Koobi Fora Research Project, Volume 6: The Fossil Monkeys

Nina G. Jablonski and Meave G. Leakey (eds.)
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Although cercopithecoid primates first evolved in the latter part of the Miocene epoch, it was not until the Plio-Pleistocene when the two subfamilies of Old World monkeys, the colobinae and cercopithecinae, started to morphologically and ecologically diversify. This diversification is well documented in the primate fossil record, especially in the Koobi Fora Formation. In *The Fossil Monkeys*, which is edited by N. Jablonski and M. Leakey, the reader is provided with comprehensive anatomical descriptions of fossil cercopithecoids from the Plio-Pleistocene and is introduced to some interpretations of cercopithecoid evolution and paleobiology (e.g., diet). This volume centers around the >890 recovered fossil specimens that can be confidently assigned to eight genera and possibly more than 11 species of cercopithecoids; there are even more specimens that are clearly cercopithecoid but lack distinctive taxonomic affinities. Although the fossil hominins from the Koobi Fora Formation traditionally receive more attention (e.g., Spoor et al. 2007), hominins are only represented by a sample of just over 200 specimens, thus demonstrating that the cercopithecoids may have been the dominant primate fauna at this time in East Africa.

The first four chapters of *The Fossil Monkeys* include an Introduction (Chapter I) in which all measurements obtained from skulls, teeth, and postcranial elements are outlined, and the systematic paleontology (Chapters II–IV) of the fossil cercopithecoids recovered up to and including the 2004 field season. In addition to the descriptive anatomy, the systematic paleontology chapters are complemented by 1) exceptional photographs of some of the better-preserved specimens, often in multiple views, and, 2) detailed tables that include lists of specimens (by provenience and taxon) and their measurements. The Appendix at the end of the printed volume also provides a comprehensive table of measurements for each specimen, and the supplementary DVD (which can be purchased separately from the hardcover book) includes additional color photographs of specimens not illustrated in the printed text, and a searchable PDF file of the entire printed volume.

Chapter II, by N. Jablonski and M. Leakey, primarily focuses on descriptions of a new small colobine species from Koobi Fora, *Colobus freedmani*. Despite few cranial fragments, several mandibles, isolated teeth, and postcranials from both fore- and hind limbs are abundant, including a partial skeleton of a probable female, KNM-ER 5896. These authors conclude that *C. freedmani* was very similar to living *Colobus*, except that it may have been slightly larger (estimated mass of 11 kg) and that it may represent one of the first examples of a colobus monkey of modern aspect in the primate fossil record.

Chapter III, by N. Jablonski, M. Leakey, C. Ward and M. Antón, describes fossil material from previously named "large" colobine monkeys: *Rhinocolobus turkanaensis*, *Cercopithecoides williamsi*, *Cercopithecoides kimeui*, and *Paracolobus mutiwa*. Chapter IV, also by N. Jablonski, M. Leakey, and M. Antón, is dominated by numerous descriptions of *Theropithecus* material, but it also describes the few recovered, but still very important fossil guenons (*Cercopithecus*), mangabeys (*Lophocebus*), and generalized baboons (*Parapapio*). Interestingly, these authors suggest that some of the larger morphs of *Parapapio* may possibly be related to *Mandrillus*, a monkey genus that has virtually no fossil record. There is a wealth of anatomical detail in these two chapters, however, considering that previous descriptions of some of this material had been previously published when these taxa were first described, there is very little new information about the biology of these animals (e.g., body size estimates, inferences about locomotor behaviors; see Delson et al. 2000). For example, the new fossil descriptions from the expanded Koobi Fora collections reconfirm that *Rhinocolobus* was likely more arboreal than *Cercopithecoides*, and that *Theropithecus* species were extremely variable in its morphology, ecology and behavior.

Although the anatomical descriptions comprise the bulk of Chapters II–IV, the beautiful (and colorful) full body reconstruction created by Mauricio Antón included in Chapters III and IV provide nice visuals of these extinct monkeys. *Rhinocolobus* is depicted sitting on an arboreal support, while *Cercopithecoides williamsi* and *Theropithecus oswaldi* are both shown in a terrestrial stance. Each of these animals is represented by reconstructions of its bony skeleton, its muscular anatomy, and its skin and hair color. These illustrations are indeed a welcome addition to these description heavy chapters, as is the narrative of the rationale and methodology used in creating the reconstructions.

Chapter V, by N. Jablonski and G. Chaplin, comes directly after the systematic paleontology section of this volume and provides what the authors refer to as "natural language descriptions" of the fossil monkeys. Using 151 unordered and ordered multistate characters, Jablonski and Chaplin employ the DELTA (DEscription Language for TAxonomy) system (Dallwitz et al. 2000) to create a flow chart that is supposed to facilitate the identification of fossil monkeys to a given species. The authors also provide a

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comprehensive distance matrix of phenetic similarity between extant and fossil cercopithecoids generated in the program DIST. Although I find the DELTA method not as intuitive or simple as the authors perceive it to be, the 151 characters states provided by the authors could be useful for other researchers to undertake more conventional phylogenetic analyses.

Chapter VI, by M. Teaford, R. Kay and P. Ungar, reads more like a journal manuscript compared to the other chapters in this volume. Teaford and colleagues examined molar shape (i.e., shearing quotient) and molar microwear in a portion of the Koobi Fora fossil monkey sample to evaluate: 1) the dietary patterns in these Plio-Pleistocene primates; and, 2) whether shearing quotient and microwear variation in these fossil monkeys is similar to that seen in extant cercopithecoids. Their molar microwear results show that both colobines and cercopithecines lack a high incidence of pitting, a pattern that differs from earlier stem-catarrhines from the Fayum, stem-cercopithecoids (e.g., *Victoriapithecus*), and crown-cercopithecoids from older sites in East Africa. When these pits do exist in the Koobi Fora sample, they tend to be small in size. Shearing quotients also were found to lie within the range of extant cercopithecoids with the colobines having a higher shearing quotient than cercopithecines; the former also had fewer pits than the latter group. Taken together, the microwear data suggests that the Koobi Fora monkeys were not hard object feeders and the molar shape data indicates that these fossil monkeys were capable of processing foods similar to their extant counterparts. Furthermore, differences between the fossil colobine and cercopithecine monkeys were subtler than they are today.

Chapter VII, by M. Leakey, P. Gathogo, and N. Jablonski, reviews the geology of the Omo-Turkana Basin and the Koobi Fora Formation. A previous volume in the *Koobi Fora Research Project* series (Feibel et al. 1991) provides a more detailed history of this region than this chapter, but its inclusion here allows the authors to discuss the cercopithecoid assemblages in a meaningful way. Specifically, they divide the cercopithecoids into four temporal intervals that are geochronologically well dated (except for a 520–550 kyr gap within the Burgi Member). Interval A (3.94–3.45 Ma) was dominated by specimens of *Parapapio*, but there was also an abundance of *Cercopithecoides*. The least taxonomic diversity is seen in this time interval and it contains animals of mostly small to medium body size. The authors suggest that these animals occupied wooded, well-watered and well-vegetated paleohabitats. *Theropithecus brumpti* is well represented in Interval B (3.45–2.52 Ma) and *Theropithecus oswaldi* appears to be the best sampled in Interval C (2.0–1.56 Ma) with more than 245 specimens. Both Intervals B and C show greater taxonomic diversity than Interval A, with Interval C being more diverse than Interval B. Although Interval B is suggested to have a similar paleoenvironment to Interval A, the fossil monkeys in Interval B are larger, and this pattern of increasing size continues into Interval C. For example, the larger colobines, *Rhinocolobus* and *Cercopithecoides* also are fairly well documented in Interval C. It is proposed by the authors that the greater diversity seen in Interval C could be a result of fluctuations in extreme climatic conditions. It is in Interval D (1.56–1.38 Ma) where the smaller cercopithecines (e.g., *Lophocebus*) and colobines (i.e., *Colobus freedmani*) become more prevalent, possibly due to drier environments. The large colobines begin to disappear and although *T. oswaldi* is still the most abundant of all the fossil monkeys recovered, its numbers are far fewer compared to Interval C. From this chapter, it becomes apparent to the reader that the cercopithecoid faunal assemblages changed across time intervals, and these changes were likely accompanied by changes in the paleoecology and paleobiology of the Koobi Fora fossil monkeys.

In the concluding chapter (VIII), N. Jablonski and M. Leakey discuss the importance of the cercopithecoid primate fossils from Koobi Fora in the context of primate and mammalian evolution. More importantly, they review cercopithecoid evolution in the Plio-Pleistocene with a focus on the Koobi Fora material; essentially, this last chapter serves as an extension of the previous one. The importance of ecology and environmental changes during the Plio-Pleistocene are the focus, and these authors highlight the role of competition between cercopithecoids, hominins, and ungulates. Increased competition pressures in a changing landscape are thought to be one cause for the demise of the largest monkey taxa.

Students of primate evolution, and not just cercopithecoid evolution, will find that *The Fossil Monkeys* is an excellent reference to have on their bookshelves. If you one day find yourself lucky enough to be working with fossil cercopithecoid material, this volume will definitely be a source of valuable information. And with the digital copy of this volume included on the DVD, you can easily transport the Koobi Fora fossil monkeys to any museum around the world to facilitate comparative analyses.

REFERENCES

Delson, E., Terranova, C. J., Jungers, W. L., Sargis, E. L., Jablonski, N. G., Dechow, P. C. 2000. *Body Mass in Cercopithecidae (Primates, Mammalia): Estimation and Scaling in Extinct and Extant Taxa*. Anthropological Paper No 83. American Museum of Natural History, New York.

Dallwitz, M. J., Paine, T. A., and Zurcher, E. J. 2000. *User's Guide to the DELTA Editor*. http://delta-intkey.com

Feibel, C. S., Harris, J. M., and Brown, F. H. 1991. Palaeoenvironmental context for the late Neogene of the Turkana Basin. In *Koobi Fora Research Project, Volume 3, The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments*, (ed. J. M. Harris), pp. 321–370. Clarendon Press, Oxford.

Spoor, F., Leakey, M. G., Gathogo, P. N., Brown, F. H., Antón, S. C., McDougall, I., Kiarie, C., Manthi, F., K., Leakey, L. N. 2007. Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya. *Nature* 448, 688–691.