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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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: Hystrixognathi) 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 hystriognath 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 AEGUATORIALIS, 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 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 hystriognaths, 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

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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 configuration 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*...
from the surface, due to the rounding of cusp edges during wear; ever, there is no way to measure enamel thickness with accuracy 

Epiphiomys appears to have consistently thicker enamel. How-

thickness of the enamel. This difference is most noticeable along 

shape of the lingual cusps, and also appears to differ in the 

occur at the same localities, it is most similar to 

Epiphiomys andrewsi from the early to middle Miocene of Namibia, a record 

1-5) also figured and described a skull that he attributed to 

these are likely to be 

Lavocatomys morphi. We recognize it as a new genus and species, 

from the Oligocene taxon, differing from it in both size and 

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. How-

ever, 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 Kra-

marz, 2003). Some authors have specified the Oligocene repre-

sentatives 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.

ACKNOWLEDGMENTS

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LITERATURE CITED


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

<table>
<thead>
<tr>
<th>Specimen number</th>
<th>p4/dp4</th>
<th>m1</th>
<th>m2</th>
<th>m3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phiomys andrewsi</td>
<td>AMNH 15275*</td>
<td>1.21†</td>
<td>1.02†</td>
<td>1.4</td>
</tr>
<tr>
<td>Epiphiomys aequatorialis</td>
<td>KNM RU 2100</td>
<td>na</td>
<td>na</td>
<td>1.69</td>
</tr>
<tr>
<td></td>
<td>KNM SO 600</td>
<td>na</td>
<td>na</td>
<td>1.32</td>
</tr>
<tr>
<td></td>
<td>KNM SO 603</td>
<td>na</td>
<td>na</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>KNM SO 862</td>
<td>na</td>
<td>na</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>KNM SO 865</td>
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<td>na</td>
<td>1.68</td>
</tr>
<tr>
<td></td>
<td>KNM SO 868</td>
<td>na</td>
<td>na</td>
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</tr>
<tr>
<td></td>
<td>KNM SO 870*</td>
<td>1.68</td>
<td>1.63</td>
<td>1.58</td>
</tr>
<tr>
<td></td>
<td>KNM SO 881</td>
<td>na</td>
<td>na</td>
<td>1.55</td>
</tr>
<tr>
<td>Means</td>
<td>1.69</td>
<td>1.35</td>
<td>1.67</td>
<td>1.52</td>
</tr>
<tr>
<td>Elmerimys woodi</td>
<td>KNM RU 2309*</td>
<td>1.44</td>
<td>1.08</td>
<td>1.50</td>
</tr>
<tr>
<td>Epiphiomys coryndoni</td>
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<td>Myophiomys arambourgi</td>
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<td>1.64</td>
<td>1.38</td>
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<td>KNM SO 686*</td>
<td>1.90</td>
<td>1.33</td>
<td>1.90</td>
</tr>
</tbody>
</table>

Measurments 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.


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