The Fossil Record—
Human and Nonhuman

The Primate Fossil Record

The Human Fossil Record, vol. 1. Terminology and Craniodental Morphology of Genus Homo (Europe)

Major reviews1 of the entire record of primate paleontology are few and far between. In fact, ironically, the three that would most readily have come to mind before 2002 were authored or edited either by this journal’s editor1 or your humble reviewer.2,3 Two shorter texts4,5 are less detailed and not up to date. The situation is reversed for volumes concentrating on human paleontology: The entire allotted space of this review would be required to list the majority of such works. Despite their rather similar titles, the books by Hartwig and by Schwartz and Tattersall are in fact quite distinct, but both are welcome additions to the evolutionary anthropologist’s reference shelf.

In his preface and introduction, Hartwig specifically positions his anthology as a successor to Szalay and Delson’s book2 and as a technical complement to works by Conroy,5 Fleagle,1 and others such as Martin,6 which are less focused on paleoprimatology. Hartwig’s volume includes twenty-five chapters by thirty-one authors, few of which can be individually discussed here. Only three authors contributed to more than one chapter, always in different sections (Rasmussen on primate origins and early catarrhines, Walker on lorisids and early Homo, and Begun on plio-pithecids and European hominoids).

This is a fairly unified book, with indexes to major authors and taxa, as well as a consolidated bibliography, in addition to subdivided lists of “primary references” at the end of each chapter. Following a brief survey of primate origins, mainly a review of models with passing mention of Plesiadapiformes and other archontans, there are five major sections on prosimians, anthropoid origins and platyrhines, “basal” catarrhines and Old World monkeys, hominoids, and human paleontology. Most of these have an introductory chapter with special reference to the historical emphasis that Hartwig desired, followed by three to five solid chapters reviewing a small geographic or taxonomic segment of the fossil record in semi-standardized format. This begins with a history of discovery and debate (which readers might think too long compared to later sections), followed by taxonomic and morphological detail, and concluding with a discussion of evolutionary patterns and interpretations. The taxonomy section features a classification to the species level, then a review of each included genus with discussion of the type species, and sometimes all others, proceeding from type specimen through age and geographic range to a variably detailed anatomical definition or discussion. There are no synonymies, and authorship often is not provided for subgenera or suprageneric taxa. This is in strong contrast to the unnecessary but uniform listing of type specimen catalog numbers, which will be useful only to potential revisers, who would have to go to the original sources anyway.

Space prevents discussion of most chapters here, but the section on hominoids may be of greatest interest to this journal’s readers. Pilbeam introduces the topic with an insightful review of prior studies, emphasizing some of the diverse approaches and arguments since his own last major analysis7 but avoiding or ignoring an even more influential predecessor.8 Harrison surveys late Oligocene to mid-Miocene catarrhines, arriving at several important, if controversial, conclusions. He presents in detail his previously summarized argument that Proconsul and close relatives were not hominoids, but rather derived early catarrhines, predating the hominoid-cercopithecid divergence because they lack synapomorphies with the modern apes. Afropithecines and nyanzapithecines are included in the Proconsulidae as thus conceived; these taxa are well characterized, but only in the “evolution” section of the chapter. Dendropithecidae is defined to receive some but not all of the smaller conservative Miocene catarrhines. Morotopithecus is tentatively recognized as a hominoid apparently predating the hylobatid-hominid divergence on the basis of derived features of one lumbar vertebra and an uncertainly referred scapular glenoid fragment, combined with craniodental and femoral morphology like that of proconsulids. Harrison hesitantly rejects the alternative that Morotopithecus is an afropithecine with a unique axial skeleton, convergent on hominoids perhaps due to its large mass. This taxon might be pivotal in understanding hominoid origins, especially if its age is closer to 21 Ma instead of the faunally derived 15 Ma. However, if it predates the gibbon-great ape split it would still not refute the model of hominoid (or hominid) diversification outside of Africa,9,10 followed by hominine reentry to Africa.

In addition to refining that model, Begun’s review of European hominoids surveys Dryopithecus, Oreopithecus, and Ouranopithecus (generically separated from Graecopithecus) and extends into southwest Asia to discuss Griphopithecus and Ankarapithecus. Kelley examines the Asian hominoids, overlapping Begun’s discussion of Griphopithecus but, surprisingly, ignoring Ankarapithecus while concentrating on Sivapithecus and Lufengpithecus. The last genus is placed in a new pongine tribe, but I am unconvinced, preferring to consider it, like Dryopithecus, a “stem hominid.” Although their fossils are rare, hylobatids are important both as a divergent hominoid clade and for their reflection of conservative morphology, yet neither Kelley nor any other author discusses them. Ward and Duren return to Africa to survey the later Miocene taxa. They follow Andrews11,12 by including the afro-
pithecines (*Nacholapithecus* and *Equatorius*) and kenyapithecines (*Kenyapithecus*) in Hominidae, while leaving *Olivipithecus, Samburupithecus*, and *Orrorin* of uncertain subfamily status. Generic diagnoses for the first three are long and detailed, and the evolutionary discussion clear if too brief: For example, Ward and Duren tantalizingly suggest that new fossils from Kenya may refute the "African re-entry" hypothesis. I was surprised at the lack of reciprocal referencing among these and other chapters. Ward and Duren specifically refer to both Kelley and Harrison, without supporting or refuting the latter. But all four of these chapters overlap significantly and most authors appear to be unaware of the others. That is a common problem in most collected volumes: If the editor does not supervise interaction among related chapters it will not happen, and the overall value of the book is reduced.

Another deficit of the volume is the rarity of discussion of taxonomic entities above the genus level. Subfamilies, families, superfamilies, and even ordinal-group taxa (even the few newly named ones) are not characterized or diagnosed except where some authors violate the imposed format, either with generic discussions or in their evolution sections. Such discussions are important summaries of characters linking genera both taxonomically and evolutionarily. Moreover, newly named taxa must be clearly delineated in order to be "available" systematically. If this work is designed to be a reference source, the editor should have required such discussions and convinced the publisher of their value, despite the effect on manuscript length.

On the other hand, Hartwig explicitly notes that he wants readers to develop their own ideas of primate phylogeny based on the data presented. This may explain, but in my opinion does not justify, the rarity of phylogeny diagrams, whether cladograms or trees. Such diagrams rapidly summarize large amounts of text and help the reader zero in on questions that an author may develop nearby. In Begun's chapter on European hominoids, for example, three cladograms of generic relationships differ widely but are separated by only three steps out of 480, emphasizing the potential pitfalls of using numerous characters in a parsimony analysis. Begun specifically prefers one cladogram based on "informed choice," while I worry also about the clarity and reproducibility of character-state coding. More important, however, is the question of whether readers should be left to draw their own conclusions in a book like this. I suggest that it is more valuable for authors to present and argue for their interpretations, even if some may prove ephemeral. The reader can decide which are worthwhile only if alternatives are clearly presented. Hartwig wisely allowed authors to determine their own taxonomies, rather than imposing a standard system, but he failed to follow through by encouraging clear diagrams and phylogenetic conclusions as well.

By contrast, the number of specimen illustrations in this work is high. Their quality is mixed, but usually is good for both photographs and drawings although, in some cases, neither sources nor permissions are obvious. On the other hand, maps showing site locations are entirely absent. Errors of fact exist but are not rampant; no finger-pointing is required. Ours is a fast-moving field. Hartwig's introduction includes a list of all primate genera accepted by this volume's authors in order of description, and already there are at least a Pakistani ?cheirogaleid (*Bugtilemur*), two new African cercopithecids (*Kuseracolobus* and *Piopapios*), and the presumed hominins *Arhipithecus, Kenyanthropus*, and *Sahelanthropus*. However, given the fact that *Australopithecus* is not listed, perhaps hominins are ignored in this table.

Schwartz and Tattersall do not have to worry about such ancient African taxa, as their book focuses squarely on the European segment of the human paleontology dataset. This book is the first of a planned quartet (at least) of volumes that will document the entire record of human evolution. It begins with a discussion of Schwartz and Tattersall's very different but equally standardized format. The focus of interest is the locality and the potential population it yields; specimens are described in alphabetical order by site name. Sixty-one sites are included, alphabetically from Abri Pataud to Zaffaraya and chronologically from Dmanisi (ca. 1.8 Ma) to Chancelade (mid-Magdalenian). Why certain Late Upper Paleolithic moderns are included and others ignored is never addressed. Maps showing all site locations follow drawings of the craniodental elements that label features discussed in the text.

Each sample is well illustrated, almost always by monochrome photographs taken by the senior author, although a few by other photographers are used, and several digital images of casts fill gaps that would otherwise exist. As this review was to be submitted, the original Combe Capelle 1 skull, described from such a cast, was rediscovered. The original photos are excellent, although the final quality is reduced through less than superior publishing. The remains are described in moderate detail, beginning with generalities about preservation and the entire cranium, then proceeding from the face over the vault to the base, several "endocranial compartments," the mandible, and the dentition. When numerous specimens are known from a site, one or more are used as reference standards and others briefly compared to them. The reader may be disappointed to find no sign of two other expected sections: there is no analytical synthesis and no measurements are provided, the photographs being thought sufficient to give "an adequate guide to size." Schwartz and Tattersall argue that as previous authors have not agreed on what metrical data to provide, or their developmental or functional relevance, they will offer none, preferring to concentrate on morphology alone. I can agree with the primacy of the latter, but not the abandonment of the former. Even less acceptable is their rejection of interpretation. One would hope that these respected colleagues (and personal friends), having spent years traveling the globe in order to see each specimen at first hand, would give us the benefit of their opinions on population affinities and variability, taxonomy, phylogeny, and perhaps adaptation. They do promise a "systematic analysis of the genus *Homo*" in volume two, after further description of African and Asian specimens. Volume three is scheduled to cover all "early hominids" with systematic conclusions. Yet, for the nonce, we are left like Frodo at the gates of Mordor, awaiting a guide to the dark regions within.
REFERENCES


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MEETINGS OF INTEREST

May 22–24, 2003
International Anthropological Congress: Anthropology and Society
Memorial Congress to the 60th anniversary of death of Dr. Ales Hrdlicka
Praha-Humpolec, Czech Republic
Contact address:
Charles University in Prague, Faculty of Science
Department of Anthropology and Human Genetics
Vinicna 7, 128 44 Prague 2
Czech Republic
Phone: +420 221 951 611
Fax: +420 221 951 619

June 22–28, 2003
V Congress of the International Association for the Study of Human Paleontology
Barcelona-Stiges (Spain)
Sponsored by the United Nations Educational, Scientific, and Cultural Organization and the Universität de Barcelona
The conference will focus on all topics of human evolution.
Excursions: Arago Cave, Altamira - North Spain and a visit to the new museum and replica of the Altamira Cave, Atapuerca - Burgos, Granada & Murcia.
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Phone: (34) 934 108 646
Fax: (34) 934 303 265
reunionsciencia@reunionsciencia.es
Website: http://www.faranews.com/iaashp2003/pro1.htm

July 5–12, 2003
XVth International Union of Anthropological and Ethnological Sciences Humankind/Nature Interaction: Past, Present and Future
Florence, Italy
The conference will focus on the global impact of human overpopulation.
Contact: Bruno Chiarelli
Dept. of Animal Biology and Genetics
University of Florence
email: secretariat@icaes-florence2003.com
website: www.icaes-florence2003.com

July 14–18, 2003
XVth International Conference of Ethiopian Studies
Hamburg, Germany
The conference will focus on the humanities, with several sessions devoted to various aspects of archaeology, history, religion, languages, literature, arts, anthropology and social sciences (including law and politics).
Ethiopian studies: ICES office
Hamburg University
Asia-Africa Institute
Edmund-Siemers-Allee 1
D-20146 Hamburg
Germany
Fax: +49-40-42838-5675
E-mail: ices2003@uni-hamburg.de
Web site: www.rrz.uni-hamburg.de/ICES2003

July 23–31, 2003
The XVth International Union for Quaternary Research Congress
Reno Hilton Resort & Conference Center Reno, Nevada
The Congress will host multiple symposia on various topics of Quaternary Research.
Contact:
Ms. M. Jones
Division of Hydrologic Sciences
Desert Research Institute
2215 Raggio Parkway
Reno, NV 89512 USA
Email: inqua03@dri.edu
Website: http://www.dri.edu/DEES/INQUA2003/inqua_home.htm

September 18–20, 2003
Evolutionary Changes in the Craniofa-cial Morphology of Primates
Institute of Anatomy, Ernst Moritz Arndt University, Greifswald, Germany.
To commemorate the life of Richard N. Wegner, a conference on primate craniofacial morphology will be held in the Institute of Anatomy.
Topics of papers include:
Functional morphology
Pneumatization
Growth & Development
Dentition
Primate collections
Contact: Thomas Koppe
Institute of Anatomy
Ernst Moritz Arndt University
Friedrich-Loeffler-Strasse 23c
D-17489 Greifswald, Germany
email: thokoppe@mail.uni-greifswald.de
website: http://www.dur.ac.uk/t.c.rae/CT/Wegner/

November 19–23, 2003
102nd Annual Meeting of the American Anthropological Association
Chicago Hilton and Towers. Chicago, IL
Contact: AAA
4350 North Fairfax Drive, Suite 640, Arlington, VA 22203-1620
phone: 703/528-1902
fax: 703/528-3546
Website: http://www.aaanet.org/mtgs/mtgs.htm
Come and see the fossil remains of your ancestors! This archive contains digital media and information about the fossil record of humans that spans over six million years. It is a collaborative initiative with curatorial institutions from around the world to provide access to digital images, 3D models and virtual copies of bones and teeth of our ancestors and non-human primate relatives. It is a resource for scientists, educators and the public to learn more about the fascinating evolutionary history of the human species. The conditions for use of the digital data vary by institution and can be transitional fossils in the human fossil record are distinguished at both the genus and species level. This group includes the extinct genera Ardipithecus and Australopithecus and the current genus Homo. All species except Homo sapiens are extinct. Much of the recent study of early humans focuses on the transition from Ardipithecus (Ardi) to Australopithecus (Lucy and similar fossils) and from Australopithecus to Homo, the genus that led eventually to us. Each of these modifications is diagnostic of humans and easily recognizable in the fossil record in specimens for which these anatomical areas are present. Ardipithecus ramidus and the Origins of Bipedality. Upper Pleistocene human fossils are still very scarce in the Philippine archaeological record, but excavations in Tabon Cave in Palawan and Callao Cave in Luzon have given the oldest human remains known so far from the Philippines (Dizon et al. 2002; Détroit et al. 2004; Mijares et al. found in Callao Cave compared with extant Asian H. sapiens and nonhuman catharrines and ursids. Upper Pleistocene Human Remains from Tabon and Callao Caves and Their Potential Relatedness with the Philippine Negritos. Tabon Cave (Quezon, Palawan). Part of a series on. Paleontology. Paleontology PortalCategory. v. t. e. The following tables give an overview of notable finds of hominin fossils and remains relating to human evolution, beginning with the formation of the tribe Hominini (the divergence of the human and chimpanzee lineages) in the late Miocene, roughly 7 to 8 million years ago. As there are thousands of fossils, mostly fragmentary, often consisting of single bones or isolated teeth with complete skulls and skeletons rare, this