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Differentiation of *Phiomys andrewsi* from *Lavocatomys aequatorialis* (n. gen., n. sp.) (Rodentia: Thryonomyoidea) in the Oligo-Miocene Interval on Continental Africa

SHORT COMMUNICATION

DIFFERENTIATION OF *PHIOMYS ANDREWSI* FROM *LAVOCATOMYS AEQUATORIALIS* (N. GEN., N. SP.) (RODENTIA: THRYONOMYOIDEA) IN THE OLIGO-MIOCENE INTERVAL ON CONTINENTAL AFRICA

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Phiomys andrewsi Osborn, 1908 (Mammalia: Rodentia: Hystricognathi) was originally described from the early Oligocene of the Jebel Qatrani Formation, Fayum Province, Egypt, and based on the holotype specimen AMNH 13275. Subsequently, Schlosser (1910, 1911) and Wood (1968) ascribed additional specimens from the same area to Osborn's species, *P. andrewsi*. These later attributions comprise a morphologically diverse group, and Wood (1968) revised the species in such a way that it was envisioned as a highly variable species that could have given rise to all later African hystricognath rodents (e.g., Wood, 1974, 1985).

In his revision of East African Miocene rodents, Lavocat (1973) referred a number of dentaries and a skull from the early Miocene Kenyan localities of Rusinga, Songhor, and Koru to the species *Phiomys andrewsi*. He recognized the apparent variability of Wood's concept of *P. andrewsi* and discovered that he could find no way to distinguish between the East African specimens and *P. andrewsi* as illustrated by Wood (1968).

Lavocat (1973) noted that it is interesting to find in the Miocene such a primitive Oligocene form, and we further note how unusual it would be to find a small mammal species with such a long temporal range. The type locality of *Phiomys andrewsi* is Fayum Quarry B in the early Oligocene Jebel Qatrani Formation of Egypt, with an age of approximately 33.7 Ma based on Seiffert's (2006) magnetostratigraphic correlation. The Kenyan localities of Rusinga, Songhor, and Koru are all 20 Ma or younger (Drake et al., 1988), implying a more than 13 million year range for *P. andrewsi*. Recent studies have suggested that mean and/or median mammalian species duration is between 2.1 and 2.6 million years (Alroy, 2000; Vrba and DeGusta, 2004) and that duration may be related to patterns of orbital forcing of climate (van Dam et al., 2006); taxonomic decisions suggesting unusually long species durations merit closer attention. Species durations in excess of 13 million years are not unknown (Vrba and Degusta, 2004), but such long-lived species are certainly not the norm.

In order to determine whether *Phiomys andrewsi* is an unusually long-lived rodent species, we have made a series of metric and morphologic comparisons of the Egyptian and East African specimens attributed to this taxon. For the purposes of this comparison, we restrict ourselves to Osborn's holotype specimen to represent *Phiomys andrewsi* and draw contrasts solely with it, excluding both Schlosser's and Wood's referred specimens, which have been recognized as likely representing additional taxa (e.g., Holroyd, 1994; Winkler et al., 2005). Based on these comparisons, we conclude that the East African Miocene specimens are distinct at both the genus and species level.

Abbreviations—Teeth of the upper and lower dentitions are indicated by upper and lower case letters, respectively. Tooth nomenclature follows Figure 1. **AMNH**, American Museum of Natural History, New York, New York; **KNM**, Kenyan National Museum, Nairobi, Kenya; **KNM SO**, KNM specimens from Songhor; **KNM RU**, KNM specimens from Rusinga; **YPM**, Yale Peabody Museum, New Haven, Connecticut.

SYSTEMATIC PALEONTOLOGY

RODENTIA Bowdich, 1821
HYSTRICOGNATHI Tullberg, 1899
THRYONOMYOIDEA Pocock, 1922
LAVOCATOMYS AEQUATORIALIS, gen. et sp. nov.
Fig. 2B

Phiomys andrewsi Lavocat 1973
"*Phiomys andrewsi*" Winkler, MacLatchy, and Mafabe, 2005

Other illustrations—KNM RU 2100, Lavocat (1973:plate 28, fig. 4).

Type specimen—KNM SO 879, right dp4-m3 (Fig. 2B).

Type locality—Songhor, Kenya, early Miocene.

Other localities—Rusinga, Kenya, early Miocene.

Referred specimens—KNM RU 2100, right m1-m3; KNM SO 600, left m1 or m2; KNM SO 603, right p4-m3; KNM SO 862, left m2; KNM SO 865, left m1-m2; KNM SO 868, left m1-m2; KNM SO 872, right m2; KNM SO 881, left m2-m3.

Diagnosis—Differs from Oligocene *Phiomys andrewsi* (Fig. 2C) in larger size, in lacking evidence of replacement of dp4 by p4 and relatively larger dp4; relatively smaller m3 relative to m1, and posterior arm of the protoconid/mesolophid arising from the ectolophid rather than the protoconid, and posterior arm of the protoconid/mesolophid consistently longer. Differs from early Miocene *Kenyamys* in larger size and in having an incomplete mesolophid. Differs from early Miocene *Simonimys* in smaller size and in having a more anterolingually directed hypolophid and better developed postmetacristid. Differs from early Miocene *Elmerimys* and *Myophiomys* in having more poorly individualized cusps on lower dentition. Also differs from *Myophiomys* in having a relatively larger m3 and from *Elmerimys* in larger size. Differs from early Miocene *Epiphiomys* (Fig. 2A) in possessing a crest in the position of the anteroconid on dp4, sharper buccal cusp margins on the molar protoconids and hypoconids, accompanied by a longer ectolophid. Lower molars are also slightly broader for their length than in *Epiphiomys* and enamel appears approximately half as thick. Differs from early Miocene *Ugandamys* in larger size and in having a relatively wider dp4.

Etymology—generic epithet in honor of René Lavocat, in recognition of his contributions to the study of African rodent evolution; specific epithet in reference to the geographic proximity of the type locality to the equator.

Description—Like most hystricognaths, the anteriormost cheek tooth in *Lavocatomys* is a retained dp4 (noted as p4 in Lavocat, 1972). The metaconid and anteroconid form the anterior edge of the tooth and the protoconid lies immediately posterior and slightly labial to the anteroconid. These three cusps are joined by
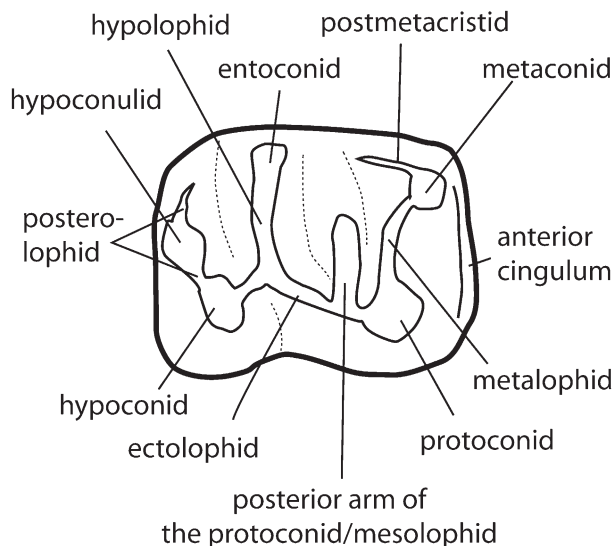
FIGURE 1. Schematic right lower molar illustrating dental nomenclature used here.

a low crest that is continuous with the ectolophid. A complete mesolophid arises off the ectolophid and extends to the lingual edge of the tooth. The posterior portion of the tooth is the widest part and is formed by a large fossetid that represents approximately 1/3 of the tooth's length and is bounded anteriorly by the hypolophid and posteriorly by the posterolophid.

On the lower molars, the metalophid is complete and exhibits a prominent anterior deviation in the course of this lophid immediately anterior to the protoconid. Directly anterior to the protoconid is a subtle anterolabial shelf or crest, most pronounced on m1. The hypolophid runs to the anterior portion of the entoconid which is canted anteriorly. There is also a distinct crest arising from the ectolophid that is in the position of the mesostylid and arises posterior to the protoconid. This configu-

ration is in contrast to the condition seen in many Oligocene hystricognaths in which the posterior arm of the protoconid arises from the protoconid itself. This crest is variable in length among specimens attributed here to *Lavocatomys*, stopping at or before the steep posterior margin of the metaconid and with wear often forming a fossetid that is bounded anteriorly by the metalophid. On m1 of the type specimen, a tiny protospur is visible on the posterior arm of the protoconid/mesostylid crest. The protospur is also variably present on m1 and m2 of other specimens attributed to *Lavocatomys*. Some specimens also have a small spur-like projection arising from the hypolophid and projecting posteriorly. The cheek teeth of *Lavocatomys* are longer than wide and decrease in length posteriorly along the tooth row.

Part of the dentary is preserved in the holotype. This portion of the specimen is not fully prepared, but the following aspects of morphology can be observed. The depth of the dentary beneath p4 and anterior to the angular process is 4.1 mm. Two small mental foramina are present, one positioned immediately anterior to the dp4 and approximately 1.7 mm below it, the second positioned below the posterior edge of dp4 and approximately 2.7 mm below it. The base of the angular process is present, arising beneath the dp4-m1 and diverging from the dentary lateral to the plane of the incisor as is typical of hystricognathous rodents. Incisor morphology cannot be observed.

Discussion—Statistical comparisons of the *Lavocatomys* sample values to the type of *Phiomys andrewsi* and other similarly-sized Miocene rodents (Table) was made using a Student's t-test for comparison of a single observation with the mean of a sample (see Sokal and Rohlf, 1981: Box 9.7). Even with the small sample size available, *Lavocatomys* was found to be significantly larger than *P. andrewsi* in m1 length and width ($p < 0.01$) and all values for *P. andrewsi* are less than the observed range for all other molars, resulting in the much shorter overall tooth row length observable in Figure 2. Notably, m2 is the longest lower molar in the type specimen of *P. andrewsi,* whereas m1 is the longest lower molar in all specimens referred to *Lavocatomys.* In comparison to the Miocene forms, *Elmerimys woodi* is significantly smaller in all measurements ($p < .05$), *Epiphiomys* is significantly smaller only in m1 width ($p < 0.05$), *Myophiomys*
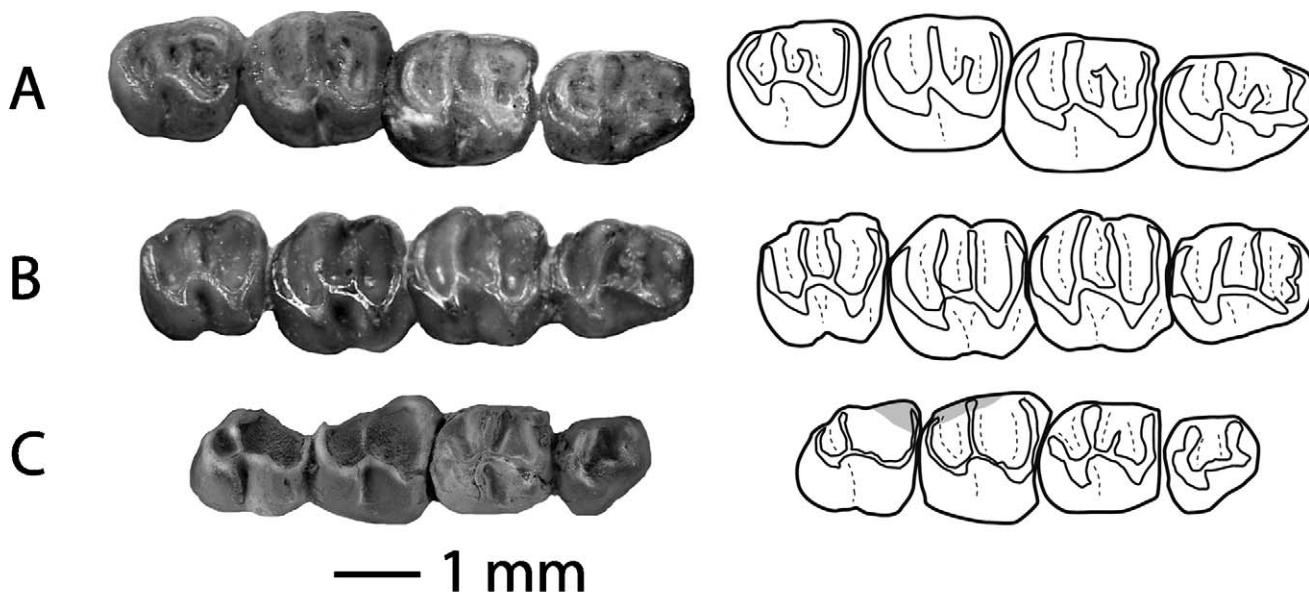

FIGURE 2. Comparison of early Miocene **A**, *Epiphiomys coryndoni* (KNM RU 2253), right dp4-m3, and **B**, *Lavocatomys aequatorialis* holotype (KNM SO 879), right dp4-m3, **C**, early Oligocene *Phiomys andrewsi* holotype (AMNH 13275), right p4-m3. Anterior is to the right.

TABLE. Dental measurements for early Miocene *Lavocatomys aequatorialis* hypodigm, early Oligocene *Phiomys andrewsi* holotype, and other selected early Miocene East African rodents

Specimen number	p4†/dp4 length	p4†/dp4 width	m1 length	m1 width	m2 length	m2 width	m3 length	m3 width
Phiomys andrewsi								
AMNH 13275*	1.21†	1.02†	1.4	1.24	1.46	1.41	1.43	1.27
Lavocatomys aequatorialis								
KNM RU 2100	na	na	1.69	1.53	1.68	1.63	1.52	1.45
KNM SO 600	na	na	na	na	1.73	1.73	na	na
KNM SO 603	1.69	1.32	1.65	1.5	1.52	1.5	1.51	1.35
KNM SO 862	na	na	na	na	1.5	1.45	na	na
KNM SO 865	na	na	1.7	1.56	1.69	1.64	na	na
KNM SO 868	1.68	1.37	1.65	1.53	1.59	1.55	na	na
KNM SO 872	na	na	1.68	1.5	na	na	na	na
KNM SO 879*	1.69	1.35	1.63	1.5	1.58	1.53	1.5	1.42
KNM SO 881	na	na	na	na	1.55	1.43	1.46	1.33
Means	1.69	1.35	1.67	1.52	1.61	1.56	1.50	1.39
Elmerimys woodi								
KNM RU 2309*	1.44	1.08	1.50	1.25	1.29	1.12	na	na
Epiphiomys coryndoni								
KNM RU 2253*	na	na	1.70	1.45	1.65	1.42	na	na
Myophiomys arambourgi								
KNM RU 2304*	1.64	1.38	1.57	1.47	1.51	1.41	1.36	1.33
Simonimys genovefae								
KNM SO 686*	1.90	1.33	1.90	1.55	1.92	1.73	na	na

Measurements were recorded using a National DC2-456H stereomicroscope bundled with Motic Images Plus (version 2.0) software.
Accuracy of measurements is on average +/− 0.01 mm.
*Denotes holotype specimen; † - p4 (all others are dp4); na-not available.

arambourgi is significantly longer in dp4 length and shorter in m1 and m3 length ($p < 0.05$), and *Simonomys genovefae* is significantly longer in dp4, m1, and m2 length ($p < 0.025$). Thus, *Lavocatomys* significantly differs in at least some tooth measures from *P. andrewsi* as well as from penecontemporaneous forms.

A number of other specimens have been attributed to *Phiomys andrewsi* from Kenyan localities including Songhor, Rusinga, Legetet, Mteitei Valley, and Chamtwara. Many of these are likely to be *Lavocatomys*. Lavocat (1973:plate 41, figs. 1-5) also figured and described a skull that he attributed to *Phiomys andrewsi*, KNM SO 884. Based on size and general morphology, this specimen could be either *Epiphiomys* or *Lavocatomys*, although it possesses enamel thickness more consistent with the thinner enamel that we see in the lower dentitions we attribute to *Lavocatomys*. At this time, we do not feel confident in assigning any of these upper dentitions to *Lavocatomys*.

Stromer (1926) also noted the presence of cf. *Phiomys andrewsi* from the early to middle Miocene of Namibia, a record that was repeated by Hopwood (1929). We have not had the opportunity to examine these specimens, but we suspect they may also be distinct from the early Oligocene taxon.

CONCLUDING REMARKS

Reexamination of early Miocene specimens previously attributed to *Phiomys andrewsi* clearly indicates that these are distinct from the Oligocene taxon, differing from it in both size and morphology. We recognize it as a new genus and species, *Lavocatomys aequatorialis*. In comparing *Lavocatomys* with taxa that occur at the same localities, it is most similar to *Epiphiomys*, from which it differs primarily in the length of the metalophids, shape of the lingual cusps, and also appears to differ in the thickness of the enamel. This difference is most noticeable along the buccal edge of the buccal cusps, where at most stages of wear *Epiphiomys* appears to have consistently thicker enamel. However, there is no way to measure enamel thickness with accuracy from the surface, due to the rounding of cusp edges during wear; only high resolution computerized tomography or destructive

analysis would allow this difference to be reliably quantified. The subtlety of the differences between *Epiphiomys* and *Lavocatomys* may indicate these are closely related taxa.

The affinities of *Lavocatomys* among other thryonomyoids are both beyond the scope of the present study and also problematic due to the fact that phylogenetic studies of thryonomyoids may have used a long-lived concept of *Phiomys andrewsi*. Many studies have used *Phiomys* to establish character polarities or root phylogenetic analyses (e.g., Winkler, 1992; Vucetich and Kramarz, 2003). Some authors have specified the Oligocene representatives of *Phiomys* (e.g., Marivaux et al. 2002, 2004) or have expressly indicated that some of the Miocene specimens we here refer to *Lavocatomys* are included in their scorings (e.g., López Antoñanzas et al., 2004). Removal of early Miocene specimens from *Phiomys andrewsi* provides a more restrictive set of character states for this taxon, a development that promises to refine future studies of thryonomyoid systematics.

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