

KAHAWAMYS MBEYAENSIS (N. GEN., N. SP.) (RODENTIA: THRYONOMYOIDEA) FROM THE LATE OLIGOCENE RUKWA RIFT BASIN, TANZANIA

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Paleogene micromammal-bearing deposits from Afro-Arabia have until recently been largely restricted to a limited number of localities in Saharan Africa and Oman (e.g., Osborn, 1908; Wood, 1968; Jaeger et al., 1985; Fejfar, 1987; Thomas et al., 1989; Holroyd, 1994; Seiffert et al., 2008; but see also Gunnell et al., 2002). Research in the Rukwa Rift Basin of Tanzania has begun to reveal a diverse late Paleogene vertebrate fauna below the equator. This work has produced evidence of primate (Stevens et al., 2005), macroscelidean (Stevens et al., 2006a) and hyracoid mammals, and in particular, an interesting array of rodent taxa (Stevens et al., 2008). Teeth attributed to the phiomorph rodent *Metaphiomys* have been recorded in the study area (Stevens et al., 2006b), along with a number of smaller thryonomyoid rodent specimens, many of which are severely worn, hampering precise taxonomic assessment. The recent discovery of a fairly complete, modestly worn thryonomyoid mandible allows us to recognize the presence of a new taxon from the Rukwa Rift Basin deposits. This find is significant in that it represents the first novel Paleogene rodent genus and species described from East Africa, and documents a critically under-represented temporal gap in African faunal evolution (e.g., Seiffert, 2006).

Location

The specimen described herein was recovered from the locality TZ-01S in the Nsungwe Formation of the Red Sandstone Group of southwestern Tanzania, a continental rift-fill sequence in the southeastern portion of the Rukwa Rift Basin (Fig. 1). The TZ-01 site is located at approximately 8°56'S, 33°12'E (precise locality coordinates are on file at Ohio University). Previous workers have suggested various ages for the Red Sandstone Group, ranging from Jurassic to Miocene-Pliocene (e.g., Spence, 1954; Pentelkov, 1979; Wescott et al., 1991; Kilembe and Rosendahl, 1992; Damblon et al., 1998). Ongoing geologic investigations associated with this project include resolving the tectonic and stratigraphic history of the Rukwa Rift Basin (Roberts et al., 2004), indicating the Red Sandstone Group can be subdivided into two distinct stratigraphic units (Roberts et al., 2004), the Galula and Nsungwe formations. A Cretaceous fauna has been recovered from the Galula Formation (O'Connor et al., 2006). A Paleogene depositional age is inferred for the Nsungwe Formation, via radiometric dating of intercalated ash beds and detrital zircon geochronology (Roberts et al., 2007a), supporting biostratigraphic evidence for an Oligocene age for

the upper Nsungwe Formation (Stevens et al., 2005, 2006a, b). Specifically, an ash flow tuff positioned 7 m below the top of the sequence at TZ-01S has yielded a late Oligocene age of 24.95 Ma (Roberts et al., 2007a, b).

Specimens from the TZ-01S were hand-quarried from a 3-4 meter thick interval of richly fossiliferous, poorly sorted, muddy, medium-coarse grained massive sandstone beds that can be correlated to other localities in the field area. The TZ-01S site is located <10 m from the top of the 300+ m thick Nsungwe Formation, and is interbedded with a series of thin (0.1-2 m thick) claystones, siltstones, and tuffs, as well several small, moderately sorted, channelized sandstone bodies (~2 m thick x 25 m wide). Fossil bearing horizons are interpreted as sheet flood deposits associated with a small, flashy discharge river system draining into a local wetland or lake system. Faunal evidence includes a diverse association of such aquatic and semi-aquatic taxa as fish (Gottfried et al., in press), freshwater crustaceans (Feldmann et al., 2007), frogs (Simons et al., 2006), and mollusks. Facies associations along with the presence of aquatic fauna suggest a variable, semi-arid climate with perennial availability of water (Choh, 2007).

MATERIALS AND METHODS

Measurements were recorded using a Nikon SMZ 1500 stereomicroscope bundled with SPOT Advanced (version 3.5) software. The accuracy of measurements is on average +/- 0.01 mm. Reference specimens and casts were borrowed from collections at the American Museum of Natural History, Yale Peabody Museum, Carnegie Museum of Natural History, Duke University Vertebrate Collections, Namibian Geological Survey Museum, and Southern Methodist University, and included holotype and/or representative specimens of numerous taxa including *Phiomys* Osborn, 1908, *Metaphiomys* Osborn, 1908, *Diamantomys* Stromer, 1922, *Pomonomys* Stromer, 1922, *Lavocatomys* Holroyd and Stevens, in press, *Phiocricetomys* Wood, 1968, *Paraphiomys* Andrews, 1914, *Gaudeamus* Wood, 1968, *Paraulacodus* Hinton, 1933, *Myophiomys* Lavocat, 1973, *Epiphomys* Lavocat, 1973, *Simonimys* Lavocat, 1973, and *Elmerimys* Lavocat, 1973. Comparisons were supplemented with published photographs for less accessible taxa.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, USA; DUCP, Duke University Vertebrate Collections, Durham, North Carolina, USA; KNM, Kenyan National Museum, Nairobi, Kenya; NGS, Namibian Geological Survey Museum, Namibia; RRB, Rukwa Rift Basin Project, with permanent repository in National Museums of Tanzania; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

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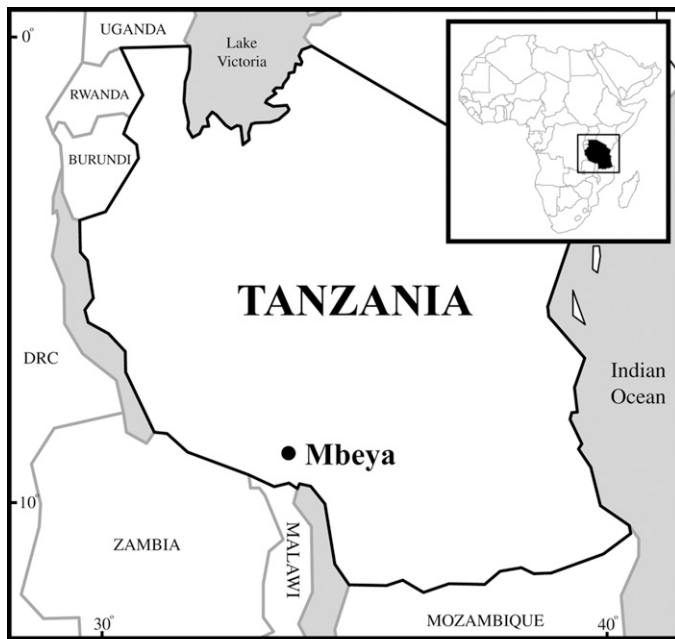


FIGURE 1. Map indicating locality for RRBP 07161. Field area 15 km southwest of the town of Mbeya.

SYSTEMATIC PALEONTOLOGY

RODENTIA Bowdich, 1821
HYSTRICOGNATHI Tullberg, 1899
THRYONOMYOIDEA Pocock, 1922
Family indet.

KAHAWAMYS MBEYAENSIS, new genus and species.

Fig. 2

Type and Only Specimen—RRBP 07161, right dentary preserving dp4-m2 (Fig. 2) and partial incisor alveolus.

Type Locality—TZ-01 South, late Oligocene Nsungwe Formation of Red Sandstone Group, Mbeya Region, southwestern Tanzania.

Etymology—Generic epithet incorporates both the Kiswahili word for the locally grown coffee (“kahawa”), and the Latin term for mouse (“mys”). Specific epithet refers to the Mbeya Region of Tanzania from which the type specimen was recovered.

Diagnosis—Differs from early Oligocene *Phiomys* species in having stronger cresting on the lower molar teeth, with a well developed postmetacristid that lingually closes the molar basin. Also differs from *P. andrewsi* in lacking the posterior arm of the protoconid/mesolophid. Differs from *P. paraphiomyoides* in having a less well-developed anterior cingulid. Differs from *Metaphiomys* in smaller size and in preserving no posterior arm of the protoconid/mesolophid.

Differs from early Miocene *Kenyamys* and *Simonimys* in absence of posterior arm of protoconid/mesolophid on molars, and in generally less pronounced cresting on dp4 and m1. Additionally differs from *Kenyamys* in larger size and in having a proportionally larger m2 relative to m1. Additionally differs from *Simonimys* in smaller size and in lacking pronounced anterior cingulid on molars. Differs from *Myophiomys* and *Elmerimys* in smaller size, in lacking a pronounced anterior cingulid, and in having a more anteriorly positioned molar protoconid. Also differs from *Myophiomys* in having less differentiated cusps on dp4 and m1. Differs from *Epiphomys*, *Lavocatomys*, *Diamantomys* and *Pomonomys* in smaller size and in preserving no evidence of a posterior arm of protoconid/mesolophid on the molars. Addi-

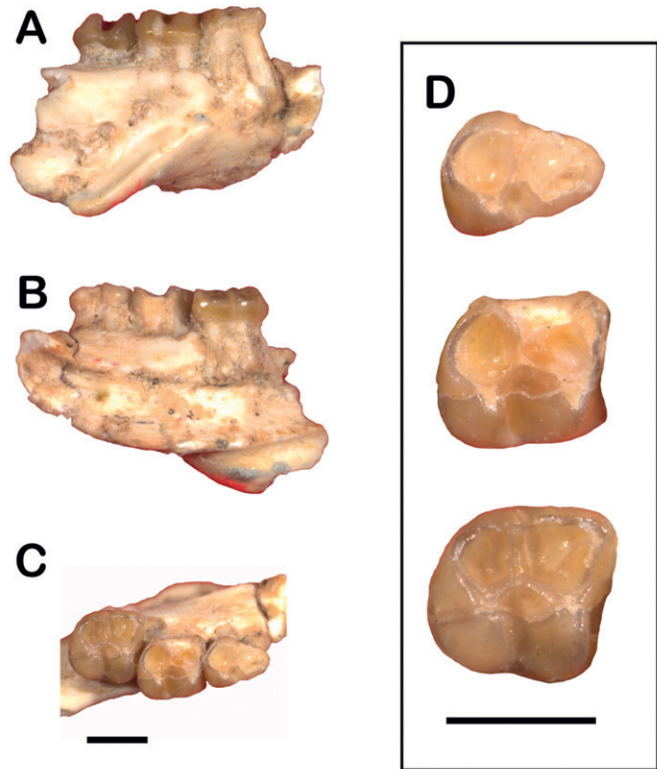


FIGURE 2. Type specimen of *Kahawamys mbeyaensis* (RRBP 07161), right dp4-m2. **A**, lingual view; **B**, buccal view; **C**, occlusal view; **D**, close-up occlusal views of (top to bottom) p4, m1 and m2. Scale bars equal 1 mm.

tionally differs from *Epiphomys* in possessing more anteriorly narrow dp4, and from *Lavocatomys*, *Diamantomys* and *Pomonomys* in having shallower basins, or markedly less pronounced cresting on the dp4 and molar teeth overall. Differs from *Ugandamys* in smaller size and in having a more anteriorly positioned dp4 metaconid.

Description—RRBP 07161 is a partial right mandible preserving a moderately worn dp4 and m1, each missing a portion of enamel from the lingual edge of its occlusal surface, and a complete and relatively unworn m2. Teeth are low crowned with cusps largely subsumed in crests. Taking breakage into account, the dp4 is wider posteriorly than anteriorly, with a length of 1.13 mm and a maximum width in the posterior half of the tooth of approximately 0.89 mm. The tooth also preserves a prominent anteroconid on dp4, with a fine crest extending posteriorly to connect with the protoconid, which is in turn positioned posteriorly relative to the metaconid. There is no evidence of a developing p4 in the dentary, and it is possible that, like many later thryonomyoids, *Kahawamys* did not replace dp4 with a permanent p4. However, given the limited wear on m2, more conclusive assessment of dp4 replacement is not possible at this time. The m1 is 1.15 mm in length and approximately 1.08 mm in width, and preserves a very faint anterolabial cuspule. There is no anterior cingulid or cuspule on m2. The m2 measures 1.25 mm in length and 1.23 mm in width, and exhibits a very faint bulge approximately halfway along the posterior aspects of both the metalophulid I and hypolophid. Molars preserve a straight metalophulid I angled posterobuccally due to the more anteriorly positioned metaconid relative to the protoconid. Both molars preserve a strong postmetacristid and basins are generally enclosed by high crests. No cresting is however visible in the position of the poste-

rior arm of the protoconid/mesolophid on m1 or m2. The ectolophid is positioned near the center of the tooth. The entoconid and hypolophid are located posterior to the midline of the tooth. The posterolophid is strongly curved without a noticeable thickening associated with a distinct hypoconulid.

The dentary is partially preserved and appears hystricognathous. The base of the angular process of the dentary is positioned lateral to the alveolus of the incisor; and has a groove for the passage of the pars reflexa of the superficial masseter muscle to its insertion on the medial surface of the angle.

Discussion—*Kahawamys* is here conservatively classified as a thryonomyoid, without assignment to family. Family-level taxa of African Paleogene and Neogene hystricognathous rodents are several in number, have not yet been diagnosed in reliably operational ways, and have been used in different senses and to comprise different sets of taxa by different authors (e.g., Wood, 1968; Lavocat, 1973; and discussion in Winkler et al., 2005).

CONCLUDING REMARKS

Rodent fossils from the late Oligocene interval on continental Africa are critical for linking the richly diverse early Paleogene faunas of Saharan Africa and Oman with the diverse and well-sampled Miocene faunas throughout Afro-Arabia and beyond (e.g., Stromer, 1926; Flynn et al., 1986; Winkler, 1992; Winkler et al., 2005). A comprehensive phylogenetic study of *Kahawamys* and other African thryonomyoids is beyond the scope of the present study and must await reassessment of the alpha taxonomy of a number of thryonomyoid species and genera (see e.g., Holroyd, 1994; López-Antoñanzas et al., 2004; Holroyd and Stevens, in press). *Kahawamys* possesses an interesting mix of features seen in both Paleogene and early Miocene taxa. In size and the relative proportions of its teeth, *Kahawamys* is generally similar to smaller Paleogene “phiomyids” described from northern Africa and the Arabian Peninsula. It is distinct from these older taxa in having better developed crests, and even from more crestiform early Oligocene taxa (e.g., *Metaphiomys* and *Gaudeamus*) in having crests that rim and more fully enclose the molar basins. In this feature it closely resembles early Miocene *Lavocatomys* and *Epiphomys*, although it is much smaller than either of those taxa (e.g., Lavocat, 1973; Holroyd and Stevens, in press).

The discovery of late Oligocene *Kahawamys mbeyaensis* in the Rukwa Rift Basin of Tanzania is of note in that it represents the first Paleogene rodent taxon known exclusively from East Africa. The Nsungwe Formation of the Red Sandstone Group has previously yielded fragmentary late Oligocene rodent material provisionally attributed to the taxon *Metaphiomys* (Stevens et al., 2006b), a genus also known from the early Oligocene of North Africa and the Arabian Peninsula, along with a small anthropoid humerus that is similar in size and morphology to some of the smallest anthropoids from the early Oligocene of Egypt (Stevens et al., 2005). These initial finds suggested a fauna quite similar to that of the early Oligocene of North Africa and the Arabian Peninsula. Yet *Kahawamys* hints at a greater distinctiveness for the Rukwa mammalian fauna from older Paleogene taxa, and its morphological similarities to small-bodied rodents from the early Miocene of Kenya suggests the possibility of faunal continuity with younger faunas in East Africa. This hypothesis is also supported by the recovery of macroscelideans that help bridge the morphologic gap between earlier Paleogene and younger Neogene taxa (Stevens et al., 2006a) and can be tested as more of the fauna becomes sufficiently known to permit detailed comparisons.

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LITERATURE CITED

- Andrews, C. W. 1914. On the Lower Miocene vertebrates from British East Africa, collected by Dr. Felix Oswald. Geological Society of London Quarterly Journal 70:163–186.
- Bowdich, T. E. 1821. An analysis of the Natural Classifications of Mammalia for the Use of Students and Travellers. J. Smith, Paris, 115 pp.
- Choh, A. M. 2007. Palaeoenvironment and Paleoclimate of the Red Sandstone Group in the Rukwa Rift Basin, Tanzania. Unpublished Honours Thesis, University of the Witwatersrand, Johannesburg: 66 pp.
- 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 Sciences 26:387–396.
- Gottfried, M. D., P. M. O’Connor, E. M. Roberts, N. J. Stevens, and R. Chami. In press. A Cretaceous record of *Neoceratodus* (Dipnoi, Ceratodontidae) from the Rukwa Rift Basin, Tanzania. Acta Zoologica.
- Fejfar, O. 1987. Oligocene rodents from Zallah Oasis, Libya. Münchner Geowissenschaftliche Abhandlungen Reihe A: Geologie und Paläontologie 10:265–268.
- Feldmann, R. M., P. M. O’Connor, N. J. Stevens, M. D. Gottfried, E. M. Roberts, S. Ngasala, E. L. Rasmussen, and S. Kapilima. 2007. A new freshwater crab (Decapoda: Brachyura: Potamonautidae) from the Paleogene of Tanzania, Africa. Neues Jahrbuch für Geologie und Paläontologie 8:71–78.
- Flynn, L. J., L. L. Jacobs, and I. U. Cheema. 1986. Baluchimyinae, a new tenodactylid rodent subfamily from the Miocene of Baluchistan. American Museum Novitates, 2841:1–58.
- Gunnell, G. G., B. F. Jacobs, P. S. Herendeen, J. J. Head, E. K., C. P. Msuya, F. A. Mizambwa, T. Harrison, J. Habersetzer, and G. Storch. 2002. Oldest placental mammal from sub-Saharan Africa: Eocene microbat from Tanzania—Evidence for sophisticated echolocation. Palaeontologia Electronica. 5:1–10. http://palaeo-electronica.org/2002_2/africa/issue2_02.htm
- Hinton, M. A. C. 1933. Diagnoses of new genera and species of rodents from Indian Tertiary deposits. Annual Magazine of Natural History, Series 10, 12:620–622.
- Holroyd, P. A. 1994. An Examination of Dispersal Origins for Fayum Mammalia. Ph.D. dissertation, Duke University, Durham, North Carolina, University Microforms 9510984, 328 pp.
- Holroyd, P. A., and N. J. Stevens. In Press. Differentiation of *Phiomys andrewsi* from *Lavocatomys aequatorialis* (n. gen., n. sp.) (Rodentia: Thryonomyoidea) in the Oligo-Miocene interval on continental Africa. Journal of Vertebrate Paleontology.
- Jaeger, J. -J., C. Denys, and B. Coiffat. 1985. New Phiomorpha and Anomaluridae from the late Eocene of North-West Africa: Phylogenetic implications. In: W. P. Luckett and J. -L. Hartenberger (eds.), Evolutionary Relationships Among Rodents: A Multidisciplinary analysis. Plenum Press, New York. pp. 567–588.
- Kilembe, E. A., and B. R. Rosendahl. 1992. Structure and stratigraphy of the Rukwa rift. Tectonophysics 209:143–158.
- Lavocat, R. 1973. Les Rongeurs du Miocène d’Afrique Orientale. I. Miocène inférieur. Mémoires et Travaux de l’Institut de Montpellier de l’Ecole Pratique des Hautes Etudes 1:1–284.
- López-Antoñanzas, R., S. Sen, and P. Mein. 2004. Systematics and phylogeny of the cane rats (Rodentia: Thyronomyidae). Zoological Journal of the Linnean Society 142:423–444.
- O’Connor, P. M., M. D. Gottfried, N. J. Stevens, E. M. Roberts, and S. Kapilima. 2006. A Cretaceous fauna from Southwestern Tanzania. Journal of African Earth Sciences 44:277–288.

- Osborn, H. F. 1908. New fossil mammals from the Fayum Oligocene, Egypt. *Bulletin of the American Museum of Natural History* 24:265–272.
- Pentelkov, V. G. 1979. New data on age and correlation of Mesozoic rocks of the Rukwa trough, southwestern Tanzania. *Doklady Akademii Nauk USSR* 245:113–116.
- Pocock, R. I. 1922. On the external characters of some hystricomorph rodents. *Proceedings of the Zoological Society, London* 1922: 365–427.
- Roberts, E. M., P. M. O'Connor, M. D. Gottfried, N. J. Stevens, S. Kapilima, and S. Ngasala. 2004. Revised stratigraphy and age of the Red Sandstone Group in the Rukwa Rift Basin, Tanzania. *Cretaceous Research* 25:749–759.
- Roberts, E. M., P. M. O'Connor, R. A. Armstrong, N. J. Stevens, and M. D. Gottfried. 2007a. U-Pb geochronology of detrital zircons from the Rukwa Rift Basin, Tanzania: New data on the pre-Neogene tectonic and sedimentary evolution of the Western Branch of the East African Rift System: *Geological Society of America, Abstracts with Programs*:39.
- Roberts, E. M., P. M. O'Connor, T. Hieronymus, M. D. Gottfried, and N. J. Stevens. 2007b. Taphonomy of two Cretaceous dinosaur quarries, Tanzania, Africa: New insights into regional paleoclimate, paleoenvironments, and paleogeography: *Journal of Vertebrate Paleontology* 27(suppl.):135–136A.
- Seiffert, E. R. 2006. Revised age estimates for the later Paleogene mammal faunas of Egypt and Oman. *Proceedings of the National Academy of Sciences of the United States of America* 103:5000–5005.
- Seiffert, E. R., T. M. Bown, W. C. Clyde, and E. Simons. 2008. Geology, paleoenvironment, and age of Birket Qarun Locality 2 (BQ-2), Fayum Depression, Egypt. In: Elwyn Simons, *A Search for Origins, Developments in Primatology: Progress and Prospects*. pp. 71–86.
- Simons, V. F. H., J. A. Holman, M. D. Gottfried, and N. J. Stevens. 2006. Locomotor morphology and ecological implications of Paleogene African frogs. *Journal of Vertebrate Paleontology* 26(3 suppl.): 125A.
- Spence, J. 1954. The geology of the Galula coalfield, Mbeya District, Tanganyika. *Geological Survey Department B*, 25:34 pp.
- Stevens, N. J., P. M. O'Connor, M. D. Gottfried, E. M. Roberts, and S. Ngasala. 2005. An anthropoid primate humerus from the Rukwa Rift Basin, Paleogene of southwestern Tanzania. *Journal of Vertebrate Paleontology* 25(4):986–989.
- Stevens, N. J., S. Ngasala, M. D. Gottfried, P. M. O'Connor, and E. M. Roberts. 2006a. Macroscelideans from the Oligocene of southwestern Tanzania. *Journal of Vertebrate Paleontology* 26(3 suppl.): 128A.
- Stevens, N. J., P. M. O'Connor, M. D. Gottfried, E. M. Roberts, S. Ngasala, and M. Dawson. 2006b. *Metaphiomys* (Rodentia: Phiomidae) from the Paleogene of southwestern Tanzania. *Journal of Paleontology* 80:407–410.
- Stevens, N. J., M. D. Gottfried, E. M. Roberts, S. Ngasala, S. Kapilima, and P. M. O'Connor. 2008. Paleontological exploration in Africa: A view from the Rukwa Rift Basin of Tanzania. In: Elwyn Simons, *A Search for Origins, Developments in Primatology: Progress and Prospects*. pp. 159–180.
- Stromer, E. 1926. Reste Land- und Süßwasser-bewohnender Wirbeltiere a. d. Diamantenfeldern Deutsch-Südwestafrikas. in E. Kaiser, *Die Diamantenwüste Südwestafrikas II*, 107–153 pp. Berlin.
- Thomas, H., J. Roger, S. Sen, C. Bourdillon-de-Grissac, and Z. Al-Sulaimani. 1989. Decouverte de vertebres fossiles dans l'Oligocene inferieur du Dhofar (Sultanat d'Oman). *Geobios*, 22:101–120.
- Tullberg, T. 1899. Über das System der Nagethiere, eine phylogenetische Studie. *Nova Acta Regiae Societatis Scientiarum Uppsalensis* 3:1–514.
- Wescott, W. A., W. N. Krebs, D. W. Engelhardt, and S. W. Cunningham. 1991. New biostratigraphic age dates from the Lake Rukwa rift basin in western Tanzania. *American Association of Petroleum Geologists Bulletin* 75:1255–1263.
- Winkler, A. J. 1992. Systematics and biogeography of middle Miocene rodents from the Muruyur beds, Baringo district, Kenya. *Journal of Vertebrate Paleontology* 12:236–249.
- Winkler, A. J., L. MacLachy, and M. Mafabi. 2005. Small rodents and a lagomorph from the early Miocene Bukwa locality, eastern Uganda. *Palaeontologia Electronica* 8.1. 24A:1–12. http://palaeoelectronica.org/paleo/2005_1/winkler24/issue1_05.htm.
- Wood, A. E. 1968. Early Cenozoic mammalian faunas, Fayum Province, Egypt, Part II: the African Oligocene Rodentia. *Peabody Museum Bulletin* 28:23–105.

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