



The Primate Fossil Record

reviewed by Mary T. Silcox

Edited by Walter C. Hartwig
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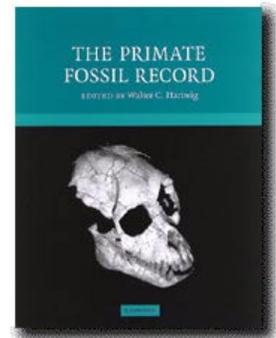
Walter Hartwig has brought together an impressive list of experts in primate paleontology to make a book that will undoubtedly be the central reference in the discipline for some years to come. Indeed, gaining cooperation from such a long list of key researchers was undoubtedly a major organizational undertaking, which is unlikely to be repeated any time soon, and Hartwig deserves kudos for succeeding in this undertaking. Having said that, however, there are a number of holes or shortcomings to this book that make it less useful than it could have been.

The Primate Fossil Record is made up of a series of individually authored chapters that fall into two categories. The bulk of the book consists of chapters that review the fossil record in clumps defined by a combination of time, location, and taxonomy. The division of the record into these clumps is not always entirely even. For example, it is unclear why are the hominoids so extensively subdivided, when the adapoids and omomyoids are afforded only one chapter each. All but one fossil primate taxon (*Plesiopithecus*) are included somewhere, however, with the major exception of the whole Plesiadapiformes (discussed below). Within the context of each of these chapters there is an introduction, a historical section, an overview of the taxonomy to be used, a listing for each taxon with distinguishing morphological features, and a discussion of the evolution of the included forms. The taxonomic listings at the generic level include a standard set of headings: genus, included spe-

cies, type species, type specimen, age and geographic range, and anatomical definition. Note that these are not formal taxonomic discussions, because they lack any information on synonymy, etc. of names. In format these chapters are quite similar to the manner in which Janis et al. (1998 and in press) organized their look at the Tertiary

North American mammalian fossil record. There are, however, a couple of key differences, which are strengths of the Janis books and weaknesses here.

First, in addition to the taxonomic framework used by each author, the contributors to the Janis et al. (1998) volume each included a cladogram with labeled nodes. Hartwig has explicitly avoided including phylogenetic trees, painting this as a plus to support objectivity and to avoid pushing a particular agenda. However, this is a false savings. The authors of the chapters still often manage to bring across their own agendas (see below), and in fact, the use of *any* taxonomic framework will always require some decisions to be made about how things are thought to be related to one another. As such, not including trees simply makes the pattern of relationships that are inevitably assumed by each author less clear, with no benefits in terms of



actually fostering objectivity. And including tree diagrams does not necessarily have to mean accepting a particular phylogeny. They can be used to clearly illustrate differences of phylogenetic opinion, for example, in the manner employed by Terry Harrison in this book.

The second major difference from the Janis book is in the age and geographic range section for each taxon. The contributors to the *Evolution of the Tertiary Mammals of North America* included information on every site where specimens for each species have been found in a coded list, providing a great wealth of distributional information. The range data from this listing was then also included in range charts. In the Hartwig book, interpretation of the information relevant to "age and geographic range" differs markedly from author to author. In some cases a very limited amount is included, while others provide more details. For example, Jay Kelley provides only limited range and locality information for Asian hominoids, while Fleagle and Tejedor provide more details, including Land Mammal Ages, for early platyrrhines. It would be nice to be able to assume that one could go to this book with a cast of a specimen from a particular locality, and figure out where the authors think it belongs. This is not generally possible, however, and is made more difficult by the lack of a central index of localities. As it stands, Szalay and Delson (1979), McKenna and Bell (1997), Fleagle (1999) and the relevant chapters from Woodburne (1988) and Volume 2 of *Evolution of Tertiary Mammals of North America* (Janis et. al., in press, when it becomes available) are all more useful references about the detailed ranges of fossil primate taxa than this book, particularly for the early parts of the record.

Finally, the authors in the Janis et al. (1998) book included some dental size information for each genus (usually a measurement of M_2), which is very useful for making quick comparisons of relative body mass. There is nothing comparable given in the generic listings here.

In spite of these criticisms, the review chapters are generally well written and coherently put together, and will be extremely useful as centralized sources of morphological information. The second set of chapters are overviews that deal with major topics (e.g., primate origins by Rasmussen) or sections of the record (e.g., the Miocene by Pilbeam). The content and utility of these chapters is much more uneven. McHenry, writing about the fossil record of human ancestry, gives a charmingly brief and clear overview that will be useful to the non-expert. Dagosto contributes the clearest discussion I have ever read on why there is a debate on anthropoid origins. Pilbeam, on the other hand,

provides a very long and gloomy "Perspective on the Miocene Hominoidea" that will probably serve only to depress and confuse experts and non-experts alike. And Rosenberger gives us a diatribe on what everyone else is doing wrong in the study of platyrrhine evolution. I would argue that, if space limits were an issue in putting together this book (as Hartwig indicates), some different choices should have been made. Rather than trying to have overview chapters, which mostly include either opinion-laden ramblings or information that is available in other chapters, I would have preferred to have seen two major holes filled. The first is the lack of detailed range and locality information discussed above. The second is the absence of a key chapter, whose lack has already rendered this book out of date. I'm referring to the fact that a chapter on the earliest and one of the most speciose and diverse radiations of fossil primates, the Plesiadapiformes, is entirely missing.

Rasmussen and Covert's overview chapters on the origin of Primates and the "earliest" fossil primates (respectively) do briefly mention the Plesiadapiformes, and provide the only explanation available as to why a specific chapter on the group was excluded. These authors allude to taxonomic and phylogenetic debates that have caused some authors to exclude plesiadapiforms from primates for philosophical or systematic reasons. Particularly, two influential papers published in 1990 suggested a closer relationship between at least some plesiadapiforms and a modern order of gliding mammals (Dermoptera) than either share with primates (Kay et al. 1990; Beard 1990). However, two points need to be made about this debate. The first is that there is a difference of perspective between paleontologists and anthropologists in terms of how to deal with this issue. In my experience, anthropologists took up the opportunity to exclude plesiadapiforms from primates with glee, because it allowed them a simpler definition of primates and a more restricted range of taxa to worry about. Paleontologists, on the other hand, have been less ready to accept the shifting taxonomic status of the group. McKenna and Bell (1997), for example, included them in Primates, and in fact most plesiadapiforms in fossil collections are still catalogued as such.

Second, the phylogenetic and taxonomic debate on the position of plesiadapiforms is far from over. As Rasmussen actually notes (p. 7), the arguments for the dermopteran-plesiadapiform relationship have been "effectively rebutted" (e.g., Krause 1991; Runestad and Ruff 1995; Stafford and Thorington 1998; Hamrick et al. 1999; Bloch and Silcox 2001; Bloch and Boyer 2002; Silcox

2001, 2003). More recent and/or comprehensive phylogenetic analyses have upheld a sister-taxon position for some or all plesiadapiforms with euprimates, rather than dermopterans (Silcox 2001; Bloch and Boyer 2002). And with these new analyses the taxonomic tide is turning back to support inclusion of the group in the order Primates (Silcox 2001, 2003 and in press; Bloch and Boyer 2002). It is actually rather ironic in light of recent discoveries to read Rasmussen's "wish list" of fossils he feels would be needed to clarify early primate evolution (p. 9): "...we need new fossils of very early primates. More than just a few teeth or jaws are required—the primate assemblage of traits cannot be fully assessed in fossils without having crania and partial hand and foot skeletons." Although I disagree with his dismissal of the importance of teeth and jaws, more complete skeletons of exactly this type are becoming available for plesiadapiforms, which are proving key to a better understanding of early primate evolution (e.g., Bloch and Boyer 2002).

Faced with this debate, Hartwig had two choices. He could assume that the "plesiadapiforms are non-primates" camp would win out and exclude the group, or he could play it safe and include a chapter on plesiadapiforms in spite of the uncertainty that still surrounds their taxonomic and phylogenetic status. Fleagle (1999) chose to do the latter in his revision of his text on primate evolution, and the book is stronger for it. Hartwig chose the former route. I would argue that doing so left a major hole in this book. Even if one chooses to exclude plesiadapiforms from the Primates for philosophical reasons, if they are the sister taxon to euprimates, they are the key group for considerations of the earliest phases of primate evolution, because they provide the context against which the characteristics of the earliest euprimates must be interpreted. As such, plesiadapiforms are central to an understanding of the order in which characteristic euprimate features such as nails and the postorbital bar were added, and to elucidating the adaptational scenario that accompanied these morphological changes (Bloch and Boyer 2002; Silcox, in press). For these reasons, no matter which taxonomic camp one is allied with, those interested in the primate fossil record cannot ignore plesiadapiforms, no matter how messy and difficult they may be to deal with.

This discussion raises a more general issue that needs to be brought to the attention of users of this book, which is particularly relevant to non-experts. Unlike other major existing overviews of the primate fossil record (Szalay and Delson 1979; Fleagle 1999), a single unifying taxonomy that is

consistent from chapter to chapter is not employed in this book. Trying to do so would probably have been impossible, due to lingering disagreements between experts on the application of many taxonomic labels, but the end result is the quite variable use of some taxonomic names. The most obvious is the family name Hominidae. The traditional anthropological use of this family name (as employed in White's chapter of this book) is to include only upright-walking human ancestors as hominids. Many researchers who are interested in the broader relationships of humans within primates, and particularly to the various Miocene apes, have begun to use this term to refer to a broader group that includes some or all living apes and various fossil taxa, such as *Dryopithecus* and *Oreopithecus* (e.g., see Begun's chapter on European hominoids). This disagreement seems to be more about taxonomic practice than phylogenetic relationships. Those who restrict the hominids to "...all species derived in the human direction after the last common ancestor of African apes" (White, p. 407) seem to treat the application of the group name as sacrosanct. Other researchers use the label as simply a taxonomic name like any other, to be fitted in where appropriate in light of hypothesized relationships (i.e., see McKenna and Bell 1997). Without choosing sides, it is worth noting that the debate does exist and that the use of the family name is inconsistent in this book. Readers trying to patch together the various taxonomies from the different chapters to form one overall taxonomy of fossil primates will find it difficult or impossible to do so.

This discussion raises an important broader issue that is also worthy of note. One of the most useful aspects of this book will undoubtedly be the bibliography, which does pull together the vast majority of the key references in post-plesiadapiform primate evolution. Perhaps in recognition of the fact that this would be the case, many of the review chapter authors saw as their "brief" a comprehensive overview of various perspectives on the subjects of their chapters, with a de-emphasis on using this as a venue to express their individual agendas. Even though one taxonomic perspective must be selected, a discussion of opposing views was treated as necessary and appropriate in this framework, if only to force inclusion in the bibliography of all relevant references. Examples of pleasantly unbiased chapters that have followed this "brief" include Dunsworth and Walker's excellent discussion of the early members of the genus *Homo* and Gebo's nicely balanced contribution on the Adapiformes.

Other authors took a very different approach, however, limiting the range of their discussion by cutting out debates that they apparently feel are settled, even if a significant number of other researchers would disagree. White, for example, is utterly unapologetic in using a very "lumped" taxonomy for all early human ancestors except *Ardipithecus*, and dismisses those who support a more "bushy" phylogeny as practicing "X-files paleontology" (p. 412). Beard similarly fails to even mention the very active current debate on the anthropoid vs. adapoid status of *Pondaungia* and *Amphipithecus* (e.g., Ciochon et al. 2001) and the anthropoid status of *Eosimias* (e.g., Gunnell and Miller 2001). It is rather ironic, in fact, that the latter debate is reflected elsewhere in the book, when Rasmussen (p. 206) refers to *Eosimias* as an "Asian tarsoid"! Although researchers familiar with these debates will probably not be surprised with the approaches these authors have taken, it is unfortunate that some key references are left out of the bibliography as a result.

Next to the bibliography, the aspect of this book that will probably be of the most use to many readers will be the illustrations. This volume does bring together many excellent and useful images that are quite helpful in demonstrating the morphological points made by the various authors. Having said that, the quality of the illustrations is a bit uneven. There are a few illustrations that are really quite awful, particularly in light of the high cost of the book. Figure 5.2, a drawing of the skull of *Necrolemur*, for example, bears some kind of odd interference pattern, likely from improper scanning of a printed image. In a few cases the images appear over-exposed or too contrasty (e.g., Figures 9.6C and 11.9A, B), which should have been fixed in the process of publication. My biggest gripe, however, relates to the inappropriate scaling of teeth in many cases. A significant number of the figures of teeth are reproduced at much too small a size to see morphology (Figures 6.1, 11.3A, 12.9, 14.18 are just a few examples), while a few are rather absurdly too large (e.g., Figure 19.7, which shows five isolated teeth that together take up the entire 8 1/2 x 11" page). This is not a universal fault, and a few chapters are quite excellently illustrated, but in a book this expensive it would have been nice to see more consistency. I have to wonder sometimes why people are illustrating teeth at all if they make them too small to see details. For most people teeth do not have the same emotional weight as a skull or a skeleton, so including them should serve some functional purpose. If illustrations of teeth are too small to make morphological

comparisons possible they are essentially without value.

In spite of these criticisms, and the VERY high price of this book, I suspect that it will be a key reference for any anthropologists and Cenozoic paleontologists who have some interest in primates. I have already made use of this book as a reference in a Primate Evolution class, and my students found it a very valuable resource in the preparation of their papers. It is a "must buy" item for libraries in institutions with paleontology and anthropology programs, and many researchers will likely find it necessary to include it in their personal libraries as well.

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