

Hominid Adaptations and Extinctions

David W. Cameron

Sydney: University of New South Wales Press, 2004, 260 pp. (hardback), \$60.00.

ISBN 0-86840-716-X

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According to David W. Cameron, the goal of his book *Hominid Adaptations and Extinctions* is “to examine the evolution of ape morphological form in association with adaptive strategies and to understand what were the environmental problems facing Miocene ape groups and how these problems influenced ape adaptive strategies” (p. 4). Cameron describes himself as being “acknowledged internationally as an expert on hominid evolution” and dedicates the book to his “teachers, colleagues and friends” Peter Andrews and Colin Groves. He has participated in fieldwork at the late Miocene sites of Rudabanya (Hungary) and Pasalar (Turkey). His Ph.D. at Australian National University was devoted to “European Miocene faciodental fossils.” He has published a number of articles on Miocene hominoids, mainly in the pages of *Primates*, *Perspectives in Human Biology*, and the *Journal of Comparative Human Biology*. From the outset, it bears mentioning that Cameron’s use of the word hominid refers not only to humans and their ancestors but to great apes and their progenitors as well. This book is really about Miocene hominoids.

The introductory chapter (pp. 1–19) lays out the author’s conceptual framework, including the classification of the Hominidae into subfamilies (Ponginae, Gorillinae, Paninae, Homininae), how the molecular clock works, and a simplified depiction of the ‘*Ramapithecus*’ saga. In a perversion of paleoanthropological history that is so fraught with irony that it borders on the surreal, Cameron credits David Pilbeam for our current understanding of divergence dates within the Hominoidea, including the realization that “the emergence of the earliest proto-humans from their proto-chimp cousins was proposed to be as late as 6 to 5 million years ago” (p. 5). Tertiary paleogeography and climates are reviewed, especially with respect to the demise of Paleogene prosimians at the “Grande Coupure” and the emergence of early anthropoids in the Fayum. Some of the discussion of primate evolution here is not particularly accurate or informative, including the suggestion that *Amphipithecus* and *Qatrania* closely resemble each other. Cameron places within the Proconsulidae a hodgepodge of taxa, including “*Proconsul*, *Rangwapithecus*, *Turkanapithecus* and the fossil small-bodied East African apes,” in essence ignoring the substantial and significant differences between *Dendropithecus* and *Simiolus* (on the one hand) and *Proconsul* (on the other hand) in terms of distal humerus articular morphology. The influence of Peter Andrews and Colin Groves on the author’s work is quite clear. The Miocene “Hominidae” are placed into four tribes: Afropithecini (at the base of the “hominid” radiation), Kenyapithecini (a side group), Sivapithecini (ancestral to *Pongo*), Dryopithecini (between

Asian and African great apes), and the subfamily Gorillinae (*Graecopithecus*). Cameron states that “the aim of this book, however, is to re-examine and if necessary revise this tentative evolutionary scheme” (p. 10). With regard to his inclusion of the Proconsulidae in the Hominoidea, Cameron cites as evidence “the presence of a frontal sinus” and that “they have an increased potential for raising arms above the head” (p. 10). Sadly, Cameron seems unaware of the fact that the frontal sinus has been demonstrated to be a primitive feature for Old World higher primates (Rossie et al. 2002). Also, no clear evidence exists for the enhanced arm-raising abilities of proconsulids compared to their contemporaries, including the victoriapithecids. In wrapping up his discussion of the Proconsulidae, Cameron unwittingly and inexplicably cites a 1983 book chapter about *Australopithecus africanus* by Tim White, Don Johanson, and Bill Kimbel as evidence that *Proconsul* lacks a tail (p. 10).

Many of the views expressed in this book are iconoclastic and, in my opinion, unlikely to be true. The genus *Homo* is claimed to be represented in the Pliocene by *Homo ergaster* (p. 2). In reality, “*Homo ergaster*” first appears in the early Pleistocene, approximately 1.8–1.7 MA (both at Koobi Fora in Kenya and at Dmanisi in Georgia, where it has been named *Homo georgicus*; Gabunia et al. 2002). Pliocene examples of the genus *Homo* more closely resemble *Homo habilis* and “*Homo rudolfensis*.” An early *Homo* cranium from Koobi Fora (KNM-ER 1470) is said to represent an “unnamed hominid genus” (p. 2). *Graecopithecus* is described as resembling extant African apes despite the fact that this genus retains primitive conditions of the supraorbital and subnasal regions. The early robust australopithecine from the Turkana Basin (*Paranthropus aethiopicus*) is referred to as “*Paranthropus walkeri*” (p. 18). The later *Paranthropus* species (presumably *P. robustus* and *P. boisei*) are described as having had “some knuckle-walking and tree-climbing abilities” (p. 18). Cameron contends that *Kamoyapithecus* may turn out to belong to the Afropithecini but the basis of this inference is not clear. We also learn from Cameron that *Dryopithecus* includes species from Spain that are ancestral to *Pongo* while species of *Dryopithecus* from France, Germany, and Hungary “belonged to the African clade.” The discussion concerning *Oreopithecus* is disappointing in that it fails to mention the suggestion, based on a complex suite of dentognathic similarities, that *Oreopithecus* is descended from an African ancestor such as *Mabokopithecus*.

In addition, there are numerous instances of confused thinking, made even less clear by garbled writing. After discussing the diverse radiation of African hominoids during the early-middle Miocene, Cameron suggests that “by 8

million years ago, however, this explosion was countered by a contraction, with only a few relict populations still managing to hold on." In fact, this is a misconception. The fossil record of African late Miocene vertebrates is poorly known in general; it is not hominoids in particular that "contracted." Postcranial remains of *Otaviipithecus* are described as "suggesting that it should be considered hominoid, rather than hominid; i.e., more primitive" (p.16). Equating primitiveness with a more inclusive taxonomic rank (the Superfamily Hominoidea) is simply illogical. It makes about as much sense as saying "suggesting that it should be considered human, rather than female; i.e., more primitive."

The second chapter "Adaptation and Evolution" (pp. 20–43) reviews the concepts of adaptation and species as well as discussing some fundamental aspects of bone biology. The methodology of cladistics also is presented. The examples chosen for demonstration of cladistic methodology involve detailed aspects of the morphology of Miocene "hominid" genera, including *Kenyapithecus*, *Afropithecus*, "*Heliopithecus*" (a junior synonym of *Afropithecus*), "*Morotopithecus*" (a junior synonym of *Afropithecus*), and "*Equatorius*" (a junior synonym of *Kenyapithecus africanus*). Unfortunately, many of the character states are clearly incorrect. Contrary to Cameron, *Kenyapithecus africanus* ("*Equatorius*") does not have higher molar relief than *Afropithecus*, the zygomatic insertion of *K. africanus* is not more forwardly positioned than in *Kenyapithecus wickeri*, and *K. wickeri* does not have relatively smaller premolars than *K. africanus*.

The most substantive parts of the book are chapters concerning Miocene hominoids, especially their craniofacial anatomy. Chapter 3 is devoted to "The African Early Miocene Large-Bodied Proconsulidae" (pp. 44–74). Cameron states that "*Heliopithecus*" is the earliest hominoid known outside of Africa but no mention is made of other candidates, such as *Platodontopithecus* or *Dionysopithecus*. The contention that primates are not "originally endemic to Africa" and "must have come from elsewhere, most likely Asia" would be more convincing if the Paleocene and Eocene mammalian paleontology of Africa was better known.

It appears (based on the acknowledgments and legends to tables and illustrations) that Cameron did not study the original specimens of Miocene hominoids from Africa, Spain, and France. Perhaps for this reason, the book suffers several shortcomings. *Ugandapithecus*, a genus erected in 2000 by Brigitte Senut and colleagues for the largest species of early Miocene African hominoid traditionally referred to *Proconsul major* (Senut et al. 2000), is too easily dismissed. *Proconsul nyanzae* is listed as being known from Rusinga and Mfangano and possibly Fort Ternan. As demonstrated by Pickford, however, the record of *Proconsul nyanzae* from Fort Ternan is an upper canine that represents a male individual of *Kenyapithecus wickeri*. Contrary to Cameron, Fort Ternan dates to about 13–12 MA, not 15 MA. Cameron states that "additional *Proconsul*-like specimens have also been excavated from the other middle Miocene locality on Maboko Island, Kenya" and claims that these were allocated to *Proconsul major* by Lawrence Martin in 1981. The

specimens that Martin allocated to *P. major* come from the early Miocene (ca. 19 MA) site of Koru, not from the middle Miocene (ca. 15 MA) site of Maboko. In fact, there are no *Proconsul*-like specimens known among the approximately 4,000 primate fossils from Maboko. Another example of the author's unfamiliarity with African Miocene hominoids is when he claims that Pilbeam described the central incisors of *Proconsul major* as being broad. The main specimen that Pilbeam described as *P. major* is the large-bodied hominoid from Moroto, a creature that does not represent *Proconsul*.

Comments on the dietary and locomotor adaptations of the early Miocene African hominoids lack insight. Cameron claims that "the molar morphology alone suggests" that *Turkanapithecus* "was predominately a folivore." The molars of *Turkanapithecus* are heavily worn, however, so whether the molar shear crests were very long (an indicator of folivory) cannot be ascertained from currently available samples. The author suggests that *Proconsul major* engaged in above-branch arboreal locomotion based on the assumption that this species' adaptations would be identical to those of smaller species of *Proconsul*.

Metric data for African early Miocene hominoid craniofacial, mandibular, and dental specimens are provided in three tables (pp. 50–55). The validity of at least some of these data is questionable. For example, values for a dimension called "mid-supraorbital tori thickness" are provided for *Turkanapithecus kalakolensis* and *Pongo pygmaeus* despite the fact that these taxa manifestly lack supraorbital tori. Illustrations in the chapter on early Miocene African hominoids are of uneven quality. There are stippled sketches of the type specimens of *Proconsul africanus*, *P. nyanzae*, and *Rangwapithecus gordonii*. These are labeled but not precisely. For example a line extending to the buccal side of the second maxillary molar of *Proconsul africanus* is labeled as "Molar cusp." Unfortunately, the end of that line falls somewhere between the paracone and the metacone. The *Proconsul* skull that was collected by Mary Leakey from Rusinga Island in 1948 is rendered in a cartoon-like drawing. The only photograph of an African early Miocene hominoid is a murky shot of a cast of the skull of *Turkanapithecus kalakolensis*, labeling non-existent supraorbital tori as present.

In a highly confused and often inaccurate way, Cameron attempts to reconstruct the ancestral condition for hominoids and then proceeds to compare the early Miocene African forms to this reconstruction. This reconstruction is based, according to Cameron on outgroup comparison to "three Old World Monkey genera, *Cebus*, *Colobus*, and *Macaca*." The fact that Cameron does not even know that *Cebus* is a platyrrhine (New World) monkey is alarming and casts doubt on the validity of his inferences and conclusions. It is also disturbing to see that "no frontal sinus" is listed as a feature of the "hominoid bauplan." This confused trend continues when "a well defined *crista obliqua*" (a consistent feature of non-cercopithecoid primate four-cusped upper molars) is treated as a dental synapomorphy of *Proconsul*, *Rangwapithecus*, and *Turkanapithecus*. Loss of the *crista obliqua* is a derived characteristic of Victoriapithecidae, the formative Old World monkeys known from the early and

middle Miocene of Kenya, Uganda, Egypt, and Libya (Benefit & McCrossin 2002). Contrary to Cameron, Harrison viewed *Rangwapithecus* as ancestral to the middle Miocene oreopithecids *Mabokopithecus* (including its junior synonym *Nyanzapithecus*), rather than as a stem catarrhine. Cameron's suggestion that "*Turkanapithecus kalakolensis* should be called *Rangwapithecus kalakolensis*" lacks credibility.

Chapter 4 (pp. 75–103) is devoted to the author's second-hand appraisal of "The African Early and Middle Miocene Hominoids." Frankly, this chapter is so filled with inaccuracies that it is difficult to review. Benefit and McCrossin are cited in the text as referring specimens from Nachola and Samburu to *Kenyapithecus africanus*. But no such reference appears in the bibliography at the end of the book. In fact, Hidemi Ishida and colleagues referred the Nachola material to *Kenyapithecus africanus* in a series of publications prior to their recognition of *Nacholapithecus* as a distinct genus. The genus *Equatorius*, with a maxilla from Maboko Island as its type specimen, is a junior synonym of *Kenyapithecus africanus*. Combining *Griphopithecus* and *Kenyapithecus* into the "African Eurasian tribe Kenyapithecini" (p. 75) is only possible for people who lack first-hand knowledge of the samples of middle Miocene large-bodied African hominoids collected in the last two decades. No uniquely derived features are shared by *Griphopithecus* and *Kenyapithecus*.

By far the most misleading and inaccurate sections of this book pertain to the pivotal middle Miocene hominoids of Africa, especially *Kenyapithecus*. It does not help that these sections are also plagued by some of the worst writing in the book. For example: "recent dates for the Tugen Hills ... have recently been dated" (p. 85). The assertion that postcranial remains of *Kenyapithecus africanus* first came to light in 1999 is dumbfounding considering that Le Gros Clark and Leakey published descriptions of humeri and femora of this taxon in 1951. In fact, these specimens were the first limb bones of an African fossil ape to be collected (in the 1930s, by Walter Owen). Most egregious is the attribution of terrestrial adaptations in *Kenyapithecus* to the work of Rich Sherwood and colleagues. Recognition and elucidation of the terrestrial adaptations of *Kenyapithecus* resulted from collections of new postcranial remains from Maboko Island in the 1990s, especially elements of the shoulder, arm, elbow, wrist, and hand (McCrossin & Benefit 1997; McCrossin et al. 1998). Although Cameron claims that "the preserved postcranial morphology of *Kenyapithecus* indicates that it had the primitive hominoid condition ... based on above-branch quadrupedalism" (p. 93), the only known postcranial fossil of *Kenyapithecus wickeri* (a distal humerus) clearly exhibits terrestrial adaptations in the posterior orientation of the medial epicondyle (McCrossin & Benefit 1997). The skeletal remains of "*Equatorius*" from Kipsaramon in the Tugen Hills, in contrast, are largely undiagnostic of substrate preference. Missing also from the discussion of *Kenyapithecus* is the identification of dentognathic adaptations for sclerocarp foraging (McCrossin & Benefit 1997; McCrossin et al. 1998).

Discussion of the paleoenvironment of middle Mio-

cene localities is heavily biased toward the work of Peter Andrews. Andrews' work was conducted during the 1970s, was based on small collections (often involving misidentifications of fauna), and was informed by simplistic analogies between ancient and modern environments. No mention is made, for example, of recent work by Retallack et al. (2002) on Maboko paleosols. In recent years a number of investigators have come to the realization that the adaptive history of hominoids during the Miocene epoch is best understood within the context of all catarrhines living at that time, especially the victoriapithecids. This realization has not yet reached Cameron.

Metric data for *Afropithecus*, "*Morotopithecus*," "*Helio-pithecus*," "*Equatorius*," *Kenyapithecus*, and *Griphopithecus* craniofacial, mandibular, and dental specimens are provided in three tables (pp. 79, 82, 84). Data for *Afropithecus* come from a cast. Illustrations continue to be of uneven quality. There is a stippled sketch of the type specimen of "*Morotopithecus*" that is printed in an upside down orientation (incisors toward the bottom, molars toward the top). The *Afropithecus* skull from Kalodirr is rendered in a cartoon-like drawing that would be appropriate for a children's book on Miocene hominoids.

Taxonomic conclusions include the erection of new familial, subfamilial, and tribal categories. Little or no evidence can be marshaled in support of Rangwapithecidae, *Afropithecidae*, *Equatorinae*, etc. I do not expect to see these terms employed by people who work on African early-middle Miocene hominoids, now or in the future.

Throughout the book, some concepts and terms are employed in ways that are confusing or imprecise. Cameron refers to the condition of "the upper face being directly hafted onto the frontal bone" (p. 39) as "often referred to as airohynchynchy". I have never heard anyone define airohynchynchy in this way. Instead, airohynchynchy involves dorsal rotation of the splanchnocranium on the antero-posterior axis of the cranial base (Bruner et al. 2004). This misconception about the hafting of the upper face to the frontal bone persists in sections devoted to descriptions of fossil taxa. *Afropithecus* is referred to as having an upper face that is not hafted "directly onto the frontal bone" (p. 77). This is quite simply incomprehensible. The bones of the upper face of *Afropithecus* (nasals, maxillae, zygomatics) are joined by sutures to the frontal bone just as they are in every other primate. The frontal anatomy of *Afropithecus* is itself misconstrued by Cameron. Rather than having a "well-developed supraorbital torus" and "frontal sulcus" (by which I think he means post-toral sulcus), *Afropithecus* exhibits supraorbital costae (rib-like superciliary processes) and a frontal trigon.

Cameron persistently confuses body weight estimates of the African Miocene hominoids. Citing an estimate based on a distal tibia from Napak (Uganda), Cameron notes that *Proconsul major* may have weighed about 75 kg. He then goes on to say that *P. major* "would have been about the size of a female orangutan." Some female orangutans weigh approximately 75 lbs (not kg); their average body weight is approximately 37 kg. As is widely recognized, the

75 kg weight estimate for *Ugandapithecus* places this creature in the size range of female gorillas. At approximately 11 kg, *Proconsul heseloni* is said to be “within the range of the smaller Asian gibbons.” In reality the 11 kg figure for *Proconsul heseloni* is based mainly on the subadult skeleton (KNM-RU 2036) from the pothole site on Rusinga Island. Adults of this species certainly weighed more. Moreover, a body weight of 11 kg is comparable to that of the largest Asian gibbons, the siamang. The smaller Asian gibbons, e.g., *Hylobates lar*, weigh about a third of this amount. With regard to *Heliopithecus*, Cameron states that “we have no estimate of its body weight, but the size of its dental complex is similar to that of *P. nyanzae*, tentatively suggesting it was probably about the size of a large gibbon.” This makes no sense whatsoever, in light of the fact that *Proconsul nyanzae* is estimated to have weighed approximately 30–40 kg and the siamang (the largest of the hylobatids) weighs about one-third to one-quarter that amount. “Equatorius” is described as weighing about 40 kg and Fleagle’s (1999) textbook is credited with this conclusion. In reality, the Maboko sample of *Kenyapithecus africanus* probably weighed between about 17 and 36 kg based on regression analyses of molar and postcranial dimensions (McCrossin et al. 1998). Accordingly, *Kenyapithecus africanus* (aka “Equatorius”) was slightly larger than *Mandrillus sphinx* (the largest living Old World monkey) and slightly smaller than *Pan paniscus* (the smallest living great ape).

Typographical errors (or downright misspellings) are not extremely numerous in the text but you can count on finding one every few pages (I stopped documenting them after the first few chapters): “temporonucal” (p. 17), “pleismorphic” (p. 29), “undeveloped” (p. 56), “Oliogocene” (p. 65), “Nyacatch” (p.76), “Turanapithecus” (p. 100), “Equatorini” (p. 100). Typos abound, however, in the references. Here we see things like “Hominiodea” (p. 239) and “Tores-Menalla” (p. 247). Readers might also feel sorry for the treatment meted out to authors with French or Japanese surnames, such as “Dugus” (Dugas), Ishia (Ishida), “Nakatskasa” (Nakatsukasa), and “Sent” (Senut).

Subsequent chapters delve into “The Asian Miocene Hominids” (pp. 104–134), “The European Later Miocene Hominids” (pp. 135–161), “Miocene Ancestors to the African Extant Great Apes?” (pp. 162–179), “Hominins at the Miocene-Pliocene Transition” (pp. 180–198), and “Hominid Adaptations and Extinction” (pp. 199–210). Space does not permit me to elaborate on these chapters. Suffice it to say that the scientific accuracy of these chapters is consistent with those I have already reviewed. The illustrations actually decline in quality. A photograph of *Ankarapithecus* is printed so dark that it is barely visible. A colleague once facetiously threatened to model a *Victoriapithecus* cranium out of Play-Do if I did not quickly send him a photograph for his textbook. Drawings of the skull of *Oreopithecus* (p. 152), the cranium of *Sahelanthropus* (p. 183), KNM-ER 1470 - termed “*Kenyanthropus rudolfensis*” (p. 196), and KNM-ER 1813 (p. 198) actually look like Cameron sculpted them out of modeling clay. Just when you think it could not get any worse there are hairy drawings, called “reconstructions,”

of *Dryopithecus brancoi* (p. 142) and “*Praeanthropus afarensis*” (p. 189) that look like weird mythical creatures.

In conclusion, this book has admirable goals. Integration of the fossil record of hominoids from the earlier parts of the Miocene with that of early hominids from the late Miocene–early Pliocene is certainly a worthy endeavor. But this book’s failings far outnumber its strengths. The combination of factual errors, generally poor scholarship, and bad writing results in a worse-than-average book, even by the standards of popular treatments of paleoanthropology. If this book is remembered for anything, it may be for how it represented a high-water mark of sorts for the Eurocentric model of African ape and human evolution. That model originated when the late Miocene record of ape and human evolution was poorly known. Recent fossil discoveries and more rigorous analyses have demonstrated that African apes and humans, not surprisingly, originated and diversified in Africa. In all likelihood the hominoids of the Eurasian late Miocene, including *Dryopithecus* and *Ouranopithecus*, went extinct without issue and were not in any way ancestral to African apes and humans. I definitely would not recommend this book to serious students of primate and human evolution. This book also is not suitable for adoption as a textbook. Finally, it is a good idea to discourage libraries from squandering their scarce resources on this poorly written book.

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