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NOTE

AN ANTHROPOID PRIMATE HUMERUS FROM THE RUKWA RIFT BASIN, PALEOGENE OF SOUTHWESTERN TANZANIA

NANCY J. STEVENS[1], PATRICK M. O'CONNOR[2], MICHAEL D. GOTTFRIED[3], ERIC M. ROBERTS[4], SIFAEL NGASALA[5], [1]Department of Biomedical Sciences, 228 Irvine Hall, College of Osteopathic Medicine, Ohio University, Athens, Ohio 45701, U.S.A., stevensn@ohio.edu; [2]Department of Biomedical Sciences, 228 Irvine Hall, College of Osteopathic Medicine, Ohio University, Athens, Ohio 45701, U.S.A., oconnorp@ohio.edu; [3]Department of Geological Sciences and Museum, West Circle Drive, Michigan State University, East Lansing, Michigan 48824, U.S.A., gottfrie@msu.edu; [4]School of Geosciences, University of Witwatersrand, Wits 2050, Johannesburg, South Africa, roberts@geosciences.wits.ac.za; [5]Department of Geological Sciences, University of Dar es Salaam, Tanzania, siengas@yahoo.co.uk

African early Tertiary paleontological sites are notoriously patchy, both spatially and temporally. The vast majority of Paleogene primate fossils have been recovered from sites in the northern portion of the continent (e.g., Thomas et al., 1991; Godinot and Mahboubi, 1992; Hartenberger and Marandat, 1992; Godinot, 1994), with the most extensive record from the Fayum Depression of Egypt (e.g., Osborn, 1908; Simons and Kay, 1983; Simons et al., 1994; Simons, 1995; Simons and Rasmussen, 1995; Simons et al., 2001). Sub-equatorial deposits are relatively sparse, and no primate postcranial remains have been described from Paleogene deposits in sub-Saharan Africa. The rarity of Paleogene strata from much of Africa poses problems not only for understanding the geographical extent and evolutionary significance of faunas occupying the majority of the continental landmass, it also provides obstacles to reconstructing biogeographic histories of a variety of clades, including primates (Stevens and Heesy, 2000; Ducrocq, 2001; Gunnell and Miller, 2001; Heesy et al., in press).

In contrast, numerous sites in East Africa have provided a wealth of information concerning the Neogene primate record (e.g., Fleagle and Simons, 1978; Leakey et al., 1995; Harrison, 1997; MacLatchy and Pilbeam, 1999; Kingston et al., 2002). Until relatively recently, the earliest Tertiary faunas reported from East Africa were Miocene in age. New finds from older Tertiary sites suggest that this region also holds keys to understanding issues deeper in paleontological history (e.g., Leakey et al., 1995b; Murray, 2000; Harrison et al., 2001; Gunnell et al., 2002; Kappelman et al., 2003; Stevens et al., 2004).

Here we describe a diminutive anthropoid primate humerus recovered from Paleogene deposits in southwestern Tanzania. In many features this specimen resembles basal anthropoids described from the Paleogene Jebel el Qatrani Formation of Egypt, constituting the first primate postcranial record from the Paleogene of sub-Saharan Africa.

Location

The specimen described herein derives from richly fossiliferous fluvial and floodplain strata in the Rukwa Rift Basin, Mbeya Region, southwestern Tanzania (Fig. 1). The locality (TZ-01) is situated in the Songwe Valley at approximately 8º 56' S, 33º 12' E (precise locality coordinates are on file at Ohio University). The fossil-bearing beds are part of a laterally continuous series of proximal fluvial and overbank deposits that comprise Unit II of the Red Sandstone Group (Roberts et al., 2004). The specimen was discovered within a tabular, two meter-thick muddy sandstone bed that is interpreted as a repeating sequence of intra-channel flood-stage fluvial deposits. A range of other exquisitely preserved isolated and articulated microvertebrate fossils has been recovered from this locality. The TZ-01 fauna is characterized by small (< 4 cm) cranial and postcranial remains, including numerous teeth, jaws, and postcranial elements from a variety of vertebrate clades (Stevens et al., 2004; Stevens et al., in press).

Age estimates for red sandstones in the study area have ranged from the mid-Jurassic to late Cenozoic (e.g., Tiercelin et al., 1988; Ebinger et al., 1989; Damblon et al., 1998; Morley et al., 1999). Recent work by our team has refined the geological and paleontological context of deposits in the region, clearly documenting the presence of both Cretaceous and Paleogene sequences (O'Connor et al., 2003; Roberts et al., 2004; Stevens et al., 2004). A Paleogene age is inferred based on the presence of *Metaphiomys,* a phiomorph rodent previously restricted to early Oligocene deposits in northern Africa and Oman (Wood, 1968; Holroyd, 1994; Stevens et al., in press). This age assignment is consistent with thermal history reconstructions of the Rukwa and Malawi rift flanks by Van der Beek et al. (1998). Based on apatite fission-track data, they document a phase of rapid cooling and denudation of rift flanks between 40–50 Ma, relating to an early Cenozoic tectonic event and subsequent sedimentation. The TZ-01 deposits likely relate to re-activation of preexisting basement structures and extensional basin development during this early Tertiary tectonic event. A Paleogene age estimate is also supported by middle Eocene to early Oligocene K-Ar dates for nepheline basalts capping sedimentary deposits in the southern part of the field area (Tiercelin et al., 1988).

METHODS

The specimen (National Museums of Tanzania TNM 03100) was collected by standard paleontological hand-quarrying methods and mechanically prepared at the Stony Brook University vertebrate preparation facility. Measurements were recorded using a Nikon SMZ 1500 stereomicroscope bundled with SPOT Advanced (version 4.0) software. The accuracy of measurements is on average +/- 0.01 mm. Comparative material consisted primarily of reference specimens and casts of representative fossil and Recent primate and non-primate mammalian humeri examined from the following institutions: American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CM), Duke University Primate Center Division of Fossil Primates (DPC), Smithsonian Museum of Natural History (NMNH), and Stony Brook University Vertebrate Collections (SBU). These observations were supplemented with photographic comparisons of less accessible specimens.

SYSTEMATIC PALEONTOLOGY

Order PRIMATES Linnaeus, 1758
Suborder ANTHROPOIDEA Mivart, 1864

Referred Material—Right distal humerus, TNM 03100, from locality TZ-01.

Description—TNM 03100 is the distal half of a right humerus (Fig. 2). The specimen preserves the medial two-thirds of the distal articular surface, a shallow, broad olecranon fossa, and approximately 11 mm of the humeral shaft proximal to the superior border of a prominent entepicondylar foramen. The long axis of the foramen measures 1.46 mm, the short axis 0.86 mm. The humeral shaft broadens and flattens distally, displaying evidence of a prominent supinator crest and a modestly developed brachialis flange. The radial and coronoid fossae are both slightly perforated, separated by a subtle bony strut arising from the lateral aspect of the entepicondylar foramen. Cracks are present along the bony arch above the entepicondylar foramen and along the proximal

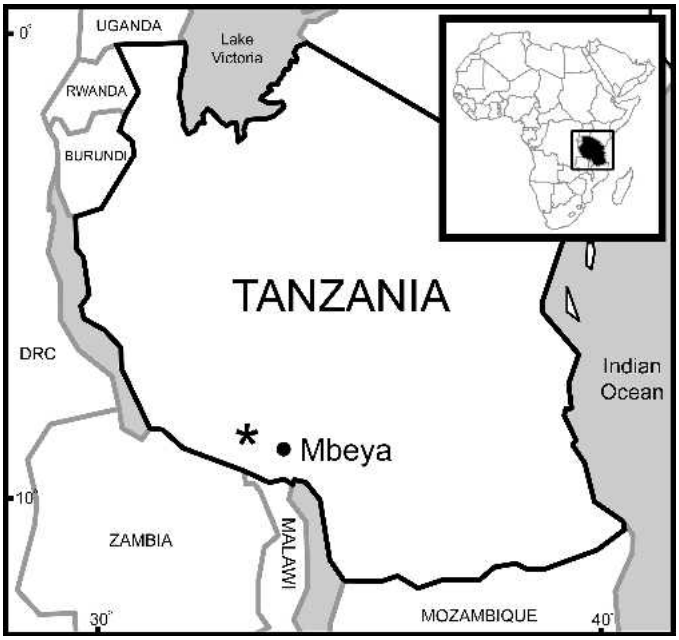

FIGURE 1. Field site (TZ-01) location in the Rukwa Rift Basin, southwestern Tanzania, indicated by star.

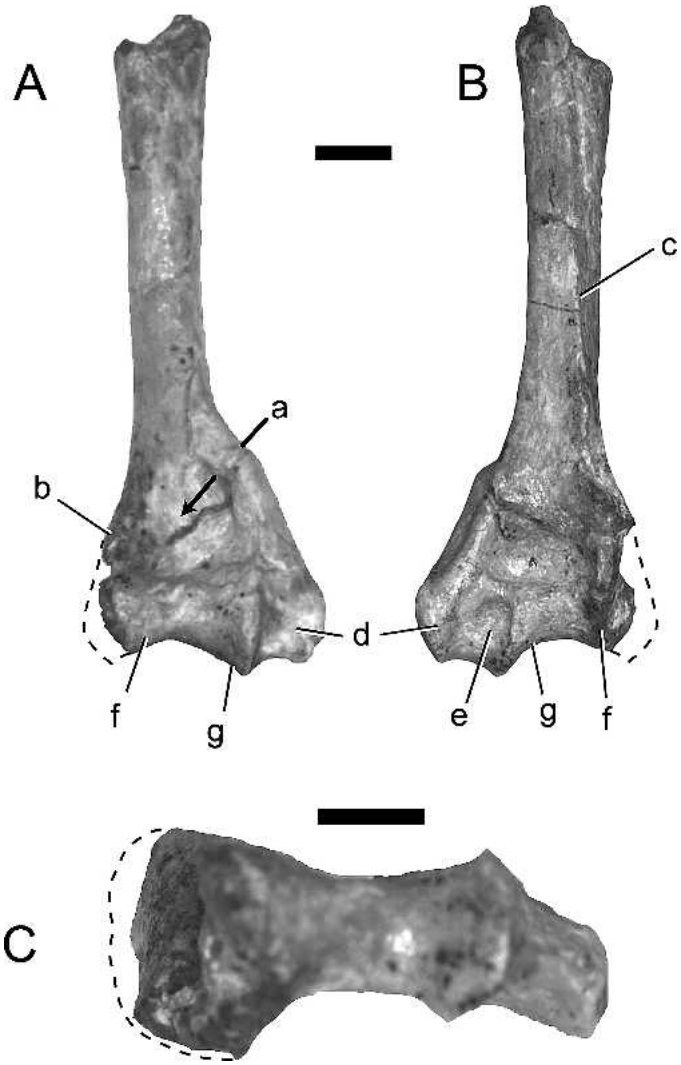

FIGURE 2. Partial right distal humerus TNM 03100. **A**, ventral; **B**, dorsal; and **C**, distal views. **Abbreviations**: **a**, entepicondylar foramen; **b**, supinator crest; **c**, brachialis flange; **d**, medial epicondyle; **e**, dorsoepitrochlear fossa; **f**, capitulum; **g**, trochlea. Scale bars equal 1 mm.

border of the olecranon fossa, slightly distorting the orientation of the distal articular surfaces relative to the humeral shaft, but these do not appear related to perforations of the radial and coronoid fossae. The medial epicondyle is prominent and perfectly preserved. It is directed posteriorly at an angle of approximately 20º, and exhibits a deep epitrochlear fossa on its dorsal surface that measures 0.98 mm across. The distolateral aspect of the specimen is abraded to the level of the entepicondylar foramen, disrupting the lateral half of the capitulum, lateral epicondyle, and lateral edge of the supinator crest. The articular surface preserves a complete trochlea and the medial portion of the capitulum. The medial edge of the trochlea is confluent with the bony strut defining the medial wall of the entepicondylar foramen. The trochlea flares distally, displaying a fairly prominent medial lip measuring 2.79 mm dorsoventrally and 2.46 mm proximodistally. The trochlea is conical in shape, narrowing to 1.77 mm dorsoventrally and 1.65 mm proximodistally at midtrochlea. The trochlea is largely continuous with the capitulum, separated on the ventral articular surface by only a faint ridge. In dorsal view, the trochlea is concave between its medial lip and the lateral aspect of the dorsoepitrochlear fossa.

Diagnostic Morphology—The distal humeral morphology of TNM 03100 is distinct from described African non-primate mammals of similar size and age. For example, the specimen preserves a prominent entepicondylar foramen for the transmission of the median nerve and brachial artery, a feature not observed in hystricognath rodents (Lavocat, 1973:pl. 21.7; Schneider, 1984). Moreover, TNM 03100 differs from macroscelideans in preserving a more oblique orientation of the entepicondylar foramen, in addition to possessing an unperforated olecranon fossa and a dorsoepitrochlear fossa for the insertion of the ulnar collateral ligament. The element is distinct from most carnivorans in its diminutive size alone as well as in bearing a more proximally placed entepicondylar foramen and prominent posteriorly-directed projection of the medial epicondyle (Conroy, 1976; Rose, 1987). It differs from tenrecoideans in possessing a deep dorsoepitrochlear fossa and a more proximally placed entepicondylar foramen. Finally, the relative distance between the lateral border of the trochlea and the medial margin of the capitulum in TNM 03100 is shorter than in metatherian taxa (e.g., Szalay and Dagosto, 1980).

In contrast, TNM 03100 does share a suite of features with early anthropoid taxa described from the late Eocene and early Oligocene Jebel el Qatrani Formation of Egypt (see, e.g., Conroy, 1976; Fleagle and Simons, 1982a, 1982b; Gebo, et al. 1994; Fleagle and Simons, 1995; Seiffert et al., 2000). For example, the well-developed entepicondylar foramen of TNM 03100 is similar in shape and position to that exhibited in many anthropoids. This structure is present in most prosimians, platyrrhines, and some primitive catarrhines, but absent in all extant catarrhines. The medial wall of the entepicondylar foramen is confluent with the medial lip of the trochlea, a condition observed in *Proteopithecus* and parapithecids but not propliopithecines or oligopithicines/cids (Seiffert et al., 2000), and the foramen lies in a relatively more proximal position on the humeral shaft than in lorisids (e.g., Szalay and Dagosto, 1980). The medial lip is also less obliquely oriented, similar to the condition observed in *Qatrania* and *Proteopithecus* (Seiffert et al., 2000:fig. 1). The specimen differs from adapiforms and resembles anthropoids in preserving a posteriorly-angled medial epicondyle (Ciochon and Gunnell, 2002). TNM 03100 preserves a prominent dorsoepitrochlear fossa, similar to many Fayum anthropoids, omomyids, and platyrrhines, but rarely exhibited in strepsirhines and catarrhines (Conroy, 1976; Fleagle and Simons, 1982a; Ciochon and Gunnell, 2002). As in other early anthropoids, the morphology of the olecranon region is similar to that of extant platyrrhines, shallower than in many catarrhines but deeper than in most strepsirhines and omomyids (Conroy, 1976; Rose, 1988; Fleagle and Simons, 1995). Taken together, these features of TNM 03100 are shared with parapithecids, *Proteopithecus*, and extant platyrrhines. Parapithecids are generally considered stem anthropoids that are basal to the platyrrhine/catarrhine divergence (e.g., Simons and Kay, 1988; Miller and Simons, 1997; Simons, 1997). *Proteopithecus* represents a generalized taxon with oligopithecine-like molar cusp morphology, yet the retention of para-

pithecid-like dental formula and postcranial attributes results in its placement as a more basal anthropoid, lacking features that definitively exclude it from platyrrhine ancestry (Simons and Rasmussen, 1995; Miller and Simons, 1997; Simons, 1997; Seiffert et al., 2004).

DISCUSSION

Functionally, many features of TNM 03100 suggest that it belonged to a small, arboreal quadrupedal primate. The shallow, distal articular surface, combined with a broad olecranon fossa are both indicative of elbow extension greater than that observed in most leaping primates, yet less than that seen in terrestrial forms (Fleagle and Simons, 1995). In this regard, TNM 03100 is most similar to extant platyrrhines and Fayum anthropoids. Slight perforations in the radial and coronoid fossae indicate an elbow adapted for habitual flexion, compatible with arboreal quadrupedal locomotion (Fleagle and Simons, 1995). This is underscored by the relatively deep radial fossa and proximal capitular articular surface preserved on the specimen. The size and angulation of the medial epicondyle in TNM 03100 is also indicative of arboreal quadrupedalism—intermediate in form between the larger, medially directed condition observed in suspensory and clinging species and the smaller, posteriorly directed condition observed in terrestrial quadrupeds (Fleagle and Simons, 1982b; Fleagle and Simons, 1995). Certain aspects of trochlear surface morphology of TNM 03100, including the prominent medial lip act to enhance elbow stability during pronation and are important for arboreal quadrupedalism (Conroy, 1976; Fleagle and Simons, 1982a; Fleagle and Simons, 1995). A deep dorsoepitrochlear fossa, the attachment area for the ulnar collateral ligament, also implies an enhanced degree of joint stabilization consistent with a habitually flexed forelimb posture (Conroy, 1976).

This combination of functionally important features is also observed in the smallest anthropoid humeri described from the late Eocene and early Oligocene of Egypt, including the tamarin-sized *Proteopithecus sylviae* (DPC-18256 and DPC-20191; Seiffert et al., 2000:fig. 1) and the small-bodied parapithecid *Qatrania fleaglei* (DPC-1311; Fleagle and Simons, 1995:figs. 1h, 2h). TNM 03100 is, however, distinct from these taxa in preserving a more prominent medial lip of the trochlea and an anteroposteriorly expanded medial aspect of the capitulum, perhaps reflecting scaling considerations in a taxon only 60—80% the size of these other primates. Based on body mass estimates derived from dental specimens, several Paleogene early anthropoid taxa are reported in the size range represented by TNM 03100, including *Biretia, Arsinoea, Tabelia, Algeripithecus, Abuqatrania*, and *Qatrania wingi* (Fleagle, 1999). To date, however, no humeri from these taxa have been described. As such, a more precise taxonomic assignment for TNM 03100 awaits the discovery of additional specimens.

CONCLUSIONS

We announce the discovery of a diminutive anthropoid primate distal humerus from the Paleogene Red Sandstone Group of the Rukwa Rift Basin, southwestern Tanzania. The specimen represents a small arboreal quadruped, sharing a number of features with basal anthropoid taxa from the Paleogene Jebel el Qatrani Formation of Egypt, and is the first postcranial specimen of a fossil primate recovered from the Paleogene of sub-Saharan Africa. Given the paucity of sites of this age in subequatorial Africa, the vertebrate fauna emerging from the Paleogene terrestrial deposits of the Rukwa Rift Basin provide an interesting window into the evolutionary history of primates and other African vertebrate taxa.

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LITERATURE CITED

Ciochon, R. L., and G. F. Gunnell. 2002. Eocene primates from Myanmar: historical perspectives on the origin of Anthropoidea. Evolutionary Anthropology 11:156–168.

Conroy, G. C. 1976. Primate postcranial remains from the Oligocene of Egypt. Contributions to Primatology 8:1–134.

Damblon, F., P. Gerrienne, H. D'Outrelepont, D. Delvaux, H. Beeckman, and S. Back. 1998. Identification of a fossil wood specimen in the Red Sandstone Group of southwestern Tanzania: stratigraphic and tectonic implications. Journal of African Earth Science 26 (3): 387–396.

Ducrocq, S. 2001. Palaeogene anthropoid primates from Africa and Asia: new phylogenetical evidences. Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la Terre et des Planètes 332:351–356.

Ebinger, C., A. Deino, R. Drake, and A. Tesha. 1989. Chronology of volcanism and rift basin propagation: Rungwe Volcanic Province, East Africa. Journal of Geophysical Research 94:15785–15803.

Fleagle, J. G. 1999. Primate Adaptation and Evolution. Second Edition. Academic Press, London, 608 pp.

Fleagle, J. G., and E. L. Simons. 1978. *Micropithecus clarki*, a small ape from Miocene of Uganda. American Journal of Physical Anthropology 49:427–440.

Fleagle, J. G., and E. L. Simons. 1982a. The humerus of *Aegyptopithecus zeuxis*: a primitive anthropoid. American Journal of Physical Anthropology 59:175–193.

Fleagle, J. G., and E. L. Simons. 1982b. Skeletal remains of *Propliopithecus chirobates* from the Egyptian Oligocene. Folia Primatologica 39:161–177.

Fleagle, J. G., and E. L. Simons. 1995. Limb skeleton and locomotor adaptations of *Apidium phiomense*, an Oligocene anthropoid from Egypt. American Journal of Physical Anthropology 97:235–289.

Gebo, D. L., E. L. Simons, D. T. Rasmussen, and M. Dagosto. 1994. Eocene anthropoid postcrania from the Fayum, Egypt; pp. 203–233 in J. G. Fleagle and R. F. Kay (eds.), Anthropoid Origins. Plenum Press, New York.

Godinot, M. 1994. Early North African primates and their significance for the origin of Simiformes (= Anthropoidea); pp. 235–296 in J. G. Fleagle and R. F. Kay (eds.), Anthropoid Origins. Plenum Press, New York.

Godinot, M., and M. Mahboubi. 1992. Earliest simian primate found in Algeria. Nature 357: 324–326.

Gunnell, G. F., and E. R. Miller. 2001. Origin of Anthropoidea: dental evidence and recognition of early anthropoids in the fossil record, with comments on the Asian anthropoid radiation. American Journal of Physical Anthropology 114:177–191.

Gunnell, G. F., B. F. Jacobs, P. S. Herendeen, J. J. Head, E. Kowalski, C. Msuya, F. A. Mizambwa, T. Harrison, J. Habersetzer, and G. Storch. 2002. The earliest placental mammal from sub-Saharan Africa: Eocene microbat from Tanzania—evidence for early evolution of sophisticated echolocation. Paleontologica Electronica 5(3):1–10.

Harrison, T. (editor) 1997. Neogene Paleontology of the Manonga Valley, Tanzania: a Window into East African Evolutionary History. Plenum Press, New York, 418 pp.

Harrison, T., C. P. Msuya, A. M. Murray, B. F. Jacobs, A. M. Baez, R. Mundil, and K. R. Ludwig. 2001. Paleontological investigations at the Eocene locality of Mahenge in north-central Tanzania, East Africa; pp. 39–74 in G. F. Gunnell (ed.), Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats (ed.). Kluwer Academic/Plenum, New York.

Hartenberger, J.-L., and B. Marandat. 1992. A new genus and species of an early Eocene primate from North Africa. Human Evolution 7: 7–16.

Heesy, C. P., N. J. Stevens, and K. E. Samonds. in press. Biogeographic origins of primate higher taxa; in J. G. Fleagle and S. Lehman (eds.), Primate Biogeography. Kluwer, New York.

Holroyd, P. A. 1994. An examination of dispersal origins for Fayum Mammalia. Ph.D. dissertation, Duke University, Durham, North Carolina, 328 pp.

Kappelman, J., D. T. Rasmussen, W. J. Sanders, M. Feseha, T. Bown, P. Copeland, J. Crabaugh, J. Fleagle, M. Glantz, A. Gordon, B. Jacobs, M. Maga, K. Muldoon, A. Pan, L. Pyne, B. Richmond, T. Ryan, E.

Seiffert, S. Sen, L. Todd, M. Wiemann, and A. Winkler. 2003. Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia. Nature 426:549–552.

Kingston, J. D., B. F. Jacobs, A. Hill, and A. L. Deino. 2002. Stratigraphy, age and environments of the late Miocene Mpesida Beds, Tugen Hills, Kenya. Journal of Human Evolution 42:95–116.

Lavocat, R. 1973. Les rongeurs du Miocène d'Afrique Orientale. I. Miocène inférieur. Mémoires et Travaux Ecole Pratique des Hautes Etudes, Institut Montpellier 1:1–284.

Leakey, M. G., C. S. Feibel, I. McDougall, and A. Walker. 1995a. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. Nature 376:565–571.

Leakey M. G., P. S. Ungar, and A. Walker. 1995b. A new genus of large primate from the late Oligocene of Lothidok, Turkana District, Kenya. Journal of Human Evolution 28:519–531.

MacLatchy, L. M., and D. P. Pilbeam. 1999. Renewed Research in the Ugandan Early Miocene; pp. 15–25 in P. Andrews & P. Banham (eds.), Late Cenozoic Environments and Hominid Evolution: a Tribute to Bill Bishop. The Royal Geological Society, London.

Miller, E. R., and E. L. Simons. 1997. Dentition of *Proteopithecus sylviae*, an archaic anthropoid from the Fayum, Egypt. Proceedings of the National Academy of Science, USA 94:13760–13764.

Morley, C. K., S. M. Cunningham, R. M. Harper, and W. A. Westcott. 1999. Geology and geophysics of the Rukwa Rift, East Africa. Tectonics 11:69–81.

Murray, A. M. 2000. Eocene cichlid fishes from Tanzania, East Africa. Journal of Vertebrate Paleontology 20:651–664.

O'Connor, P. M., M. D. Gottfried, E. M. Roberts, N. J. Stevens, F. Jackson, and E. Rasmussen. 2003. Closing the African Gap: a new Cretaceous vertebrate fauna from Tanzania. Journal of Vertebrate Paleontology 23(3, supplement):84A.

Osborn, H.F. 1908. New fossil mammals from the Fayum Oligocene, Egypt, Bulletin of the American Museum of Natural History 24: 265–272.

Roberts, E. M., P. M. O'Connor, M. D. Gottfried, N. J. Stevens, S. Kapilima, and S. Ngsala. 2004. Revised stratigraphy and age of the Red Sandstone Group in the Rukwa Rift Basin, Tanzania. Cretaceous Research 25:749–759.

Rose, K. D. 1987. Climbing adaptations in the early Eocene mammal *Chriacus* and the origin of Artiodactyla. Science 236:314–316.

Rose, M. D. 1988. Miocene hominoid postcranial morphology: monkey-like, apelike, neither, or both; pp. 405–417 in R. L. Ciochon and R. Corruccini (eds.), New Views of Ape and Human Evolution, Plenum Press, New York.

Schneider, E. E. 1984. Comparative and Functional Morphology of the Appendicular Skeleton in Oligocene Fayum Rodentia. M.S. thesis, Stony Brook University, Stony Brook, New York, 44 pp.

Seiffert, E. R., E. L. Simons, and J. G. Fleagle. 2000. Anthropoid humeri from the late Eocene of Egypt. Proceedings of the National Academy of Science, USA 97:10062–10067.

Seiffert, E. R., E. L. Simons, and C. V. M. Simons. 2004. Phylogenetic, biogeographic, and adaptive implications of new fossil evidence bearing on crown anthropoid origins and early stem catarrhine evolution; pp. 157–181 in C. Ross and R. F. Kay (eds.), Anthropoid Origins: New Visions. Plenum Press, New York.

Simons, E. L. 1995. Egyptian Oligocene primates: a review. Yearbook of Physical Anthropology 38:199–238.

Simons, E. L. 1997. Preliminary description of the cranium of *Proteopithecus sylviae*, an Egyptian late Eocene anthropoidean primate. Proceedings of the National Academy of Science, USA 94:14970–14975.

Simons, E. L., and R. F. Kay. 1983. *Qatrania*, New Basal Anthropoid Primate from the Fayum, Oligocene of Egypt. Nature 304:624–626.

Simons, E. L., and R. F. Kay. 1988. New material of *Qatrania* from Egypt with comments on the phylogenetic position of the Parapithecidae (Primates, Anthropoidea). American Journal of Primatology 15: 337–347.

Simons, E. L., and D. T. Rasmussen. 1995. A whole new world of ancestors: Eocene anthropoideans from Africa. Evolutionary Anthropology 3:128–139.

Simons, E. L., D. T. Rasmussen, T. M. Bown, and P. S. Chatrath. 1994. The Eocene origin of anthropoid primates: adaptation, evolution, and diversity; pp. 179–201 in J. G. Fleagle and R. F. Kay (eds.), Anthropoid Origins. Plenum Press, New York.

Simons, E. L., E. R. Seiffert, P. S. Chatrath, and Y. Attia. 2001. Earliest record of a parapithecid from the Jebel Qatrani Formation, Northern Egypt. Folia Primatologica 72:316–331.

Stevens, N. J., and C. P. Heesy. 2000. Biogeographic origins of primate higher taxa. Journal of Vertebrate Paleontology 20(3, supplement): 71A.

Stevens, N. J., M. D. Gottfried, P. M. O'Connor, E. M. Roberts, and S. D. Kapilima. 2004. A new Paleogene fauna from the East African Rift, southwestern Tanzania. Journal of Vertebrate Paleontology 24(3, supplement):118A.

Stevens, N. J., P. M. O'Connor, M. D. Gottfried, E. M. Roberts, and S. Ngasala. In press. *Metaphiomys* from the Paleogene of southwestern Tanzania. Journal of Paleontology.

Szalay, F. S., and M. Dagosto. 1980. Locomotor adaptations as reflected on the humerus of Paleogene primates. Folia Primatologica 34:1–45.

Thomas, H., S. Sen, J. Roger, and Z. Al-Sulaimani. 1991. The discovery of *Moeripithecus markgrafi* Schlosser (Propliopithecidae, Anthropoidea, Primates) in the Ashawq Formation (Early Oligocene of Dhofar Province, Sultanate of Oman). Journal of Human Evolution 20:33–49.

Tiercelin, J. J., J. Chorowicz, H. Bellon, J. P. Richert, J. T. Mwanabene, and F. Walgenwitz. 1988. East African Rift System: offset, age and tectonic significance of the Tanganyika-Rukwa-Malawi intracontinental transcurrent fault zone. Tectonophysics 148:241–252.

Van der Beek, P., E. Mbede, P. Andreisson, and D. Delvaux. 1998. Denudation history of the Malawi and Rukwa Rift flanks (East African Rift System) from fission track thermochronology; pp. 363–385 in D. Delvaux and M. A. Khan (eds.), Tectonics, Sedimentation and Volcanism in the East African Rift System. Journal of African Earth Science 26.

Wood, A. E. 1968. The African Oligocene Rodentia. Bulletin of the Peabody Museum of Natural History 28:23–105.

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