsal rotator cuff muscles on the greater tubercle of A.L. 333-107.

Larson (1995) reports that the lesser tubercle is shaped differently in apes compared to other anthropoids or humans. As shown in Fig. 17.6, the insertion facet for subscapularis on the lesser tubercle is longer proximodistally in apes (the human mean is significantly different from those of either African ape with $p < 0.001$). Larson (1995) relates this elongation of the lesser tubercle to the internal functional differentiation displayed by subscapularis in chimpanzees (Larson and Stern 1986; Larson 1988), arguing that variation in the impact of different regions of subscapularis on humeral motion is due to the gradual transition of the direction of fiber insertion from the top to the bottom of the lesser tubercle. Also shown in Fig. 17.6 (see also Fig. 17.5) are the shapes of the subscapularis insertions facet of Sts 7 and OMO 119-73-2718. Both are similar to those of apes, but only Sts 7 is statistically

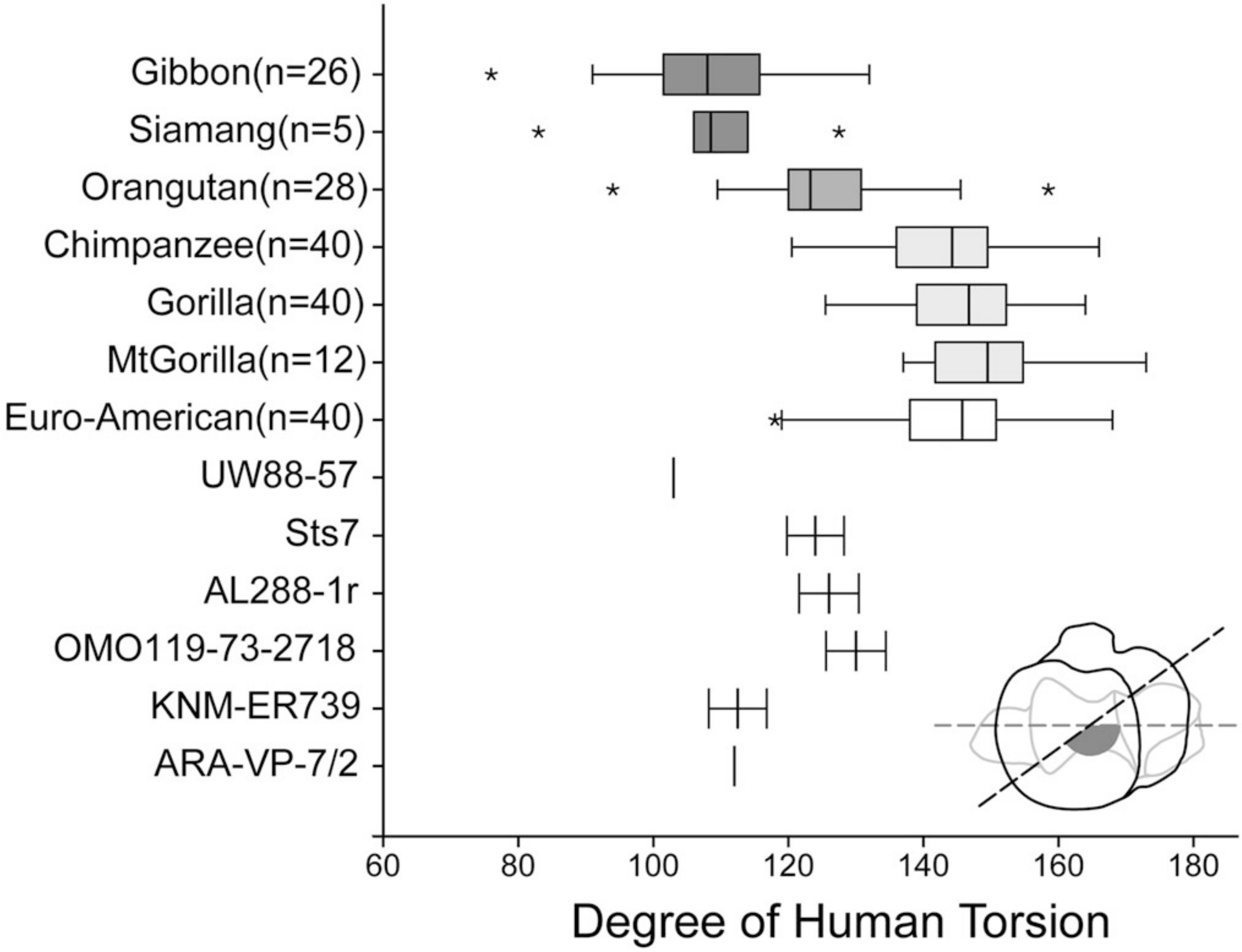

Fig. 17.7 Box and whisker plots of humeral torsion for comparative samples of apes, modern humans, and fossils. Torsion value for UW88-57 is from Berger et al. (2010) and for ARA-VP-7/2 is from Lovejoy et al. (2009). Comparative extant data and other early hominin fossil torsion estimates are from Larson (1996). *Error bars* for the latter early hominins represent possible ranges of torsion values based on mean absolute percent prediction errors derived from regression analysis

different from that of humans ($p < 0.05$). Broom et al. (1950) have also described the lesser tubercle of Sts 7 as being prominent. Although they do not comment on the shape of the subscapularis insertion facet, Pickford et al. (1983) report that the Chemeron proximal humeral fragment, KNM-BC 1745, similarly displays a relatively large lesser tubercle, as do Johanson et al. (1982) in regard to the A.L. 288-1r proximal humerus. It seems reasonable, therefore, to project that the configuration of the humeral tubercles in the last common ancestor was like that of apes, and this morphology continued to be displayed by early hominins.

In regard to humeral head shape, all hominoids have rounded humeral heads, although those of apes tend to be either absolutely round, or slightly broader than tall, while in modern humans the humeral head is typically slightly taller than wide. The functional implications of this difference are unclear, however. To the degree that it can be determined, the humeral heads of all known early hominin humeri are elliptical like those of humans rather than spherical or broad as in extant apes. If the humeral head of the last common ancestor was similar to that of the extant apes, then is appears that early hominins display a more derived humeral head shape.

African apes are distinct from humans in displaying a deep and tunnel-like intertubercular groove. The intertubercular grooves of early hominin humeri tend to be shallow, similar to modern humans. However, it is unclear whether this represents a derived condition for early hominins since this feature of African ape humeri also distinguishes them from other extant apes. It is possible, therefore, that the last common ancestor of African apes and humans also displayed a shallow intertubercular groove, and the tunnel-like configuration represents a derived condition for African apes only, perhaps in some way related to knuckle-walking.

A marked degree of humeral torsion is another trait that is associated with a dorsal scapular position, and so is said to characterize all apes and humans. However, the lesser apes actually have a low degree of torsion, and torsion is at an intermediate level in orangutans (Evans and Krahl 1945; Larson 1988). Only the African apes and humans can be truly said to display a high degree of humeral torsion (Fig. 17.7). While this has been taken as evidence that a high degree of humeral torsion is a derived trait for the African ape/human clade, humeral torsion in early hominins is only low to modest, more comparable to that of orangutans (Larson 1996; Lovejoy et al. 2009; Berger et al. 2010). In addition, it has recently been shown that humeri from early *H. erectus* exhibit low degrees of humeral torsion (Larson et al. 2007; Lordkipanidze et al. 2007). This supports the contention that the high degree of torsion in modern humans is a more recently acquired characteristic, and its similarity to that of African apes is due to convergence (Larson 1996). According to this proposal, the high degree of humeral torsion in modern humans evolved in response to the habitually medially rotated shoulder position used during manipulation of objects, whereas the high degree of torsion in African apes is related to the need to maintain a sagittal orientation of their elbow joints in a knuckle-walking posture. This leaves unanswered what the primitive condition in regard to humeral torsion was for the last common ancestor of the African ape/human clade. If the absence of a high degree of torsion in early hominins is taken to represent retention of the primitive condition, this could be viewed as evidence against a quadrupedal/knuckle-walking ancestry for hominins as some have proposed (Sarmiento 1988, 1994; Gebo 1992, 1996; Richmond and Strait 2000, Richmond et al. 2001). However, since there is some developmental plasticity in humeral torsion (Krahl 1947; Edelson 2000), it is possible that the degree of torsion underwent a decrease following the transition from a quadrupedal/knuckle-walking stage to bipedality in response to changes in the functional demands on the shoulder.

Noting that humeral torsion is related to scapular position and elbow joint orientation, Ward (2002) has speculated that differences in the degree of humeral torsion between early hominins and modern humans could be related to a difference in scapular position due to differences in thoracic shape. According to Schmid (1983), *A. afarensis* had a funnel-shaped thorax somewhat similar to African apes rather than a barrel-shaped thorax as in modern humans. A possible relationship between thoracic size and scapular position has been suggested for Neanderthals by Vandermeersch and Trinkaus (1995) and Churchill (1996). Since Neanderthals are characterized by humeral torsion values somewhat lower than those of modern humans, these authors suggest that the cold climate adaptation of an enlarged chest resulted in a more laterally positioned scapula. However, Larson (2007) has argued that the degree of humeral torsion in Neanderthals is not low when compared to non-industrialized modern human populations, and that the characteristic elongated clavicles of Neanderthals were able to compensate for their enlarged chest size to maintain a dorsal scapular position. While there is indeed an association between the position of the scapula on the thorax and the degree of humeral torsion (see Larson 2007; Larson et al. 2007), the only relationship between scapular position and thoracic shape that has ever been described is the lateral position of the scapula on a dorsoventrally deep thorax as in monkeys, and the dorsal position of human and ape scapulae on their mediolaterally broad thoraces (Schultz 1956). Extant hominoids vary in thoracic shape and in degree of humeral torsion, but all have dorsally positioned scapulae. For example, the large bodied apes have funnel-shaped thoraces, but while the African apes have high humeral torsion, torsion is only modest in orangutans (Evans and Krahl 1945; Larson 1988). Humans have a more barrel-shaped thorax and high humeral torsion, yet humeral torsion is low in hylobatids (Evans and Krahl 1945; Larson 1988) who also have a barrel-shaped thorax. While one can not entirely rule out the possibility of interaction between thoracic shape and scapular position as both changed in the course of human evolution, at this point, the limited evidence available indicates a retained high dorsal scapular position in early hominins.

Overview of Early Hominin Shoulder Morphology

The pectoral girdle/shoulder of early hominins appears to have retained many features of the presumed ancestral condition. Judging on Vrba's (1979) interpretation of the coracoid of Sts 7, and on the absence of the single inferior curve in the A.L. 333x-6/9 clavicle, the scapula was probably positioned high on a funnel-shaped thorax (see also Schmid 1983). The clavicle was therefore obliquely oriented, and in the absence of evidence to the contrary, was probably still relatively short. The glenoid fossae of early hominin scapulae were ovate, evenly curved, and cranially directed (Oxnard 1968; Robinson 1972; Vrba 1979; Stern and Susman 1983). In regard to the scapular blade, the infraspinatus neck width was wide (Larson 1995), although not as wide as in modern humans, and based on the DIK-1-1 juvenile scapula, the scapular fossae were still ape-like in size (Alemseged et al. 2006; Green and Alemseged 2012). However, the proximal humerus of early hominins displays a mix of features including a more human-like elliptical humeral head and relatively shallow bicipital groove, but with greater and lesser tubercles that are more similar to extant apes. Unlike either humans or African apes, however, the humerus displays low to modest torsion. If the high degree of humeral torsion in African apes and perhaps their tunnel-like bicipital grooves are features directly related to knuckle-walking, and the high level of humeral torsion in humans is related to manipulation, then the shoulder of early hominins appears to be that of an ape that neither walked quadrupedally nor displayed accommodations to a dependence on tools.

As can been seen from Table 17.1, the amount of fossil shoulder material known for early hominins is limited, and even where multiple specimens do exist, as is the case with proximal humeri, taxonomic attributions are often unclear (e.g., Omo 119-73-2718). In addition, much of the shoulder material is fragmentary and damaged, all of which makes it essentially impossible to evaluate diversity in pectoral girdle/shoulder morphological among the known early hominin taxa.

The situation is no better for *Homo habilis* (Table 17.1). However, among the limited material available is OH 48, a nearly complete clavicle (Fig. 17.1). Napier (1965) describes OH 48 as basically human-like except for the cross-sectional shape of the medial end. Based on the orientation of the long axis of this cross-section, he concludes that the clavicle would have been rotated slightly around its longitudinal axis and the shoulder positioned higher than in modern humans to sit on a thorax with a steep inlet (i.e., funnel-shaped thorax). Oxnard (1969) reports a significantly higher degree of torsion in the OH 48 clavicle than in modern humans, and concurs that it would have been twisted cranially and the shoulder positioned more superiorly, which he interprets as reflecting some ability for upper limb suspension. In response to Oxnard, Day (1978b) argues that the missing ends of the specimen make any measure of torsion unreliable, and emphasizes the basically human appearance of the fossil, a view echoed by Ohman (1986). However, Voisin (2001) reports that OH 48 does not display the distinctive single inferior curvature of modern humans, and concludes that the scapula of *H. habilis* was situated higher on the thorax than in modern humans.

The only other shoulder remains attributed to *H. habilis* are the lateral portion of a clavicle and a small piece of scapula from the KNM-ER 3735 partial skeleton. Noting the thickness of the preserved scapular spine along with the large size of other forelimb features of KNM-ER 3735, Leakey et al. (1989) suggest that *H. habilis* may have displayed substantial climbing ability. In sum, although little can be said with certainty based on this very limited sample, the fossil evidence suggests that earliest *Homo* continued to possess a largely primitive shoulder configuration like that of earlier hominins. Nonetheless, with the emergence of early *H. erectus* in Africa, as represented by KNM-WT 15000, the scapula had undergone a transformation in appearance and probably also in position, and the configuration of the pectoral girdle had changed dramatically (Larson 2007; Larson et al. 2007).

Discussion

Of all the regions of the early hominin upper limb, the shoulder perhaps displays the largest number of primitive features. As such, can it contribute to resolution of the debate as to whether primitive features in early hominins have simply been retained because no selective force has acted to change them, or are they instead persisting functionally valuable traits indicating the continued importance of arboreal behaviors to their survival?

In the course of this review of early hominin shoulder morphology, various traits have been described as more similar to or different from extant apes perhaps inadvertently implying that the living apes are all very similar in shoulder morphology. This is decidedly not true. Larson (1998) has argued that there is a higher level of postcranial variability than is generally appreciated among hominoids that likely reflects a substantial amount of parallelism in the course of their individual evolutionary histories. Despite this diversity within apes, Young (2008) has recently shown that at least in regard to scapular form, hominoids as a group are distinct from other anthropoids except *Ateles* in displaying dorsal scapular fossae that are more equal in size, a craniocaudally tall rather than broad blade, an oblique scapular spine, a large projecting coracoid and acromion, and a round, shallow, cranially directed glenoid fossa. In addition, all apes have a shoulder that is positioned high on the thorax with an oblique clavicle that is relatively short except for orangutans, which have clavicles that are uniquely elongated among nonhuman primates (see note added in proof). Although the African apes display a high degree of humeral torsion, this is related to their quadrupedal habits. The Asian apes have only low to modest degrees of humeral torsion. The attachment sites for the rotator cuff musculature on the greater and lesser tubercles of ape humeri are distinctive reflecting the important roles that these muscles play during various arboreal and voluntary behaviors. These features characterizing ape shoulders in general can all be loosely related to use of the upper limb in overhead postures and behaviors.

The habitual pendant posture and purely manipulatory role of the upper limb in modern humans is associated with a shoulder positioned lower on the thorax. The clavicle is elongated and nearly horizontal; the scapula has a horizontal spine, small supraspinous and large infraspinous fossae, a very wide infraspinous scapular neck, and a laterally directed ovoid, shallow glenoid fossa. The muscle insertion sites on the greater tubercle of the proximal humerus are fairly continuous, the lesser tubercle is only modestly elongate, and the humeral head is slightly elliptical and displays a high degree of torsion. Since early hominins were also bipedal, their upper limbs would have similarly hung in a pendant posture and they no doubt used their hands for manipulation of objects. Yet their shoulder remained essentially ape-like. Is this an indication of the continued importance of climbing and other arboreal behaviors, or is this assemblage just so much baggage? The implication of the latter view is that this collection of primitive features must have been functionally neutral, that is, it did not directly contribute to behaviors important to the survival of the species, but it also did not detract from effective use of the upper limb.

While there is nothing obvious about a high shoulder, a cranially facing glenoid or large supraspinatus that would inhibit upper limb manipulatory ability in early hominins, a low degree of humeral torsion does have some negative consequences. If a humerus with a low degree of torsion articulates with a dorsally positioned scapula (whether the glenoid faces cranially or laterally), the elbow joint will have a "lateral set" (Larson 1988), that is, the cubital fossa will face laterally and the forearms will be splayed out to the sides. This is the condition seen in gibbons at rest (see Larson 1988, Figs. 9 and 10; Larson 2007). While this lateral set can be overcome by medial rotators of the shoulder to bring the hand into a better position for manipulation, this is a more energy costly solution than having a humerus with a higher degree of torsion. In addition, while a humerus with a low degree of torsion confers a large range of lateral rotation at the shoulder, it limits the range of medial rotation (Larson 2007). Therefore, if the upper limb of early hominins was freed from all locomotor functions and was used solely for foraging and other manipulatory activities, one would expect the humerus to have had a higher degree of torsion to facilitate a habitually medially rotated posture for the upper limb. It might be argued that unlike selection on the lower limb favoring features related to bipedal locomotion, selection on the shoulder for improved manipulatory abilities was not yet sufficiently strong to modify the inherited primitive condition. However, humeral torsion displays developmental plasticity (Krahl 1947; Edelson 2000), and systematic changes in the degree of humeral torsion in humans have been demonstrated in association with certain habitual behaviors, such as throwing (Pieper 1998; Crockett et al. 2002; Osbahr et al. 2002; Reagan et al. 2002). The fact that early hominins had only low to modest humeral torsion indicates that other selective forces were maintaining this configuration of the proximal humerus and of the shoulder region in general. It is hard to imagine what such selective forces could have been other than a continuing role for the upper limb in arboreal locomotion and posture.

Note added in proof

Kagaya et al. (2010) have recently analyzed relative clavicular length in apes and report that when scaled to body mass chimpanzee clavicles are not elongated while those of orangutans are, as observed in the present study. However, while clavicular length relative to humeral length in hylobatids is not unusual, when scaled to body mass their clavicles are quite elongated, reflecting the marked elongation of all their upper limb elements.

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Chapter 18
Age and Sex Differences in the Locomotor Skeleton of *Australopithecus*

Elizabeth H. Harmon

Abstract Skeletons of juvenile hominoids recovered from the past can provide much information about locomotor patterns, including when and in what order adult morphology appears in the skeleton, how locomotor repertoire during growth affects the skeleton, and how ontogeny relates to the evolution of new locomotor behaviors. The goal of this review is to assess whether the pattern of growth in the *Australopithecus* skeleton as can now be perceived provides insight into previously developed locomotor hypotheses derived from the adult skeleton. Hypotheses about the developmental underpinnings of skeletal differences between *Australopithecus*, apes, and humans are also explored. Based on current evidence reviewed here, *Australopithecus afarensis, Australopithecus africanus,* and *Australopithecus garhi* were habitually bipedal, but incorporated arboreal grasping postures into their behavior, whether locomotor or positional. Finally, the proposal that hind limb growth in recent *Homo* species is heterochronic extension of the *Australopithecus* pattern is probably oversimplified and is confounded because the phylogenetic relationship among *A. afarensis, A. africanus, A. garhi*, and *Homo* is not understood.

Keywords Bone functional adaptation • Development • Genetics • Growth • Hominin • Locomotion • Ontogeny • Phenotypic plasticity

Introduction

There are at least three kinds of information about locomotor patterns that can be obtained from the juvenile hominoid skeleton. The first is how and when adult morphology appears in development. The second is how locomotor behaviors during growth affect the skeleton. The third is how the pattern and pace of growth relate to evolutionary changes in locomotion. Such ontogenetic perspectives have been instructive for understanding the locomotor variation among apes and humans (e.g., Schultz 1924; Doran 1992; Inouye 1992; Simpson et al. 1996; Tardieu and Preuschoft 1996; Tardieu 1997; Williams and Orban 2007). However, even though there are many postcranial fossils from the Pliocene taxa *Australopithecus afarensis* and *Australopithecus africanus*, little is known about the juvenile skeleton of early hominins, which is unfortunate because the skeleton provides the best information about locomotor behavior. Ontogenetic observations are, of course, hard to make in early hominins because there are few subadult elements, and even fewer that are associated with cranial material. The newly reported *A. afarensis* DIK 1-1 skeleton (Alemseged et al. 2006) has and will continue to provide fresh insight into growth and development because it represents a nearly complete individual at an early developmental stage that can be compared to adult specimens, such as A.L. 288-1.

The current state of knowledge about the juvenile skeleton in the genus *Australopithecus* is presented in this review. The goal is to assess whether evidence for pattern of growth in the *Australopithecus* skeleton provides insight into locomotor hypotheses derived from the adult skeleton and to explore hypotheses about the developmental underpinnings of the skeletal differences between *Australopithecus*, apes, and humans. The context for this discussion is phenotypic plasticity, genetically defined adaptive complexes, and evolutionary trajectories in growth and development. The adult locomotor morphology of *Australopithecus* is discussed in

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this volume by Ward (2013) and can be found elsewhere (e.g., McHenry and Berger 1998; Lovejoy et al. 2002; Richmond et al. 2002; Ward 2002; Organ and Ward 2006; Green et al. 2007).

The Role of Ontogeny in Producing Skeletal Morphology

Ontogenetic changes arise through multiple pathways. Growth changes unfold as part of the genetic "plan" for the development of tissues (Lovejoy et al. 1999, 2003). They also occur as part of the feedback system between environmental cues (e.g., nutrition) and genetic mediation, such as via hormonal responses (Lovejoy et al. 1999; Sultan and Stearns 2005). With respect to hard tissues, locomotor behaviors or other external factors during development can induce skeletal changes (Lieberman 1997; Lovejoy et al. 1999; Skerry 2001; Ruff 2003; Pearson and Lieberman 2004; Sultan and Stearns 2005).

It is often difficult to know which of these three processes or which combination of processes underlies the pattern of ontogenetic change that is observed in the skeleton. Broadly considered, growth and development can be viewed as a continuum wherein ontogenetic changes are the result of interrelated processes that originate in the genes and gene-environment interactions, but may be the outcome of external factors independent of genetics as well (Sultan and Stearns 2005). Nevertheless, it is desirable to document the pattern of growth and development and attempt to partition ontogenetic changes according to the responsible process, to the extent that it is possible.

It is through growth studies that we understand when and how pattern differences in adult morphologies manifest. For example, longer human legs (compared to chimps) are achieved through faster and extended growth, according to a comparative ontogenetic study by Simpson et al. (1996). The similar forelimb lengths of humans and chimpanzees are attained through short, fast growth in chimpanzees, compared to the longer, slower growth period in humans (Simpson et al. 1996).

Ontogenetic studies are particularly helpful for addressing behavioral questions in fossil species because morphology that is behaviorally labile can be identified and tracked over developmental time. Such studies of living species provide examples of the influence of activity on the structural properties and shape of the skeleton (e.g., Jungers et al. 2002; Ruff 2003; Raichlen 2005; Shapiro and Raichlen 2006; Young 2006; Cowgill 2007). For example, compared to exercised adults, exercised juvenile humans, sheep, and pigs build more cortical bone (Ruff et al. 1994; Lieberman and Pearson 2001; Lieberman et al. 2001, 2003). Some evidence, reviewed in Pearson and Lieberman (2004), suggests that activity early in life sets the stage for adult morphology, which is comparatively unresponsive to loading, while other studies, such as those on phanageal curvature (e.g. Richmond 2003, 2007), suggest otherwise.

While activity patterns may be an important component of bone apposition and shape of long bone shafts and joints, another prime source is body mass. For example, the adolescent growth spurt in humans is associated with a corresponding increase in cortical thickness, which may relate in turn to the increase in body size (Ruff et al. 1994; Trinkaus et al. 1994), although increases in both body mass and cortical thickness may simply be a result of the same hormonal changes associated with the growth spurt. Either way, these findings demonstrate that the skeleton is labile and alters in response to repetitive activity, such as locomotor behaviors, as well as internal factors such as an increase in body mass. Skeletal alteration in response to external factors such as locomotion, is often referred to as phenotypic plasticity. The value of phenotypic plasticity is particularly clear if the interest is in identifying actual behaviors practiced by *Australopithecus.* If a skeletal trait is shaped by a specific activity, the presence of it in *Australopithecus* probably indicates that the activity was practiced.

Lovejoy and colleagues (Kalmey and Lovejoy 2002; Lovejoy et al. 2002, 2003) caution that the relationship between loading regimes and bone structure is often overdrawn. Citing experimental studies (e.g., Rubin et al. 2001), Lovejoy et al. (2002, 2003) argue that there may not be a consistent relationship between strain magnitudes and bone apposition, which makes them skeptical that the role of external loads in producing bony change is understood, and even more skeptical that bone can be shaped simply by activity. They further contend that the shape of bony structures, including under loading regimes, is very often under genetic control. Thus, it is important to limit a discussion of the relationship between activity and ontogenetic change to well-documented cases.

The ideas of Lovejoy and colleagues are greatly influenced by the burgeoning field of evolutionary developmental biology, in which morphogenesis of the mammalian skeleton is being revealed (Shubin et al. 1997; Wolpert 1998; Carroll et al. 2001). Studies of morphogenesis show that morphology in place at the earliest stages of development (i.e., before substantial behavioral input) reflects genetically integrated aspects of the ontogenetic program. When taxa differ in fetal skeletal characteristics, the differences are likely to be due to be genetic differences. Such observations provide clues to selective histories in lineages. As an example, Young's (2008) study of growth in anthropoid scapulae shows that taxon-specific adult morphology is in place early in development, with subsequent growth resulting in relatively minor changes. Taxon-specific infant morphology is largely the product of developmental programs that differ due to separate evolutionary trajectories (Young 2008).

Divergent adult morphologies can also reflect genetic differences, but other processes (such as phenotypic plasticity) can also be responsible. In contrast to the anthropoid shoulder, Tardieu et al. (2006) report that the epiphysis of the human distal femur alters significantly in shape and proportion during the course of development. Perhaps the distal femur is more affected by external factors, such as locomotor behaviors, than the scapula, which can only be explored through the study of young and adult skeletons. If so, then ontogenetic studies of the *Australopithecus* skeleton could potentially help identify actual behavior during life (via phenotypic plasticity), genetically integrated morphologies (via early ontogenetic morphology), and selective histories (via comparative ontogenies).

Cranial and Dental Evidence for Growth Pace in *Australopithecus*

Studies of cranial and dental development in *Australopithecus* provide some information about pace and duration of growth, which appears to be closer to an ape, than human, pattern (see Bromage 1987, 1989; Anemone et al. 1996; Dean et al. 2001; Robson and Wood 2008). Robson and Wood (2008) emphasize that the similarity in body mass between early hominins and *Pan*, and presumably the last common ancestor, provides additional evidence for a faster pace of growth in *Australopithecus* compared to modern humans. Given the possibility of an apelike growth pattern, it is reasonable to infer that life history features of modern humans, such as long childhood and long adolescence, were absent in *Australopithecus* (Bogin 2003). Accordingly, life history-related variables such as social organization and reproductive patterns, among others, probably differed significantly between early hominins and later taxa with growth rates closer to that in modern humans (Leigh 2001; Bogin 2003).

The rate and pattern of growth of the *Australopithecus* postcranium has been mainly inferred on the basis of cranial, dental, and body size evidence. The possibility exists that postcranial and cranial growth are separately controlled and are responsive to different environmental stimuli (Leigh 2001), making inferences from the cranium and dentition not necessarily applicable to postcranial growth. Further, although the pace of growth may have been more like that of apes, the pattern clearly differs because the outcome of growth—the australopith skeleton—is radically different from that of apes. The important goal is to understand how the skeletal differences arise. Thus, the postcranial studies that address growth pace and pattern in *Australopithecus* are part of the discussion below.

Postcranial Ontogeny and Phenotypic Plasticity in *Australopithecus*

Locomotor behavior in *Australopithecus* has been studied intensely in the adult skeleton (see reviews in Stern 2000; Ward 2002), but the nature of the skeletal evidence makes it difficult to resolve the question of how much, if any, arboreal behavior was part of the hominin locomotor repertoire. According to Ward (2002, 2013), the difficulty, in part, is construal of the evidence. Does the presence of anatomy used by apes in arboreal locomotion indicate arboreal behaviors in a hominin taxon that possesses a similar morphology?

One way to reconstruct behavior in early hominins is to focus on anatomical traits that are affected by behavior. These are phenotypically plastic and generated in response to activity, rather than being under direct genetic control. Age variation in phenotypically plastic anatomy is a valuable indicator of the chronology of adoption of particular behavioral patterns. This is because the presence of the trait at a particular growth stage indicates the adoption of the behavior that induced the trait. Such analysis is difficult in *Australopithecus* because of the lack of juvenile specimens, but simple comparisons between the very young and adult are possible.

It is not entirely clear which anatomical traits are modified as a consequence of behavior, but for bipeds the bicondylar angle is one good candidate (Tardieu and Trinkaus 1994; Berge 2002; Lovejoy 2007). The presence of the bicondylar angle in bipeds is a well-documented behaviorally induced trait (Tardieu and Trinkaus 1994; Tardieu and Damsin 1997; Tardieu 1998, 1999; Lovejoy et al. 2002). In bipeds the femoral shaft (identified as a plane that bisects the condylar surface) deviates from a parasagittal plane on average 8–11°, compared to the shafts of apes which deviate from this plane less (1–5°) (Tardieu and Trinkaus 1994; Tardieu 1999; Shefelbine et al. 2002; Lovejoy 2007). The bicondylar angle starts to develop with the acquisition of walking and results from increased loading on the medial condyle and concomitant bone apposition mediodistally (Tardieu and Trinkaus 1994; Shefelbine et al. 2002). The angle effects flexion and extension in a parasagittal plane, at the same time maintaining the center of gravity at the midline of the body (Tardieu and Trinkaus 1994; Lovejoy et al. 2002). Adult *A. africanus* and *A. afarensis* exhibit a bicondylar angle (Lovejoy 1975; Lovejoy et al. 1982). Adolescent and young adult *A. afarensis* femora also express a bicondylar angle (Tardieu 1998, 1999; Alemseged et al. 2006; Harmon, personal observation). Generally, the angle is higher than that of modern humans owing to the shorter legs and wider acetabulae in early hominins (Tardieu and Trinkaus 1994; Lovejoy 2007). The Dikika baby (*A. afarensis* DIK-1-1) adds to understanding of the ontogenetic development of this trait in early hominins. At 3 years, this individual already exhibits a bicondylar angle and must have engaged in bipedal locomotion (Alemseged et al. 2006).

Curvature of bones of the hands and feet may be a developmental response to arboreal behaviors (Stern et al. 1995; Jungers et al. 2002; Richmond 2003, 2007). Richmond (2003) found that curvature increased postnatally in hominoids, but in secondarily terrestrial African apes, decreased as larger body size and concomitant increased terrestriality were obtained. A recent analysis by Richmond (2007) demonstrates that phalangeal curvature reduces bending strain during grasping. The biomechanics of phalangeal curvature and the epigenetic production of this trait combine to suggest that the possession of this morphology signifies that grasping is regularly practiced.

The phalanges of the Dikika baby are curved (Alemseged et al. 2006). The phalanges of adult *A. afarensis*, *A. africanus*, and *Australopithecus anamensis* are also curved (Bush et al. 1982; Ward et al. 1999, 2001). While not formally quantified, the phalanges and metapodials from young (infant and adolescent) individuals in the *A. afarensis* assemblage from A.L. 333 appear to be more curved than those of recent humans and are comparable to juvenile chimpanzees (Fig. 18.1). It seems likely that metacarpal and metatarsal curvature is produced through the same process as phalangeal curvature. A modest degree of curvature is described among adult and juvenile *A. afarensis* metacarpals and metatarsals as well (Bush et al. 1982; Latimer et al. 1982; Drapeau et al. 2005; see Fig. 1). Apparently, in *A. afarensis*, grasping was undertaken at an early age. Curved phalanges could be associated with the grasping of arboreal supports, or grasping of the mother's coat as commonly occurs in extant primates, as it is possible that hairlessness had not yet evolved in *Australopithecus* (Wheeler 1992; Jablonski 2004). However, the persistence of curved phalanges into adulthood makes arboreal grasping the most reasonable cause among older individuals.

There are other skeletal features that appear to be altered in response to behavioral demands. Humeral torsion, which refers to the orientation of the head relative to the distal end of the shaft, changes from the juvenile stage to adulthood, possibly in response to activity (Larson 1998, 2007; Rhodes 2006; Cowgill 2007). According to Tardieu et al. (2006) and Lovejoy (2007) the elliptical profile of the lateral condyle of the distal femur in adult humans is generated, at least in part, from bipedal walking, and is not present in very early pre-walking stages. Unfortunately, sample limitations do not permit examination of young and adult humeral torsion or lateral condyle morphology in *Australopithecus*.

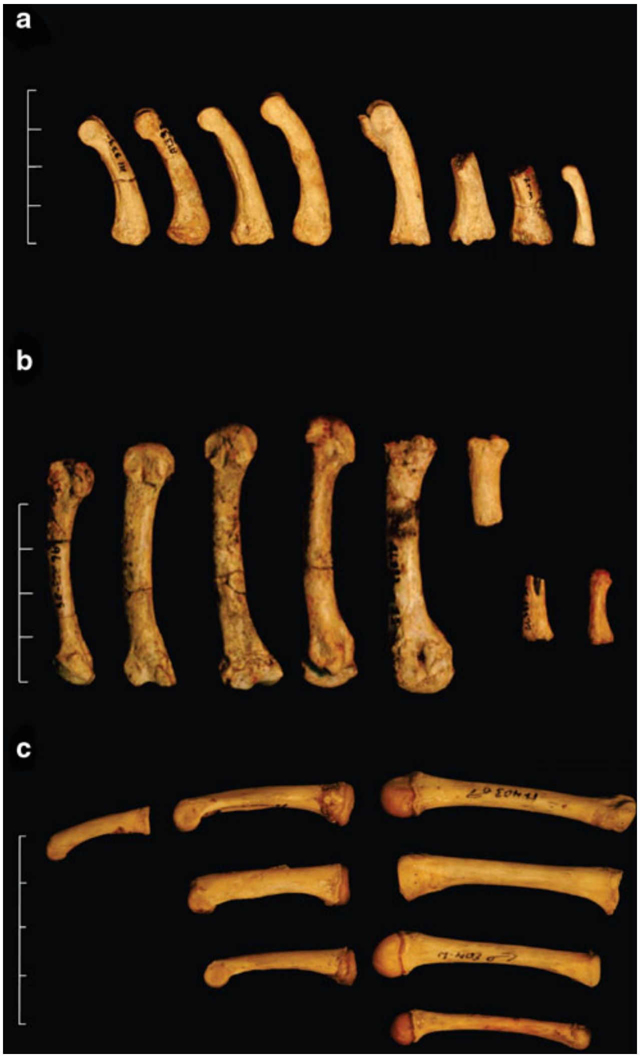

Fig. 18.1 Manual phalangeal curvature. **a** *A. afarensis* proximal phalanges; **b** *A. afarensis* metacarpals. The four bones on the *right hand side* of both images are juvenile. *Extreme right*: Infant. **c** Juvenile (adult M1 erupted) chimpanzee metacarpals and phalanges. *Scale bars*: 4 cm

Assuming that the traits described above accurately reflect behavioral practice, the Dikika baby and other juvenile hand bones provide evidence that both bipedality and arboreality were established at a young age in *A. afarensis*. The presence of traits that are induced during arboreal behaviors early in development makes other explanations, such as the retention of primitive traits, less likely.

Genetically Mediated *Australopithecus* Morphology and Evolution of Developmental Programs

Among anthropoids, adult features of scapular morphology appear very early in development, suggesting that scapular morphogenesis is genetically mediated and phylogenetically meaningful (Young 2003, 2008). This finding is interesting in light of the description of scapular morphology of the *A. afarensis* skeleton DIK-1-1 (Alemseged et al. 2006). The glenoid fossa is cranially oriented, the infraspinous fossa is narrow (both features that are similar to apes) and the spine is not as horizontally oriented as it is in humans (Alemseged et al. 2006). Alemseged et al. (2006) describe the morphology as unique, but closer to gorillas than to humans. Features shared by DIK-1-1 and apes, such as cranial orientation of the glenoid fossa, have been linked to frequent overhead arm movements associated with suspension and climbing (Larson 1993, 2013). The shape of the juvenile *A. afarensis* scapula records genetically generated form that is the result of selection for arboreal behavior in the evolutionary history of the lineage. Alemseged et al. (2006) interpret the scapular morphology as evidence for an arboreal component in this otherwise bipedal taxon (Green and Alemseged 2012). However, the possibility that *A. afarensis* retained these features from an arboreal ancestor, but did not engage in frequent arboreal behaviors cannot be rejected on the basis of shoulder morphology alone.

Genotypic variation is hypothesized to explain differences in the hominoid pelvis and pelvic growth patterns (Williams and Orban 2007). As is the case with anthropoid scapular morphology (Young 2008), shape differences among taxa, such as the long ilium of apes and the short ilium and ischium of humans, are present very early in ontogeny (Williams and Orban 2007). Pelvic elements are rare in fossil taxa and the only juvenile examples (MLD 7 and MLD 25) are attributed to *A. africanus*. According to Williams and Orban (2007) juvenile *Australopithecus* differs from both humans and great apes in having a long ischium and short ilium, a pattern that is continued in adult pelves, and is particularly accentuated in *A. afarensis* (A.L. 288-1) compared to *A. africanus* (Sts 14). Based on the juvenile pelves and the adult Sts 14, the *A. africanus* pattern of growth included rapid early expansion of anterior ilium length as in great apes. However, the length of the ilium is short in adult *A. africanus* and compares best with that of modern humans (Williams and Orban 2007). Thus, the ultimate shape of the *Australopithecus* ilium is short and broad as expected for a bipedal pelvis, but to the extent that it can be determined, the growth pattern (such as rapid early expansion of the anterior ilium) is apelike.

Berge (1998) also argued that pelvic growth in *Australopithecus* was apelike. She proposed that the evolution from *Australopithecus* to recent *Homo* in pelvis growth and morphology reflected growth pattern extension (heterochrony). The basis of the argument is the form of the acetabulo-cristal buttress, which is the same in adult *A. afarensis* and juvenile (but not adult) recent humans (Berge 1998). Thus, the morphological similarity of adult *Australopithecus* and juvenile *Homo sapiens* is evidence for an extension of the *Australopithecus* pattern in *Homo*.

Williams and Orban (2007) agree that adult human and juvenile *Australopithecus* pelves are similar, but they argue that the two groups have different ontogenetic trajectories. The *Australopithecus* trajectory includes a unique growth pattern and shape of the ischium coupled with an apelike rate of expansion of the anterior ilium, which cannot be reconciled with the human trajectory by invoking simple heterochrony (Williams and Orban 2007). Both studies of the *Australopithecus* pelvis infer an apelike pace for pelvic growth. Berge goes further and attempts to explain the mechanism (heterochrony) that ultimately leads to the modern human pattern, an interpretation that is not supported by Williams and Orban (2007).

From studies of the hind limb it appears that *Australopithecus* lacks the adolescent growth spurt that characterizes recent humans (Berge 1998, 2002; Tardieu 1998). In recent humans, the adolescent growth spurt effects the elongated hind limb and broad ilium. In *Australopithecus* the broad ilium is obtained prior to adolescence (Williams and Orban 2007), but the hind limb is not elongated. The hind limb of *Australopithecus garhi* may be elongated (Asfaw et al. 1999), and it remains to be seen whether this taxon is an exception to the apparent *Australopithecus* pattern of early and rapid growth. That is, the elongated hind limb may have come about through an extended growth period relative to other taxa. An alternative mechanism would be early growth of the hind limb in *A. garhi* that was even faster than that of other *Australopithecus* species, such that a relatively longer hind limb was the result.

In recent humans the pronounced lateral lip of the distal femur resists lateral patellar pull during extension on a valgus knee (Gresalmer and Weinstein 2001; Lovejoy 2007). Lovejoy (2007) identifies a fully expressed lateral lip in *A. afarensis* distal femora and describes this feature as a genetically controlled characteristic of bipeds. On the other hand, Tardieu (1998, 1999) suggests that *A. afarensis* lacks a fully projecting lateral lip. To Tardieu, the weak form of the lateral lip in *A. afarensis* (A.L. 129-1, A.L. 333-4) is evidence for her hypothesis about the pattern of selection in the knee joint (Tardieu 1999). The hypothesis states that the minor degree of lateral lip projection in *A. afarensis* (as described by Tardieu) shows that some epigenetic remodeling in the knee joint took place due to bipedal locomotor behaviors (Tardieu 1999). That is, walking generates the bicondylar angle, which causes the lateral femoral condyle to bear more weight. The pressure of the patella against the lateral condyle induces growth of the lateral lip (Tardieu 1999). Later in hominin evolution, lateral lip projection was independently incorporated into the genome through selection related to striding bipedality (Tardieu 1999; Garron et al. 2003, Glard et al. 2005; Tardieu et al. 2006).

Tardieu's (1998, 1999) hypothesis is meant to account for the pronounced lateral lip in modern humans, and the lack of a pronounced lateral lip in *Australopithecus*. Further, absence of a significantly projecting lateral lip in *A. afarensis* is argued as evidence for absence of the adolescent growth spurt. This is because in humans, the adolescent growth spurt is the time during which the distal epiphysis fuses and the lateral lip reaches adult proportions. The absence in *Australopithecus* implies that the corresponding growth period did not occur (Tardieu 1998). The implication about growth pattern in *Australopithecus* makes sense in the context of a heterochronic model for the differences in growth between early and later hominins (as in the description of pelvis evolution), which may be an inadequate model (see below).

In contrast, Lovejoy (2007) argues that the lateral lip is clearly present in *A. afarensis*, which indicates that the knee joint operated as it does in modern humans, with increased contact (compared to apes) between the tibia and femur, and flexion–extension occurring in the midline. He explains that the failure of some scholars (e.g., Tardieu) to recognize the lateral lip is due to incorrect means of trait assessment. Because humans develop the flared lateral lip early in ontogeny, Lovejoy (2007) suggests that this feature is part of the hind limb developmental program and alteration from the ape condition is due to selection.

A different pattern of selection is envisioned for the posterior attachment of the meniscus on the hominin tibia (Tardieu 1999). Only recent humans (and possibly fossil *Homo*) possess a crescent shaped lateral knee meniscus with both anterior and lateral attachment to the tibial spine, which is part of the locking mechanism of the bipedal knee (Senut and Tardieu 1985; Aiello and Dean 1990; Tardieu 1999; Lovejoy 2007). Our closest relatives have a ring-shaped meniscus with a single attachment (Aiello and Dean 1990; Tardieu 1999). The shape of the meniscus in *Australopithecus* is unknown, but only a single attachment site appears on the tibial intercondylar eminence in *A. afarensis* and *A. anamensis* (Senut and Tardieu 1985; Tardieu 1999; Ward et al. 2001). Tardieu (1999) suggests that striding bipedality, which came later in hominin evolution, drove selection for a change to the meniscus that resisted the forces of external tibial rotation and allowed for full knee extension. Implicit in this argument is that the character of *Australopithecus* bipedality was very different from recent humans and required less knee mobility and stability. On the other hand, Holliday and Dugan (2003) have shown that the presence of the posterior notch on the intercondylar eminence is equivocal or absent in nearly 20 % of a sample of modern humans, suggesting that the absence of the trait in *Australopithecus* is not necessarily an indication of non-human meniscus morphology.

Like Berge (2002), Tardieu (1998) proposes that the extension of the early hominin growth pattern explains the evolutionary shift from *Australopithecus* distal femoral morphology to that of modern humans. The shift relates to features found in recent humans such as exaggerated projection of the lateral lip of the lateral condyle, and the anteroposterior lengthening and increased curvature of the condylar surface. Ontogenetic study of human femora demonstrates that these features arise during the adolescent growth spurt (Tardieu 1998). Perhaps because it is difficult to ascertain whether *Australopithecus* had a comparable growth spurt in the cranium or postcranium, time hypermorphosis is presented to explain human knee morphology. Thus, Berge (2002) and Tardieu (1998) invoke extension of the early hominin growth pattern (heterochrony), and in particular an extended adolescence, to explain evolutionary changes in hind limb morphology.

An informal examination of adult and juvenile *A. afarensis* distal femora supports Lovejoy's (2007) contention that a pronounced lateral lip is present in adults. There is some evidence for an extended lateral lip in DIK-1 (Alemseged, personal communication). However, the degree of lateral lip expansion awaits formal assessment and comparison to juvenile humans to determine if humans and *A. afarensis* are ontogenetically comparable in this trait. At this point, it is not clear whether the lateral lip visible in *A. afarensis* is simply the result of bipedal walking, as Tardieu suggests, or if it is part of the genetic developmental program, as Lovejoy contends.

The hypothesis of heterochrony is difficult to evaluate because the growth patterns of *A. garhi* and *A. anamensis* are completely unknown and may deviate from those of *A. afarensis* and *A. africanus*. Moreover, heterochronic change rests on the assumption of an ancestral and descendant relationship between *A. afarensis*, *Homo erectus* (KNM-ER 15000), and *H. sapiens*. While this relationship may or correct in general, it is certainly oversimplified as there are numerous other potentially related taxa, such as, *A. africanus*, *A. garhi*, and *H. rudolfensis*.

Berge (2002) in particular structures her argument around a perception of the morphological intermediacy of *A. afarensis* and *A. africanus* between the last common ancestor and recent humans, which is meant to support the inference of an intermediate growth pattern. The mosaic nature of the adult skeleton of these taxa, which includes, apelike, humanlike, and unique traits (Abitbol 1991; Harcourt-Smith and Aiello 2004; Drapeau et al. 2005; Lovejoy 2005; Harmon 2009) make it difficult to uncritically agree that *Australopithecus* is merely paedomorphic relative to modern humans. The relationship between growth patterns in *Australopithecus* and in *Homo* is likely to be complex.

Conclusion

Based on the high bicondylar angle and curved phalanges, which develop in response to behavior, arboreal grasping and bipedality probably constituted the locomotor regime of *A. afarensis* and *A. africanus*. Based on current evidence, *A. afarensis* and *A. africanus* were habitually bipedal, but incorporated arboreal grasping postures into their repertoire. *A. afarensis*, at least, acquired these skills at a young age, as demonstrated by the 3-year-old DIK-1-1 (Alemseged et al. 2006). Further confirmation of some arboreal component in *A. afarensis* comes from this individual's scapular morphology (Alemseged et al. 2006). Postcranial remains from Bouri, Ethiopia, possibly belonging to *A. garhi*, exhibit the same phenotypically plastic morphology, but in the context of an elongated hind limb, among other limb proportion differences (Asfaw et al. 1999). Despite the differences, curved phalanges indicate that arboreal grasping and bipedality constituted the locomotor regime of this taxon as well.

It could be argued that the apelike shoulder morphology in DIK-1-1 is a retention from an earlier ancestor, and does not necessarily indicate arboreal behaviors during life. However, Alemseged et al. (2006) favor a behavioral, rather than primitively retained, explanation, and phenotypically plastic morphology present in *Australopithecus*, such as the bicondylar angle (e.g., Tardieu and Trinkaus 1994) and phalangeal curvature (e.g., Jungers et al. 2002; Richmond 2007), undermines the notion that these characteristics were merely phylogenetic baggage of little use to these habitual bipeds.

It is evident from cranial, dental, and limited study of the postcranium that the slow recent human growth pattern did not evolve in *Australopithecus*. Even though the pace of growth in *Australopithecus* was closer to that of apes, the morphological outcome of skeletal growth was very different. Growth outcomes that radically differ from those of apes are evident in the adult *Australopithecus* skeleton, such as derived pelvic and knee joint morphology. Of these, the short broad ilium and long ischium are present in juvenile *A. africanus* (Williams and Orban 2007) and may have been present in juvenile skeletons of other *Australopithecus* as well, which will become clearer once the DIK-1-1 skeleton is fully prepared and examined. Early developmental evidence of adult morphology confirms that pelvic morphology changes from the ape condition (although the condition of the last common ancestor is unknown) were incorporated into the genome and were the consequence of selection operating in favor of locomotor/postural changes.

The genesis of the anteriorly projecting lateral lip of the distal femur is less clear. This feature, which is part of the genetically controlled morphogenetic program of humans (Tardieu et al. 2006; Lovejoy 2007), is present in some adult *A. afarensis* femora. The juvenile condition is not quantified, but some degree of expansion is evident. The idea, suggested by Tardieu (1999), that the force of the patella on the lateral lip during bipedal knee extension generated the anterior projection in *A. afarensis* is not unreasonable but cannot be fully evaluated with the present evidence. It also remains unclear when in hominin evolution the posterior attachment of the lateral meniscus of the knee was incorporated into the developmental program.

The idea that hind limb growth in recent *Homo* is heterochronic extension of the *Australopithecus* pattern is probably oversimplified and is confounded because the phylogenetic relationship among *A. afarensis, A. africanus, A. garhi*, and *Homo* is not at all understood. While developmental programs are conserved (Lovejoy et al. 1999, 2003), there are variable skeletal morphologies among early hominin taxa (McHenry and Berger 1998; Richmond et al. 2002; Harcourt-Smith and Aiello 2004; Drapeau et al. 2005; Green et al. 2007; Harmon 2009), and between early hominins and recent humans (Bramble and Lieberman 2004; Richmond and Jungers 2008). Such variability makes it very difficult to invoke simple heterochrony as the sole explanation for these possibly variable ontogenies. Advances in evolutionary developmental biology and the addition of juvenile fossil material like DIK-1-1 will help to determine if additional processes such as heterotopy can help explain evolutionary developmental changes in hominins.

Addendum

The present chapter was finished and reviewed at the time of the author's tragic death. Will Harcourt-Smith kindly incorporated the reviewers suggestions and comments.

Kaye Reed wrote the abstract. Elizabeth's final contribution to the field is appreciated by all of us who worked with her and knew her.

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