J. Paleont., 80(2), 2006, pp. 407–410

0022-3360/06/0080-407$03.00

METAPHIOMYS (RODENTIA: PHIOMYIDAE) FROM THE PALEOGENE OF SOUTHWESTERN TANZANIA

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INTRODUCTION

THE EVOLUTIONARY history of the living African rodent families is a topic of considerable debate, yet it is generally agreed that the modern cane rats (*Thryonomys* Fitzinger, 1867) and dassie rats (*Petromus* Smith, 1831) have an evolutionary history within the infraorder Phiomorpha (e.g., Wood, 1968). Phiomorphs possess hystricognathous mandibular morphology, multiserial incisor enamel, and hystricomorphous attachment of the masseteric musculature (e.g., Lavocat, 1978; Holroyd, 1994). In his initial work on the group, Wood (1968) placed all phiomorph taxa into a single family, and named a handful of morphologically diverse species based mainly on size. Lavocat (1978) later revised the taxonomy of the group, raising many of the differences among species to the family level. More recently, Holroyd (1994) observed that these contrasting views likely stemmed from the fact that Wood's phiomorph work emphasized the overall similarity of Paleogene specimens from the Fayum of Egypt, whereas Lavocat endeavored to explain the diverse Miocene rodent faunas from East Africa, envisioning that each of the Miocene forms had an ancestor among the Paleogene taxa. In this paper we adopt Holroyd's (1994) revised version of family-level relationships among the phiomorphs.

A variety of well-preserved specimens pertaining to phiomorph evolutionary history have been described from the Paleogene of northern Africa and Oman (Osborn, 1908; Wood, 1968; Jaeger et al., 1985; Fejfar, 1987; Holroyd, 1994) and Asia (e.g., Flynn et al., 1986; Jaeger, 1988; Marivaux et al., 2002; Marivaux and Welcomme, 2003). However, Paleogene terrestrial deposits in sub-Saharan Africa are extremely rare, hence this constitutes the earliest phiomorph record from East Africa. Here we announce a new microsite in the Mbeya Region of southwestern Tanzania, preserving *Metaphiomys* Osborn, 1908, a rodent taxon previously described exclusively from the early Oligocene of Egypt, Libya, and Oman (Wood, 1968; Fejfar, 1987; Thomas et al., 1989). Not only does this represent a significant geographic extension of the taxon, it also constitutes the first rodent material described from the Paleogene of East Africa.

Location.—The specimen described herein derives from a laterally extensive, richly fossiliferous, muddy sandstone unit (TZ-01) located in the Songwe Valley portion of the Rukwa Rift Basin, Mbeya Region, southwestern Tanzania (Fig. 1). TZ-01 is located at approximately 8°56′S, 33°12′E (precise locality coordinates are on file at Ohio University). These fossil-bearing strata pertain to Unit 2 of the Red Sandstone Group, a series of proximal fluvial and overbank deposits (Roberts et al., 2004). A range of isolated to articulated microvertebrate fossils have been recovered from this locality, primarily from a tabular, 2 m thick sandstone bed, interpreted as either channel lag or flood-stage fluvial deposits. The TZ-01 fauna is characterized by small (<4 cm) cranial and postcranial remains, including numerous jaws, teeth, and limb elements from a variety of vertebrate groups.

Although age estimates for red sandstones in the study area have ranged from the Jurassic to the late Cenozoic (e.g., Tiercelin, 1988; Ebinger et al., 1989; Morley et al., 1992; Damblon et al., 1998), recent work has refined the geological and paleontological context of deposits in the region, clearly documenting the presence of both Cretaceous and Paleogene sequences in the primary study area (O'Connor et al., 2003; Roberts et al., 2004; Stevens et al., 2004). These age assignments are 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 and 50 Ma, associated with an early Cenozoic tectonic event and subsequent sedimentation. The TZ-01 deposits are most likely associated with reactivation of preexisting basement structures and basin development during a Paleogene tectonic event. This age estimate is also supported by Tiercelin et al. (1988), who reported a middle Eocene to early Oligocene age for nepheline basalts capping sedimentary deposits in the southern part of the field area.

Abbreviations.—AMNH, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; TNM, National Museums of Tanzania, Dar es Salaam; YPM, Yale Peabody Museum, New Haven, Connecticut.

MATERIALS AND METHODS

The specimen (TNM 03111) was collected by standard hand-quarrying methods and mechanically prepared at the Stony Brook Vertebrate Preparation Facility. Length and width 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, the Carnegie Museum of Natural History, the Duke University Primate Center, and Southern Methodist University, and included holotypes and/or representatives of numerous genera including *Phiomys* Osborn, 1908, *Metaphiomys*, *Diamantomys* Stromer, 1922, *Phiocricetomys* Wood, 1968, *Paraphiomys* Andrews, 1914, *Gaudeamus* Wood, 1968, *Paraulacodus* Hinton, 1933, *Myophiomys* Lavocat, 1973, and *Elmerimys* Lavocat, 1973.

SYSTEMATIC PALEONTOLOGY

Suborder HYSTRICOGNATHI Tullberg, 1899
Infraorder PHIOMORPHA Lavocat, 1962
Family PHIOMYIDAE Wood, 1955
Genus METAPHIOMYS Osborn, 1908
METAPHIOMYS cf. M. BEADNELLI Osborn, 1908

Metaphiomys beadnelli OSBORN, 1908, fig. 5; WOOD, 1968, fig. 8.

Description.—TNM 03111 is fragmentary and moderately

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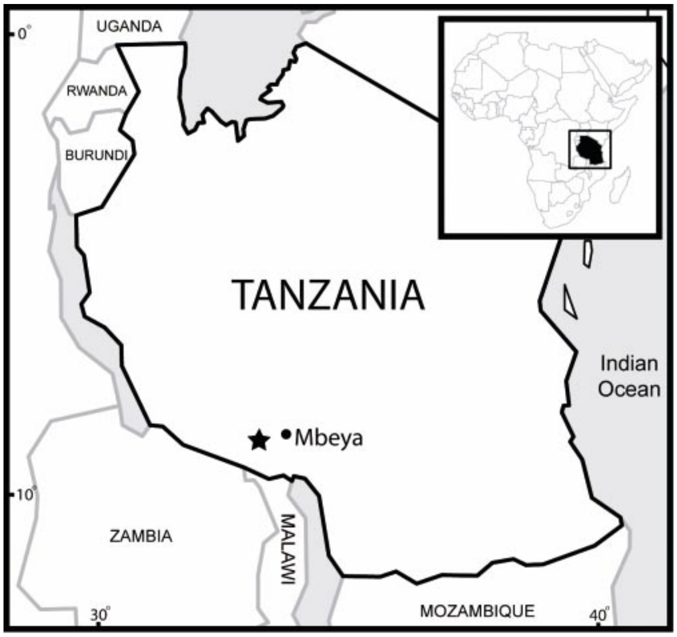

FIGURE *1*—Field site (TZ-01) location in the Rukwa Rift Basin, southwestern Tanzania, indicated by star.

worn, preserving the protoconid, metaconid, and part of the hypoconid (Fig. 2.1). The anterior cingulum is strong. The buccal aspects of both protoconid and hypoconid are sharp in outline, exhibiting relatively thin enamel (Fig. 2.2). The posterior arm of the protoconid arises anterior to the cusp along the metalophid, extending posterolingually before recurving anteriorly toward the metaconid. A weak protospur is present at the recurve. Although the occlusal surface is incomplete, approximate length ($\sim$3.0 mm) and width ($\sim$2.7 mm) measurements can be estimated for the crown.

Material examined.—Partial left lower molar, TNM 03111, from locality TZ- 01.

Discussion.—Although consisting of only a partial molar, this specimen is confidently referred to the genus *Metaphiomys* based on the combination of its size with characteristics including the presence of a prominent posterior arm of the protoconid with a posteriorly directed protospur (Wood, 1968). TNM 03111 is similar to the *M. beadnelli* hypodigm specimen YPM 18226 (Fig. 2.3), in that the posterior arm of the protoconid arises from the metalophid more anteriorly than in the holotype (AMNH 13273), or in any of the specimens referred to *Metaphiomys schaubi* Wood, 1968.

TNM 03111 is similar in size to specimens referred to *M. beadnelli*, and is approximately half the size of the morphologically similar *Diamantomys* (Table 1). TNM 03111 also differs from *Diamantomys* in having a wider angle between the buccal margins of the protoconid and hypoconid (see Lavocat, 1973). TNM 03111 differs from *Phiomys andrewsi* Osborn, 1908 in its larger size and by exhibiting less inflated buccal margins of the protoconid and hypoconid. Wood (1968) proposed that *Phiomys andrewsi* gave rise to *Metaphiomys schaubi*, which in turn gave rise to *Metaphiomys beadnelli*. Holroyd (1994) agreed that specimens attributed to *M. schaubi* and *M. beadnelli* represent points along a lineage increasing in size. However, with a larger sample she found no distinct characters to justify separate species designations, and synonymized the taxa into *M. beadnelli* (Holroyd, 1994). In both size and morphology, TNM 03111 most closely

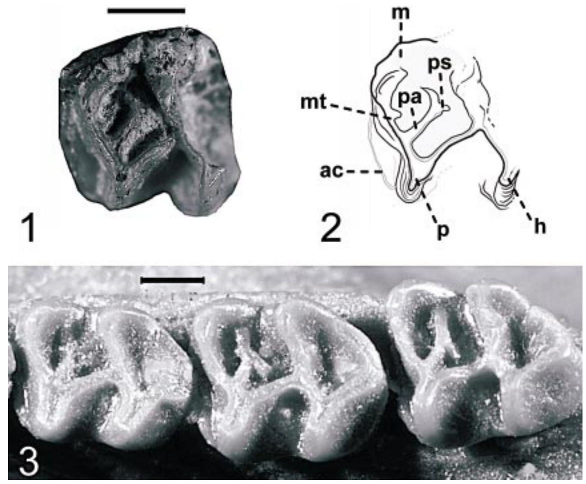

FIGURE *2*—*1,* Occlusal view of partial left lower molar (TNM 03111) from Tanzania, assigned to *Metaphiomys* cf. *M. beadnelli*. *2,* Line drawing of TNM 03111. Abbreviations: ac = anterior cingulum, h = hypoconid, m = metaconid, mt = metalophid, p = protoconid, pa = posterior arm of protoconid, ps = protospur. *3,* Left lower molars (m1-m3) of YPM 18226, hypodigm specimen of *M. beadnelli* from lower Oligocene Jebel el Qatrani formation, Egypt. Scales equal 1 mm.

resembles YPM 18226, an undisputed specimen of *M. beadnelli*. Hence we tentatively refer TNM 03111 to this species, pending recovery of additional and more complete specimens. TNM 03111 is thus the first East African record of the genus *Metaphiomys*.

CONCLUSIONS

Here we announce the discovery of a new Paleogene microsite in the Mbeya Region of southwestern Tanzania, preserving dental remains of a phiomorph rodent taxon (assigned here to *Metaphiomys* cf. *M. beadnelli*) best known from the early Oligocene Jebel el Qatrani Formation of Egypt. This find represents a significant geographic extension of the taxon. Moreover, given the scarcity of sites of this age in sub-Saharan Africa, richly fossiliferous Paleogene terrestrial deposits in the Mbeya Region may prove critical for understanding the evolutionary history of rodents and other vertebrate taxa.

ACKNOWLEDGMENTS

We would like to thank our Tanzanian colleagues, particularly S. Kapilima (University of Dar es Salaam), R. Chami (National Museums of Tanzania), and H. Gideon (COSTECH). Special thanks to T. Hieronymus, E. Rasmusson, V. Simons, and Y. Tulu for field assistance. G. Gunnell (University of Michigan) and T. Harrison (New York University) provided advice on logistical arrangements during the preliminary stages of this project. Thanks also go to D. Krause and the expert fossil preparation skills of V.

TABLE *1*—Length and width measurements of lower molars (in mm) for TNM 03111 and selected reference species (means taken from [a]Holroyd, 1994; [b]Lavocat, 1973).

	m1		m2		m3	
Taxa	Length	Width	Length	Width	Length	Width
TNM 03111			3	2.7		
Phiomys andrewsi[a]	1.44	1.22	1.6	1.41	1.68	1.42
Metaphiomys beadnelli[a]	2.61	2.08	2.87	2.55	2.98	2.53
Metaphiomys schaubi[a]	2.4	2.19	2.48	2.4	2.57	2.4
Diamantomys luederitzi[b]	4.5	3.7	4.5	4.5	5.8	4.2

Heisey (Stony Brook University Vertebrate Preparation facility). We appreciate access to the Fayum collections at the Duke University Primate Center Division of Fossil Primates (DUPC). We thank E. Simons and J. Fleagle for helpful discussions. For access to museum collections, we thank S. Bell and B. Burger (AMNH); S. McLaren, J. Wible, and C. Beard (CM); and P. Chatrath (DUPC). L. Jacobs, B. Jacobs, and A. Winkler (Southern Methodist University) also provided access to specimens in their care and helpful comments. This manuscript greatly benefited from reviews by P. Holroyd and A. Winkler. Finally, D. Pratt and J. Brown (Ohio University College of Osteopathic Medicine) assisted with figure preparation. Support for this research was provided by the following sources: National Geographic Society Committee for Research and Exploration, Office of the Vice-President for Research and Graduate Studies at Michigan State University, Ohio University Research Council, Ohio University College of Osteopathic Medicine, and LSB Leakey Foundation.

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ACCEPTED 17 FEBRUARY 2005