Winfried Henke · Ian Tattersall (Eds.)

Handbook of Paleoanthropology

Volume III
Phylogeny of Hominids

In collaboration with Thorolf Hardt

With 113 Figures and 26 Tables

Springer

Preface to Volume 3

The first two volumes of the *Handbook of Paleoanthropology* dealt with principles, processes and methods, and with our primate relatives that provide the context within which human evolution must be understood. In this final volume of the series, we come to the human fossil record itself, and once again we have asked our authors to represent their distinctive points of view on the topics addressed, while acknowledging the diversity of perspectives that exists in this often contentious arena. As ever, this has meant that different contributions often represent different points of view in areas of overlap (contrast, for example, the notions of *Homo erectus* presented by Susan Antón and colleagues, and by Ian Tattersall), and we ask our readers to accept divergent views such as these as evidence of the dynamism and the spirit of active inquiry that informs the entire field of paleoanthropology. This is not an area of science that has settled into a state of comfortable domination by a body of canonical works—and we both expect and hope that it never shall be. Science is always a work in progress, and the ongoing ferment in paleoanthropology exemplifies this essential fact. Indeed, our authors are even far from agreement on the matter of the rank at which the taxon that includes *H. sapiens* and its non-ape living and extinct relatives should be recognized. One group of molecular biologists, not represented here, would go so far as to include all of these forms in the genus *Homo*; at the other end of the spectrum lie those (such as ourselves) who believe that they are so numerous and diverse that they warrant the familial distinction as Hominidae that they were accorded throughout most of the twentieth century. In the middle are those who believe that our closest ape relatives, at least, should be admitted to Hominidae and that consequently we and our extinct relatives should be allocated to the subfamily Homininae. To a large extent these differences stem more from a philosophical "top-down versus bottom-up" disagreement than from a dispute over phylogeny; we have thus not insisted on a standard usage here, and must ask the reader to indulge the resulting rather flexible terminology: it should in any case be obvious what the authors' meanings are.

Volume 3 opens with a review by George Koufos (Chapter 1) of the fossil record pertaining to hominid origins, starting with the Early Oligocene *Aegyptopithecus* which, despite its very early date, he views as a potential ancestor for the Micocene hominoid radiation. Among the earliest representatives of the latter he finds that in a rather spotty record *Proconsul* spp. provide the most plausible connection to later Miocene forms such as *Ouranopithecus* (and

possibly *Dryopithecus*) that he views as lying close to the common ancestry of both hominids and the living great apes. He notes that particular similarities between *Ouranopithecus* and *Sahelanthropus* suggest hominid affinity for the former, but at the same time he finds that the tantalizingly fragmentary nature of the hominoid fossil record of the later Miocene makes highly provisional any inferences drawn. Jeffrey H. Schwartz (Chapter 2) tackles the matter of hominid origins and ancestry from a rather different perspective, providing an historical overview of how today's received wisdom was acquired, and proposing a suite of mostly postcranial and dental characteristics that may be regarded as hominid synapomorphies. He notes the hazards of indirectly inferring upright bipedal locomotion from fragmentary and cranial evidence, and reviews the craniodental features that have been used to argue that one or another latest Miocene hominoid has specifically hominid affinities. In doing this, he points out the dangers inherent in analyzing character states in the light of prior assumptions about relationship, and exposes the rather fragile nature of many cherished notions about very early hominid evolution. In concluding, he provides a detailed analysis of the morphology of the recently discovered *H. floresiensis* that underlines the oddly assorted features of this hominid. In asking the question of whether this curious creature is properly allocated to the genus *Homo*, Schwartz raises vital questions as to the morphological criteria that have been used to define the family Hominidae itself.

However exactly it originated, the family Hominidae was the product of an environment or set of environments to which its earliest representatives had to accommodate. Bogusław Pawłowski (Chapter 3) contributes a general discussion of the environmental forces that may have shaped or influenced early hominid evolution, particularly in such areas as body size, sexual dimorphism, the masticatory system, social structure, and above all the locomotor system. He sees in future a closer integration of paleoanthropology and genetics that will allow us to decipher the first appearance of derived hominin traits and to determine more precisely the selection pressures that acted upon them. Elisabeth Vrba (Chapter 4) follows with a consideration of ways in which evolutionary changes may be linked to external environmental change and adaptive strategies. She emphasizes that hominoids should be studied within the contexts of the biotas and environments in which they lived, and that changes in biotic factors should be examined in relation to events in the physical world. She also notes the need for an expanded theoretical framework to allow a better understanding of the dynamics of causality and effect among the various levels of evolutionary action from morphogenesis up through faunal turnovers. Given the discovery of early bipeds in forest contexts, some have expressed doubts about whether the origin of bipedality was linked to environmental stimuli. However, Vrba shows how such linkage might be

maintained even so; and following a review of relevant physical and biotic factors she presents both theoretical and empirical arguments to sustain the notion that in diverse ways hominids have been responsive to environmental stimuli throughout their evolutionary history.

Vrba's thoughtful review serves as prelude to Will Harcourt-Smith's (Chapter 5) consideration of the hominid postcranial skeleton and the morphological evidence for early bipedal locomotion and posture among hominids. Harcourt-Smith finds that this evidence indicates a qualitative shift between an early form of locomotion that represented a sort of compromise between terrestrial bipedality and arboreal climbing, and a later obligate bipedalism that completely sacrificed arboreal agility for a striding locomotion suited to open savanna habitats. He links the origin of striding locomotion to the emergence of the genus *Homo*; and, after examining the remarkable variety of hypotheses that have been put forward to account for the adoption of upright terrestrial locomotion, concludes that this new behavior was at least strongly linked to the availability of new, more open habitats. He also notes that this radical adaptive shift is unlikely to have been associated with a single factor alone, but that it most probably occurred in the context of a broader ecological strategy to cope with changing environments.

Nowadays the adoption of upright bipedality, at least in its original facultative manifestation, has become more or less synonymous with the origin of Hominidae itself. As a result, more or less any hominoid fossil that displays evidence of upright terrestriality has a claim upon early hominid status. Brigitte Senut (Chapter 6) surveys a wide range of early claimants to hominid status, concluding that among the three latest Miocene contenders, *Orrorin tugenensis*, *Sahelanthropus tchadensis*, and *Ardipithecus kadabba*, only the first has a clearly demonstrated claim to having moved bipedally. Because of the evidence that *Orrorin* had lived in a rather moist and forested environment Senut is skeptical of the notion that hominid bipedality evolved in a savanna setting, and on the basis of some apelike isolated teeth from 12- to 6-million year-old sites in Kenya, she suggests that the split between the human and African ape lineages may have occurred rather earlier than generally believed.

The substantive hominid fossil record begins with the appearance of the genus *Australopithecus* at a little over 4 Ma. The term "australopiths," which was originally introduced by Clark Howell to avoid the subfamilial status implicit in the term "australopithecine," has now become even more problematic than the term it was intended to replace. This is largely because it is unclear whether early hominids or putative hominids other than *Australopithecus* and *Paranthropus* species should be embraced by the name (and, if so, which). William H. Kimbel (Chapter 7) firmly lays the problem to rest by adopting a restricted definition not only for "australopiths" but by sinking *Paranthropus* (yet

again) into *Australopithecus*. For him, then, "australopith" is simply an informal term to embrace all members of a comprehensive (and possibly paraphyletic) genus *Australopithecus* (plus the stray *Kenyanthropus platyops*, which he finds to be morphologically isolated), the earliest member of which is *A. anamensis*. Kimbel reviews the taxonomic history of the genus and follows with outlines of the salient craniodental morphologies of the eight australopith species that he recognizes. However, he cautions that uncertainties originating one way or another in the incompleteness of the record make it difficult to discern the precise pattern of the hominid evolutionary record during this early phase. He finds only two cases in which it is currently possible to suggest evolutionary pattern within the australopith group. One of these cases is the anagenetic transformation of *A. anamensis* into *A. afarensis*; and the other is splitting of a "robust" lineage rooted in *A. aethiopicus* into southern (*A. robustus*) and northern *(A. boisei*) clades.

Mark Collard and Bernard Wood (Chapter 8) broach the ever-elusive problem of defining our own genus *Homo*. Despite the evident centrality of this issue to the human identity, our genus has essentially been defined in the breach, as it were. For most of the early history of paleoanthropology the genus *Homo* remained highly exclusive, necessarily containing *H. sapiens* and at best also including the large-brained *H. neanderthalensis*, more or less as a courtesy. At the same time, as the hominid fossil record slowly grew, hominid genera proliferated to accommodate the new finds. But at the midpoint of the twentieth century, everything changed. As the Evolutionary Synthesis swept all in paleoanthropology before it, the genus *Homo* briefly came to embrace the entire known hominid fossil record (Mayr 1950; see Henke, Volume 1 of this series). As sanity returned, the australopiths were hived off once more into their own genus or genera, and the focus of *Homo* narrowed again until the controversial addition in 1964 of *H. habilis*, driven by Louis Leakey's predilection for the notion of "Man the Toolmaker." The initial acceptance of *H. habilis* was generally reluctant, for both good reasons and bad; but once the species gained general currency, the way was open for the genus *Homo* to become a wastebasket for a whole miscellany of fossils dated to the period immediately following the invention of stone tools at about 2.5 Ma. In this volume, Collard and Wood expose the fragility of the criteria that have been applied to the recognition of early putative members of *Homo*, consider the various ways in which genera have been defined, and review the early fossil materials that have been allocated to *Homo*. They recommend restricting our genus to *H. ergaster* and subsequent forms, to the exclusion of such dubious candidates as *H. habilis*, "*Homo rudolfensis*," and the recently described *H. floresiensis*. Friedemann Schrenk, Ottmar Kullmer, and Timothy Bromage (Chapter 9), too, are conscious of the problems attendant on including many

fossils of the 2.5- to 1.5-Ma period in *Homo*, but they take a more ecumenical approach than Collard and Wood, and argue for a broad interpretation of the species *H. habilis* and for the inclusion in *Homo* of the Malawi and Kenyan materials often assigned to *H. rudolfensis*, which they consider distinct from the former. They review the morphology of the fossils involved in some detail, and present a scenario of ecogeographic differentiation among the hominids that straddled the Plio-Pleistocene boundary in Africa.

As the first truly archaic hominid species to be described, *H. erectus* from Java has occupied an iconic position in the history of paleoanthropology. It is quite understandable that, at a time when nothing much was known of the hominid evolutionary past beyond the Neanderthals and some ancient European *H. sapiens*, this form should have been widely considered a lineal ancestor of our own species. Whether it appropriately occupies this position today is much more arguable, especially in light of the enormous growth of the human fossil record. Ian Tattersall (Chapter 10) briefly reviews the history of study of this species, then goes on to consider the variety of morphologies that have been shoehorned into it over the last century. He concludes not only that the inclusion in *H. erectus* of the early African forms now often known as *H. ergaster* is unwarranted, but that a variety of distinct morphs can be perceived even within the classic eastern Asian hypodigm of *H. erectus* (as well as among the African materials widely attributed to *H. ergaster*). He stops short of advocating that the species *H. erectus* should be limited strictly to the Trinil type specimen and others of like morphology, but he does present substantial grounds for regarding *H. erectus* as an endemic and terminal eastern Asian species rather than an Old World-wide phase of human evolution. He also points to reasons for rejecting the notion that the remarkably diverse hominid fossils from Dmanisi in the Caucasus can usefully be subsumed under the umbrella of *H. erectus*. Susan C. Antón, Fred Spoor, Connie D. Fellmann, and Carl C. Swisher (Chapter 11) adopt an opposite perspective, arguing that little reason exists for differentiating between *H. erectus* and *H. ergaster* (although they experience difficulty in finding a satisfactory morphological definition of the enlarged taxon). These authors suggest instead that a relationship exists between brain size and a variety of cranial features, and that apparent differences between African and Asian *H. erectus* in such features may be related to large brain size in the first-discovered Asian specimens. Focusing particularly on the relationship between body and brain size, Antón and colleagues find a time-related trend toward increasing brain size within the species as broadly defined; and although they discover a distinct gulf between *H. erectus* and *H. sapiens* in the scaling relationship between body and brain size, at an earlier period they find it difficult to discern a similar distinction between large individuals of *H. habilis* and the smallest and earliest "African *Homo erectus*." Clearly

the problem of the precise identity of *H. erectus* is not one that will reach a consensus solution any time soon.

Philip Rightmire (Chapter 12) covers some of the same ground in his review of later Middle Pleistocene *Homo*, but concentrates mainly on *H. heidelbergensis*, which he distinguishes from *H. erectus* by a suite of cranial traits that he considers to be derived. These features, he believes, indicate that *H. heidelbergensis* originated from *H. erectus* (in the broadest sense) in a splitting event. The core group of fossils (Kabwe, Bodo, Saldanha; Ndutu as a possible female) that underpins Rightmire's notion of this cosmopolitan *H. heidelbergensis* comes from Africa, but he readily associates with these fossils such European specimens as Arago and Petralona (and even Mauer, hence the species' name). He is a little hesitant to include such eastern Asian specimens as Dali and Jinniushan in this group, but more boldly proposes that it also embraces the amazing sample of hominids from the Sima de los Huesos at the Spanish locality of Atapuerca. For Rightmire, these latter fossils provide a potential link between *H. heidelbergensis* and *H. neanderthalensis*, although Katerina Harvati's discussion (Chapter 13) demonstrates that a distinct morphological divide exists between the Neanderthals and the *H. heidelbergensis* core group. Harvati also shows quite clearly that the Neanderthals represent a distinct and endemic European lineage whose last common ancestor with *H. sapiens* existed quite deep in the Middle Pleistocene, and thus warrant specific distinction from the latter. As the best known of all extinct hominid species, *H. neanderthalensis* gives us a unique insight into both biological and behavioral variation of hominid species other than our own, and Harvati summarizes evidence in both categories before tackling the tricky subject of cognition, on which she wisely hesitates to be doctrinaire. She discusses the generally negative molecular evidence, both from Neanderthal aDNA and from comparative studies of modern human populations, for possible Neanderthal admixture with *H. sapiens*, and reviews hypotheses relating to Neanderthal exinction.

One of the hottest debates of the last decade has concerned Multiregional Evolution versus single-origin models of modern human emergence. Günter Bräuer (Chapter 14) begins his survey of the evidence for the origin of *H. sapiens* with early twentieth century "presapiens" notions, but quickly focuses in on the more recent controversy, which has still not been resolved to everyone's satisfaction. Bräuer's own preferred formulation for modern human emergence tries to accommodate as wide a range of concerns as possible as he rejects hard-line formulations at both ends of the spectrum in favor of a middle-of-the-road solution. He accepts the by now virtually unarguable evidence for abrupt replacement of the Neanderthals in Europe, by modern humans whose roots ultimately lay in Africa. Further, his examination of the evidence for regional transition in

China and Australasia fails to substantiate the notion of continuity in these regions. But within Africa itself he does find support for "a continuous early modernization process." In this he is aided by maintenance of a concept of "archaic *Homo sapiens*" that, in sharp contrast to Rightmire's assessment of the matter, is broad enough to include such specimens as the 600-ka-old cranium from Bodo. For Bräuer this fossil represents the first of three successive "grades" within *H. sapiens* that evolved, in "mosaic" fashion, through such forms as Florisbad, Omo 2, and Singa, to more fully modern populations such as those represented at Klasies River Mouth and Border Cave (BC 1). Taking these various analyses together, then, it appears that even though the Multiregional model has clearly failed as a general paradigm of modern human emergence, there is a vast range of possible takes on the single-origin alternative. In this area, as in so many others in paleoanthropology, it will evidently be a very long time before anything resembling a consensus emerges on the matter.

The first part of this volume of the *Handbook* is devoted to studies that are directly based on the hominid fossil record. But the interpretation of hominid evolutionary history does not stop there, and in the volume's second half a variety of studies is presented that help round out our picture of hominid evolution—and the ways in which we understand it—from a variety of complementary points of view. David Strait, Frederick E. Grine, and John G. Fleagle (Chapter 15) survey the development of concepts of human evolution, starting with notions of the evolutionary process itself and with the influence of the expectations that stem from them. They then proceed to examine the effects of cladistic approaches, traditional and quantitative, on the interpretation of human phylogeny. From this overview they gratifyingly conclude that such analyses are "converging on a common set of relationships," and that "the broad strokes of early hominid phylogeny are perhaps better understood than is commonly acknowledged." However, they do point out that announcements of new hominids—and especially early hominids—tend not to be accompanied by either comprehensive or testable hypotheses of their relationships. They thus assess the relationships of a variety of hominids discovered over the last decade or so using cladistic methodologies. And, while they acknowledge that the slender information so far available makes this attempt a highly provisional one, they conclude that although the overall topography of the hominid family tree appears relatively stable, the relationships of many of these forms, including *Sahelanthropus tchadensis*, *Ardipithecus kadabba* and *Orrorin tugenensis*, and perhaps most especially *Kenyanthropus platyops* and *Australopithecus garhi*, will continue to be vigorously debated.

Todd R. Disotell (Chapter 16) turns his attention to biomolecules and what they can tell us about human evolution. He points out that there are three areas in

which molecular studies have made specific contributions so far: the nature and timing of the split between the hominid lineage and its ape relatives; the status of the Neanderthals and their probable date of divergence from the lineage leading to *H. sapiens*, as based on the extraction and sequencing of aDNA; and the history of diversification and migration of *H. sapiens* populations via the comparative study of groups alive today. Disotell reviews the various techniques and lines of evidence available for approaching these questions, and points out some of their flaws and pitfalls as well as those areas in which signal contributions have been made. While powerfully making the case for the utility of molecular genetic studies in paleoanthropological studies, not least because of the enormous amount of data available, Disotell concludes that we will make most progress by integrating biomolecular data with what we can learn from the fossil record. From the perspective of population genetics, Alan R. Templeton (Chapter 17) examines various molecular data sets relevant to paleoanthropology, and concludes that over the past 2 million years hominids have expanded out of Africa on three occasions: the initial diaspora of the *H. ergaster/erectus* group; another episode some half-million years later, which he identifies with the exodus of the Acheuleans; and a third in which "modern" traits became disseminated around the world. The two later expansions involved interbreeding of the newcomers with the earlier emigrants, so Templeton envisages some continuity of gene flow throughout this demographic history. Accordingly, he is not prepared to accept that the aDNA evidence is conclusive evidence of the distinctness of the Neanderthals. In the molecular as well as the morphological realm, the continuity versus replacement debate continues. The vexed question of the Neanderthals reopens the question of what species actually are, a matter that Colin Groves reviews at some length in Chapter 18. He notes that a range of mechanisms may be involved in speciation but that, as a generally short-term phenomenon, under most definitions speciation itself is something we are unlikely to witness in the fossil record. Groves reviews the implications of speciation style for expected and observed patterns in the fossil record, and points out the degree to which the former may determine perceptions of the latter; the inevitable conclusion is that many "classic" instances of anagenesis in the fossil record may well require reexamination. He points out that gradualism is surprisingly hard to justify on theoretical grounds; but he also makes it clear that, given the many uncertainties of the fossil record, it may not always be easy to choose among scenarios based on gradualist versus punctuationist assumptions.

Wolfgang Nentwig (Chapter 19) takes the volume in a new direction with a consideration of the potential and measurable environmental impacts of increasing human population size through the Paleolithic and Neolithic periods. Such impacts are most clearly demonstrable after *H. sapiens* appeared on the scene, and

Nentwig discusses notions of megafaunal overkill at the end of the Pleistocene as a prelude to considering the sequelae of settled life, starting with Epipaleolithic/Mesolithic and Early Neolithic societies. These periods of human prehistory witnessed the most radical change ever in the nature of the relationship between humans and the environments around them. For the first time, human beings found themselves in an adversarial relationship with Nature; and in the course of describing changing patterns of environmental exploitation from the Paleolithic through the Early Iron Age, Nentwig shows how increasing economic intensification has amplified human vulnerability to environmental fluctuation. Nentwig confines himself largely to the Old World record, but another major and fateful event that occurred around the end of the Pleistocene was the initial occupation of the New World. The origin and pattern of this major episode is examined on the basis of dental morphology by Christy G. Turner and G. Richard Scott (Chapter 20), who offer evidence of separate migrations to Arctic and sub-Arctic North America, and to regions of the New World lying further south. On the basis of a general homogeneity of dental characteristics Turner and Scott infer that a single migration into the southerly zone was quickly followed by rapid population expansion in North America and rapid penetration throughout the South American continent.

The archive of human behavioral evolution is the archeological record, and in Chapter 21 Nicholas Toth and Kathy Schick review the development of stone-working technology and its inferred associated behaviors from the simple beginnings of stone tool making, some 2.6 Ma ago, through the Upper Paleolithic and the earliest evidence of symbolic activities. Many other chapters in these volumes refer to aspects of the archeological record, but here Toth and Schick provide the larger perspective within which these developments need to be understood. They not only provide a descriptive account of the stone tool succession but also sketch the larger behavioral background to which the stone tools and other material expressions bear witness. Steven Mithen (Chapter 22) takes up in greater detail the question of how the material record reflects wider behavioral complexities. In discussing the early stages of hominid evolution Mithen focuses on the relationships among general behavioral categories such as bipedalism and the broader aspects of sociality; at later stages, he stresses the relationship between material culture and cognitive processes. Throughout, Mithen is concerned to emphasize the interdependence (his preferred term is coevolution) of body, brain, language, and culture; and he finds that the most radical behavioral departure in the hominid record came with the sedentary behaviors ushered in at the end of the last glacial period. While Mithen's chapter looks at patterns of hominid behavioral evolution throughout prehistory, Nicholas Conard (Chapter 23) examines the evidence, mainly African and European, for the advent of cultural and

technological "modernity" in the record of the late Middle and Late Pleistocene. Conard points out the difficulty with concepts of behavioral "modernity," and suggests that, whatever exactly this behavioral pattern implies, it may well have been neither limited to nor universally characteristic of beings whom we would accept as "modern" on anatomical grounds. He evokes a very complex pattern of behavioral innovation in the latest Pleistocene, with multiple divergent and convergent regional developments: something which has, of course, characterized the behavioral history of *H. sapiens* ever since.

The volume's final contribution, by Mathias Gutmann and Michael Weingarten (Chapter 24), raises the epistemological context within which we understand and interpret the diverse and voluminous mass of paleoanthropological subject matter. Most particularly these authors examine, within a specifically philosophical context, the issue of "modernity" (alternatively, "human versus non-human") raised by Conard. Modern human beings are, without doubt, strikingly distinguished skeletally from all other hominids known. Yet there can be no question that it is in our unique mode of cognition that we are most radically distinguished from even our closest relatives in Nature. Gutmann and Weingarten thus recognize true human uniqueness as residing in the cultural realm, which is where we must seek the fundaments of the "non-human-human transformation." However, reviewing both the empirical evidence and the philosophical background they find that paleoanthropology—indeed, biology in general—has failed to furnish us with an adequate basis for ethics, largely because a definition of "humanity" based on any simple listing of criteria fails us in this task. Their philosophical approach underlines the weakness of "modular" concepts of the evolution of human cognition, and reminds us that whatever it is that makes us what we uniquely are must be sought in a generalized capacity that underpins our intellectual functions—a capacity whose multifarious dimensions we are still exploring.

The three volumes of this series attempt to provide the reader with compact coverage of most of those areas of knowledge and scientific practice that are embraced by current definitions of paleoanthropology. And, like every complex project, it has itself evolved between its conception and its completion. Similarly, we hardly expect that the balance between the myriad aspects of paleoanthropology that it covers will match anyone else's ideal. Paleoanthropology is a dynamic and rapidly evolving field, and the last word in this complex domain of knowledge will never be written. But we hope that these books will provide a useful and readily accessible introduction to the field for those just joining it, and at the same time a valuable source of reference for established professionals. We could hardly expect the short individual chapters to be exhaustive accounts of the subjects covered, but one of our requests to our authors was to provide substantial

bibliographies that would serve as introductions and guides to a vast and rapidly expanding literature—and these colleagues have complied magnificently. These volumes have value as a comprehensive and authoritative account of paleoanthropology in the first decade of the twenty-first century precisely to the extent that the insights and hard work of the authors of the individual chapters have made possible. And as editors we have been hugely gratified by our authors' response. Thank you all.

Winfried Henke and Ian Tattersall
Mainz and New York City
November, 2006