



SMALL RODENTS AND A LAGOMORPH FROM THE EARLY MIOCENE BUKWA LOCALITY, EASTERN UGANDA

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ABSTRACT

Recent screen washing at Bukwa, Uganda, has produced a deciduous lower premolar, a deciduous upper premolar, and three other upper cheek teeth of tiny thryonomyoid rodents and a single fragmentary ochotonid cheek tooth. Bukwa is early Miocene in age and has a provisional radiometric date of 22 Ma. The deciduous lower premolar, deciduous upper premolar, and two upper molars are assigned to a new taxon, *Ugandamys downsi*, gen. and sp. nov. The deciduous lower premolar is morphologically distinct from a phiomyid deciduous lower premolar previously recovered from Bukwa. The deciduous upper premolar and two upper molars are very small, elongate, and have strong mesoloph. The two molars have a distinct metaconule. One molar and the deciduous upper premolar have short but distinct metaloph. The remaining upper cheek tooth has four lophs (lacks a mesoloph) and is referred to the Family Thryonomyidae. It is incomplete and heavily abraded, and thus tentatively referred to *Paraphiomys* sp. The Bukwa ochotonid is an incomplete cheek tooth that cannot be assigned confidently to genus. It is significant in being one of only a few fossil lagomorphs recovered from Uganda.

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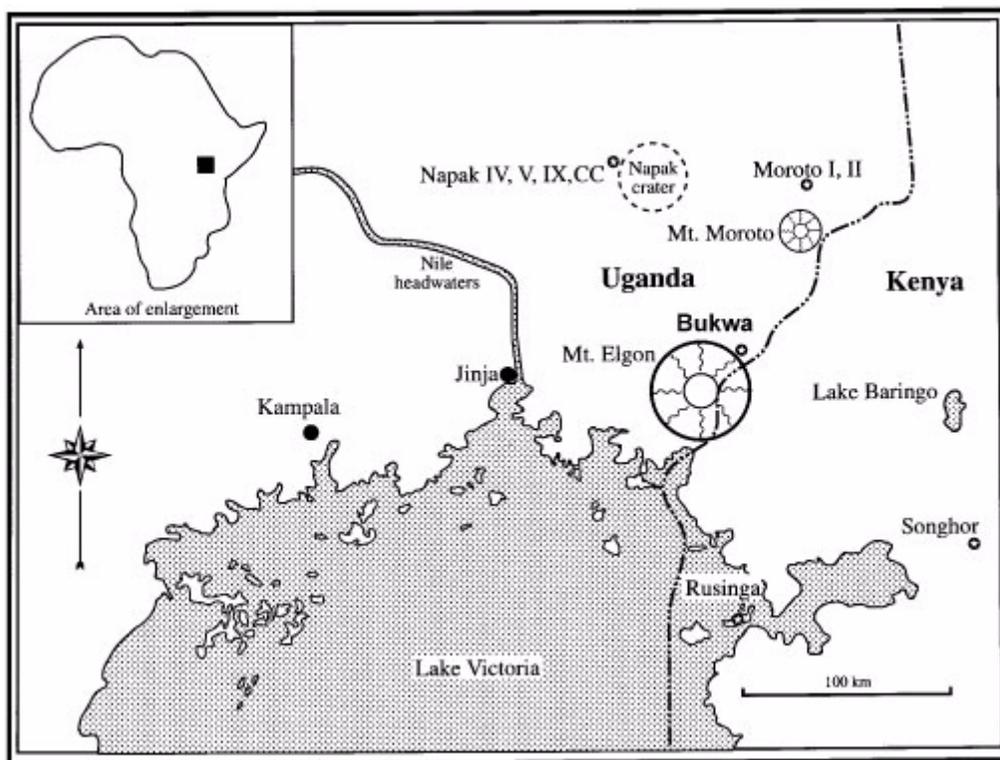


Figure 1. Map showing the location of the Bukwa locality in eastern Uganda.

INTRODUCTION

The Bukwa site is located 4.0 km east of the village of Bukwa, Kapchorwa District, eastern Uganda (34°47' East longitude, 1°17' North latitude) on the northeastern side of the extinct early Miocene alkaline volcano Mt. Elgon (Figure 1). Bukwa was first discovered in 1965 (Walker 1969). Excavations at Bukwa during the 1960s yielded an extensive mammalian fauna and paleobotanical remains, as well as invertebrates, fish, reptiles, and birds, that are dated at about 22 Ma (Walker 1969; redating of the site is in progress). The main faunal site is Bukwa II, which produced the lagomorph and rodents described here. Fossils from Bukwa II were recovered primarily from a green clay that likely represents lacustrine deposition (Walker 1969). The only rodents reported previously from Bukwa were *Megapedetes pentadactylus* (spring hare; Walker 1969), *Bathyergoides neotertiarius* (mole rat; Pickford 2002), and thryonomyoids (relatives of the modern cane rat), including *Paraphiomys pigotti*, *P. stromeri*, and some smaller unassigned taxa (Lavocat 1973).

Lavocat (1973, p. 158) briefly mentioned 12 teeth or fragments of teeth collected by Walker and associates from Bukwa in 1968. Lavocat assigned most of these specimens to either the thryonomyids *Paraphiomys pigotti* or *P. stromeri*. Four teeth

were considered similar to *P. stromeri*, but of smaller size and sometimes of slightly different morphology.

The specimens described here were collected in 2002 from Bukwa II by L. MacLatchy, W. Downs, R. Kityo (Makerere University, Uganda), and E. Mushiime (Uganda Museum). At Bukwa II, Will Downs collected two burlap bags of the green clay (Bukwa IIA) and two bags that included green clay plus overlying brown marl (Bukwa IIB). Will believed the bone was coming from the junction of the two units. In map view, Bukwa IIA and B are about 5 m apart. This sediment was dried in the field then washed through tandem screen boxes at Makerere University; the fine fraction was washed repeatedly in the United States. The coarse fraction was sorted in Uganda. Will Downs sorted the fine fraction under a dissecting microscope at the Museum of Northern Arizona University. In addition to rodents, Bukwa IIA also yielded an upper cheek tooth of *Myohyrax oswaldi* (Macroscelididae), a frog humerus, and fish teeth and vertebrae; Bukwa IIB produced rodents, a lagomorph, and fish vertebrae.

The Bukwa rodents and lagomorph described here are housed at the Uganda Museum, Kampala, under the acronym BUMP (Boston University/Uganda Museum/Makerere University Paleontol-

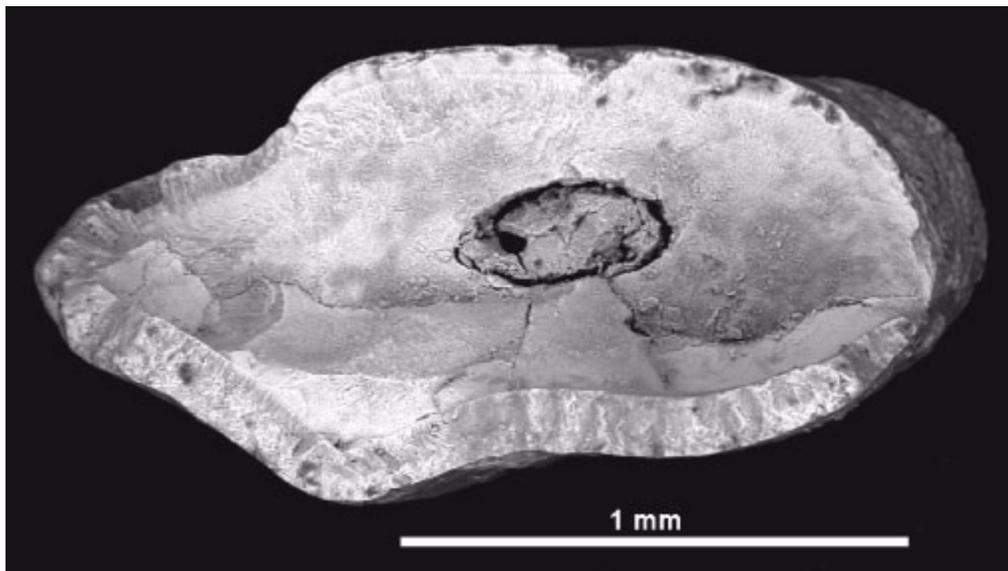


Figure 2. Ochotonidae, genus and species undetermined. Occlusal view of trigonid of left lower cheek tooth, BUMP 1021, from Bukwa IIB. Anterior is to the top of the figure.

ogy Expeditions). Other abbreviations: AMNH, American Museum of Natural History, New York; N, number of specimens; SO or KNM SO, Songhor locality, Kenya.

SYSTEMATIC PALEONTOLOGY

Order LAGOMORPHA
 Family Ochotonidae Thomas, 1897
 Genus and species undetermined
 Figure 2

Referred material. BUMP 1021, trigonid of left lower cheek tooth (either a p4, m1, or m2) from Bukwa IIB.

Description. The only specimen is fragmentary. It is wider than long: width is 1.80 mm and length is 0.92 mm. Most of the anterior border is convex anteriorly and there is a distinct antero-external fold, which is not filled with cement. The posterior border has a sharp posterior inflection (postprotoconid crista of Mein and Pickford 2003, or “rib”) about one-third of the way from the labial side. Enamel is relatively thin along the anterior border of the tooth but is thickened labially. The posterior border has thick enamel, which projects as a ridge. Enamel along the ridge is smooth and unbroken, indicating that it was not continuous with the talonid (i.e., the trigonid and talonid were separated by cementum).

Remarks. The earliest African lagomorphs are early Miocene records of the ochotonids (pikas) *Kenyalagomys* (Kenya: MacInnes 1953; Namibia: Hende 1978; Morocco: Janvier and De Muizon

1976; Israel: Tchernov et al. 1987; Libya: Wessels et al. 2003, cf. *Kenyalagomys*) and *Austrolagomys* (Namibia; Stromer 1926; Hopwood 1929; Hende 1978; Mein and Pickford 2003). Mein and Pickford (2003) considered *Kenyalagomys* to be a junior synonym of *Austrolagomys*. The leporids (rabbits and hares) are unknown in Africa until the late Miocene (Winkler 2003). Fossil lagomorphs are extremely rare from Uganda. Earlier collecting at Bukwa by A. Walker and colleagues produced at least one specimen (Walker, personal commun., 2002), but this specimen(s) has not yet been relocated.

BUMP 1021 is extremely fragmentary and cannot be assigned confidently to species. It is assigned to Family Ochotonidae based on presence of a distinct antero-external fold. Comparable development of this fold is more commonly, although not exclusively, seen on ochotonids than on leporids (e.g., may be distinct in the leporids *Serengetilagus* and *Pronolagus*). Development of the antero-external fold on BUMP 1021 is within the range of variation seen on “*Kenyalagomys*” *minor* and “*K.*” *rusingae*. The fold is a more gentle curve on the type of *Austrolagomys hendeyi* (AD 418’99; Mein and Pickford 2003, figure 1) and on the holotype of *A. simpsoni* (AMNH 22528; this species considered synonymous with *A. inexpectatus* by Mein and Pickford 2003).

Order RODENTIA
 Suborder Hystricognathi
 Superfamily Thryonomyoidea

The small rodents from Bukwa are most similar in morphology and size with members of the Family Phiomyidae. Membership within the Phiomyidae, and the higher level systematics of this group are controversial (Holroyd 1994) and beyond the scope of the present paper. We follow Holroyd's (1994) proposed phylogeny for the Fayum thryonomyoids, which includes *Phiomys*, *Metaphiomys*, and a new genus as members of the Phiomyidae. Holroyd (1994) did not include a detailed study of the East African Miocene phiomyids. The Bukwa rodents described here are compared with published descriptions and illustrations (primarily) and casts of phiomyids from Uganda (Bukwa; Lavocat 1973), Kenya (Lavocat 1973), Egypt (Wood 1968; Holroyd 1994), Libya (Fejfar 1987), Oman (Thomas et al. 1989; 1999) and Algeria (Jaeger et al. 1985). Stevens et al. (2004; in press) have reported phiomyids from Tanzania, but only a lower molar has been described (no comparable tooth position from Bukwa is reported here).

The best sample of phiomyids, both numerically and taxonomically, is from the late Eocene to early Oligocene Jebel Qatrani Formation, Fayum, Egypt. The seminal work on the Fayum rodents was by Wood (1968). Extensive new collecting in the Fayum lead to a major revision of the Fayum rodents by Holroyd in her dissertation (1994). This revision has not yet been formally published. Holroyd (1994) conservatively left the Fayum rodents in the Superfamily Thryonomyoidea, and proposed grouping them into two families, the Phiomyidae (which she revised) and the Thryonomyidae.

Fejfar (1987) reported 28 molars and premolars and 40 incisors of phiomyids from Oligocene deposits near the Zallah Oasis, southern Libya. The rodents and large mammals from these deposits suggested correlation with the Jebel Qatrani Formation, Fayum, Egypt. The Libyan rodents include *Metaphiomys schaubi*, *Phiomys andrewsi*, and *Phiomys paraphiomyoides*, with *Metaphiomys* the dominant taxon. Fejfar (1987) illustrated, but did not describe the specimens. Holroyd (1994, p. 324) disagreed with the identification of *Phiomys andrewsi* and suggested that *M. schaubi* was synonymous with *M. beadnelli*.

Phiomyids are known from two early Oligocene localities in Oman (Thaytiniti and Taqah; Thomas et al. 1989; 1999). Thomas et al. (1999) provided the most recent faunal list, but did not describe or illustrate any specimens. Holroyd (1994, p. 326) suggested a late Eocene age for the sites. The phiomyid fauna from Thaytiniti includes *Phiomys* cf. *P. andrewsi*, *P.* cf. *P. lavocati*, and cf. *Metaphiomys* spp. 1 and 2. The phiomyid fauna

from Taqah includes those species plus *M.* cf. *M. schaubi* (*M.* sp. in Thomas et al. 1989).

Jaeger et al. (1985) described *Protophiomys algeriensis* based on 23 isolated teeth from the late Eocene Bir el Ater (= Nementcha) locality, eastern Algeria. Holroyd (1994) suggested that the hypodigm of *Protophiomys algeriensis* may actually include more than one taxon.

Stevens et al. (2004) reported multiple phiomorph rodent taxa from a site in the Mbeya Region, southwestern Tanzania. They noted that these taxa suggest a late Paleogene age for the locality. An isolated incomplete lower molar of *Metaphiomys* cf. *M. beadnelli* was described (Stevens et al., in press).

Family PHIOMYIDAE Wood, 1955
Ugandamys, gen. nov.
Figures 3, 4

Type and only species. *Ugandamys downsi*.

Diagnosis. As for type and only species.

Etymology. “Uganda,” the country where it is found plus “mys,” Greek for mouse.

Ugandamys downsi, gen. and sp. nov.

Holotype. BUMP 1022, right Dp4.

Referred material. BUMP 1023, RM1 or M2; BUMP 1024, LM1 or M2; BUMP 1025, RDP4. All from Bukwa IIB.

Diagnosis. Small size; proportionally elongate teeth. Dp4 – trigonid narrower than talonid; preprotocristid absent (primitive); metaconid opposite protoconid (derived); protoconid significantly reduced in size relative to metaconid; short metalophid; ectolophid present (derived) and relatively labial in position; strong mesolophid originating from the ectolophid and extending transversely to the lingual border of the tooth (derived); mesoconid present (primitive); triangular shaped talonid with a deep circular basin. Upper fourth premolar and M1 or M2s – strong mesoloph present.

Type locality and age. Green clay unit, Bukwa IIA, 4.0 km east of the village of Bukwa, Kapchorwa District, eastern Uganda (34°47'East longitude, 1°17'North latitude); early Miocene, about 22 Ma (Walker 1969).

Etymology. “downsi” for Will Downs who recovered the specimen; in gratitude for his dedication to the recovery of small mammal fossils from Uganda and elsewhere.

Description. Tooth terminology for the Bukwa rodents is adapted from Flynn et al. (1986). Polarity



Figure 3. *Ugandamys downsi*, gen. and sp. nov. Occlusal view of right Dp4, BUMP 1022, from Bukwa IIA. Anterior is to the top of the figure.

of character states is from Holroyd (1994, table 4.14).

Lower Fourth Premolar

The Dp4 is 1.44 mm long x 0.92 mm wide. This tooth is long and slender, with the trigonid narrower than the talonid. The mesial edge of the tooth is incomplete, but there appears to be a very low indistinct shelf along the metaconid. The metaconid occupies much of the mesiolingual portion of the tooth. It is the second largest cusp. The protoconid is significantly reduced. Some enamel along its mesiolabial edge is missing, but even if com-

plete the protoconid would still be much smaller than the metaconid. The protoconid and metaconid are adjacent to each other; i.e., the metaconid is not anterior to the protoconid. Short low crests extend distally from the more medial aspects of the metaconid and protoconid. Each crest contacts a cuspule. These cuspules are joined as a short metalophid, and the lingual cuspule has a tiny crest continuing distally to the mesial side of the mesolophid, just lingual to its midpoint. A low crest projects distally from the metaconid to contact the entoconid, which is the largest cusp on the tooth. The ectolophid is low and extends distally from the

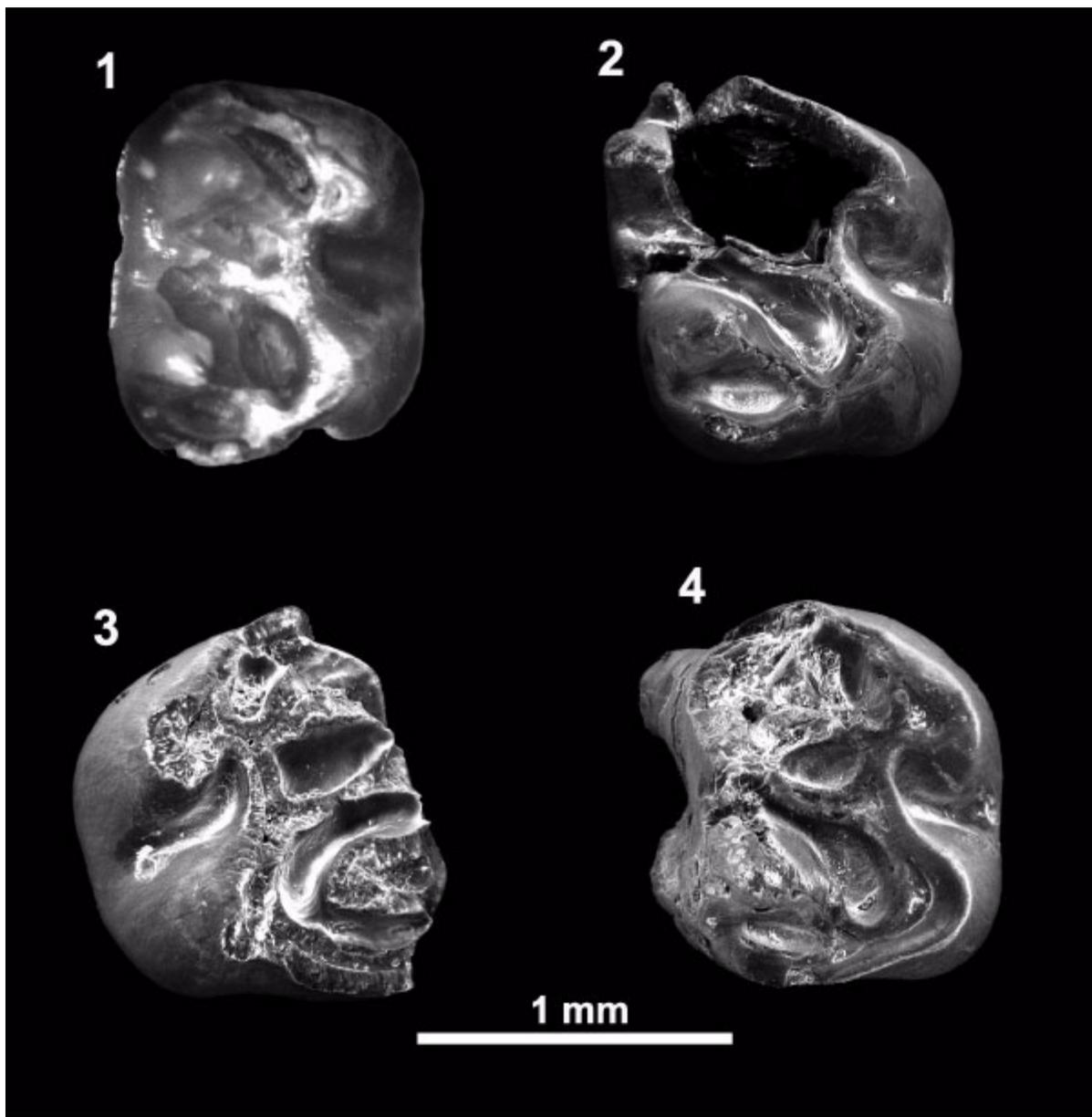


Figure 4. *Ugandamys downsi*, gen. and sp. nov. Occlusal views. 1 and 2, right DP4, BUMP 1025; tooth measures 1.52 mm length x 1.20 mm width. 1, conventional digital photograph of the complete tooth. 2, higher quality SEM image taken after the tooth was damaged. 3, left M1 or M2, BUMP 1024. 4, right M1 or M2, BUMP 1023. All from Bukwa IIB. Scale bar is for 4.2-4.4, SEM photographs. Anterior is to the top of the figure.

protoconid along the labial side of the tooth. It curves slightly lingually to contact a long mesolophid, which continues transversely to the crest along the lingual side of the tooth. This crest is called a mesolophid (versus the posterior arm of the protoconid, protospur, or metalophid II) because of its close proximity to the mesoconid. Continuing distally from the mesolophid, the ectol-

ophid contacts a small mesoconid at the junction with the hypolophid. The hypolophid joins the entoconid to the hypoconid; the latter is the third largest cusp on the tooth. The hypoconid is staggered distolabial to the entoconid. There is a strong mesially concave posterolophid connecting the hypoconid and entoconid. At the distal apex of the posterolophid the enamel is thickened and

likely represents a hypoconulid. These three cusps (plus the mesoconid) and their associated lophs define a roughly triangular talonid, which borders a deep circular basin. Roots of the Dp4 are not preserved.

Upper Fourth Premolar, M1, and M2s

BUMP 1023 (M1 or M2) is 1.44 x 1.16 mm and BUMP 1025 (DP4) is 1.52 x 1.20 mm. BUMP 1024 is too incomplete to measure but is similar in size to BUMP 1023 and 1025. These teeth are approximately rectangular in occlusal outline and longer than wide; BUMP 1025 (DP4) is proportionally slightly longer. The mesial and distal sides are gently convex. None of the teeth are complete. The delicate crown of BUMP 1025 (Figure 4.1-4.2) was originally complete but was damaged during preparation for SEM study. Much of the detailed structure of the occlusal surface of BUMP 1024 (Figure 4.3) is obscured by breakage.

These teeth have four distinct cusps, plus other minor cusps, and five crests. The lingual side of the occlusal surface has worn more quickly than the labial side. Thus, on BUMP 1023 (Figure 4.4) and 1025 the lingual side is relatively flattened, but the major labial cusps (paracone, metacone) are still prominent and bulbous. The protocone and hypocone are crescent shaped with occlusal wear. The protocone-paracone and metacone-hypocone pairs are approximately opposite each other. The paracone is larger than the metacone, and the protocone is slightly larger than the hypocone. An oblique anteroloph extends from the protocone to the labial side of the tooth. On BUMP 1025 this crest has two cuspids; the more lingual is heavily worn. There is a short protoloph connecting the protocone to the longitudinal crest. This short longitudinal crest, just lingual to the midline of the tooth, connects the protocone to the metaconule, and then continues from the metaconule to the hypocone. The metaconule is smallest on BUMP 1025, but more distinct on BUMP 1023 and 1024. The mesoloph is long and slightly oblique. It originates from the metaconule and continues to the labial side of the tooth where it ends in a mesostyle on BUMP 1024 and 1025. This area of the tooth is damaged on BUMP 1023. A distinct posteroloph extends from the hypocone to the labial side of the tooth, contacting the metacone. There is a hypoconule at the junction of the posteroloph with the metaloph on BUMP 1025. A short but distinct metaloph is present on BUMP 1023 and 1025. A metaloph is lacking, or at most represented only by an extremely low indistinct crest, on BUMP 1024.

There is a strong lingual root supporting both the protocone and hypocone. Separate smaller

roots are present under the paracone and metacone.

Remarks

Ugandamys downsi is best placed within the Family Phiomyidae. Holroyd (1994) recently proposed an emended diagnosis of the Phiomyidae (originally diagnosed by Wood 1955; emended by Wood 1968). Her revised diagnosis uses characters of the Dp4 to distinguish it from the Dp4 of the Family Thryonomyidae: 1) generally smaller size; 2) Dp4 replaced by p4 primitively; 3) metaconid less anteriorly placed; 4) relatively stronger hypolophid; and 5) less lingually placed ectolophid. It is unknown if *Ugandamys* replaced the Dp4. The metaconid of the Dp4 of *Ugandamys* is adjacent to the protoconid, similar to the condition in the Phiomyidae, and unlike the anteriorly placed metaconid of the Thryonomyidae. The hypolophid of the Dp4 of *Ugandamys* is distinct, and the ectolophid is along the labial border of the tooth. The small size and presence of a mesoloph on the DP4 and M1 or M2s is consistent with assignment to the Phiomyidae.

Holroyd (1994, p. 97) proposed placement of the genera *Diamantomys*, *Metaphiomys*, and a new genus (and excluding *Pomonomys*) into the subfamily Diamantomyinae (new rank, rediagnosed), within the Family Phiomyidae. The Diamantomyinae were distinguished in part from the Phiomyinae (new rank, rediagnosed by Holroyd 1994, p. 83) by their larger size and consistently having a mesolophid. The diamantomyine Dp4 has the protoconid and metaconid aligned labiolingually, a preprotocristid consistently present, and a relatively wider trigonid. The Dp4 of *Ugandamys* has a strong mesolophid, the protoconid and metaconid are aligned labiolingually, and size is close to, but still smaller than, that of Holroyd's (1994, table 4.6) proposed new genus. Although the Dp4 of *Ugandamys* lacks a preprotocristid, and has a relatively narrow trigonid, the Dp4 of *Ugandamys* fits best within Holroyd's proposed Subfamily Diamantomyinae. Based on their strong mesoloph and size close to that of Holroyd's (1994, table 4.6) proposed new genus, the BUMP DP4 and these two upper molars are also best considered within this subfamily.

Comparisons

Dp4: Of the published phiomyids, the Bukwa Dp4 is most similar to, but still distinct from, the morphology represented by the Dp4 of AMNH 13271, "*Phiomys andrewsi*," from the Fayum (Wood 1968, figure 1G). As originally noted by Wood (1968), and supported by Holroyd (1994), the original

hypodigm of "*Phiomys andrewsi*" actually consists of more than one taxon. Holroyd (1994) suggested that material from the original hypodigm, plus additional specimens, represent the genus *Phiomys* (emended diagnosis) and a new unpublished genus (Holroyd 1994, p. 102). AMNH 13271 was considered by Holroyd (1994) to belong to the new genus, within her Subfamily Diamantomyinae.

Like AMNH 13271, the Bukwa Dp4 is elongate, has the metaconid and protoconid opposite with a metalophid connecting them posteriorly. The mesolophid is long and extends to the lingual side of the tooth. In comparison with AMNH 13271, BUMP 1022 has a distinctly smaller protoconid, lacks a preprotocristid, probably has a more labially placed ectolophid, has a mesoconid, and has a triangular talonid defining a circular basin. In addition, BUMP 1022 is from 7 to 17% shorter (N of the new genus is 6 to 16 for two species) and from 18 to 22% narrower (N = 6 to 18) than the mean values given by Holroyd (1994, table 4.7) for the genus to which AMNH 13271 belongs. Compared to species of the genus *Phiomys* from the Fayum (Holroyd 1994, table 4.2), *Ugandamys* is 10% shorter to 17% longer (N=1 for each of two species, 3 for a third species), and ranges from 23% narrower (N=4), comparable in width (N=2), to 24% wider (N=1).

Ugandamys is distinct from a Dp4 illustrated, but neither specifically named nor described, from prior collections at Bukwa (Lavocat 1973, p. 158, figure 28.7; specimen B9). Lavocat (1973, p. 158) assigned his right Dp4 to "*Paraphiomys stromeri* of small size." Compared to Lavocat's specimen (B9), BUMP 1022 is comparable in length but is slightly narrower. Approximate measurements of B9 from Lavocat's photograph are 1.5 x 1.1 mm. On BUMP 1022 the protoconid is much smaller than the metaconid; these cusps are of more comparable size on B9. On B9 the area between the protoconid/metaconid and hypoconid/entoconid is obscured, so it is unknown if there is a metalophid or mesolophid. The strong labial ectolophid observed on BUMP 1022 is absent, or is more medial in position and obscured on B9. Unlike *Ugandamys*, B9 has a gently concave distal end, and instead of a circular basin the talonid has a narrow valley, which opens lingually.

Lavocat (1973) described two taxa of phiomysids from the early Miocene of Kenya. *Andrewsimys parvus* was reported from only two incomplete maxillae from Songhor; the lower dentition is unknown. *Phiomys andrewsi* was described from a skull, upper jaw, and mandibles from Songhor, Rusinga, and Koru. Holroyd (1994) considered *A. parvus* to be a valid genus within the Phiomysidae.

Although she accepted the Kenyan "*Phiomys andrewsi*" in the Phiomysidae, she thought it distinct at both the generic and specific levels.

Unfortunately, Lavocat (1973, figure 28.4) did not illustrate the Dp4 of the Kenyan "*Phiomys andrewsi*," although the m1-m3 are shown. His measurements for the Dp4 of one specimen, SO 879, are 1.55 x 1.45 mm. BUMP 1022 is slightly shorter than the Dp4 of SO 879, but the Bukwa tooth is significantly (63%) narrower. It is noteworthy that there are strong mesolophids on the lower molars, although they extend only halfway across the m1. Posterolophids contact the entoconid, enclosing a mesiodistally compressed basin on m1 and a more transverse valley on m2 and m3.

Fejfar (1987) illustrated four Dp4s of *Metaphiomys schaubi* (Dp4s not reported for the other taxa) from Zallah, Libya (Fejfar 1987, figure 1.1-1.4). The Zallah Dp4s (smallest is about 2.3 x 1.6 mm; Fejfar 1987, figure 2) are all appreciably larger than BUMP 1022. Like BUMP 1022, the protoconid and metaconid are opposite, but these cusps are comparable in size on the Libyan specimens. Compared to *Ugandamys*, the Zallah specimens also differ in at least three of them having a distinct preprotocristid. The specimens also have a small to absent mesolophid, a more lingually placed ectolophid, and a proportionally wider trigonid. Three of four specimens from Zallah have a triangular talonid defining a circular basin, similar to *Ugandamys*.

The rodent fauna from Thaytiniti, Oman, includes two Dp4s referred to *Phiomys* cf. *P. andrewsi*, which are illustrated (one specimen) and briefly described by Thomas et al. (1989). Holroyd (1994, p. 85) did not consider this material referable to *P. andrewsi*. The one measurement given by Thomas et al. (1989), 1.45 x 0.94 mm, is comparable to that of *Ugandamys*. *Ugandamys* differs from the Oman tooth in that the latter has the protoconid and metaconid of comparable size, the protoconid has a distinct mesio-internal projection, the metalophid is stronger, the ectolophid is more oblique and more lingual, the hypolophid is longer, and the hypoconulid larger. The mesolophids cannot be adequately compared with the available illustration of the Oman specimen.

BUMP 1022 is distinct from the Dp4 of *Protophiomys algeriensis* from Algeria (Jaeger et al. 1985). Compared to BUMP 1022, the Dp4 of *Protophiomys algeriensis* is proportionally wider (mean measurements 1.60 x 1.73 mm, N = 3), has a more anterior and proportionally smaller metaconid, lacks a metalophid connecting the metaconid and protoconid, lacks a mesolophid, has a

more lingual ectolophid, lacks the triangular talonid, and has a stronger hypoconulid.

DP4 and M1 or M2s: Compared to the Fayum phiomyids (Wood 1968; Holroyd 1994), the DP4 and M1 or M2s of *Ugandamys* are most similar to Holroyd's (1994, e.g., figure 4.7, DPC 8170) proposed new genus. The new genus includes three species; lengths of the BUMP specimens are within the range of the Fayum material (Holroyd 1994, table 4.6), but the BUMP specimens are proportionally slightly narrower. The mesoloph is usually present on the species represented by DPC 8170 but is variable in development. It may be as strong as the consistently long mesoloph in *Ugandamys*. The species represented by DPC 8170 does not have a distinct metaconule, but *Ugandamys* has a small to distinct (2 of 3 specimens) metaconule. An incomplete metaloph is also present on Holroyd's (1994) new genus, but it may be stronger and join the area of origin of the mesoloph in addition to joining the posteroloph.

Lavocat (1973, plate 28.6, 28.8, 28.9) illustrated, but did not describe, two isolated small thryonomyoid upper molars from Bukwa. Plate 28.8 (B12) is a right upper molar referred to a thryonomyoid "a little smaller than *Paraphiomys stromeri* of small size and of a form a little different" (Lavocat 1973, p. 158; translated from French). Figure 9 (B11) is a "left upper molar of *P. stromeri* of small size with the mesoloph reaching the border of the crown" (Lavocat 1973, p. 158; translated from French). Measurements of these specimens are not given, but approximate measurements from the Plate are B12, 1.40 x 1.20 mm and B11, 1.60 x 1.70. It is probable that these teeth belong to the same species, with the differences ascribable to intraspecific variation. B12 is comparable in size to BUMP 1023 (1.44 x 1.16 mm) and BUMP 1025 (1.52 x 1.20 mm). B11 is comparable in length but wider. None of the BUMP specimens have the lingual side of the tooth as proportionally short compared to the labial side, as seen on B11. Overall morphology of B11 and B12 and *Ugandamys* is similar. Especially notable is the long mesoloph, which extends to the labial border of the crown (B11 also has a mesostyle) and a short metaloph. The anteroloph is better developed on B11 than B12. The anteroloph on B11 is comparable to that of BUMP 1025, the DP4. The labial part of both BUMP 1023 and 1024 is damaged, so detailed comparisons of the anteroloph are not possible. Definitive presence or absence of a metaconule cannot be determined from the photographs of B11 and B12. It is possible that Lavocat's (1973) B11 and B12 are referable to *Ugandamys*, with the differences related to intraspecific variation.

Lavocat (1973, plate 41.6) described and illustrated the upper dentition of "*Phiomys andrews*" from Songhor, Kenya. He noted the strong development of the mesoloph, a distinct mesocone (= metaconule in the terminology used here), and a short metaloph. Lavocat (1973, table 14) provided measurements for one upper dentition (specimen number not given): DP4 (P4 of Lavocat) 1.6 x 1.7 mm, M1 1.6 x 1.75 mm, M2 1.5 x 1.7 mm. These teeth are proportionally wider than *Ugandamys* (acknowledging that it is unknown if the BUMP specimens are M1 or M2s). Length to width ratios for his specimens are DP4, 0.94; M1, 0.91; M2, 0.88. Length to width ratio for BUMP 1025 DP4 is 1.27, BUMP 1023 is 1.24. The posterior portion of Lavocat's "*P. andrews*" differs significantly from *Ugandamys* in formation of a circular basin bounded mesially by a connection between the metaloph and the metaconule or the mesoloph near where it contacts the metaconule.

Lavocat (1973, plate 42.4) also described and illustrated two incomplete maxillae of *Andrewsimys parvus* from Songhor, Kenya. This taxon is diagnosed by its small size and distinct cusps. The lophes (e.g., the mesoloph) are reduced, although the mesoloph looks strong on the photograph of "P4" (Lavocat 1973, plate 42.4). A metaconule and short metaloph are present. Lavocat considered the specimens to have P4s, not DP4s, although he was uncertain. His "P4s" of *A. parvus* are 1.1 x 0.95 mm and 1.15 x 1.1 mm; the M1s are 1.2 x 1.1 mm and 1.15 x 1.25 mm (Lavocat 1973, table 14). If Lavocat's specimens are DP4s, they are about 27% shorter and proportionally wider (length to width ratios 1.04 and 1.16) than BUMP 1025. The M1s of *Andrewsimys parvus* are about 18% shorter and proportionally wider (length to width ratios 1.09 and 0.92) than the M1 or M2 (BUMP 1023) of the BUMP taxon.

The sample of phiomyids from Zallah Oasis, Libya (Fejfar 1987), did not include any DP4s. Two M1 or M2s of *Metaphiomys schaubi* were illustrated (Fejfar 1987, figure 1.19, 1.20). Measurements for three specimens of this taxon are significantly larger (Fejfar 1987, figure 2; smallest specimen about 2.31 x 2.65 mm) than *Ugandamys*, and no further comparison is given here. An upper molar of *Phiomys paraphiomomyoides* was also illustrated (Fejfar 1987, figure 1.17; no tooth position given, but likely M1 or M2). This specimen is closer in size (about 1.45 x 1.4 mm from Fejfar 1987, figure 2) to BUMP 1023. *Phiomys paraphiomomyoides* was diagnosed (in part) by Wood (1968, page 41) by the metaloph connecting with both the posteroloph and mesoloph. This connection appears to be present in Fejfar's specimen, which

also has a very short mesoloph and is squarer in outline than *Ugandamys*.

Thomas et al. (1989) illustrated and briefly described the upper molars of some phiomyids from Thayitini and Taqah, Oman. *Phiomys* cf. *P. lavocati* was reported from both sites (total of three specimens). This material differs significantly in smaller size from *Ugandamys* (e.g., M1 from Taqah 0.97 x 1.02 mm) and squarer outline, shorter or interrupted mesoloph, and connection of the metaloph to the posteroloph and mesoloph/metaconule, helping form a circular basin in the Oman material. Thomas (1989, figure 11.a) also referred an M1 to cf. *Metaphiomys* sp. 1. Holroyd (1994, page 102) considered this specimen to belong to her proposed new genus of phiomyid. The M1 of cf. *Metaphiomys* sp. 1 (1.52 x 1.66 mm) is comparable in length but wider than BUMP 1023. Like *Ugandamys*, the Oman tooth has a metaloph, metacone (= metaconule), and a strong mesoloph reaching the labial wall. However, the M1 of cf. *Metaphiomys* sp. 1 has a more complicated occlusal pattern, including a short crest between the anteroloph and the protoloph, a distal elongation of the protocone, and a metaloph connecting to both the mesoloph and the posteroloph (in part forming a circular basin).

The description of *Protophiomys algeriensis* from Algeria (Jaeger et al. 1985) included three DP4s and six M1 or M2s. The morphological variability of the illustrated M1 or M2s (Jaeger et al. 1985, plate 1.6-1.8) may reflect presence of more than one taxon. Thus, comparisons of this taxon with the Bukwa upper cheek teeth would be misleading. However, it should be noted that the diagnosis of *Protophiomys algeriensis* includes upper molars lacking a mesoloph (strong on Bukwa specimens), and the metaloph never connected to the posteroloph (always connected on Bukwa specimens).

Family Thryonomyidae Pocock, 1922
cf. *Paraphiomys* sp.
Figure 5

Referred material. BUMP 1026, right upper cheek tooth, from Bukwa IIA.

Description. BUMP 1026 is incomplete, especially along the labial side. Minimum measurements are 1.4 x 1.2 mm. This tooth is etched, suggesting digestion or the effect of postdepositional soil acids. Some smooth polishing of the sides of the tooth suggests postmortem transport. There are four major nearly transverse lophs: anteroloph, protoloph, metaloph, and posteroloph. The third loph is considered a metaloph, because it goes

directly to the metacone and does not seem to originate from a central cusp (metaconule). BUMP 1026 lacks the strong mesoloph seen on the other upper molars described here from Bukwa. The protoloph and metaloph connect to a longitudinal crest located lingual to the midline of the tooth. All cusps are worn flat, and the hypocone is completely missing (broken). A strong root is present under the protocone. Another root is present under the hypocone and likely also under the distolabial aspect of the tooth. The rest of the underside of the tooth is damaged.

Discussion

The occlusal pattern of this tooth (e.g., four nearly transverse lophs) is comparable to a small species of *Paraphiomys* (i.e., *P. stromeri* size or smaller), but incompleteness of the specimen precludes specific assignment. *Paraphiomys* is a common component of early Miocene and, to a lesser extent, middle Miocene African faunas (e.g., Lavocat 1973; Winkler 1992; Mein et al. 2003; López Antoñanzas et al. 2004). *Paraphiomys simonsi* was reported from the Fayum of Egypt (Wood 1968). Holroyd (1994) proposed transferring this species to a new genus, but López Antoñanzas et al. (2004) retained it within *Paraphiomys*. Whatever the allocation of *P. simonsi*, the Bukwa tooth is smaller and has a strong metaloph (metaloph lacking in *P. simonsi*; Holroyd 1994 and López Antoñanzas et al. 2004).

CONCLUSIONS

Screen washing of a relatively small sample of sediment from the Bukwa locality, Uganda, has yielded two taxa of thryonomyoids and an ochotonid. The number of Bukwa rodent specimens described here is admittedly small. However, this collection, especially in combination with the Bukwa rodents illustrated by Lavocat (1973), is important in demonstrating the potential of this site for increasing our knowledge of the rare smaller sized rodents in the early Miocene East African fauna. Although ochotonids are known from early Miocene deposits elsewhere in Africa, this is the first published description of a specimen from Uganda.

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Figure 5. Family Thryonomyidae, cf. *Paraphiomys* sp. Occlusal view of right upper cheek tooth, BUMP 1026, from Bukwa IIA. Anterior is to the top of the figure.

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