Chapter 14
Natural Selection as Agent of Evolutionary Change: A View from Paleoanthropology

Ian Tattersall

Abstract Following the triumph of the Modern Evolutionary Synthesis in the 1940s and 1950s, natural selection became viewed by most anglophone evolutionary biologists as the primary or even the only instrument of evolutionary change. Under the "hardened" version of the Synthesis as it was absorbed into paleoanthropology after 1950, generation-by-generation change under selection's guiding hand became not only a necessary but a sufficient vehicle for explaining the unilinear pattern of human evolution that was perceived under the allied notion that the human "niche" was too broad to admit the existence of more than one hominid species at any one point in time. Subsequent additions to the hominid fossil record, as well as a better understanding of evolutionary process itself, have in contrast revealed a pattern of hominid diversity over time much better explained by sorting propelled by drift and external environmental change than by species-intrinsic natural selection as classically envisaged. Indeed, selection—a mathematical certainty in any population in which more individuals are born than reproduced—very plausibly acted among extinct hominids much more as a crucial homeostatic mechanism ("stabilizing selection"), than as an agent of change.

Keywords Natural selection · Evolution · Modern synthesis · Adaptation · Human fossil record · Paleoanthropology · Phyletic gradualism · Punctuated equilibria

14.1 Introduction

The reductionist human mind loves nothing better than a good story; and a major aspect of Charles Darwin's multifaceted genius was to be an inspired storyteller. Of the many scientific stories Darwin told, none was more effective in selling the idea of evolution to an initially skeptical mid-nineteenth-century audience than his account

I. Tattersall (✉)
Division of Anthropology, American Museum of Natural History, New York, NY, USA
e-mail: iant@amnh.org

of natural selection. Of course, Darwin's thumbnail definition of evolution as "descent with modification" captures the two essential attributes of evolution without making reference to any mechanism of change whatever, selection or otherwise; and it still remains incomparably the best capsule formulation of the phenomenon it describes. But nonetheless, in explanatory terms, it is hard to match the sheer "why didn't I think of that?" power of the notion that better adapted individuals leave behind more offspring sharing their hereditary features than less well-favored ones do and that the effect multiplies over the generations. After all, natural selection is a mathematical certainty in any population in which more offspring are born than survive to reproduce; and in the form articulated by Darwin, it is an agency that logically should make gradual change within lineages of organisms virtually inevitable over time.

Accordingly, although the young Darwin had been acutely—and uncomfortably—aware of the many complexities of the natural world that make any reductionist explanation of evolutionary phenomena risky (see Eldredge 1995, 2016), by the time he was goaded by the arch-adaptationist Alfred Russel Wallace (1858) into publishing *On the Origin of Species* in 1859, the mature Darwin had more or less convinced himself that competition among organisms for reproductive success was, and continued to be, the principal driver of evolutionary change, despite, as Ernst Mayr (2001) pointed out, a notable dearth of available and provable examples at the time. Among other things (see Bellon, Chap. 3; Delisle, Chap. 4, Schwartz, Chap. 12), it was this lack of direct evidence for natural selection that prompted ongoing opposition from a wide variety of prominent critics such as the saltationist St George Mivart (1871); but by the end of the nineteenth century, the view of natural selection as *the* agent of evolutionary change had gained considerable public and scientific traction, not only in the anglophone UK and USA but also throughout Europe, not least through the efforts of the conflicted Ernst Haeckel (see Levit and Hossfeld, Chap. 5; Schwartz, Chap. 12).

The Darwinian notion that evolutionary change has usually—or even, if you are an ultra-Darwinian, invariably—been driven by natural selection depends on the phenomenon of heredity, whereby the distinctive biological characteristics of parents are often passed along to their offspring more or less intact. That this was, and is, the case had of course been well-known to animal and plant breeders and genealogists from time immemorial; and such knowledge was enough by itself to allow Wallace and Darwin to formulate their ideas of evolution by natural selection in the absence of an accurate notion of heredity. But a fuller understanding of process in evolution depended on a precise understanding of exactly *how* hereditary characters are transmitted between generations; and the dawning of this key comprehension had to await the turn of the twentieth century and the rediscovery of Mendel's principles by the early geneticists (see the account by Mayr 1982; see also Ochoa, Chap. 6).

By that point, the notion that the living biosphere was in some way the product of evolution had become widely accepted by scientists and educated public alike, partly thanks to the seductive powers of the natural selection concept. But the initial rise of the science of genetics produced some bumpy conditions for selectionists, as the

nascent field became polarized between the single-gene "mutationists" in the Mendelian tradition, who fixated on the inheritance of discrete and discontinuous characters (e.g., wrinkled vs. smooth seed pods), and the "biometricians" whose interests lay in continuously varying traits such as body size or stature (for more discussion, see Schwartz, Chap. 12). During the early days, the Mendelians were in the ascendant; and these scientists were in general less receptive than the biometricians to the idea that natural selection was the major propulsive force in evolution. In the end, however, the balance shifted.

What appears in retrospect as the tipping point came in 1918, when the mathematical geneticist R.A. Fisher, confronted with the need to reconcile the results of the Mendelians and the biometricians, came up with what is now known as his "infinitesimal model" of the behavior of genes within populations. Fisher's formulation acknowledged the experimental importance of the single genes of interest to the Mendelians, but it swung the focus back upon the vast majority of traits that were determined by numerous different alleles acting together. In combination, those multiple alleles produced continuous and normally distributed ranges of phenotypes in the populations concerned; and, in its turn, this realization opened the door to quantitative modeling of the action of natural selection (and of other putative influences, such as "mutation pressure") within such populations. The infinitesimal model also led eventually to the recognition of the "norm of reaction," which sees the genotype as specifying a range of potential outcomes among which the environment selects (see Clausen and Hiesey 1958).

In a period of lively debate over evolution, and of natural selection's role in it (see Ceccarelli, Chap. 7), the rise of quantitative population genetics also paved the way for what eventually became known as the "Modern Evolutionary Synthesis" (Huxley 1942; see discussion by Adams, Chap. 8; Schwartz, Chap. 12). This convergence began during the 1920s and 1930s, as the theoretical modeling of Fisher and other luminaries such as Sewall Wright (see account by Provine 1986) and J. B. S. Haldane (see account by Clark 2011) was integrated with empirical data from genetics (Dobzhansky 1937), systematics (Mayr 1942), and paleontology (Simpson 1944) to produce what was later proclaimed (not least by Mayr 1963, 1982) to be a coherent and comprehensive account of the evolutionary process (but see Schwartz, Chap. 12). Most anglophone evolutionary biologists came quite rapidly to subscribe to this account, but while it had been fairly nuanced in its earlier manifestations (for discussions on differences of viewpoint among its founders, see discussions by van der Meer, Chap. 11; Ochoa, Chap. 10; Schwartz, Chap. 12; see also Levit and Hossfeld, Chap. 9; see Granovitch, Chap. 13, for some interesting non-anglophone views), by mid-century, the Synthesis had "hardened," to use Steve Gould's (1983) memorable term, into a simple formula that had shed many of the complexities recognized by earlier naturalists (and summarized by Schwartz, Chap. 12) in favor of reducing the multifaceted evolutionary process (or, rather, processes) to little more than the action of natural selection within gradually transforming lineages of organisms. As Esposito (Chap. 2) implies, this reductionist outcome may well reflect an unduly tidy view of history; and the actual intricacies of the real world are clearly reflected in the myriad popular misunderstandings of

evolutionary process elaborated by Watts (Chap. 16). Nonetheless, the ultimate reductive formulation, as energetically promoted by Mayr, was compelling enough that most working systematists were happy to accept that, while identifiable (albeit normally polytypic) at any one point in their history, species actually lost their individuation with time, as they gradually transformed themselves into distinctive new species as selection did its inexorable work.

So persuasive was the reductionist natural selection metaphor as thus deployed (time + natural selection = evolution) that it was many years before the dictates of the Synthesis and the canonical authority of its founding fathers began to be seriously questioned. The inevitable rethinking was eventually set in train by Niles Eldredge and Steve Gould (1972), both invertebrate paleontologists, who pointed out in a now classic but then frequently reviled paper that the Emperor of the Synthesis had been remarkably flimsily clad from the very start (see also Schwartz, Chap. 12). Extrapolating empirically from the invertebrate fossil record, Eldredge and Gould contended that fossil species, instead of gradually evolving into new forms under natural selection, typically showed stasis—non-change—over their frequently quite extended lifetimes. In Eldredge and Gould's view, species characteristically have births (at speciation), histories (as basically stable entities), and deaths (at extinction). During their life spans, they might give rise to descendant species in short-term speciation events, and they might even persist alongside those descendants for long periods of time. But what they do not do is gradually evolve themselves out of existence as envisaged by the Synthesis. In other words, where the Synthesis had taken away the immemorial notion that species were bounded entities, Eldredge and Gould re-established ancient wisdom by arguing on empirical grounds that species really do have real, objective, existences in nature.

In articulating this perspective, Eldredge and Gould also, and inevitably, questioned the role of natural selection as the dominant force guiding evolutionary change. Indeed, they viewed species and populations as basically "homeostatic systems," suggesting that essentially stochastic events, such as invasions of new environments by geographically peripheral populations, were more plausible than selection as drivers of such well-established phenomena of change as adaptive radiation and morphological trends. What's more, in empirically basing their argument on invertebrate fossils, Eldredge and Gould forcefully reinstated the fossil record as the major arbiter of evolutionary mechanism. Under the Synthesis, paleontology had been relegated to the essentially clerical role of documenting the products of the "Phyletic Gradualism" propounded by the geneticists and systematists who produced the basic underpinnings of the Synthesis (the influential mammal paleontologist G. G. Simpson is usually credited as one of the founding triumvirate of the Synthesis, and he certainly achieved a major advance in eliminating orthogenetic echoes from paleontology; but while his *Tempo and Mode in Evolution* (1944) showed that he acutely appreciated the importance of the major discontinuities in the fossil record, the ultimate thrust of the book was to bring paleontology into line with gradualist thinking; see also Ochoa, Chap. 10). Under Eldredge and Gould's "Punctuated Equilibria" model, in contrast, paleontology resumed center stage as the key repository of information about evolutionary process, which was, of course, highly

appropriate; paleontology is, after all, our only direct means of accessing, however incompletely, the historical record of how biological history has actually unfolded and on what time scales.

Subsequently, Eldredge (e.g., 1978) took to characterizing the two contrasting views of evolutionary process in slightly modified and more accurately descriptive terms, as "transformational" vs. "taxic," the former depending on long-term natural selection as classically envisaged and the latter relegating selection at best to ephemeral episodes of speciation. Under the taxic paradigm advocated by Eldredge, evolution is principally about the origin of new species and much less about the differential reproductive success of individuals within old ones.

Coincidentally—but not inconsequentially—Eldredge and Gould published their broadside not long after the long-ascendant "expert judgment" paradigm of systematics had begun to be supplanted by the more rigorous demands of the newly surgent cladists. This new breed of systematists insisted that relationships among species should be reconstructed using synapomorphies to link sister taxa (Hennig 1966) and thus that phylogenies should be testable rather than simply declarative and based on little more than informed subjective opinion. And even if Eldredge and Gould's views of evolutionary process had not on their own begun to change minds, the intrusion of cladistics would, by itself, have been bound to throw the emphasis in evolutionary biology back upon taxa as discrete entities, each one defined by characters and with an individuated history. The twin conceptual revolutions in systematics and evolutionary theory of the late 1960s and early 1970s were ontologically unrelated (indeed, some radical cladists even insisted that evolution was not a necessary prerequisite for understanding pattern in nature), but in synergy they radically transformed both the invertebrate and the vertebrate branches of paleontology within a remarkably short space of time. As usual, though, paleoanthropology remained an exception.

14.2   Early Paleoanthropology

Invertebrate paleontology was largely born within the science of geology, while most early vertebrate paleontologists emerged from the very different realm of comparative anatomy. Nonetheless, despite their great disparity in origins, the two disciplines shared from the beginning a profound appreciation of the importance of diversity in nature. After all, the processes of distinguishing among species, and of establishing relationships within larger groups, were of equal importance to the scientists who were, on the one hand, trying to sort out facies and biostratigraphic sequences on varying scales and to those who, on the other hand, were attempting to make evolutionary sense of the bewildering range of structural variations on the basic vertebrate and invertebrate themes. In dramatic contrast, the roots of paleoanthropology lay in the study of human anatomy. This latter field had traditionally been a branch of the medical sciences; and the issues of systematic and functional diversity in nature as a whole had never been perceived as very relevant to its

practice. Indeed, to anatomists whose focus was on the minutiae of variation and function within one single species, systematics barely seemed to be relevant at all. As the hominid fossil record enlarged, and it became increasingly evident that the hominids were a pretty diverse clade, this limiting perspective should clearly have altered among paleoanthropologists; but in the event, any fossil that was recognizably human—and that its discoverers had therefore sent to someone with an anatomical background for analysis—was usually seen simply as a variation of some kind on the basic progressive human theme. If, of course, it did not more probably lie somehow directly in the line of descent that culminated in *Homo sapiens*.

From the beginning, the idiosyncratic origin of paleoanthropology promoted a marked degree of insularity in the viewpoint of its practitioners. So marked, indeed, that it would hardly be unfair to characterize that viewpoint as "paleoanthropological exceptionalism." For while paleontologists of other stripes were acutely aware that the very first thing that needed to be done in the case of any newly found fossil was to determine exactly where it had fit into the riotous natural diversity of the world in which it had lived, paleoanthropologists saw no such imperative. To scientists in this blinkered specialty, the subtleties and procedures of systematics and classification, painfully honed through efforts to understand non-hominid organisms, apparently seemed largely irrelevant—if, indeed, they thought about them at all.

The reason for this was simple. For while most other paleontologists saw their job as in one way or another to explain how the vibrant diversity of the biosphere had emerged, paleoanthropologists remained fixated on one single species, *Homo sapiens*. Little else mattered. After all, because it is incontestable that the world today contains only one hominid species, the strong temptation is and was to project that single species back into the past by the simple expedient of fitting fossils into the human lineage according to their chronological positions, rather than by trying to make phylogenetic sense of their morphological characteristics. It was, indeed, no accident that such linear concepts as aristogenesis and orthogenesis found some of their strongest proponents in the ranks of the paleoanthropologists, or at least in paleoanthropological contexts (c.f. Osborn 1915; Weidenreich 1947; see also Ochoa, Chap. 10). A major corollary of this linear mode of thinking was to divert paleoanthropological attention away from issues of morphology and evolutionary mechanism in evolution and toward a minor obsession with stratigraphy. To give one simple but eloquent example, while you will find a vast amount of detailed information about fossil hominid sites and their stratigraphies in the leading anatomist Arthur Keith's influential 1915 book *The Antiquity of Man*, you will search his index in vain for any mention whatever of "natural selection." Indeed, Keith's title says it all: his book is all about human antiquity and the anatomical features of fossils, rather than about evolution and the means by which it might have occurred in the hominid family.

Unsurprisingly, given the resulting profound lack of interest in the proper practice of systematics among students of human evolution (or, perhaps more properly, of human antiquity), the first half of the twentieth century saw a vast proliferation of names in the paleoanthropological literature: a proliferation that was entirely out of scale with the expansion of the hominid fossil record itself, as practically every

Table 14.1 Generic terms commonly in use in the pre-war literature for members of the three genera *Australopithecus*, *Paranthropus*, and *Homo* as generally recognized today

Australopithecus africanus
Plesianthropus transvaalensis
Paranthropus robustus
Pithecanthropus erectus
Meganthropus palaeojavanicus
Sinanthropus pekinensis
Atlanthropus mauritanicus
Palaeoanthropus palestinensis
Palaeanthropus heidelbergensis
Protanthropus neanderthalensis
Cyphanthropus rhodesiensis
Javanthropus soloensis
Telanthropus capensis
Africanthropus helmei
Homo spelaeus

new find was baptized with its own zoological name, regardless of any resemblances it might have borne to fossils already discovered. As quoted by his American Museum of Natural History colleague Ernst Mayr (1950: 109), Franz Weidenreich, the distinguished describer of the Peking Man fossils, puts it this way: "[in anthropology] it always was and still is the custom to give generic and specific names to each new type without much concern for the kind of relationship to other types formerly known." By the mid-twentieth century, there were accordingly at least 15 generic labels in use for members of the three genera *Australopithecus*, *Paranthropus*, and *Homo* as recognized by most paleoanthropologists today (see Table 14.1), not to mention dozens more species names. Paradoxically, this welter of nomina would have given the proverbial observer from Mars the impression of an entirely fictitious diversity of organisms—in a field whose practitioners were signally uninterested in natural diversity as it was understood by other paleontologists! Clearly, some kind of major rethinking was long overdue.

14.3   Paleoanthropology and the Synthesis

The necessary nomenclatural surgery was carried out in 1950 by Ernst Mayr, an ornithologist and evolutionary theorist who unabashedly confessed to "not possessing any first-hand knowledge of paleoanthropology" (Mayr 1950: 109). Instead, Mayr brought the authority of a co-founder of the Synthesis to the self-imposed task of sorting out the "simply bewildering diversity of names" regularly in use by hominid paleontologists, via the expedient of "giv[ing] the categories species and genus a new meaning in the field of anthropology, namely, the same one which in recent years has become the standard in other branches of zoology" (Mayr 1950: 109). By "new meaning," he was referring to the "population thinking" that was a

central feature of the Synthesis (and had, indeed, been a major legacy of Darwin's thought). This viewpoint downplayed typology in favor of emphasizing intra-species variability among individuals. In this perspective, according to Mayr, if several species of the fruit fly *Drosophila* were blown up to human size, "it would be apparent even to a lay person that they are probably more different from each other than are the various primates and certainly more than the species of the suborder Anthropoidea." Having thus arbitrarily (and apparently with a straight face) disposed of form as a criterion for recognizing putative (and expectedly polytypic) hominid species and genera, Mayr proceeded to claim that, across the board, genera and even species were much more importantly distinguished by their "adaptive zones" than by their morphologies. His colleague and fellow architect of the Synthesis, Theodosius Dobzhansky, had already surveyed the fossil hominids and concluded that "there is no reason to suppose that more than a single hominid has existed on any time level in the Pleistocene" (Dobzhansky 1944: 264), and Mayr upped the ante by declaring that the hominid adaptive zone/ecological niche is so broad as to obviate *in principle* the existence of more than one hominid lineage at any one point in time. As he put it: "The ecological versatility of man and his slowness in acquiring reproductive isolating mechanisms have prevented the breaking up of *Homo* into several species" (Mayr 1950: 117). See Baravalle (Chap. 15) for an overview of the issues of "cultural evolution" that inevitably intrude in this context.

The systematic conclusion was inevitable: in Mayr's view, only one lineage had ever existed in the entire long history of the hominid family. All members of that consistently evolving polytypic lineage had belonged to the genus *Homo*, within which he perceived a gradually transmuting succession of three species. *Homo transvaalensis* (what we would nowadays call the australopiths) had gradually given rise to *Homo erectus* (as then known from Java and China), which in its turn had insensibly changed over time into *Homo sapiens* (a species that, as Dobzhansky had already proposed, also included the Neanderthals, now differentiated merely at the level of subspecies). Here was the hardened synthesis with a vengeance: a braided stream of hominids flowing and reticulating across time, driven all along by natural selection that somehow contrived simultaneously to respond to local conditions and to maintain the biological coherence of the lineage.

Delivered at an enormously influential conference held on Long Island in 1950, Mayr's diatribe dropped on paleoanthropology like a bombshell. Coming just after the huge disruptions of World War II, and at a time when the old guard of anatomists was ageing out of the profession, the blow had been delivered at what was a propitious moment for the Synthesis. Younger paleoanthropologists, in particular, were vulnerable to the implied—and entirely accurate—accusation that their elders had been operating in what was essentially a theoretical vacuum, and they were traumatized accordingly. From far-away South Africa, John Robinson (1953) did complain that the robust and gracile australopiths formed two demonstrably separate lineages, and Mayr (1953) himself actually conceded this with remarkable rapidity, albeit rather grudgingly and in a footnote. Nonetheless, he still felt obliged to reproach Robinson by tossing in the canard that the latter had not addressed "the serious problem of competition" (Mayr 1953: 281): a "problem" that, of course,

existed only if one fixated on Mayr's own unilinear model. Still, aside from Robinson and such odd outliers as Solly Zuckerman (see Ashton and Zuckerman 1951), the capitulation of anglophone paleoanthropology to Mayr's new scenario was both sudden and effectively complete—to such an extent that, for more than a decade, hominid paleontologists hardly dared to use zoological names for the objects of their study, warily avoiding taxonomic designations and referring to individual fossil specimens by their site identifiers (see Tattersall 2018a).

Such was the shock inflicted by Mayr that his minimalist nomenclatural strictures still unhappily reverberate in paleoanthropology some 70 years later, even as the human fossil record, and our perspective on it, has vastly expanded. Still, the fallout from his attack was not limited to the naming and recognition of taxa at the species and genus levels. This was because a major, and much more salutary, effect of Mayr's criticism was to make paleoanthropologists keenly aware of the importance of mechanism in evolutionary studies of all kinds, including their own. Accordingly, as the new generation of hominid paleontologists took over, ideas of natural selection and adaptation entered their discipline to a far greater extent than they had ever done before, and indeed, selection and adaptation (each of them implying and affirming the other) have been the primary foci of interest in modern human evolutionary studies ever since—even as, on the minus side, chronology still rules the day, and it remains distinctly unfashionable to "argue about names" regardless of the self-evident fact that, if you are ever going to properly understand the evolutionary/ecological play, you will first need to have a pretty accurate idea of who the actors are.

Despite this checkered legacy, there can be no doubt that Mayr's intrusion reinvigorated paleoanthropology. There is a distinctly liberated quality to many paleoanthropological publications from the middle 1950s onward, largely due to an overt acknowledgment that the fossils under scrutiny had once been part of living, breathing individuals whose lives could be reconstructed from multiple lines of evidence. Raymond Dart (1925, 1947) and even Franz Weidenreich (1939) had, in their time, exhibited fine fertile imaginations in the domain of ancient hominid behavior, but what was truly new after midcentury was an acceptance that paleoanthropology was a multifaceted science that could substitute empirical fact for imagination and still come up with a dramatic story. Emblematic of this awakening was the early work of F. Clark Howell (1951, 1952), whose studies of European late-middle-to-late Pleistocene hominid fossils possessed a range and a tone that had been missing in pre-war days, integrating morphologies, faunas, environments, and the gradualist evolutionary model to create a picture of a hominid lineage that had flourished through changing and challenging times by diversifying regionally via local adaptation while still retaining its (phylo)genetic coherence.

Howell told a wonderful and erudite story that was both underpinned and animated by a firm Mayrian faith that natural selection could simultaneously act to promote both diversification and coherence within variable and ever-changing lineages. Yet, inevitably, this perspective appears in retrospect as at best incomplete. The reason for this is that when you give primacy in this way to adaptation (usually simply assumed: if it's there, it's an adaptation) in any evolutionary scenario, you

run the obvious risk of distracting attention away from the critical taxic aspect of evolution that Niles Eldredge emphasized in 1978. Species are the central actors in the evolutionary play by virtue of being effectively discrete participants in the ecological drama at any one point in time; and their fates depend on the kind of organism they are overall (and with whom they happen to be competing and in what kind of environmental circumstances), rather on the individual excellences of their components, or on what paleontologists might later conclude they became. After all, species consist of populations of organisms that interact with their environments and their peers as integrated wholes, and not as individual characteristics in which we can track change over time.

As a result, while scientists might find it convenient to atomize both taxa and individuals into discrete characters for the purposes of understanding adaptation and other elements of their biology, when they do so, they always run the risk of missing the bigger and more important picture. This is because every individual is an astonishingly complex concatenation of features; and he or she will much more likely succeed or fail in the reproductive stakes as the sum total of them all, rather than because he or she possesses or lacks any one of them. It is, after all, presumably of little survival or reproductive benefit to be the fastest runner in your group if you are also the shortest-sighted or, perhaps even more importantly in the longer term, if your species as a whole is being outcompeted into extinction. What's more, physical characteristics almost invariably turn out to have very complex genomic backgrounds (see discussion in Tattersall and DeSalle 2019), so that there are typically huge constraints on what constitutes a viable change.

Half a century ago, the neurolinguist Eric Lenneberg articulated this key fact with a subsequently unmatched clarity and brevity. He made his remarks in the context of a seminal discussion of the origins of language, but his observations apply much more broadly, and all are as pertinent today as when he wrote:

> We can no longer reconstruct what the selection pressures were or in what order they came, because we know too little that is securely established by hard evidence about the ecological and social conditions of fossil man. Moreover, we do not even know what the targets of actual selection were. This is particularly troublesome because *every genetic alteration brings about several changes at once, some of which must be quite incidental to the selective process*. (Lenneberg 1969: 643; italics added)

Sadly, Lenneberg's sage admonition went largely unheeded by paleoanthropologists who, still in thrall to Mayr, continued diligently dreaming up essentially untestable adaptationist scenarios. For example, it is in the reductionist neo-Darwinian spirit lamented by Lenneberg that the interminable debate over why hominids became bipedal has persisted in churning on, apparently unstoppably. Darwin himself famously thought in terms of a key advantage: he felt that the defining benefit of bipedality was the ability it conferred on individuals to wield clubs for both attack and protection. This attractive proposition has since become empirically indefensible, at least as concerns its timing; but nonetheless, Darwin's successors continue to look for an alternative adaptive advantage that made terrestrial bipedality beneficial for an ancestrally quadrupedal (or perhaps more properly quadrumanous) form living at a time when continuous forest cover was shrinking in Africa, with the

consequent expansion of more open woodland and bushland habitats. Raymond Dart (1959) favored the view that standing upright had allowed diminutive hominids to see danger approaching from farther away; Gordon Hewes (1961) thought that the advantage of upright posture lay in the ability it conferred to carry food over long distances; Frank Livingstone (1962) proposed that gorilla-like bipedal display was defensively beneficial at expanding but dangerous forest edges; Cliff Jolly (1970) and others such as Kevin Hunt (1994) have concluded that bipedality in one way or another represented a helpful feeding strategy for a terrestrial primate; Peter Rodman and Henry McHenry (1980) saw improved locomotor efficiency as the fundamental issue; Owen Lovejoy (1981) liked the idea that male provisioning provided the critical advantage in the context of pair bonding; Nancy Tanner (1981) favored phallic display and infant carrying; Pete Wheeler (1984) made a powerful argument for thermoregulation; and the notion (proposed by Alister Hardy in 1960 and later popularized by Elaine Morgan in 1982) that early hominids waded upright in shallow water to exploit aquatic resources still refuses to go away (Kuliukas 2013).

All of these diverse scenarios, and many more, focus on individual key advantages to hominid bipedality, and each one is clearly underpinned, in one way or another, by the notion that adopting this unusual way of getting around was somehow propelled by natural selection acting on a particular feature of the organism. The fallacy is evident, as Lenneberg clearly realized, but from the resulting mindset sprang such extraneous and misleading concepts (rarely mooted outside paleoanthropology but distressingly frequently heard within it) as "mosaic evolution," the nebulous idea that different parts of organisms evolve at different rates. Atomistic notions of this kind are made possible only by transformational views of evolution, and it does not take much reflection to realize just how absurd they are. As already emphasized, morphological (or, for that matter, behavioral) features do not have independent existences. They are packaged into the entire organism. And it is the entire organism, not the feature, that interrelates with the environment and succeeds or fails on the ecological and social stages. When we favor a view of evolution that eliminates the role of whole taxa as interactors, we ignore a crucial dynamic in evolutionary histories, and in the specific context of hominid bipedality, we also lose sight of the fact that once a hominoid has become upright, it enjoys *all* the advantages—and all of the significant *dis*advantages—of the new locomotor strategy. Almost certainly most, if not all, of the posited "key benefits" of bipedality must surely have entered in some way into determining the overall viability of the new locomotor mode; and ultimate evolutionary success or failure (necessarily of the individual and species, not of the feature) must have involved a balance of all of those characteristics that were truly relevant to ecological success.

Adopting the taxic perspective clearly shifts the terms of the debate. The essential question then becomes "Why did the primordial hominid adopt bipedality in the first place?" Clearly a quadrupedal or quadrumanous ape did not come down to the ground to seek new resources and then decide that it would be advantageous to stand tall so that it could see farther, or thermoregulate better, or more effectively attract the ladies. A committed quadruped might facultatively have done any or all of those things; but to escape danger, or to travel any distance, it would have instantly

dropped to all fours and scampered away. The only conceivable reason why a hominoid would have stood upright on the ground and would have remained committed to that posture even for traveling was simply that it felt most natural for it to do so (see Tattersall (2016a) for more extensive discussion). And that would only have been the case if the hominoid in question was already highly suspensory and therefore habitually held its body erect for feeding, balancing, and moving around in the trees (see also Tuttle 1981; Thorpe et al. 2007). In turn, this would have made the origins of its putative terrestrial pre-adaptations entirely irrelevant to its later adoption of the new locomotor style. Inevitably, the relevant novel anatomical features had been acquired in another context entirely, only later to be recruited to their new postural and locomotory uses. In this perspective, natural selection cannot have been a driving agent of the change observed. Instead, an adventitious change in environment made an existing structure "adaptive" in an entirely new and unanticipated context. Indeed, it is possible to argue that *everything* we later recognize as an *ad*aptation has to come into existence as an *ex*aptation, that is to say, entirely randomly with respect to any use for which it might be co-opted after becoming fixed in the population. Mutations are, after all, stochastic events.

14.4   Recent Paleoanthropology

After some admittedly fairly shrill initial complaints (e.g., Malmgren et al. 1983; H. Robinson 1986), vertebrate and invertebrate paleontologists quite rapidly and comfortably incorporated both punctuated evolutionary models and cladistics into their world views—not as procedural Holy Grails but simply as additional weapons in their phylogenetic armamentaria alongside emerging technologies such as molecular systematics. As a result, both fields today look very different from their predecessors in the mid-twentieth century. Not so paleoanthropology, which remained generally unreceptive to cladistics and punctuated evolutionary models. Resistance to both remains tenacious, even as such highly selectionist alternatives as the "multiregional" notion of hominid evolution (Wolpoff et al. 1984) have tended to fade or to transmute. True, many paleoanthropologists have adopted at least the terminology of cladistics, along with some of the quantitative phylogenetic modeling methods to which trait-based phylogenetic reconstruction opened the door (e.g., Dembo et al. 2015); and, perhaps even more importantly, the sheer abundance of new morphologies represented in a rapidly expanding human fossil record has by now forced the general recognition of more than two dozen extinct hominid species (see review by Tattersall 2018a). But the overwhelming tendency in paleoanthropology is still to think of the human fossil record in the most minimalist terms possible and to cleave to Mayr's transformationist and linear injunctions to the maximum practical extent. Paleoanthropology is, in other words, still somewhat in thrall to the tired old formula: time + natural selection = evolution.

The ongoing paleoanthropological reluctance to think taxically, and thereby also to bring the systematics of Hominidae (or, if you must, Homininae; in this context

the difference is notional) into line with that of other mammalian (sub)families, finds expression in many ways. But perhaps the most egregious example is the apparently inexhaustible willingness of paleoanthropologists to cram ever more diverse morphologies into the already bulging single genus *Homo*, the addition of each new morphology making the genus more "variable" and thus easier to force further ones into. True, Ernst Mayr lost the battle to subsume the australopiths into *Homo* very early on; and a decade and a half after his tirade was published (a period during which anglophone paleoanthropologists hardly dared utter a formal species name), Louis Leakey et al. (1964) had the temerity to apply the new nomen *Homo habilis* to a dental australopith from Olduvai Gorge. Decades later, Meave Leakey and her colleagues (M. Leakey et al. 2001) even dared to propose the new genus *Kenyanthropus*, which was met with a deafening silence where it was not roundly criticized. But otherwise, and very much in the Mayrian spirit, the tendency among paleoanthropologists has increasingly been to dichotomize most hominid fossils into *Australopithecus* vs. *Homo*. The prevailing systematic algorithm seems to be: if it isn't one, it *has* to be the other—regardless of what it actually looks like.

Evidence for the seductive power of this mindset is everywhere. For example, other than that they are plainly not *Australopithecus*, there is precious little morphological or phylogenetic justification for shoehorning the diminutive and tiny-brained hominids from Liang Bua in Flores (Brown et al. 2004) or Rising Star in South Africa (Berger et al. 2015) into the genus *Homo* (Tattersall 2015). The recently announced *Homo luzonensis* (Detroit et al. 2019) also presumably belongs in this category. Perhaps worse yet, there is even less reason for cramming any of the morphologically diverse hominids from Georgia's Dmanisi into the genus that is defined by *Homo sapiens*, let alone into the designated species *Homo erectus*; none of the Dmanisi specimens even remotely resembles the *Homo erectus*-type material from Trinil, in Java (see Schwartz and Tattersall (2005) and Tattersall (2015) for discussion). Indeed, if one were to seek a prime example of systematic exceptionalism in paleoanthropology, one could do no better than to point to the fact that the describers of the most complete and distinctive of the Dmanisi hominid crania (D4500/2600) saw fit to place this remarkable specimen in its own "sub-subspecies"—an otherwise unheard-of taxonomic rank—as *Homo erectus ergaster georgicus* (Lordkipanidze et al. 2013). Even the early anatomists might have scratched their heads at this mind-boggling move; but paleoanthropology itself is left with a systematic disaster, the resolution of which will only be in sight when its practitioners start to admit that Hominidae is a very diverse clade indeed and that more genera than the simple *Australopithecus*/*Homo* dichotomy allows will be needed to express the complex structure that lies within it (Tattersall 2017a). Sadly, the seductive power of the reigning adaptationist/selectionist paradigm helps very effectively to disguise this necessity, and it is clear that in paleoanthropology our received neo-Darwinian assumptions about selection continue to resonate far beyond the immediate fields of evolutionary process and theory.

14.5 Natural Selection and Hominid Phylogeny

A glance at an approximate but fairly mainstream hominid family tree (Fig. 14.1) shows how far, despite our gradualist preferences recent empirical findings in a rapidly expanding fossil record have obliged us to come, in recognizing that ancient hominids really were diverse. Far from reflecting a slow and steady process of refinement over the years, this fairly speciose tree is witness to a story of vigorous
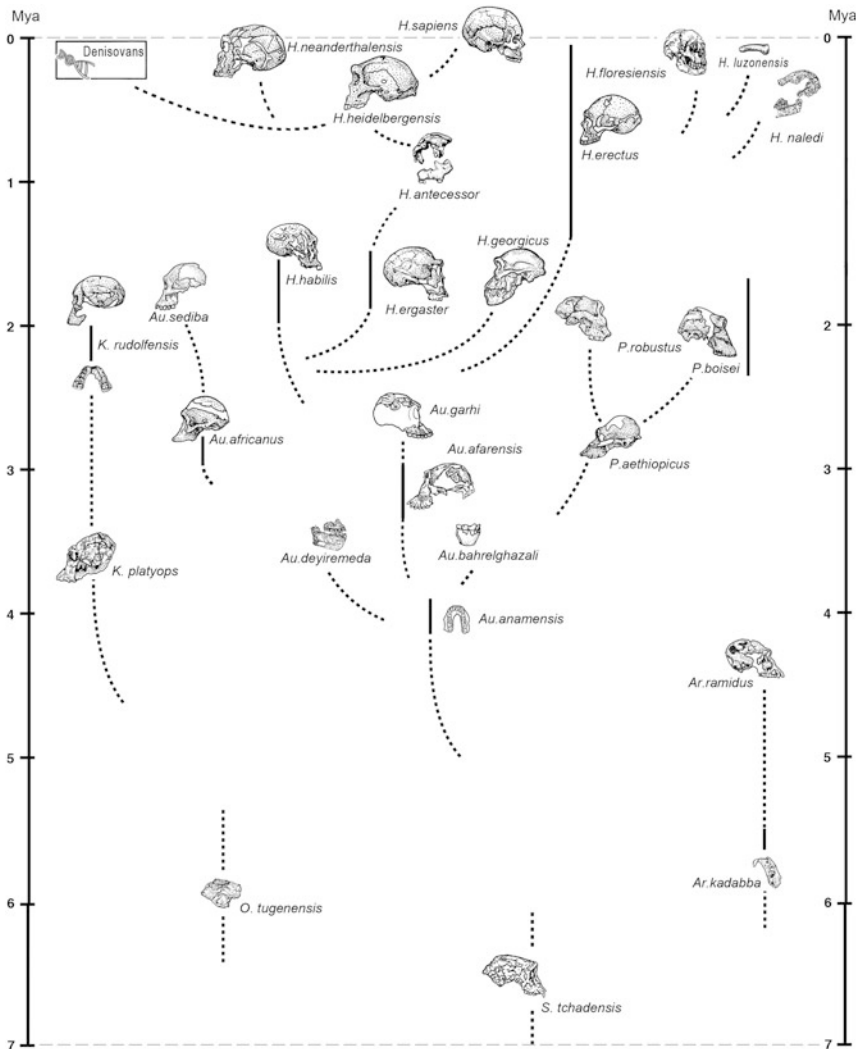
Fig. 14.1 Schematic tree of hominid evolution, showing how, typically, multiple hominid species have shared the planet at any one point in time. It is *Homo sapiens* that is truly unique in being alone in the world. Art by Kayla Younkin

evolutionary experimentation, in which new variations on the hominid theme (new species) were repeatedly generated, and pushed out into the ecological arena to thrive or to perish. Individual taxa in this schema may or may not have been competitively superior to one another, or to unrelated contenders for ecological space; but the overall topography of the tree does little to suggest that the major pattern involved the steady adaptive enhancement of a central evolutionary mainstream.

The belief that natural selection is a major agent of evolutionary change is often as much a matter of faith as of established fact (see also Delisle, Chap. 4). As Mayr pointed out in 1982, there were signally few documented examples of selection-driven change in Darwin's day; and, perhaps oddly, there are not many additional ones now. Such phenomena as industrial melanism and antibiotic resistance are hard to refute, of course, because the cause-effect relationship in such exceptional cases is unusually clear-cut. But it remains true that the best grounds we have for believing in selection-driven change in the ancient past are inferential, rather than observable. That something we can justifiably call Darwinian adaptation is at some level an important part of evolutionary process is pretty strongly suggested by the rampancy of morphological convergence in the natural world. But while the gradualist influence of natural selection might in principle be most powerfully inferred from within-lineage morphological trends observed in the fossil record, the paleoanthropological literature actually yields remarkably few such instances. References to the "mosaic evolution" of fossil hominids abound in the literature, most commonly in the context of functional analyses (e.g., Kivell et al. 2011); but as far as I am aware, there is only one explicit recent test of anagenesis in the human fossil record (Kimbel et al. 2006). Once again, this example was likely compromised by a leaning toward minimalist systematics in the Mayrian tradition (see Schwartz and Tattersall 2005); and it has actually been refuted on the basis of fossil discovery (Haile-Selassie et al. 2019). Without an adequate systematic framework, inferences concerning pattern in the fossil record are essentially worthless.

This having been said, there is one particular line of putative evidence for the long-term transformative action of natural selection that remains, without any question, an intuitively satisfying one. I refer, of course, to the apparent documentation of long-lasting within-lineage morphological trends in the fossil record. But caution is always advisable when interpreting evidence of the kind available. This is because gaps in osteodental morphology between closely related species are typically small, so that in a spottily sampled record, a pattern of continuous change may be closely mimicked by multiple samplings over time of a diversifying clade. Nonetheless, the human fossil record, and specifically that of the genus *Homo* [as rationally defined to exclude anything that is not a reasonably close relative of *Homo sapiens*: see discussion in Collard and Wood (2015) and Tattersall (2016b)] provides us with one of the most striking examples of an evolutionary trend in all of paleontology: the apparently inexorable increase in the volume of hominid brains over the course of the Pleistocene. Australopith cranial volumes in the period before two million years ago already hovered around the 450 ml mark (about a quarter larger than in the very first hominids and the living great apes). A mere couple of

hundred thousand years later, early members of *Homo* had brains in the 800 ml range. By a million years ago, the figure was up to around 1000 ml, and by the end of the Pleistocene, the brains of both *Homo sapiens* and *H. neanderthalensis* had reached a mean of about 1500 ml.

In the absence of an adequate systematics of the genus *Homo* (which will only be achieved when the final traces of the linear/selectionist paradigm of human evolution are finally erased), it is impossible to achieve a testable interpretation of the tendency that is somehow buried in these figures. However, within the genus *Homo* as reasonably defined, it is notable that trends toward increasing brain sizes proceeded *independently* in at least three separate lineages: those leading to late *Homo erectus* in eastern Asia to *H. neanderthalensis* in western Eurasia and to *H. sapiens* in Africa. In each lineage, earlier members had smaller brains than later ones. From this we can, I think, legitimately conclude that there is some feature common to members of the genus *Homo* that predisposed all of its constituents to increasing brain size with the passage of time. Exactly what that feature might have been is currently impossible to specify; but it certainly seems reasonable to suggest that natural selection, operating similarly in each lineage because of some shared behavioral or physiological apomorphy, might somehow have been involved in generating the pattern observed. However, while it is also reasonable to surmise that, in some sense, increasing "intelligence" was implicated in the process of brain enlargement in *Homo* (and a stepwise increase in technological complexity is simultaneously documented in the archaeological record), it was certainly not intelligence of the specifically modern human variety. Not only did the very different Neanderthals have brains identical in size (though not in shape) to those of early *H. sapiens*, but the *H. sapiens* brain has shrunk in average volume (by almost 13%) since the archaeological record suggests the modern symbolic cognitive algorithm began to express itself (Tattersall 2018b). And, in any case, only one lineage of the three became fully symbolic.

From a gradualist perspective, the overall trend may seem somehow suggestive; but, given the deficiencies of our existing systematic frameworks, it is difficult to reach any definite conclusions on the action of transformative selection as a guiding force in this aspect of hominid evolution. We can certainly infer that long-lived hominid paleospecies were adequately adapted to their circumstances; but that is very different from claiming that they were in any way optimized for anything (or were even on a trajectory toward optimization) through the action of neo-Darwinian transformative natural selection. And of course, the trick in evolution is evidently not necessarily to be optimized (it is no accident that extinction rates are higher among stenotopes than among eurytopes like hominids), but simply to be good enough to deal successfully with whatever varying conditions present themselves. Evolution is not about engineering; it is about survival and successful reproduction under immediate circumstances, not only at the individual level but at that of the species as well. This means above all maintaining a fit population, rather than merely assuring the success of the "fittest" individuals within it. And it is here that natural selection—which, as we've seen, must inexorably take place in any

population in which more individuals are born than survive—almost certainly plays its most vital role in most evolutionary histories.

In obeisance to Ronald Fisher's infinitesimal model, nearly every variable biological feature of every population exhibits a normal distribution (see discussion in Tattersall and DeSalle 2019); and the most critical function of natural selection in any successful species is almost certainly to keep the population fit by trimming off the extremes of those distributions at both ends, in the process maintaining a stable mean (Eldredge and Gould's "homeostasis"). What is more, for the population as a whole (whether locally or as a species), the crucial thing is not how well adapted in their individual features its most outstanding and reproductively successful members are; it is its own unitary success as a whole, something that necessarily involves the entire constellation of its characteristics and members. For while the individual succeeds or fails in the reproductive stakes as the sum of its parts, as far as the species is concerned, the most important role of natural selection is to keep the mean values of relevant characters in the most advantageous positions for the competitiveness of the entire population. This function of selection looms even larger when one considers that, in a hazardous world, the fates of individuals and even of entire populations are often very much at the mercy of chance events.

None of this entirely obviates any potential role for transformational selection in evolution; but given that gradual evolution by natural selection is acknowledged by all to be a very slow process, and that we now know that over hominid history environments have tended to change dramatically and unpredictably on very short time scales, it appears that the external conditions necessary for gradual directional evolution were relatively rare over the tenure of our family. For most of the evolution of the genus *Homo*, certainly, its members seem to have existed in tiny populations that were spread across vast tracts of territory and that were buffeted hither and yon by capricious changes in climate and environment—changes that were entirely random to their existing adaptations or proclivities. In aggregate, those circumstances would have provided ideal conditions not only for genetic drift but for evolutionary change via diversification, reintegration, and competition among and within populations belonging to a clade that was both remarkably flexible behaviorally and highly generalist ecologically. In all likelihood, the form of the hominid family tree in Fig. 14.1 reflects a complex ramifying history of this kind, rather than a basically linear history significantly influenced by gradual and transformational natural selection.

14.6 Conclusion

Independently derived from the study of human anatomy, and isolated from mainstream paleontology and evolutionary theory for the first century of its existence, paleoanthropology has been in thrall to a reductionist version of the Modern Evolutionary Synthesis since 1950. The "hardened" form of the Synthesis involved emphasizes straight-line evolutionary pathways guided by directional natural

selection over long periods of time. Despite major developments in evolutionary and systematic theory in the interim, 70 years later, the resulting linear and minimalist mindset continues to dominate human evolutionary studies—which still tend to be largely focused in one way or another on adaptation and the assumed results of transformational selection. This narrow orientation has led to an obsession with the evolution of individual characters and character complexes that are, in reality, inextricably bound up in the whole organisms apart from which they cannot have independent evolutionary histories. And, perhaps predictably enough, it has also led to the chasing of red herrings such as "mosaic evolution," to the effective exclusion both of systematics and of the adequate appreciation of the role of whole individuals and taxa in evolution.

Nonetheless, on a pragmatic level, over time, the pressures of discovery have obliged paleoanthropologists to recognize a certain diversity of species in the hominid fossil record: a diversity that, although still regrettably muted by strong minimalist tendencies, clearly suggests just on its own that the history of the hominids has typically been one of vigorous evolutionary experimentation with the hominid potential, rather than one of the fine-tuning of a major central lineage by classical neo-Darwinian processes. Accordingly, it is hardly surprising that putative long-term evolutionary trends within the human family give equivocal support at best to the idea that transformational natural selection has had the largest effect on human evolution. Instead, it increasingly appears that in an uncertain, unpredictable, and rapidly changing world, natural selection has functioned principally as a force that vitally acts to keep entire populations fit and stable, rather than as one that has favored change over time in individual features we might choose to regard as adaptive. As predicted by Ronald Fisher's century-old infinitesimal model of genotypes and phenotypes, most of the variable characteristics that affect the survival or reproductive success of organisms within a population turn out to be normally distributed. And natural selection—which necessarily operates in any population in which more individuals are born than reproduced—appears to perform the essential function of keeping populations fit by trimming away the maladaptive extremes of those distributions and thereby promoting population homeostasis.

Still, it is undeniable that hominids have come a very long way over the course of the Pleistocene. Indeed, no other species in the world today is phenotypically more dissimilar from its own ancestor of two million years ago than *Homo sapiens* is. And this, of course, leaves us with the issue of explaining this unusually high aggregate rate of change. I have suggested (Tattersall 2017b) that a major cause may have been the unique hominid ingredient of material culture, though not in the gene/culture co-evolutionary context often invoked by evolutionary psychologists. Instead, my suggestion is an essentially demographic one. Namely, that, in a period when tiny hominid populations were thinly spread over vast landscapes, material culture would have permitted wider dispersal than would otherwise have been possible in propitious times. In contrast, it would have provided an incomplete buffer against habitat change in less favorable ones. This effect would have exacerbated the population fragmentation/recoalescence cycle in which genetic novelties could be fixed and sorted, and it would thereby have maximized the probabilities both of evolutionary

innovation within hominid populations and of competition among them. In this perspective, hominid evolution was driven to a much greater degree by a combination of demographic and extrinsic factors, than by elements of intrinsic excellence and transformational selection.

References

Ashton EH, Zuckerman S (1951) Some cranial indices of *Plesianthropus* and other primates. Am J Phys Anthropol 9:283–296

Berger LR, Hawks J, de Ruiter DJ, Churchill SE, Schmid P et al (2015) *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. eLife 4:e09560. https://doi.org/10.7554/eLife.09560

Brown P, Sutikna T, Morwood MJ, Soejono RP, Jatmiko SEW, Due RA (2004) A new small-bodied hominin from the late Pleistocene of Flores, Indonesia. Nature 431:1055–1061

Clark R (2011) J.B.S. The life and work of J. B. S. Haldane. Bloomsbury Books, London

Clausen J, Hiesey WM (1958) Experimental studies on the nature of species, Volume IV: Experimental structure of ecological races. Carnegie Institution of Washington, Publ 615, Washington, DC

Collard M, Wood BA (2015) Defining the genus *Homo*. In: Henke W, Tattersall I (eds) Handbook of paleoanthropology, vol 3. Springer, Heidelberg, pp 2107–2144

Dart RA (1925) *Australopithecus africanus:* the man-ape of South Africa. Nature 115:195–199

Dart RA (1947) The osteodontokeratic culture of *Australopithecus prometheus*. Transvaal Museum Memoir 10:1–105

Dart RA (1959) Adventures with the missing link. Harper, New York

Darwin C (1859) On the origin of species by natural selection. John Murray, London

Dembo M, Matzke NJ, Mooers AO, Collard M (2015) Bayesian analysis of a morphological supermatrix sheds light on controversial fossil hominin relationships. Proc R Soc B 282:20150943. https://doi.org/10.1098/rspb.2015.0943

Detroit F, Mijares AS, Corny J, Daver G, Zanolli C, Dizon E, Robles E, Grun R, Piper PJ (2019) A new species of *Homo* from the late Pleistocene of the Philippines. Nature 568:181–186

Dobzhansky T (1937) Genetics and the origin of species. Columbia University Press, New York

Dobzhansky T (1944) On the species and races of living and fossil man. Am J Phys Anthropol 2:251–265

Eldredge N (1978) Evolution: Taxic or transformational? Syst Zool 27:130–132

Eldredge N (1995) Reinventing Darwin: discovering the tree of life. Norton, New York

Eldredge N (2016) Eternal ephemera: adaptation and the origin of species from the nineteenth century through punctuated equilibria and beyond. Columbia University Press, New York

Eldredge N, Gould SJ (1972) Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf TJM (ed) Models in paleobiology. Freeman Cooper, San Francisco, pp 82–115

Fisher RA (1918) The correlation between relatives on the supposition of Mendelian inheritance. Proc Roy Soc Edinburgh 52:399–433

Gould SJ (1983) The hardening of the evolutionary synthesis. In: Grene M (ed) Dimensions of Darwinism. Cambridge University Press, Cambridge, pp 173–204

Haile-Selassie Y, Melillo SM, Vazzana A, Benazzi S, Ryan TM (2019) A 3.8-million-year-old hominin cranium from Woranso-Mille, Ethiopia. Nature 573:214–221

Hardy AC (1960) Was man more aquatic in the past? New Scientist 174:642–645

Hennig W (1966) Phylogenetic systematics. University of Illinois Press, Urbana, IL

Hewes GW (1961) Food transport and the origins of hominid bipedalism. Am Anthropol 63:687–710

Howell FC (1951) The place of Neanderthal man in human evolution. Am J Phys Anthropol 9:379–416.

Howell FC (1952) Pleistocene glacial ecology and the evolution of "Classic Neanderthal" man. Southwest J Anthropol 8:377–410

Hunt KD (1994) The evolution of human bipedality: ecology and functional morphology. J Hum Evol 26:183–202

Huxley J (1942) Evolution: the new synthesis. Allen and Unwin, London

Jolly CJ (1970) The seed-eaters: a new hypothesis of hominid differentiation based on a baboon analogy. Man 5:1–26

Keith A (1915) The antiquity of man. Williams and Norgate, London

Kimbel WH, Lockwood CA, Ward CV, Leakey MG, Rak Y, Johanson DC (2006) Was *Australopithecus anamensis* ancestral to *A. afarensis*? A case of anagenesis in the hominin fossil record. J Hum Evol 51:134–152

Kivell TL, Kibii JM, Churchill SE, Schmid P, Berger LR (2011) *Australopithecus sediba* hand demonstrates mosaic evolution of locomotor and manipulative abilities. Science 333:1411–1417

Kuliukas AV (2013) Wading hypotheses of the origin of human bipedalism. Hum Evol 28:213–236

Leakey LSB, Tobias PV, Napier JR (1964) A new species of the genus *Homo* from Olduvai Gorge. Nature 202:7–9

Leakey MG, Spoor F, Brown FH, Gathogo PN, Kiarie C, Leakey LN, McDougall I (2001) New hominin genus from eastern Africa shows diverse middle Pliocene lineages. Nature 410:433–440

Lenneberg E (1969) On explaining language. Science 164:635–643

Livingstone FB (1962) Reconstructing man's Pliocene ancestor. Am Anthropol 64:301–305

Lordkipanidze D, Ponce de Leon MS, Margvelashvili A, Rak Y, Rightmire GP, Vekua A, Zollikofer C (2013) A complete skull from Dmanisi, Georgia, and the evolutionary biology of early *Homo*. Science 342:326–331

Lovejoy CO (1981) The origin of man. Science 211:341–350

Malmgren BA, Berggren WA, Lohmann GP (1983) Evidence for punctuated gradualism in the Late Neogene *Globorotalia tumida* lineage of planktonic foraminifera. Paleobiology 9:377–389

Mayr E (1942) Systematics and the origin of species. Columbia University Press, New York

Mayr E (1950) Taxonomic categories in fossil hominids. Cold Spring Harbor Symp Quant Biol XV:109–118

Mayr E (1953) Comments on evolutionary literature. Evolution 7:273–281

Mayr E (1963) Animal species and evolution. Harvard University Press, Cambridge, MA

Mayr E (1982) The growth of biological thought. Belknap Press, Cambridge, MA

Mayr E (2001) What evolution Is. Basic Books, New York

Mivart SG (1871) On the genesis of species. Macmillan, London

Morgan E (1982) The aquatic ape. Stein and Day, New York

Osborn HS (1915) Men of the old stone age: their environment, life and art. Charles Scribner's Sons, New York

Provine WB (1986) Sewall Wright and evolutionary biology. University of Chicago Press, Chicago

Robinson JT (1953) *Meganthropus*, Australopithecines and hominids. Am J Phys Anthropol 11:1–38

Robinson H (1986) A key to the common errors of cladistics. Taxon 35:309–311

Rodman PS, McHenry HM (1980) Bioenergetics and the origin of hominid bipedalism. Am J Phys Anthopol 52:103–106

Schwartz JH, Tattersall I (2005) The human fossil record, Vol 4. Craniodental morphology of early hominids (Genera *Australopithecus, Paranthropus, Orrorin*) and overview. Wiley-Liss, Hoboken N

Simpson GG (1944) Tempo and mode in evolution. Columbia University Press, New York

Tanner NM (1981) On becoming human. Cambridge University Press, Cambridge

Tattersall I (2015) Defining and recognizing the genus *Homo*. Gortania 36:5–22

Tattersall I (2016a) Prerequisites for hominid bipedality. In: Ribot Trafi F (ed) Homenaje al Dr Jose Gibert Clols. Una vida dedicada a la sciencia y al conocimiento de los primeros europeos. Publicaciones Diputacion de Granada, Granada, pp 83–91

Tattersall I (2016b) The genus *Homo*. Inference Int Rev Sci 2(1). http://inference-review.com/article/the-genus-homo

Tattersall I (2017a) Species, genera, and phylogenetic structure in the human fossil record: a modest proposal. Evol Anthropol 26:116–118

Tattersall I (2017b) Why was human evolution so rapid? In: Marom A, Hovers E (eds) Human paleontology and prehistory, essays in honor of Yoel Rak. Springer AG, Heidelberg, pp 1–9

Tattersall I (2018a) History and reality of the genus *Homo*: What is it, and why do we think so? Métode Sci Stud J 9:79–89

Tattersall I (2018b) Brain size and the emergence of modern human cognition. In: Schwartz JH (ed) Rethinking human evolution. MIT Press, Cambridge, MA, pp 319–334

Tattersall I, DeSalle R (2019) The accidental *Homo sapiens*: genetics, behavior and free will. Pegasus Books, New York

Thorpe SKS, Holder RL, Crompton RH (2007) Origin of human bipedalism as an adaptation for locomotion on flexible branches. Science 316:1328–1331

Tuttle RH (1981) Evolution of hominid bipedalism and prehensile capabilities. Philos Trans Roy Soc Lond B 292:89–94

Wallace AR (1858) On the tendency of varieties to depart indefinitely from the original type. Proc Linn Soc (Zool) 3:53–62

Weidenreich F (1939) Six lectures on *Sinanthropus pekinensis* and related problems. Bull Geol Soc China 19:1–110

Weidenreich F (1947) The trend of human evolution. Evolution 1:221–236

Wheeler PE (1984) The evolution of bipedality and loss of functional body hair in hominids. J Hum Evol 13:91–98

Wolpoff MH, Wu XZ, Thorne AG (1984) Modern *Homo sapiens* origins: a general theory of hominid evolution involving the fossil evidence from East Asia. In: Smith FH, Spencer F (eds) The origins of modern humans: a world survey of the fossil evidence. Alan R. Liss, New York, pp 411–484