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# EDITORIAL

As we enter a new century and millennium and **Evolutionary Anthropology** begins its ninth volume, it seems an appropriate time to take stock of both the journal and the field in general—to consider what we have done so far, and where we are going in the coming years. It is with this goal that we have designated the first two issues of Volume 9 as our Millennium Issues and are providing Volume, Subject, and Author indices for the previous issues.

**Evolutionary Anthropology** was founded in 1991 and began publication in 1992 with the aim of providing a multidisciplinary review journal to bring together, in an widely accessible style, the results of current research relevant to human evolution in the broadest sense from paleontology, archeology, geology, primatology, functional anatomy, human ecology, genetics, and other disciplines. Our goal has been to provide minireviews of current research that can be readily understood by students, teachers, and researchers from all disciplines. Our articles are explicitly aimed at students and at researchers in allied subdisciplines, who want to know about the research of their colleagues, but may not follow the original literature. Thus articles on archeology are meant to be accessible to primatologists and paleontology articles should be accessible to human ecologists. Through extensive peer review and editorial review we make every effort to publish reviews that are authoritative and reflect as broadly as possible the current status and diversity of opinion on a variety of topics. They are meant to describe the state-of-the-art. In addition to an array of articles on diverse topics, we have also attempted to provide broad coverage of a number of pertinent research areas through a sequence of related articles over several years. These include a series of articles on geological dating, a series on the natural history of great apes, and reviews of major primate radiations from earlier epochs.

Like our review articles, our book reviews are intended to be broad essays comparing several recent publications on a similar topic with the aim of framing the individual books in a broader context. We make no attempt to review all recent publications, but we list all books received.

Human evolution is a dynamic field, in which the status quo is often overly conservative and myopic. We introduced our Issues essays to fulfill the need for the presentation of more extreme views, strong opinions, and new ideas. These provide a forum for the airing of new ideas, and neglected topics, and for limited debates over controversial and polarized topics that are so far from any resolution that they could not be fairly presented in a review format. They are meant to be thought provoking and stimulating to new ideas, new syntheses and new approaches, as well as allowing people to let off steam now and then.

It is in this dual spirit of both review and provocation that we offer these Millennium Issues of **Evolutionary Anthropology.** Rather than providing long and tedious reviews of areas that been reviewed many time before during the past century, we provide a series of minireview essays that attempt to put current views and research on aspects of human evolution in a broader framework, but focus more explicitly on what the individual authors feel are the most exciting recent developments and current challenges facing evolutionary anthropology. In the first two issues of 2000, we include essays on human paleontology, paleolithic archeology, geologic dating, human ecology, primate socioecology, and primate evolution. An essay on genetics will appear later this year. As a reminder that the entire concept of humans having an evolutionary past and prehistory is a relatively young idea, and one that is by no means obvious to much of humanity, we include a special essay by James Sackett on "Human Antiquity and the Old Stone Age: the Nineteenth Century background to Paleoanthropology." We hope that these essays will provide an appropriate and enjoyable transition from the twentieth to the twenty-first century and a lively beginning of both a new millennium and a new volume of **Evolutionary Anthropology.**

John G. Fleagle, Editor

# Paleoanthropology: The Last Half-Century

IAN TATTERSALL

Leaving aside the multifarious brands of millenarian alarmism (which actually have the comforting effect of reminding us that, for better or for worse, human nature has not changed one bit since the very beginnings of recorded history), the upcoming century's end does at least have the advantage of providing us with an excellent occasion to look back over the last fifty-plus years of human evolutionary studies, and to assess how far our field has come in that time. Of course, paleoanthropology has a much longer history than this, arguably going back to Johann Blumenbach in the late eighteenth century, and certainly to the discovery and first analysis of the Feldhofer Cave Neanderthal in the mid-nineteenth. However, it was only in the post-World War II period that our science took on its recognizably modern shape.[1] For as late as the mid-1920s, for instance, Raymond Dart could still hark back to the nineteenth-century essentialist aesthetic by invoking the "harmonious" proportions of the Taung skull as evidence of its proto-human status,[2] while at about the same time, and without raising too many eyebrows,[3] Henry Fairfield Osborn could promote his orthogenetic concept of "aristogenesis" as a driving force in human phylogeny.

Interestingly, what changed around 1950 to consign such notions not simply to the wastebasket of history, but to an identifiably archaic period of paleoanthropology, was not anything intrinsic to the study of the human fossil record itself. Rather, it was the somewhat belated acceptance by paleoanthropologists of the principles of the "Evolutionary Synthesis," a movement aptly named since it had contrived during the 1930s and 1940s to unify evolutionary biology under a single conceptual umbrella. Once absorbed into paleoanthropology, the Synthesis rapidly penetrated its furthest reaches, at least in anglophone countries. And in doing so, it had the salutary effect of sweeping away a huge entrenched accumulation of mythology and misapprehension. Sadly, however, the Synthesis was doomed to harden, much like a religion, into dogma: a dogma whose heavy hand continues to oppress the science of human origins a half-century later.

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The story of the "modern" period of paleoanthropology is thus in very large part the story of the Synthesis and, latterly, of efforts to break free of its most limiting strictures. This is why the first half of this article is devoted less to the fossil record itself than to ways of thinking about it. I trust I will be forgiven for this by those who—not entirely without historical justification—look upon paleoanthropology as largely discovery-driven.

## PALEOANTHROPOLOGY AND THE SYNTHESIS

Following the rediscovery of the principles of Mendelian genetics in 1900, what was to become known as evolutionary biology entered a three-decade-long period that Ernst Mayr[4] has aptly described as "chaotic." Theories of the evolutionary process abounded, and few of them incorporated Darwin's original notion of natural selection as a significant mechanism of evolutionary change. Predictably, the paleoanthropologists of the period witnessed this ferment as little more than passive bystanders; for then, as now, their science was a consumer, rather than a producer, of evolutionary theory. And given the passion, even vituperation, with which competing notions of the evolutionary process were argued during those years, perhaps they were wise to keep their distance.

In the years around 1930, however, a group of mathematical geneticists who included J.B.S. Haldane[5] and R.A. Fisher[6] in England, and Sewall Wright[7] in the United States, laid the quantitative basis for the approaching Synthesis. The major principles of the Synthesis itself were subsequently enunciated between 1937 and 1944 in three seminal books by the geneticist Theodore Dobzhansky,[8] the ornithologist Ernst Mayr,[9] and the paleontologist George Gaylord Simpson.[10] Each of these authors had his own distinct vantage point (Dobzhansky's that of the gene, Mayr's that of the species, and Simpson's that of the origin of higher taxa),[11] and each worked in a field with its own unique data set and perspectives. However, even if sometimes reluctantly, all three scientists ultimately capitulated to the central notion that virtually the entire range of evolutionary phenomena could be reduced in one way or another to generation-by-generation modification of gene frequencies within lineages of organisms, under the guiding if not always beneficent hand of natural selection. Each author was, of course, acutely sensitive to the existence of discontinuities in nature–which is, after all, organized into the "packages" we call species, however difficult it may sometimes be to recognize them in practice. And, equally, each was aware that this fact sat rather uncomfortably with the continuities preached by the Synthesis.[11] As time passed, though, such niceties tended to become lost, and the Synthesis acquired a more hard-edged quality.

It was in its more fundamentalist form that the Synthesis was finally absorbed into paleoanthropology, partly through the efforts of Dobzhansky and Mayr themselves. As early as 1944, Dobzhansky[12] reviewed the known fossil record of *Homo*, and concluded that "no more than a single hominid species existed at any one time level" (p. 261–262). It is evident that Dobzhansky, who quite likely had never seen an original hominid fossil, was influenced in this view by his newly arrived New York neighbor Franz Weidenreich,[13] nowadays hailed as the father of "multiregional continuity." While politely interested in the intellectual developments then taking place at the American Museum of Natural History (his academic home as well as that of Mayr and Simpson), the aged and orthogenist Weidenreich was reluctant to absorb new theories of process so late in his career.[14] Still, his long-established and vigorously promoted views on human evolution as a single braided stream were in major respects highly congenial to the gradualist outlook of the Synthesis. They certainly appear to have been accepted rather uncritically by Dobzhansky,[2] who accordingly rejected the "classic" notion of human evolution as "a phylogenetic tree with many branches [of which] all . . . but one withered and became extinct" (p. 259), in favor of the idea that "the racial differentiation of living mankind had its roots at a level much antedating the attainment of the Homo sapiens [sic] 'stage' " (p. 260). What's more, Dobzhansky came very close to asserting that there *could* only ever have been one kind of hominid at any one time; and his authority was such that few demurrals were heard.

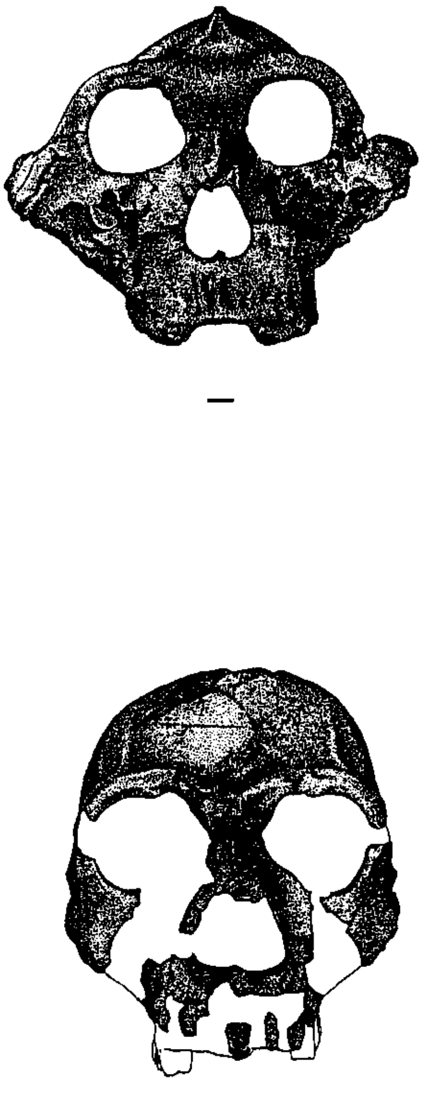

Figure 1. Front views of the crania KNM-ER 406 (above) and KNM-ER 3733 (below). The contemporaneity of these vastly different hominids finally put paid to the "single-species hypothesis." Scales are 1 cm; from Tattersall.[1]

Mayr never went quite so far as Dobzhansky in lumping fossil hominids, but he came close. In 1950 he published an influential paper[15] in which he berated paleoanthropologists for the plethora of taxonomic names littering the hominid fossil record. He argued instead that all known fossil hominids could be accommodated into a single lineage leading from *Homo transvaalensis* (the australopiths), through *Homo erectus*, to *Homo sapiens* (including the Neanderthals). Mayr emphasized his view that these sequential hominids had participated in "a very gradual process" (p. 115) of transformation, so that, for example, "To determine the exact point . . . where the *sapiens* level was reached, is quite impossible" (p. 115). To his credit, Mayr felt it necessary to inquire as to why hominids had apparently stopped speciating. But his answer was to cast a shadow over paleoanthropology for a quarter-century to come. Humans didn't speciate, Mayr claimed, because "man occupies more different ecological niches than any known animal" (p. 116). In which case, "If the single species man occupies all the niches that are open for a *Homo*-like creature, it is obvious that he *cannot* speciate" (p. 116; my emphasis).

The way was thus opened for the later proponents of what was to become known as the "single-species hypothesis" to elaborate on the notion that, from the very earliest days, the human possession of "culture" (which, indeed, constituted the "human ecological niche") had made it impossible *in principle* for more than one kind of hominid to exist at any one time. As a result, during the 1960s and 1970s a vociferous group of proponents carried on a crusade to cram the entire human fossil record (which was already quite diverse) into this single linear model.[16,17] What's more, after fossil discoveries in the mid-1970s at Kenya's Lake Turkana Basin

(Fig. 1) had made it no longer tenable to believe under any theoretical construct whatever that only one kind of fossil hominid had ever existed at one time,[18] the single-species theory was converted by its ingenious proponents into the "multiregional continuity" model with which we are still contending today.[19] Harking back to Weidenreich[13] and his belief that each of today's human "races" has roots deep in time ("Java Man" having given rise to modern aboriginal Australians, for example, and "Peking Man" to modern Chinese), multiregional continuity in its most recent incarnation claims that all evolutionary developments in the hominid line subsequent to *Homo habilis* (whatever that is) have taken place within the single species *Homo sapiens*.[19,20] The argument here is that the various geographical groups of mankind have maintained their own individuality and evolutionary tendencies over the past two million years, while at the same time remaining part of one big happy species through a process of gene flow among sublineages. Quite a trick to pull off; and if making this process even minimally biologically plausible necessitated sweeping an astonishing variety of morphologies under the rug of a species *Homo sapiens* that was thereby expanded well beyond the point of meaninglessness, that was just part of the cost of doing business.[20] One can only speculate that Dobzhansky, who wrote at a time when the hominid fossil record was a fraction of its present size and diversity, would have been appalled to know where his wartime ruminations had ultimately led.

Despite its recent reputation as a hotbed of contention, however, paleoanthropology has traditionally tended to be a consensus-seeking and thus rather boring science. The vast majority of paleoanthropologists have preferred to gravitate to the center, even when at the center nothing much actually existed. So it was with the absorption of the Synthesis. Most paleoanthropologists ultimately felt obliged to reject the reductionist excesses of the single-species hypothesis and its intellectual descendants. But at the same time they welcomed the linearity of thought that lay behind them. This heralded an era in which the recognition of systematic diversity in human evolution would be rigorously minimized, and in which dissidents would be excoriated as "typologists," or "nonbiological."

Of course, it's useless to deny that the linear approach to human evolution had certain manifest practical advantages. For one thing, it reduced the number of names with which it was necessary to deal. More importantly, though, if human fossils were to be regarded essentially as links in a chain running through time, then the critical importance of those fossils was reflected in their ages, rather than in their morphologies (which inconveniently required analysis). And while, as the hominid fossil record expanded, morphology continued to pose an increasingly intractable set of problems, the introduction of various radiometric dating techniques in the 1950s and subsequently made those ages a lot easier to determine.[21] Linearity of mindset thus offered multifarious attractions, especially when backed up by the authority and evolutionary orthodoxy of the Synthesis.

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Eventually this had to change, and it did. By 1995 no less an authority than the Editor of this Journal, a self-confessed cladist/splitter, felt it necessary to remark upon the plethora of widely-accepted systematic names that had emerged in paleoanthropology during the previous quarter-century.[22] Accurately, he attributed this situation to the enormous enlargement of the fossil record over this period. But he also invoked, as joint culprits, new methods of extracting morphological information and of statistical analysis.[22] Finally, he pointed out the effects that a growing awareness of patterns of biodiversity in general had exercised on paleoanthropological interpretation. If primates are diverse today, which they certainly are, why should they not have been equally diverse in the past? These are all significant points, but it seems to me that there was an added factor as well: one that involved a more general appreciation of the complexities of the evolutionary process.

## PUNCTUATED EQUILIBRIA

In retrospect, it seems evident that the fossil record, human or otherwise, had never truly borne out the predictions of the Synthesis in terms of perfecting adaptation within lineages over prolonged periods of time. The signal of continuity is, in fact, much weaker than the Synthesis predicts. Indeed, the fossil record is replete with major *dis*continuities, and Charles Darwin himself had resorted to special pleading to explain its lack of the predicted intermediates. According to Darwin, those intermediates had indeed existed; they just hadn't yet been discovered.[23] Well, okay. Darwin was right to the extent that the fossil record *is* incomplete, and always will be. Nonetheless, it is surely significant that in the century and a half since Darwin wrote, during which many thousands of stratigraphic sections have been investigated and untold millions of fossils collected, the situation has not materially changed. New species regularly show up, but the record itself remains gappy. Thus, by the time the 1970s rolled around, the Emperor's clothes were looking decidedly threadbare, and it was time to begin asking whether the gaps in the fossil record might not actually be conveying a biological message.

This impolitic question was raised in 1972 by two invertebrate paleontologists, Niles Eldredge and Stephen Jay Gould.[24] They had noticed that the histories of lineages tended to be marked not by change but by nonchange, or stasis. And they were unwilling to ascribe this simply to the incompleteness of the record. Instead, they contrasted the "phyletic gradualism" preached by the Synthesis with an alternative model of "punctuated equilibria," whereby most evolutionary change has taken place during short-term episodes associated with speciation. Species in the fossil record, Eldredge and Gould argued, tended like individuals to have relatively sudden origins (by speciation), varying (and sometimes very long) lifespans as recognizable entities, and deaths (by extinction). And even though some fine-tuning of the basic idea was inevitably needed (it seems likely, for example, that significant adaptive novelties are more usually incorporated into populations during the process of geographic diversification than during that of speciation[25]), subsequent analyses of the fossil record, including that of hominids, have strongly tended to bear the basic pattern out.

Of course, there was much initial resistance to Eldredge and Gould's idea ("evolution by jerks," as one unkind critic called it) among evolutionary biologists of all stripes. Punctuated equilibria was vociferously attacked as being antievolutionary (which it clearly isn't), or at least as excluding natural selection from the evolutionary mix (equally untrue). But such knee-jerk instant reactions to novel ideas are routine in all fields, and what is perhaps more surprising is how rapidly evolutionary biologists in general came to see that punctuated equilibria is complementary, rather than antagonistic, to the principles of the Synthesis. In particular, an appreciation has widely emerged of the importance of the role that punctuated equilibria permits entire populations and species to play in the evolutionary process. This role is aptly reflected in Gould and Eldredge's recent comment that "Most macroevolution must be rendered by asking what kinds of species within a clade did better than others (speciated more frequently, survived longer) or what biases in direction of speciation prevailed within a clade."[26]

In paleoanthropology, however, a different outlook has often prevailed. Slow to absorb the principles of the Synthesis, paleoanthropology has been equally slow to augment these principles with a recognition of the multifarious complexities of the evolutionary process. Once again, it seems, paleoanthropology has been willing to declare itself independent from the regularities of nature as expressed in the evolution of nonhominid organisms. Yet is this really tenable? *Homo sapiens* today is without question an extraordinary organism, and may yet prove itself so unusual that it is resistant to the normal patterns and processes of evolution. But what is clearly not true is that our remarkable species is a simple extrapolation of what went before.[27,28] There is no a priori or empirical reason to believe that earlier hominids were exempt from the constraints that have governed the evolution of all other organisms. Still, in paleoanthropology business is often conducted as though this *were* the case: as if hominids not only are, but always have been, intrinsically different from other organisms, and subject to a different set of laws. Because our species *Homo sapiens* is the lone hominid on the Earth today, we conclude that this is the "natural" state of affairs. Not so, as the record abundantly demonstrates; but while Paleolithic archaeologists have long since realized that it is entirely inappropriate to extrapolate *Homo sapiens* back into the past as a "living model" of its ancestors, this fundamental fact of life has consistently tended to elude paleoanthropologists.

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As a result of all this, the legacy of the Synthesis in paleoanthropology is a somewhat mixed one. The Synthesis certainly introduced the first coherent evolutionary paradigm into the science of human evolution. What's more, the implementation of this new view of process led to an essential intellectual and practical housecleaning, in the absence of which it is hard to see how much further progress could have been made. At the same time, however, the essential linearity of mindset inculcated by the Synthesis has channeled much thinking about the hominid fossil record into the simple search for ancestors and descendants. And in so doing, it has contrived to divert attention not only from the pressing necessity of characterizing the taxic diversity present in the known hominid fossil record, but also from the need to elucidate the evolutionary relationships that exist among the components of this diversity.

## CLADISTICS AND PHYLOGENETIC HYPOTHESES

Theoretical advances during the 1960s and 1970s were not simply confined to matters of evolutionary process, but also addressed the broader question of pattern in nature, and how to recognize it. In particular, following an initial flirtation with numerical taxonomy, which paved the way for the adoption of sophisticated quantitative methods in paleontological analysis, the way in which system-

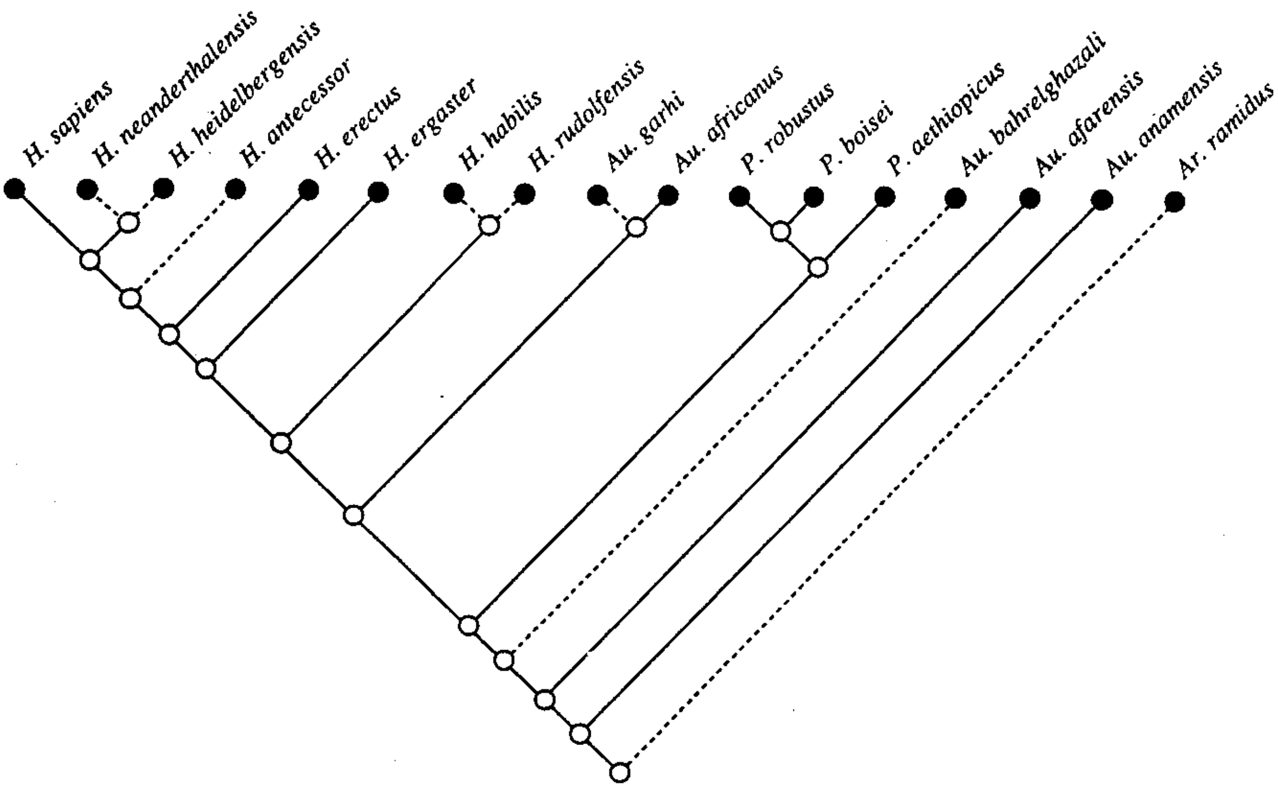

Figure 2. Highly speculative cladogram showing relationships among commonly recognized hominid species. Please note that many of the nodes shown are at best incompletely characterized or substantiated. Modified from Tattersall.[1]

atists of all kinds went about their business came eventually to be profoundly affected by the introduction of the concepts of *cladistics*. The dominance of gradualistic thought in paleontology had fostered the notion that paleontological analysis was a more or less passive correlate of discovery: find enough fossils, and the course of phylogenetic events would somehow be revealed.[29] However, the introduction into the evolutionary mix of notions of lineage splitting and diversity made it clear that phylogenies are not something that can be directly discovered in the fossil record. Instead, they reflect patterns of relationship that require morphological analysis. Of course, paleontology had come a very long way simply on the basis of a subliminal awareness that some kinds of characters were more useful in phylogenetic reconstruction than others; but this made it no less true that the field of systematics in general was lacking an articulated theoretical basis.

Such a basis was eventually supplied by the German entomologist Willi Hennig, whose influence came to the fore when his book *Phylogenetic Systematics* was translated into English in 1966.[30] Hennig pointed out that morphological characters (or more properly, character *states*) are operationally of two distinct kinds: primitive (plesiomorphic) and derived (apomorphic). Primitive states are those that were present in the common ancestor of the monophyletic group under consideration. Derived states, on the other hand, represent any deviation from the primitive condition, and are the sole arbiters of relationship, since the sharing of primitive characters tells us nothing about specific links between taxa. It is important to bear in mind that primitiveness and derivedness are not qualities specific to any particular anatomical condition: the same character state may be derived for a given group, but primitive for a subgroup within it. But if the goal of systematics is ultimately to reconstruct the great nested arrangement of monophyletic groups in the living world, then the quest for relationships had to become the explicit search for shared derived characters, rather than the largely intuitive process it had previously been.

Distributions of derived character states within a group of related organisms are expressed in a simple branching diagram known as a *cladogram* (Fig. 2). This is the only potentially testable formulation in the entire field of systematics:[31] taxon A is more closely related to B than either is to C, because A and B share derived characters not present in C. Derivedness vs. primitiveness in character states may be determined by criteria of commonality or of morphogenesis,[29] and in recent years quantitative routines have become available for phylogenetic analysis along these lines, based principally on parsimony criteria (e.g., Swofford[32]).

A more elaborate level of analysis is represented by the *phylogenetic tree* (Fig. 3). This kind of formulation adds to the information in the cladogram by specifying the nature of the evolu-

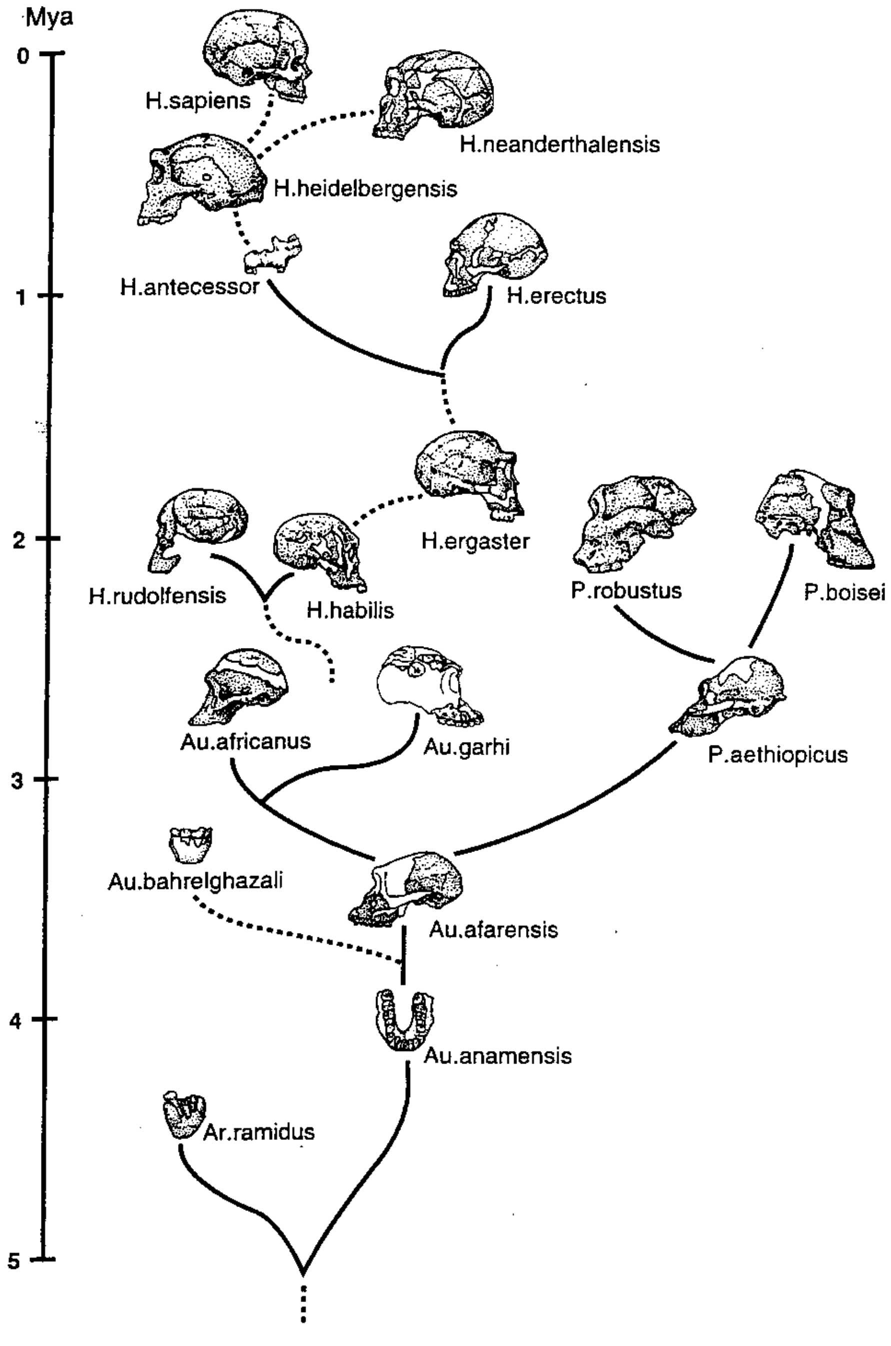

Figure 3. Hominid phylogenetic tree based on the cladogram shown in Figure 2. Everyone will be unhappy with at least some aspects of it, illustrating how much still remains to be done in the basic systematics of the hominid fossil record. Modified from Tattersall.[1]

tionary relationships postulated (i.e., ancestor-descendant, or separate descent from the same ancestor). In paleontology, trees will also factor in geological age. But while a tree is thus inherently more interesting than a cladogram, it is also less testable (because it is impossible to prove or disprove a specific kind of relationship); and indeed the information contained in a single cladogram may be translated into a variety of trees.[31]

Even more interesting and informative than the tree, but at the same time yet farther from testability, is the *scenario*, which adds to the mix everything you know about adaptation, ecology, and so forth. The resulting statements are usually so complex that they cannot be directly compared and evaluated; in effect, the ability of the storyteller becomes as important as content in determining the plausibility of the whole.[31] None of this is to suggest, of course, that trees and scenarios should be eschewed: a lifetime of cladograms would, after all, be tedious indeed. But it does emphasize that when formulating phylogenetic hypotheses it is important to start with the simple before moving on to the complex. Any phylogenetic tree should be based on a cladogram, and any scenario on a tree; in this way, it is possible to see on what basis the more complex hypotheses have been formulated, even if they are not directly testable themselves.

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In the last quarter-century the language of cladistics has quite successfully penetrated paleoanthropology, although one cannot avoid the impression that its underlying philosophy has been less thoroughly absorbed. Still, the effect has been, at least in some quarters, to refocus attention upon morphology. And although (myth to the contrary) cladistics in itself has little directly to do with the recognition of the basic units of systematic analysis–rather, it is concerned with determining the relationships among taxa—its arrival in paleoanthropology has been accompanied by the realization that our perceptions of the human biological past have been distorted by the exhortations of the Synthesis to minimize the number of species recognized. Partly as a result of this realization, and partly because an expanding fossil record has made it impossible to ignore, many paleoanthropologists have developed a concern with diversity in the human fossil record. In 1975, for example, when Eldredge and I[29] published the first (rather crude) cladistic analysis of this record, we were able to perform the modest service of pointing out that *Homo erectus*, then universally seen as the standard-issue hominid of the Middle Pleistocene, is cranially apomorphic, and unlikely to be ancestral to our species *Homo sapiens*. But at the same time, still in thrall to tradition, we adhered to prevailing norms and recognized only five species (of *Australopithecus* and *Homo*) in the entire human fossil record (excluding *Ramapithecus punjabicus*, shortly to be reallocated to the *Sivapithecus*-group). Twenty-five years later, as I've already noted, the scene has changed markedly. Many paleoanthropologists would now recognize three times as many hominid species, grouped into double the number of genera (Figs. 2, 3). Partly, this change has been due to the impressive augmentations of the hominid fossil record I've already remarked on over this period; but at the same time, beginning in the mid-1980s,[33] there has been a new willingness on the theoretical level to contemplate diversity as a fact of paleoanthropological life.[22]

The effect of this new perspective has been to alter, quite radically, the continually re-emerging picture of human evolution. For one thing, of course, a better appreciation of the actual systematic diversity that characterized the human biological past has permitted a more reliable evaluation of the sequence and pattern of historical events that ultimately gave rise to our species. But, just as importantly, these developments have also offered us freedom from the linearity of the Synthesis. The significance of this cannot be overstated, for literal adherence to the tenets of the Synthesis has had two particularly unfortunate effects. First, it has imparted a sense almost of inevitability to the arrival of *Homo sapiens*, for under the dictates of the Synthesis the story of human evolution has been effectively that of a long, dogged, singleminded trudge from primitiveness to perfection. Second, this same mindset has promoted the transformationist notion of perfecting adaptation as the underlying mechanism of change in human evolution. Yet "adaptations" cannot be independent entities whose histories can be followed independently of those of the taxa within which they are embedded.[34] Natural selection can, after all, only vote up or down on the success of the whole individual, not on that of its separate components; and the same applies to taxa. Thus, as I have previously emphasized in these pages, "the history of the hominid family . . . is not simply the abstract sum of evolutionary changes in a number of body systems that can conveniently be followed and examined independently. Instead, it is . . . the history of the differential successes of taxa that triumphed or failed as the overall sums of their parts" (Tattersall,[34] p. 115). In short, by freeing ourselves from the transformationist paradigm of the Synthesis, we are able to see human phylogeny more realistically, as a history of constant evolutionary experimentation. New hominid species have endlessly been produced, have competed (with their close relatives and with less closely related forms), and have given rise to descendant species or become extinct (or both). This is not only a truly dramatic scenario, but it has the overwhelming advantage of bringing the story of human evolution into line with what we know of the histories of virtually all other evolutionarily successful groups. And in doing so, ironically, it brings us back to something very like the "classic" schema of human evolution so vigorously rejected by Dobzhansky in 1944.[12]

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## MOLECULAR SYSTEMATICS AND THE STATUS OF HOMINIDAE

The changing complexion of the fossil record, and advances in its analysis, have done much to alter our perceptions of human evolution. But another data source—molecular comparisons—has, over the last four decades, almost as profoundly affected the way we look at humanity's place in nature. Right from the very earliest days of comparative anatomy, of course, the close morphological similarities of humans with the great apes (gorillas, chimpanzees, and orangutans) had been acknowledged. Indeed, Linnaeus himself had classified the great apes then known within the genus *Homo*.[35] By the mid-twentieth century the accepted classification placed all the great apes together in one family, Pongidae, and *Homo* by itself (with its fossil relatives) in another, Hominidae; and in those precladistic days no-one thought to question this. But in the early 1960s Morris Goodman[36] showed that apes and humans were so similar immunologically that all should be included in the same family (Hominidae). What's more, he demonstrated that by some markers humans were most similar to chimpanzees, while in other blood proteins humans were closer to gorillas. This launched a fierce debate over the classification of apes and humans that continues today and is well summarized in various contributions to Delson et al.[37] In the present article, the term "hominid" is perhaps inappropriately used in its traditional sense, to designate the taxon containing the living human species and its exclusive fossil relatives.

Even more remarkably, in 1966–1967 Vincent Sarich and Allan Wilson[38,39] proposed that albumin molecules evolve at a constant rate, and that the "immunological distances" thereby derived indicated a parting of company by the ancestors of African apes and humans a mere 5 myr ago. Coming at a time when many thought that the 12–14 myr-old *Ramapithecus* was a hominid ancestor, this finding caused considerable brouhaha. However, new fossils and analyses eventually brought a kind of reconciliation of the molecular and morphological records, and it is now widely believed that humans shared an ancestor with one of the African apes at around 6–8 myr ago.

But Wilson and his collaborators did not stop there. In 1975 they published a review[40] that found humans and chimpanzees to be astonishingly alike—indeed, more than 99% alike—at the genetic level. This is not, perhaps, so surprising when one considers that humans and chimpanzees share about 99.9999997% of their evolutionary histories in common;[41] but it had a significant effect upon paleoanthropologists' perspectives on ape/human relationships. Most notably, it provided an intellectual framework within which to consider very early hominid fossils. In later years, molecular data have also impinged on other areas of human phylogeny, most spectacularly via the recent extraction of mtDNA from the original Feldhofer Cave Neanderthal;[42] but of this, more later.

## AUGMENTATIONS OF THE HOMINID FOSSIL RECORD

When Dobzhansky and Mayr wrote, the human fossil record was but a fraction of its present size. With the effective disappearance from discussion by the 1940s of Eoanthropus ("Piltdown Man"), the major ongoing controversies in paleoanthropology at midcentury concerned the place of the newly published Mount Carmel hominids in human evolution[12,43] and Weidenreich's provocative (but almost data-free) notions of the antiquity of the modern human races.[12,13,44] Interest in the Taung juvenile *Australopithecus* was waning, while the wranglings over adult South African australopiths had only recently appeared on the horizon. From the perspective of the end of the twentieth century, then, it takes a conscious mental effort to reconstruct the fossil perspective within which the "modern" period of paleoanthropology took its start.[1] A comprehensive review of the past half-century's impressive augmentations of the paleoanthropological record is impractical in the space available here (see Tattersall[1] for such a review up to the early 1990s); but following are some of the highlights. Everyone will certainly find some favorite fossil, artifact, author, study, or technology missing from this account, and I can only apologize in advance for such inevitable lacunae.

> **. . . with long arms and extremities and relatively short legs (but broad pelvises), these early bipeds possessed a bodily conformation that would have facilitated locomotion in the trees even as they moved on their hind limbs on the ground.**

### The First Bipeds

During the early 1960s there was vociferous debate over just what it was that had set Hominidae on its unique evolutionary trajectory.[1] Some paleoanthropologists favored the appearance of the precisely manipulative hand; others the reduction of the canine tooth, possibly in association with toolmaking and manipulation. Brain size increase was also defended as the defining hominid characteristic, as was the adoption of upright bipedalism.[1] Fossil discoveries made from the mid-1960s through the 1970s seemed to settle the argument in favor of the last possibility (though nothing, it seems is forever!), to the extent that, by the end of the 1980s, it had become common for paleoanthropologists to refer to the earliest hominids (the "australopiths") as "bipedal apes."[45]

Currently the earliest pretender to hominid status is *Ardipithecus* (formerly *Australopithecus*[46]) *ramidus*, a form described from the Ethiopian site of Aramis in 1994.[47] The few fragmentary specimens of this species currently described (though more are rumored) are dated to about 4.4 myr ago, and come from what the associated fauna suggests was a relatively closed habitat.[48] Bipedalism in this species is very indirectly inferred from a tiny portion of cranial base in which the foramen magnum appears to have been forwardly positioned. However, the associated teeth are narrow and (primitively) thin-enameled, and when contrasted with those of the almost-as-old *Australopithecus anamensis* (see below) suggest that if this species is indeed hominid, it represents an early side-branch of the family—showing us that from the very beginning, hominid history has been one of evolutionary experimentation.

Even more recently described is the species *Australopithecus anamensis*, reported from deposits representing a more open environment at Kanapoi and Allia Bay, in northern Kenya. All but one of the fossils currently ascribed to this species are bracketed between 4.17 and 4.07 myr ago.[49–51] Also fragmentary, and represented primarily by (thick-enameled) teeth, *A. anamensis* has the advantage of being known from described postcranial fragments. These include a proximal tibia which shows strong indications of bipedality. Dentally, *A. anamensis* is described as having long, narrow, and parallel toothrows, indicating a strongly projecting face. However, most observers have been struck[51] by the general similarity to *Australopithecus afarensis*, the best known (and next in time) of the early hominid bipeds.

*Australopithecus afarensis* itself was described in the 1970s[52] from deposits at Hadar, Ethiopia, that are now dated between about 3 and 3.4 myr ago,[53] and at Laetoli, Tanzania (ca. 3.5 myr[54]). Most famously represented by "Lucy," a 40% complete skeleton,[55] *A. afarensis* is now known from hundreds of fossils, including a quite recently discovered robust skull, presumably male.[56] These show that while this species was unquestionably bipedal when on the ground (something also suggested by the remarkable Laetoli footprints[54]), the form of bipedalism involved was not that of modern humans. Rather, with long arms and extremities and relatively short legs (but broad pelvises), these early bipeds possessed a bodily conformation that would have facilitated locomotion in the trees even as they moved on their hind limbs on the ground.[57] The common linking factor between these locomotor/postural modes was evidently trunk uprightness. For, as the fossil record has expanded, it has become evident that australopith locomotion was not simply a "transitory" specialization between arboreal and terrestrial modes; rather, it was a stable and successful adaptation in itself, remaining essentially unchanged over at least 3 myr even as new australopith species came and went. And the Hadar hominids seem to have lived in a mosaic of closed riverine forest to woodland and bush,[58] an ideal habitat for exploiting this combination of abilities. A remarkable recent find of a partial australopith skeleton at Sterkfontein, in South Africa (whence the first adult *A. africanus* had come in 1936, though the new find was at an earlier stratigraphic level, 3.3 myr old by magnetostratigraphy as compared to maybe 2.5 myr), reveals a foot that is more derived (bipedally specialized) toward the rear, while the digits remain relatively elongated and the great toe relatively divergent.[59]

Clearly, bipedal terrestrial locomotion (eventually) paved the way for all the developments that were to come in human evolution. But there are nonetheless good reasons for characterizing the australopiths as "bipedal apes." For the crania of these hominids had large, projecting faces and relatively tiny braincases: exactly what we find among living apes, and the reverse of what we see in extant hominids. What small brain sizes imply functionally, though, is obscure. Some polished bone fragments from South Africa's Swartkrans[60] apart, there is no uncontested evidence that any australopith used tools. Thus, regrettably, the australopiths left virtually no archaeological record; and in the absence of such a record there is rather little that can be inferred about their behavior (though stable isotope analyses of South African fossils suggest that the "robust" forms were largely vegetarian,[61] while the "gracile" forms apparently included animal protein in their diet[62]). But while there is currently no way to demonstrate how far the early australopiths might have moved cognitively or manipulatively beyond the ape league, a high-protein diet on the part of the graciles might well have laid the energetic basis for the expansion of the notoriously energy-hungry brain.

**It will, of course, be years (if ever) before consensus is reached on the exact geometry of relationships among the members of the ever more diverse australopith group; but the general pattern is already becoming clear. The australopiths were not simply a monotonous early "stage" in the ascent to humanity. Rather, while maintaining a basic body plan, they represent a period of intense speciation and evolutionary experimentation in early hominid history. It is from this ferment that the human ancestor ultimately emerged.**

What drove the adoption of bipedalism among hominids? Many believe that a trend toward climatic drying and seasonality of rainfall led to the contraction of African forests and the consequent expansion of woodland and grassland following about 5 myr ago.[63] This would have created precisely the conditions necessary to have encouraged populations of forest-living hominoids to venture beyond their leafy habitat. The French paleoanthropologist Yves Coppens has, indeed, elaborated on the notion of the Dutch primatologist Adriaan Kortlandt that physiographic changes consequent on the creation of the great African Rift Valley had placed eastern Africa in the rain shadow of the west.[64]

The consequences of this are potentially significant. To the east, hominids emerged onto the burgeoning dry grasslands, while to the west the persisting forests continued to shelter arboreal hominoids, the ancestors of today's African apes. Ironically, though, a problem with this attractive scenario is posed by a fragment of lower jaw found recently by Coppens' French colleague Michel Brunet.[65] Given the name of *Australopithecus bahrelghazali*, this specimen came from a site in Chad, to the west of the Rift, that probably dates to around 3.5 myr ago. Where exactly it fits into human phylogeny remains to be determined; but it certainly makes the human family tree "bushier," as do the famous 2.6 myr-old "Black Skull" (KNM-WT 17000; Fig. 4) found at Kenya's West Turkana in the mid-1980s,[66] and the *Australopithecus garhi* fossils very recently reported[67] from 2.5 myr-old deposits in Ethiopia's Bouri Formation. The long-faced Black Skull (nowadays generally assigned to the species *Paranthropus aethiopicus*) is generally considered to lie somewhere near the ancestry of the "robust" australopith lineage, while its describers place the megadont *A. garhi* in an intermediate relationship

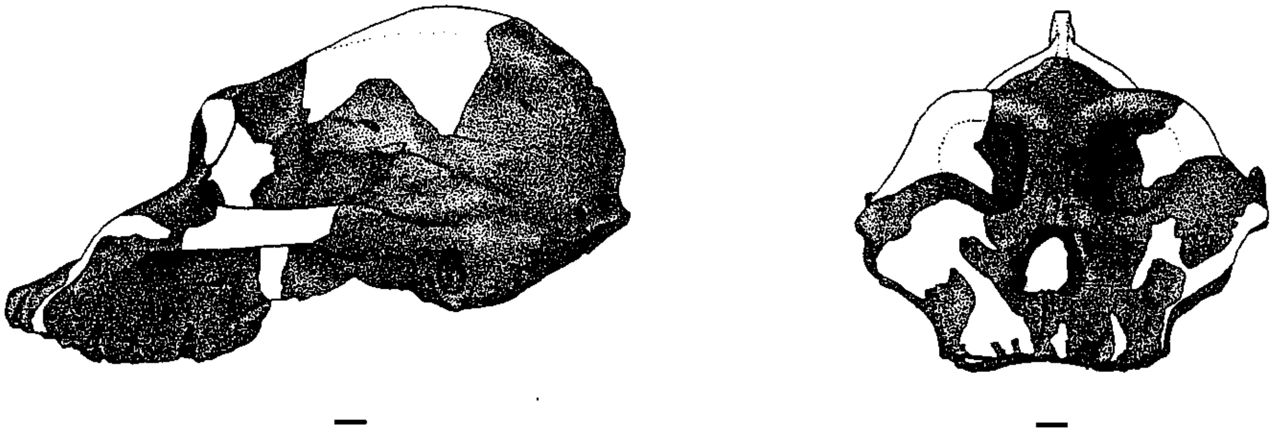

Figure 4. Side and front views of the "Black Skull," KNM-WT 17000, which pushed back the antiquity of the "robust" australopiths in East Africa. Scales are 1 cm; from Tattersall.[1]

between *A. afarensis* on the one hand, and a larger clade that includes both more recent *Australopithecus* and *Homo* on the other.

It will, of course, be years (if ever) before consensus is reached on the exact geometry of relationships among the members of the ever more diverse australopith group; but the general pattern is already becoming clear. The australopiths were not simply a monotonous early "stage" in the ascent to humanity. Rather, while maintaining a basic body plan, they represent a period of intense speciation and evolutionary experimentation in early hominid history. It is from this ferment that the human ancestor ultimately emerged.

## The First Tool Makers

One of Louis Leakey's major concerns in creating the new species *Homo habilis* in 1964[68] was to provide an identity for the maker of the crude stone tools found in Bed I of Tanzania's Olduvai Gorge. This might not have been the optimal use of a classification system normally based on the morphological identification of species, but as it turns out it was certainly practical. For a huge variety of fossils has by now been placed in the category of "early *Homo*," mostly because of age or putative association with early stone tools, rather than on the basis of any morphological characteristics that would suggest particular affinity with our own type species of the genus. Most of the fossils involved come from Olduvai Gorge and from Kenya's East Turkana region (though they are increasingly reported both to the north and the south of these sites); and it is, indeed, ironic that *Homo habilis* first became a widely accepted taxon as a result of the mid-1970s discovery of the relatively large-brained KNM-ER 1470 cranium at East Turkana.[69] Ironic because, in the wake of Wood's exhaustive researches,[70] it has become common to accept 1470 as the type specimen of the separate species *Homo rudolfensis*.[71] To this same species has also been allocated a possibly 2.5 myr-old mandible found in 1992 at Uraha, in Malawi.[72] More dubiously, a partial cranium (Stw 53) from Sterkfontein in South Africa has been referred to *Homo habilis*.[73] To the original *Homo habilis* materials from Olduvai (cranial and jaw fragments, plus a few isolated postcranial bones including most of a foot) have subsequently been added a highly fragmentary skeleton (OH 62) with staggeringly primitive limb proportions,[74,75] and a palate (OH 65) that is as yet undescribed. Among other finds, a 2.3 myr-old palate from Hadar, stratigraphically associated with stone tools, has recently been referred to *Homo* sp.[76] Interestingly, Wood and Collard[77] have lately reviewed the fossils variously referred to *Homo habilis* and *H. rudolfensis*, and, while accepting both species as valid biological entities, have concluded that neither qualifies morphologically for membership in *Homo*. Clearly, this is an area for much future research; but it is already abundantly evident that diversity was also a signature of the fossil record at this stage of human evolution.

The earliest stone tools are currently known from sites in Ethiopia and Kenya dating between about 2.3 and 2.6 myr ago.[78,79] Unfortunately, definitive association between the first crude stone tools (belonging to the Oldowan Complex, apparently beyond the cognitive abilities of living apes,[79] and consisting of simple flakes knocked from small stone cores) and particular hominid fossils is lacking. However, an important recent report[80] has placed 2.5 myr-old stone tools in close stratigraphic and geographic proximity to the newly named *Australopithecus garhi*.[67] Cut- and chop-marks on contemporaneous mammal bones demonstrate that these early tools were used in the butchering of carcasses, and long-bones show the torsional fractures caused by marrow extraction. The describers were understandably reluctant to associate the tools and evidence of butchery with their new *Australopithecus* species;[78] but it should not be forgotten that any behavioral innovation has to take place *within* a species (for where else can it happen?). Thus, as long as our criterion for membership in *Homo* is the behavioral one of stone toolmaking, the picture will inevitably remain muddy; for morphologically the first stone tool maker cannot have signifi-

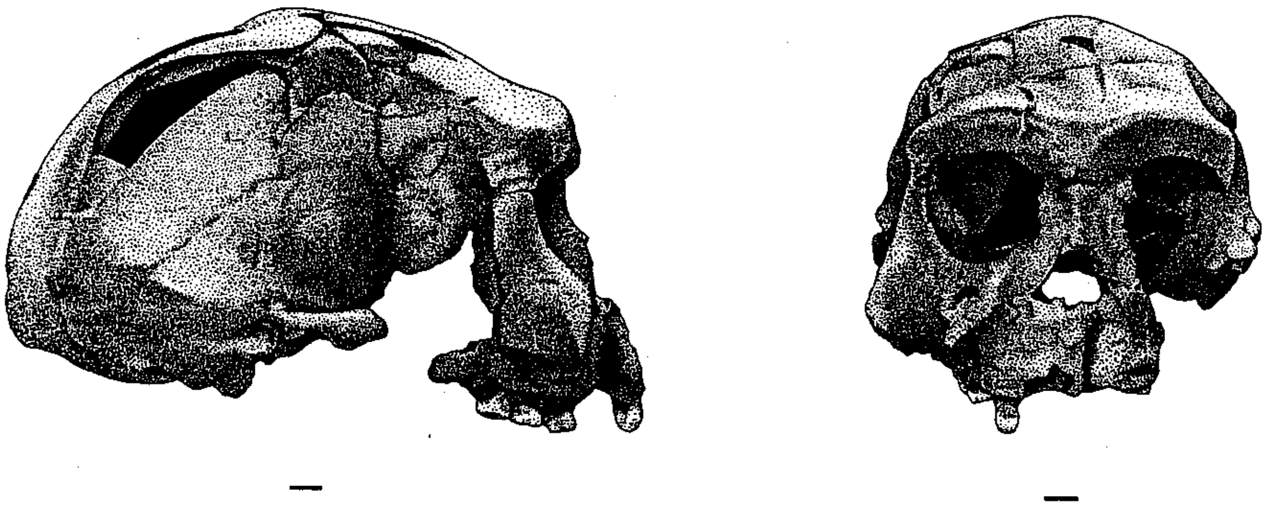

Figure 5. Side and front views of Sangiran 17, one of the two best-preserved putative *Homo erectus* crania from Java. Scales are 1 cm; from Tattersall.[1]

cantly differed from its own non-toolmaking parents.[27]

## The Earliest Humans of Modern Body Form

One of the most remarkable paleoanthropological events of the last half-century was the recovery of the KNM-WT 15000 skeleton from 1.6 myr-old deposits at Nariokotome in Kenya's West Turkana region.[80] Emerging somehow from the postcranially impenetrable "early *Homo*" morass, here finally were the remains of a tall, slender individual (adolescent, but clearly interpretable) with an essentially modern body build. See Schwartz's recent book[81] for a provocative mechanism to explain how this rapid skeletal reorganization might have come about. Earlier usually referred to as an "early African *Homo erectus*," this specimen is now frequently associated with the more primitive species *Homo ergaster*, described in 1975[82] from the 1.5 myr-old KNM-ER 992 mandible from East Turkana. Latterly this designation has increasingly been applied to such "advanced" crania from the same region as KNM-ER 3733 (about 1.8 myr old) and the slightly younger ER 3883 (and sometimes also to the SK 847 partial cranium from Swartkrans in South Africa). Future research will probably demonstrate some considerable diversity even within this group;[83] but for the moment it is sufficient to distinguish these early African forms from the later "classic" *Homo erectus* known from eastern Asia since the 1890s. Particularly significant in historical terms was the discovery of ER 3733 in East Turkana sediments that were penecontemporaneous with those that had yielded the "robust" australopith cranium ER 406. This latter is usually attributed to *Paranthropus boisei*: the species of the famous "Zinjanthropus" specimen (OH 5), the first East African "robust," discovered by Mary and Louis Leakey at Olduvai Gorge in 1959. It was the contemporaneity of these two vastly different hominids (Fig. 1) that sounded the final death knell of the single species hypothesis, at least in its purest form.

In any event, it is with *Homo ergaster* that we find the first hominid who was clearly at home in the open savanna, far from the shelter of trees, with a heat-shedding, bipedally-striding structure that included tall stature and long, slender limbs.[80] Interestingly, these physically distinctive new hominids continued to make tools that were pretty much indistinguishable from those their anatomically more primitive predecessors had made for nigh on a million years; for it was only at about 1.5 myr ago (in Africa; its spread significantly beyond that continent was sluggish) that a radically new kind of tool, the Acheulean hand axe, became common.[84] Although there are recent hints that Acheulean technology goes back as far as about 1.65 myr,[85] we appear to have here another example of a theme that has marked the history of human technology: technological innovations do not coincide with (and are thus not explained by) the arrival of new hominids.[27] Which, again, makes sense; for any technological innovator has to belong to a pre-existing species.

## Into Eurasia

Once modern body form (hence emancipation from the forest fringes) had been achieved, hominids were not slow to exploit the new possibilities.[86] For, hard on the heels of the first *H. ergaster*, controversial new dates suggest that hominids had spread not only beyond Africa but to the farthest reaches of eastern Asia, where ages as early as 1.8 myr have been reported for hominid fossils from both Java[87] and China.[88] Despite the loss of the Zhoukoudian fossils in 1941, a steady trickle of finds from eastern Asia has resulted in a fairly impressive (though poorly described) hominid fossil record from both continental and insular parts of the region (Fig. 5).[89] Indications of early hominid occupancy also come from farther west along the route of spread, notably in the form of a possibly 1.6 myr-old "*Homo erectus*" jaw from Dmanisi in ex-Soviet Georgia,[90] and crude stone tools 1.6 myr old from Riwat, in Pakistan.[91] An early (pre-Acheulean) hominid exit from Africa has the advantage of helping explain why the Acheulean never made it to far eastern Asia.[87] At the other end of the time spectrum, recent (controversial) dating of the Ngandong "*Homo erectus*" to around 40 kyr[92] at least hints at the possibility that the same fate may have overtaken these late survivors of the eastern Asian hominid radiation as befell the Neanderthals in the far west of Eurasia, at about the same time.[86]

Anomalous observations apart,[93] there is little evidence for hominid occupation of Europe before about 1 myr ago. The earliest fossil evidence from the subcontinent, from the Gran Dolina of Spain's Atapuerca Hills, consists of fragmentary (and in some ways remarkably modern-looking) specimens that are about 800 kyr old and have been allocated to the species *Homo antecessor*.[94] They are found in association with a rather crude stone tool kit, and their relationship to later European forms remains equivocal,[86] though their describers place them close to the common ancestry of Neanderthals and moderns.[94] A cranium from Ceprano, Italy, is a little younger, at about 700 kyr. Assigned by its describers[95] to *Homo erectus*, its exact affinities are unclear at this point. The European record picks up again after about 500 kyr ago, with a succession of fossils (formerly "archaic *Homo sapiens*," one of paleoanthropology's greatest and most destructive obfuscations) that are commonly referred nowadays to *Homo heidelbergensis*, the species created in 1908 by Schoetensack[96] to accommodate the German Mauer jaw ("Heidelberg man"). This species boasts brains in around the 1,100–1,200 ml range, and is first known from Ethiopia's Bodo at about 600 kyr ago; some of its more complete later representatives, such as the crania from Petralona (Greece) and Kabwe (Broken Hill, Zambia) are still uncertainly dated. In Europe, *Homo heidelbergensis* is temporally associated with early hearths and structures at sites such as France's Terra Amata,[97,98] and at Germany's Bilzingsleben.[99] Putatively it is also associated with two-meter-long, heavy, and beautifully-crafted wooden throwing spears some 400 kyr old recently discovered at Schoeningen, Germany.[100] Some *Homo heidelbergensis* (e.g., Petralona) show such enormous development of the cranial sinuses that they are ruled out of the ancestry of any later hominids; but such ancestry is presumably to be found somewhere within this motley complex.

## The Neanderthals and Their Relatives

Much recent attention has been paid to the Neanderthals, whose record is constantly being augmented, and who flourished in Europe and western Asia between about 200 and 30 kyr ago.[101] Increasing numbers of researchers are coming to see these distinctive large-brained hominids as demanding distinction as *Homo neanderthalensis*[33,102] (rather than being mere variants of *Homo sapiens*); and it has also been pointed out that in fact this species merely comprises one component of a quite diverse endemic radiation of hominids in western Eurasia.[103] Other components of this radiation include the extraordinarily-preserved Atapuerca Sima de Los Huesos specimens[104] from Spain, dated to about 300 kyr ago, and the (probably somewhat younger) fossils from Germany's Steinheim and Reilingen and England's Swanscombe, each of which shows some Neanderthal characteristics without displaying the entire suite.

Whatever the actual diversity involved, *Homo neanderthalensis* seems to have been the most successful member of this group; and after about 200 kyr ago this species appears to have had Europe to itself until disturbed by the first arriving *Homo sapiens* about 40 kyr ago (following which it was gone within not much more than 10 kyr). The Neanderthals left us a rich technological record, although not one that contains much unequivocal evidence of symbolic behaviors. However, burial of the dead (the significance of which remains equivocal) was practiced at least simply, and occasionally.[27] The rare Châtelperronian culture (which shows some Upper Paleolithic as well as Middle Paleolithic elements) was probably the work of Neanderthals,[105] but occurs only within the period (ca. 36–32 kyr ago) in which geographic (and presumably cultural) contact with moderns was already established.

Several studies have lately shed light on the Neanderthals as a distinctive morphological and evolutionary entity. Recently, for example, it has been recognized that these hominids possessed highly unusual specializations of the nasal region.[106] And although, bizarrely, this simple observation has been attacked both by those who claim that these apomorphies are not really present in Neanderthals[107] and by others who assert that they also occur in *Homo sapiens*,[108] the great distinctiveness of the Neanderthals in the nasal region (especially in possessing prominent bilateral "medial projections" just inside the lateral nasal margins, and a bulging of the nasal wall behind them), as in other anatomical complexes, is not in doubt.[109] On another front, Krings et al.[42] accomplished the technological feat of isolating some 378 bp of mtDNA from the type Neanderthal specimen from the Feldhofer Grotto (now also radiometrically dated, to about 40 kyr ago[110]). This clearly showed the Neanderthaler to represent a distant outgroup to all living human populations, and it convinced Krings et al.[42] of the specific distinctness of the two kinds of hominid. Indeed, these workers calculated a probable divergence date of the *neanderthalensis/sapiens* lineages in the range of 690–550 kyr (in contrast to 150–120 kyr for the common ancestor of all modern humans).[42,111] In light of the substantial length of the putatively pre-Neanderthal fossil record, this estimate seems quite plausible.

Evidence of this kind has not, however, caused any significant rethinking of Neanderthal/modern relationships among those of linear mindset. Experts in fallback positions, paleoanthropologists of this ilk have largely abandoned the notion that Neanderthals evolved directly into moderns, but now assert instead that Neanderthal disappearance was due to a genetic "swamping" of the latter by large numbers of invading moderns.[19] Relethford[112] has recently shown in these pages that such an effect may be plausible in principle. However, the fact remains that the anatomical "evidence" for any such effect is shaky at best, and is in fact dependent largely on inadequate characterizations of morphology.[103,111] The latest expression of the interbreeding notion is the claim that a 24.5 kyr-old infant skeleton from Lagar Velho in Portugal is somehow a member of a Neanderthal/modern hybrid population.[113] There is, however, no substantive morphological basis for this interpretation[114] (and as far as we know from fossil evidence the last Neanderthal was gone from Iberia by 29–27 kyr ago[115]); but the debate will doubtless drag on.

### The Origin of Modern Humans

The question of modern human origins has been very actively argued in recent years, especially in the wake of intriguing fossil discoveries in southern, eastern, and northern Africa, and in the Levant.[116,117] This is also a field in which new dating techniques have had a particularly significant impact.[117] The earliest putatively *Homo sapiens* (i.e., anatomically modern) fossils show up in Middle Stone Age contexts in Africa; and while many of them are either fragmentary or poorly dated,[1] when taken together they are hard to ignore. This physical record, which starts at about 130 kyr ago, is the principal data set on which the "Out of Africa" model of modern human origins is based,[116] although this notion (which sees the origin of *Homo sapiens* in an African isolate that later spread widely) also receives considerable support from molecular studies.[118] In Israel, well preserved and clearly *Homo sapiens* (but Middle Paleolithic) fossils from Jebel Qafzeh have been dated to 92 kyr ago,[119] though it should be borne in mind that there is some morphological heterogeneity at this site, as there is at Mount Carmel's Skhul, a little earlier in time. Still, anatomically indisputable *Homo sapiens* (in the form of Qafzeh 9 and allied specimens) was present in the Near East at close to 100 kyr ago. So also, apparently, were the Neanderthals, which persisted in that part of the world until something under 40 kyr ago.[120] Somehow, then, Neanderthals and moderns contrived to share the Levant for perhaps 60 kyr, although it's also possible that in warmer times the *Homo sapiens* population moved into the Levant from Africa while the Neanderthals retreated north, the reverse occurring in phases of cooler climate.[121] Whatever the case, it is at the very least interesting that Neanderthals disappeared definitively from the Near East at around the time when the Levantine Upper Paleolithic emerged, suggesting that it was behavioral rather than anatomical innovation that eventually gave the moderns their competitive edge.[27]

We should not be surprised by this, for as already noted behavioral innovations have to occur *within* pre-existing species. The first Cro-Magnons who invaded Europe about 40 kyr ago[27] clearly possessed a totally modern human sensibility, although where exactly they came from is unknown. The earliest intimations of modern behavior patterns come from Africa,[27,122] but the evidence is sparse. So is evidence for what, exactly, happened in the emergence of modern humans. Given the fact that externally modern human brains had been around for 60 kyr or more before we have unequivocal evidence for the exercise of modern human cognition, it seems most reasonable to conclude that a behavioral potential was born with modern human anatomy that was only exploited much later in time.[27,123] In terms of evolutionary process such "exaptation"[124] is, of course, entirely routine. However, it remains to be determined what the cultural releasing agent might have been. My favorite suggestion is the invention of language, something that is powerfully tied up with the unique symbolic processes of the human mind.[123] This would help explain how the remarkable human capacity spread so rapidly throughout the Old World; for this evidently advantageous cognitive condition could have spread by cultural contact among populations that already possessed the latent capacity to acquire it. No wholesale replacement of behaviorally archaic by behaviorally modern populations would have been required. Still, the mystery of the origin of the human capacity is, of course, the question of questions. And it is one that will be debated indefinitely.

## WHITHER PALEOANTHROPOLOGY?

The remarks above will have indicated some of the multitude of areas in paleoanthropology where our knowledge is sorely deficient, and where research attention will doubtless be concentrated over the century to come. It is, of course, impossible to predict what discoveries of new fossils and sites will be made, and how these will alter our outlooks on the evolution of our kind. Nobody, after all, could have imagined fifty years ago the hominid fossil record that exists today. Yet we can say with some confidence that our new theoretical perspectives will allow us to place human evolution more squarely within the evolutionary process as it is known for organisms in general. I have little hesitation, for instance, in predicting that, at all stages, an expanding record will show a strong signal of diversity, and will reveal an episodic history of evolutionary experimentation rather than a linear trudge toward perfection. And, as cladistic notions continue to permeate their science, one can at least hope that paleoanthropologists will henceforth pay more attention than has mostly been the case to the importance of basic systematics in unraveling pattern in human evolution.

On the technological front, it is equally unpredictable what new techniques in dating, dietary analysis, morphometrics, biomechanics, and so forth will offer paleoanthropology in the third millennium—although, based on the experience of the last decade alone, it is clear that the potential is enormous. But while advances in technology will offer huge potential for "gee-whiz" displays of technical expertise, and achievements to date have been impressive, it is clear that technology by itself will be no panacea for paleoanthropology's problems. To make a truly positive contribution, technical advances must be harnessed in the service of a theoretically coherent framework, and to clearly articulated sets of questions. As our still-young science matures, it is reasonable to hope that this necessity will increasingly be appreciated. It is less sure, on the other hand, that paleoanthropologists will entirely abandon their received predilections toward viewing evolution as a process that consists of little more than "adaptation-driven" fine tuning. And if I am right about this, tension will continue to exist between the basic data of the fossil and archaeological records, and paleoanthropologists' interpretations of them.

## ACKNOWLEDGMENTS

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