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Book review

Review of "The Primate Fossil Record" Edited by Walter C. Hartwig

Where do you turn when you are preparing to get acquainted with the latest omomyiform, or decipher the importance of yet another species of puffy-cusped hominoid from the Miocene of East Africa, or trying to work out (yet again!) whether adapiforms should be included in Strepsirhini (or is it Strepsirrhini)? If you are anything like me, you dust off Szalay and Delson (1979) and Fleagle (1999), try to hunt down that review article you are certain you read (but somehow the citation details escape you), harass your graduate students for downloads from their Endnote files and hit the Web of Science. Your traditional and new-fangled desktops disappear under mountains of photocopies and pdfs, respectively, your graduate students mysteriously decide to work at home and you are once more reminded how difficult it is to locate and collate information.

Thus, the time is more than ripe for an edited volume on the primate fossil record. Szalay and Delson (1979), *the* classic treatment for the last 23 years and the only single-volume game in town, is well out of date, but replacing it is a challenge. Primate fossil taxa are now so diverse that no single individual can do the record justice, necessitating an edited, multi-authored volume to provide in-depth analysis across the entire Order. Of course, edited volumes only work if the editor has a vision and brings it to fruition in a timely manner. *The Primate Fossil Record* had such an editor in Walter Hartwig. Hartwig's great contribution has been to bring together the experts who find and describe the primate fossil record, provide them with a format for presenting the necessary information, and present them with an opportunity to air their opinions on pressing issues in primate evolution. Each chapter therefore includes the author's preferred taxonomy of the target group, a historical review of the study of the group and a summary of its evolution in time, space and ecology. This structure not only makes it easy to find information in each chapter, but also provides the authors with the latitude to make the book more than an annotated bibliography of primate evolution. Indeed, this volume is as much a snapshot of ideas, theories and personal scientific philosophies as it is a compendium of the primate fossil record. It is this combination that makes the book so valuable.

Following an "Introduction" by Hartwig, Rasmussen's nicely succinct chapter summarizes ideas regarding the relationships of primates to other mammals and reviews explanations for primate origins and recent work on these questions. Up-to-date on ideas and references, it is an ideal introduction to the literature. Thereafter, contributions are grouped into five sections one per major radiation. Most sections are introduced by a topical chapter discussing important issues surrounding that radiation.

One of the book's strengths is that it does not subject us to the fossil record of the plesiadapiforms. Participants at the primate origins conference in Chicago in 2002 (Ravosa and Dagosto, nd.) opined that plesiadapiforms are diverse enough to be grouped in their own Order, so several extra chapters would have been needed to treat them in a manner consistent with the book's organization. In any event plesiadapiforms are too derived to tell us much about primate evolution. Although one can dredge up a few similarities between plesiadapiforms and some adapiforms and omomyiforms, these features always occur in the context of some decidedly

E-mail address: cross@mail.som.sunysb.edu (C. Ross).

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nonprimate specializations. The ear region is a case in point. The ectotympanic ring of plesiadapiforms resembles that of some omomyiforms and adapiforms in being intrabullar and it is omomyiform-like in being fused to the bullar wall by an annular bridge (Bloch and Silcox, 2001). However, the bulla in *Ignacius* (at least) is entotympanic (Kay et al., 1992) suggesting that the intrabullar position of the ectotympanic evolved independently. Similarly, the intrabullar circulation was probably absent not only in plesiadapiforms, but also in lorisiforms, cheirogaleids, and, by inference, possibly in the primate common ancestor as well. But in plesiadapiforms this was compensated for by an enhanced vertebral circulation (or a maxillary artery-Circle of Willis anastomosis through the orbit), whereas in cheirogaleids and lorisiforms the Circle of Willis is reinforced by the ascending pharyngeal. The skulls of plesiadapiforms also include some highly derived features of the dentition, including a reduced dental formula and enlarged, procumbent incisors, effectively excluding this group from immediate ancestry of Primates. Thus, although Silcox's (nd.) detailed phylogenetic analysis of plesiadapiform relationships places them as the outgroup to Primates, plesiadapiforms are unlikely to be representative of the animals from which the primate lineage evolved. Moreover, if Martin's (2000) estimate of 87 Myr for the haplorhine-strepsirrhine divergence time is correct, plesiadapiforms are probably too young to be of much interest with respect to primate origins. This is not to say they are not interesting in their own right, but this temporal consideration, if confirmed, is sufficient to justify their omission from this volume.

The first section of *The Primate Fossil Record* covers all nonanthropoid primates in five chapters and ca. 100 pages. Covert summarizes the adaptive and taxonomic diversity of extant prosimians and introduces one of the key (unanswered) questions in primate higher taxonomy. How are the omomyiforms and adapiforms related to extant primates? Gebo treats us to a detailed assessment of adapiform taxonomy and paleobiology, including some nice new illustrations of the fossils by Reed-Deemer. Gunnell and Rose make as much sense of omomyiforms as anyone can and the illustrations from the original literature are mostly well-chosen. Moiré patterns that have crept into a few of the figures are the only disappointments here. Gunnell and Rose place omomyiforms in the Infraorder Tarsiiformes with Tarsiidae, despite the fact that links between tarsiers and omomyiforms are tenuous. I prefer expressing this uncertainty with separate Infraorders (i.e., Omomyiformes, Adapiformes and Tarsiiformes) but their approach has historical precedent. Phillips and Walker summarize the scrappy record of lorises and galagos with a useful summary of the questions surrounding strepsirrhine biogeography and the molecular estimates of their phylogeny. Godfrey and Jungers' chapter on quaternary fossil lemurs includes good photos of many fossils and a lengthy but highly enjoyable review of the history of discovery and study of subfossil lemurs.

The remaining 325 pages of the book concern anthropoid evolution. They are grouped into four sections: anthropoid origins and diversification (including platyrrhines), Old World Monkeys and early catarrhines, hominoids, and humans. One inevitably hopes to find one's own area of research well treated. And indeed, the second section of the book, "The origin and diversification of anthropoid primates", nicely encapsulates the knotty problems surrounding the origin of Anthropoidea, Catarrhini and Platyrrhini. All sides of the debate are presented by Dagosto, with her characteristically careful consideration of the characters involved (see also (Dagosto, 1990)). Beard's treatment of early anthropoids is thorough and balanced, although I would not agree with his contention that a "strict tarsier/anthropoid clade is difficult to reconcile with available postcranial data". Parsimony analyses including all data still support a tarsier/anthropoid clade, exclusive of omomyiforms (Kay et al., 1997; Ross et al., 1998). The importance of including data from many anatomical systems is also made by Rosenberger in his historical review of studies on platyrrhine evolution. He compares cladograms of platyrrhine relationships generated by several authors and finds the highest correlations between those with data from several anatomical areas. Yet Rosenberger eschews such large scale cladistic

analyses because they atomize the evidence, subdividing a "coherent body of data … into minutia (sic) in order to extract individual character states which together form a long list rather than an integrated working unit, thus causing them to lose phylogenetic signal" (p. 156). Rosenberger's concern is shared by all of us interested in reconstructing primate evolutionary relationships, but there are ways of identifying character covariance, cliques, and other issues related to independence. Paleoprimatology includes several interesting attempts to address these issues (McCollum, 1999; Strait, 2001; Wood and Lieberman, 2001). The problem is, of course, that character complexes, whether functional or otherwise, can be assembled and disassembled through evolution, so that a complex in one part of the tree will eventually disintegrate. This must be true, otherwise we would still be soft-bodied, agnathous, filter-feeders. Robust phylogenies are the only way to trace the assembly and disassembly of these complexes.

Three chapters on platyrrhine evolution follow Rosenberger's chapter, reviewing respectively the fossil platyrrhines of southern South America (Fleagle and Tejedor), the neotropics (Hartwig and Meldrum) and the Greater Antilles and Brazil (MacPhee and Horovitz). The latter two chapters are particularly well illustrated, with especially good photos of *Caipora* and *Protopithecus*. Fleagle and Tejedor review the range of opinions about the phylogenetic placement of the non-La Venta fossil platyrrhines, Hartwig and Meldrum emphasize the functional morphology and ecology of the La Venta primate fauna and MacPhee and Horovitz reiterate their hypothesis that the Antillean platyrrhines are monophyletic. Of course, this requires that *Paralouatta* evolved its very *Alouatta*-like appearance in parallel with howlers. If morphology can be this deceiving about phylogeny, those who use fossils to recover information about phylogeny might as well give up and go home!

The section on early catarrhines and Old World monkeys is led off by Rasmussen's review of the predominantly Fayum record of early catarrhines. Rasmussen's chapter exemplifies one of the strengths of the contributions to this book: it includes not only a summary of the divergent views on the relationships of the Fayum taxa, but also the author's own views on these issues. Rasmussen classifies *Catopithecus* as an early catarrhine because it has two premolars and postcranial similarities (Seiffert and Simons, 2001), but he and Simons have also argued that its dissimilarity from tarsiers argues against the tarsier-anthropoid hypothesis (Rasmussen and Simons, 1988). If *Catopithecus* is on the catarrhine stem lineage, then it is too far away from the anthropoid stem to carry much weight in the tarsier-anthropoid debate, and if it is on the anthropoid stem, as suggested elsewhere, it does not seem to falsify the tarsier-anthropoid hypothesis (Kay et al., 1997; Ross et al., 1998).

Begun's chapter on pliopithecoid evolution is an excellent introduction to this group. They are strangely primitive and the evidence linking them to crown catarrhines is no more convincing than that for *Catopithecus*. Begun's skepticism of the phyletic valence of the "partial" ectotympanic tube is well taken, given its demonstrated parallelism in other groups. Pliopithecoids also lack a canine honing complex and have trigonids resembling those of platyrrhines, adapids and some extant prosimians, causing Begun to wonder whether pliopithecoids "may be an independent descendent lineage of the propliopithecoids, or may even be the sister clade of living anthropoids" (p. 223). Benefit and McCrossin's treatment of the Victoriapithecidae is well illustrated, and rounded off nicely with a discussion of basal catarrhine paleobiology as revealed by the teeth and postcrania. Jablonski's thorough review of Neogene Old World monkeys includes an excellent synthesis of the available evidence, fossil and molecular, of cercopithecoid evolution, including biogeography, adaptation and divergence times.

Pilbeam introduces the hominoid primate section with a comparison of the molecular and fossil evidence for hominoid divergence times and some cautionary notes regarding character polarity and parallelism. As he observes, fossil hominoids are unlike living hominoids in many ways, especially in the postcranium. Not only does this make it difficult to link fossil taxa to extant hominoids, but once they are linked, it makes it necessary to invoke parallelism to explain the similarities among the extant forms. This problem

would be lessened to some degree if we accept Harrison's argument that the swath of Oligocene-Early Miocene dendropithecoids and proconsuloids (*Proconsul*, *Heliopithecus*, *Afropithecus*, *Turkanapithecus*, *Rangwapithecus*, *Mabokopithecus* and *Nyanzapithecus*) are not actually hominoids at all, but stem catarrhines. But even this does not solve the problem completely: the humeral shaft of *Sivapithecus* is not that of a suspensory animal. The most plausible scenario at present seems to be Begun's scenario of a basal suspensory form for crown hominoids, with subsequent reversal in the *Sivapithecus* lineage.

Reading the chapters in this section of the book drove home to me how crucial well-established relationships between form and function in the postcranial skeleton and teeth are for our understanding of hominoid evolution, and in contrast, how poorly understood the functional anatomy of the face is in these taxa. Begun ventures some functional hypotheses regarding the divergence between Asian and Africa hominoids in facial anatomy, but really, we have a very poor understanding of the functional significance of even these profoundly different facial arrangements. This may be because the face does many things other than dissipate and resist feeding forces (Hylander et al., 1991; Ross, 2001), but natural selection must underlie these differences. Our comprehension of early hominoid adaptive diversity is poorer for lack of this understanding.

The final section of the book concerns "The fossil record of human ancestry". McHenry's introduction reiterates some basic trends in human evolution and echoes the views of many contributors in calling for a better understanding of characters used in phylogeny reconstruction. White's chapter on the "Earliest hominids" stands out in comparison with the others in the volume in being terse and critical. The only speculation he allows himself is the assertion that we have probably found the best fossil hominid localities already and that we are unlikely to have a comprehensive understanding of human evolution in the near future. Only time will tell whether he is a pessimist or a realist. The rich history of study of early *Homo* and Middle and Late Pleistocene humans is well summarized in separate contributions by Dunsworth and Walker and Smith, respectively.

Molecules and fossils

Recent years have seen an explosion in sequencing capacity and the use of large DNA sequence data sets to generate hypotheses regarding both the relationships among primate clades and their divergence times (e.g., Yoder et al., 1996; Porter et al., 1997; Springer et al., 1997; Chaves et al., 1999; Page et al., 1999; Yoder and Yang, 2000). The degree of congruence between these estimates and those generated from the fossil record is one of the most important issues in primate phylogeny. This volume treats this issue unevenly. In addition to Jablonski's chapter, Pilbeam nicely summarizes molecular and fossil divergence times as they relate to hominoids, and Phillips and Walker compare the molecular and fossil evidence for divergence times among major strepsirrhine clades. But molecular evidence for the divergence times and relationships of tarsiers, Platyrrhini, Anthropoidea and Primates are not discussed. The likely reason for this is that, unlike the divergence time estimated for catarrhines, divergence times for these primate higher taxa are not corroborated by the fossil record, the focus of this book. However, molecular-based divergence times for primate origins, the haplorhine-strepsirrhine split, and the strepsirrhine radiation are for time periods when the primate fossil record is essentially silent, with no capacity to either falsify or corroborate hypotheses based on molecular evidence. Do these divergence times mesh better with the primate fossil record than more traditional estimates?

Recent DNA-based phylogenetic reconstructions estimate ancient times for the divergence of primates from other mammals: $\geq$90 Myr (Hedges et al., 1996; Kumar and Hedges, 1998) and 80 Myr (Arnason et al., 1996, 1998). Martin (1993, 2000) came to a similar conclusion (90 Myr) based on a simple estimate of the completeness of the primate fossil record. When Martin (2000) used these estimates for the time of primate origins to recalibrate

Yoder's (1997) estimates of the haplorhine-strepsirrhine divergence, it was pushed back from 61 Myr to 87 Myr.

Definitive primates in the form of omomyiforms and adapiforms appear at the base of the Eocene. These two lineages of fossil primates have for many years constituted the fossil rag-bag in which researchers have groped for the origins of the three clades of extant primates, the Anthropoidea, Tarsiidae and Strepsirrhini. The dentitions of the basal omomyiforms and adapiforms are almost indistinguishable, suggesting that they shared a common ancestor some time in the Late Paleocene (ca. 58–55.5 Myr) (Rose, 1995). It is not known whether these dental contrasts were accompanied by differences in other parts of the skeleton. If adapiforms and omomyiforms did share a common ancestor in the late Paleocene, and if the lineages of extant primates arose from these two groups, then the fossil based divergence times of strepsirrhines, tarsiers and anthropoids are only slightly younger than Yoder's (1997) original haplorhine-strepsirrhine divergence date of 61 Myr. If, however, we accept Martin's (2000) recalibration of Yoder's haplorhine-strepsirrhine date back to 87 Myr, then the haplorhine and strepsirrhine stem lineages diverged approximately 30 Myr prior to the divergence of omomyiforms and adapiforms. These two lines of evidence are only in conflict if *both* strepsirrhines and haplorhines evolved out of the adapiform and omomyiform radiations. If they did not, then fossil based estimates of omomyiform-adapiform divergence times do not constrain the haplorhine-strepsirrhine divergence times. How strong, then, is the evidence for adapiform-strepsirrhine and omomyiform-haplorhine relationships?

Several postcranial features are shared by strepsirrhines and adapiforms to the exclusion of omomyiforms, anthropoids, tarsiers and putative outgroups (Gebo, 1986; Covert, 1988; Dagosto, 1988). None of the adapiforms are known to exhibit a toothcomb; the similarities between *Notharctus* and lemurs in the ear region are neither shared by all adapiforms, nor by cheirogaleids and lorisiforms; and the grooming claw documented for strepsirrhines and the Messel cercamoniine is also found in tarsiers. Moreover, a possible fossil cheirogaleid has been reported from the Oligocene of Asia (Marivaux et al., 2001) and a galagid and possible lorisid have been recovered from the late middle Eocene of Africa (Seiffert et al., 2003). These discoveries suggest that the divergence of the three major clades of strepsirrhines had occurred at least by the middle Eocene, and probably earlier (Martin, 2003). Derivation of strepsirrhines from adapiforms in this context is unlikely.

The features linking tarsiers to omomyiforms are similarly unconvincing, being either widespread through the group, and therefore primitive, or scattered among different clades (Ross and Covert, 2000). The postcrania of omomyiforms are not particularly tarsier-like, although one may find one or two similarities in different omomyiform lineages (Dagosto et al., 1999). Similarities between anthropoids and omomyiforms are also scant, and were it not for the fact that tarsiers are aligned with anthropoids, anthropoids probably would not share a clade with omomyiforms.

The ages of the earliest fossil anthropoids and tarsiers also argue against origins for these clades amongst omomyiforms and adapiforms. The earliest tarsiers (*Tarsius eocaenus* and *Xanthorhysis tabrumi*) and anthropoids (*Eosimias* and *Bahinia*) in the fossil record are middle Eocene at least, and early Eocene is likely for anthropoids (*Tabelia*, *Algeripithecus*). These taxa are all so divergent from basal omomyiforms and adapiforms as to render it extremely unlikely that they arose (almost instantaneously) from within those radiations. It is therefore possible that omomyiforms and adapiforms as currently delineated have nothing to do with the origins of tarsiers and anthropoids at all, and probably nothing to do with strepsirrhine origins either. Instead, they appear to have been a radiation of primates that occurred independently of the lineages leading to extant primates, an evolutionary dead end.

Omomyiforms and adapiforms are predominantly a Laurasian radiation that appears at the base of the Eocene from some unknown predecessor. Despite fairly intensive sampling of the Paleocene of North America and Europe, the ancestors of omomyiforms and adapiforms have not emerged. The simplest explanation for this is that they are simply not there, but somewhere else.

Asia is a possibility; it is already known to have possessed a radiation of tiny haplorhine- and anthropoid-like primates (Gebo et al., 2000). Africa is also a good bet on biogeographic grounds but the Paleocene fossil record in Africa is meager, explaining why the basal primate stock has not been found. *Altiatlasius* may be a member of that group. As Dagosto notes, various workers have hypothesized unknown groups of basal primates as anthropoid ancestors, mostly out of frustration at the possibilities provided by adapiforms and omomyiforms.

If this reconciliation of the molecular and fossil records is correct, it is both depressing and exciting for the primate fossil record. It means that we have no clear fossil record of the group that gave rise to strepsirrhines, tarsiers and anthropoids and we have no fossil record of basal primates. On the other hand, there is still a chance that the fossils documenting these events are preserved in the late Cretaceous or early Paleocene of Africa.

Continued discovery of fossils is necessary because, although DNA sequences constitute the most numerous and most direct evidence for relationships among extant primates and their mammalian kin, fossil primate species will always exceed living primates in number. Moreover, although the number of extant species will not appreciably increase, the amount of DNA sequence data available for these species will continue to grow. Because accurate identification of branching is heavily reliant on adequate taxon sampling, integration of fossil and molecular data sets is a necessity. Nowhere is this more important than in cases of long branch lengths leading back to short internode distances, where long branch length attraction is known to confound attempts to identify branching patterns (the "Felsenstein Zone"). A good example of this is the long branch leading to extant tarsiers, which is making it very difficult to come up with a definitive signal regarding their relationships either from molecular or morphological data. The only way to break up the long branch length leading to tarsiers is with new fossil discoveries.

This book is a magnificent contribution to the literature on primate evolution. Its rich mix of historical review, systematic paleontology, and paleobiology makes it as close to a synthesis as can be imagined at present. Anyone teaching or researching on primate evolution will want a copy, whether they are a student of morphology, ecology or behavior. You will, however, need to come up with your own locality maps, not an insignificant undertaking. If you're teaching undergraduates, this book is the perfect complement to Fleagle's "Primate Adaptation and Evolution". If you're looking for a text to give your graduate students to learn for their qualifying examinations, this is it. If you are looking to build a phylogeny to incorporate into your comparative analyses, this is the place to start.

The only downside of this book is that it makes it glaringly apparent how desperately our discipline needs a book of this quality on the functional morphology of extant primates. A revision of Aiello and Dean's masterful treatment of human evolutionary anatomy would be a start, but the rest of the Order should not be neglected. Walter Hartwig has done our field a signal service with "The Primate Fossil Record". What would it take to persuade him to turn his attention to organizing a comparably magisterial review of functional morphology?

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Callum F. Ross
Anatomical Sciences
Stony Brook University
USA