WINDOWS INTO SAUROPSID AND SYNAPSID EVOLUTION
Essays in honor of Prof. Louis L. Jacobs, pp. 306–331, 2023

LATE MIOCENE AND EARLY PLIOCENE RODENTS FROM THE TUGEN HILLS, WESTERN KENYA

ALISA J. WINKLER*

Roy M. Huffington Department of Earth Sciences, Southern Methodist University, Dallas, Texas, 75275, U.S.A, awinkler@smu.edu;
Department of Surgery, University of Texas Southwestern Medical Center, Dallas, Texas, 75390, U.S.A.

ABSTRACT Neogene deposits in the Tugen Hills, Kenya, have yielded a minimum of four genera of rodents from the late Miocene (Kapcheberek locality, 5.9-5.7 Ma) and eight genera from the early Pliocene (Tabarin locality, 4.5-4.4 Ma). These faunas are significant in including some of the earliest fossil records of several extant African rodent genera including the sciurid *Paraxerus* (4.5-4.4 Ma), and the murines *Arvicanthis* (5.9-5.7 Ma) and either *Grammomys* or *Thallomys* (4.5-4.4 Ma). If a specimen of cf. *Heliosciurus* from Tabarin is indeed referrable to that genus, then it would be the earliest record of this exclusively sub-Saharan African squirrel. If cf. *Mus* from Tabarin is referrable to that genus, then it is one of the earlier records of *Mus* in Africa. Assignment of the Tabarin murine *Saidomys* to the same species as that from the Manonga Valley, Tanzania, further supports affinities of these two faunas. The rodent sample from the Kapcheberek locality is very small, but the affinities of modern analogues are supportive of a savanna habitat. Rodents from the Tabarin locality suggest a woodland environment.

KEYWORDS Rodentia, late Miocene, early Pliocene, Systematics, Kenya

INTRODUCTION

Fossil vertebrates were first reported from the Tugen Hills, Baringo Basin, Kenya, by Fuchs (1950). Since then, the area has yielded fossiliferous deposits dating from 15.5 Ma to <200 ka (summarized in Hill, 1999, 2002). The area has received considerable attention because it has produced abundant fossil remains from a long Neogene stratigraphic sequence that is well calibrated by radiometric and magnetostratigraphic techniques. Hominoids occur sporadically throughout the sequence, including the critical period from the middle Miocene to early Pliocene during which hominids differentiated. Although the Tugen Hills hominoids from this period are well studied (e.g., Pickford et al., 1983; Hill, 1985; Ward & Hill, 1987; Hill et al., 1991; Ward et al., 1999; Senut et al., 2001; Hill et al., 2002; Pickford et al., 2022), other taxa, such as rodents, have received much less attention. Rodents have, however, been recovered from throughout the sequence, from sites dating from 15.5 Ma to less than 1 Ma, and they are numerically abundant and taxonomically diverse (e.g., Winkler, 1990, 1992, 2002; Mein & Pickford, 2006). Through the sequence, rodent faunas show major changes in composition and relative abundance, changes likely reflecting the immigration of new taxa from Eurasia and other parts of Africa, and *in situ* evolution and extinction (Winkler, 1994, 2002). The documentation of faunal change through time in the Tugen Hills sequence, and the development of hypotheses to explain those changes, aids in an understanding of the evolution of the East African fauna, and to a synthesis of the ecological history of East Africa.

The Tugen Hills sequence includes, from oldest to youngest, six major sedimentary units that have produced fossil vertebrates (Hill, 1999, 2002): Muruyur Formation (15.5-15 Ma), Ngorora Formation (13-8.5 Ma), Mpesida Beds (7-6.2 Ma), Lukeino Formation (6.2-5.6 Ma), Chemeron Formation (5.6-1.6 Ma), and Kapthurin Formation (700-<200 ka). Sediments intercalated with volcanic units provide age control through radiometric and magnetostratigraphic methods. Stratigraphy and paleontology of the Tugen Hills section are summarized by Hill (1999, 2002). Prior to studies by Winkler (1990), rodents were reported from the sequence (e.g., Bishop and Pickford, 1975; Pickford, 1978; Jaeger et al., 1985, Flynn et al, 1983, 1985; Hill et al., 1986; McBrearty, 1999, Denys, 1999), but not formally and/or fully studied. Winkler (1992)

---

*Corresponding author

published on rodents from the Muruyur Formation and named a new rodent from the Chemeron Formation (*Tectonomys africanus*; Winkler, 1997). Mein & Pickford (2006) described an extensive collection of micromammals from several localities (Aragai, Kapsomin, Kapcheberek) sampling the Lukeino Formation that yielded (among other taxonomic groups) 16 species of rodents.

The present paper describes the rodent fauna collected by Winkler (1990) and colleagues (in particular, Louis Jacobs) from the Lukeino (Kapcheberek locality) and Chemeron (Tabarin locality) Formations, primarily in 1987. This paper follows Deino et al. (2002) in considering Tabarin locality BPRP#77 to sample the Chemeron Formation as opposed to the Mabaget Formation. Table 1 presents the composite rodent faunal list from these collections. Figure 1 shows the location of Kapcheberek and Tabarin in the context of some other Baringo localities (e.g., Kipsaramon, Muruyur Beds; Kabarsero, Ngorora Formation). The focus of this paper is on systematics; paleobiogeographic and paleoenvironmental interpretations based on these fossils have been discussed elsewhere (Winkler 1994, 2002). Rodents from the Ngorora Formation will be described in a subsequent paper. The Mpesida Beds have not yet yielded rodents, and those from the Kapthurin Formation have not been formally described (Denys, 1999; McBrearty, 1999).

Table 1. Composite rodent fauna for the Kapcheberek (Lukeino Formation) and Tabarin localities (Chemeron Formation), Tugen Hills, Kenya, based primarily on collections described in this paper

Taxon	Locality	
	Kapcheberek (BPRP#76c)	Tabarin (BPRP#77a except as noted)
Family Sciuridae		
Cf. *Heliosciurus* sp.		X
Paraxerus meini		X
Family Nesomyidae		
Subfamily Dendromurinae		
Dendromus sp.	X	
Steatomys minus sp.	X	
Family Muridae		
Subfamily Deomyinae		
Tectonomys africanus		X
Subfamily Murinae		
Saidomys alisae	X	
Saidomys parvus		X
Arvicanthis sp.	X	
Cf. *Mus* sp.		X
Grammomys or *Thallomys* sp.		X
Family Thryonomyidae		
Thryonomys sp.		X
Family Hystricidae		
Hystrix[a] sp.		X

[a] Specimen from Tabarin sub-locality BPRP#77c

MATERIALS AND METHODS

Rodent remains of the Lukeino Formation were recovered from about 130 kilograms of matrix from the Kapcheberek locality, BPRP#76c (equivalent to Pickford's locality 2/226, in his member B, Pickford, 1975). Matrix was also collected from higher in the Lukeino section (BPRP#76d; likely near Pickford [1975] locality 2/227): that matrix yielded only fragmentary rodent teeth but looked promising. Kapcheberek locality BPRP#76c is dated between 5.9-5.7 Ma (Deino et al., 2002).

Rodents were collected near the top of BPRP#76c in a massive light tan to gray-green fossiliferous muddy fine to very fine-grained sand. This sandy matrix also produced fragments of larger vertebrates (e.g., hippopotamus), gastropods and ostracods. Ostracods were identified by Andrew Cohen and Koen Martens (pers. comm. from A. Cohen, 1988, 1989) as belonging to the genus *Sclerocypris*. This taxon suggests presence of a quiet water, moderate alkalinity lake, in addition to the fluvial input suggested by the sedimentology (see also Pickford, 1975). Pickford (1975) suggested Kapcheberek sampled a lakeshore environment.

Rodents from the Tabarin locality (BPRP#77; near the base of the Chemeron Formation) were recovered from fluvial sediments that have also yielded abundant vertebrate remains. The Tabarin locality can be divided into two main sub-localities, a and b (Mark Monaghan, pers. comm., 1987). Rodents described in this study are from sublocality BPRP#77a. Hystricids have been recovered from outside the main Tabarin area in BPRP#77c (Sagatia locality, 1.5 km south of Tabarin, in the same fossiliferous horizon; Ward & Hill, 1987), and from an undetermined Chemeron locality: those specimens are not described in this paper. Rodents from BPRP#77a were recovered from approximately 48 kilograms

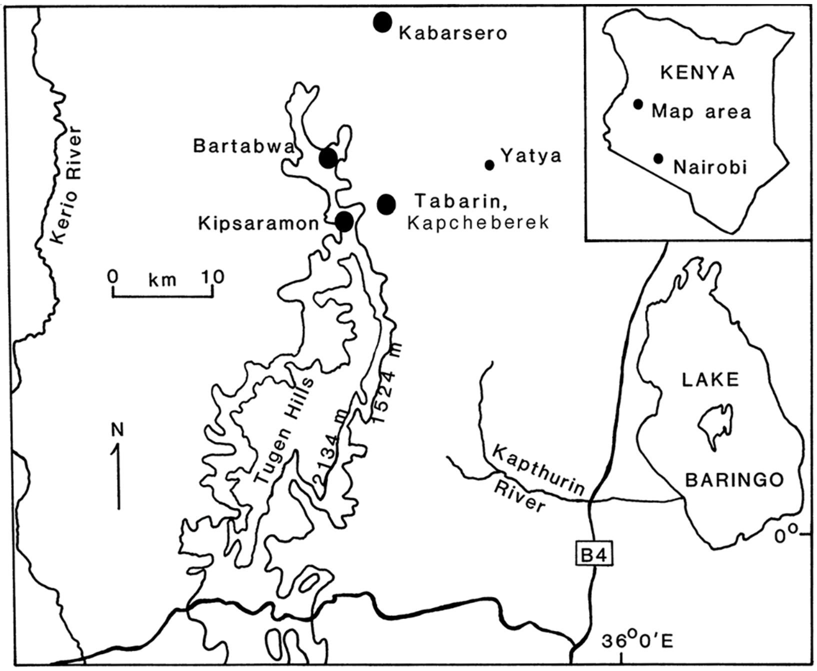

Figure 1. Location map of the Tabarin and Kapcheberek localities in the Tugen Hills, Baringo County, Kenya (after Hill, 1985).

of tan to brown fossiliferous muddy clayball and lithic gravel to very coarse-grained sand. These fluvially derived gravels extend about 181 m along strike. Below them are silts and sands, which overlie a thick tuff. Above the gravels is a brownish orange, organic-rich paleosol. The Tabarin rodents are considered 4.5-4.4 Ma based on dates for a Tabarin hominid (KNM-TH 13150), which was recovered about 10 m below the rodent level (Hill, 1999; Deino et al., 2002).

The fossiliferous matrix was processed by washing through tandem screen boxes. Most of the fine concentrate was further processed using heavy liquids (sodium polytungstate).

Most recovered specimens are isolated teeth; jaws, maxillary fragments, and post-crania are rare. Fossil teeth were measured using a microscope fitted with a reticule. Accuracy of measurement averages +/− 0.04 mm. Measurements record maximum occlusal length and width unless otherwise specified.

Fossils from the Tugen Hills were cataloged into collections at the Nairobi National Museum, Nairobi, Kenya. Casts are deposited at the Nairobi National Museum and at the Shuler Museum of Paleontology, Roy M. Huffington Department of Earth Sciences, Southern Methodist University, Dallas, Texas.

Institutional Abbreviations — **BPRP**, Baringo Paleontological Research Project; **KNM-**Nairobi National Museum collections, Nairobi, Kenya; **KNM-BC**, Baringo Basin, Chemeron Formation localities; **KNM-LT**, Lothagam localities, Kenya; **KNM-LU**, Baringo Basin, Lukeino Formation localities; **KNM-TH**, Baringo Basin, Tugen Hills localities; **LAET**, Laetoli, Tanzania, specimens formerly deposited at the Nairobi National Museum, Nairobi, Kenya, but later moved to the National Museum of Tanzania (specimens were studied while housed in Kenya).

Anatomical Abbreviations — **M**, upper molar; **m**, lower molar; **P**, upper premolar; **p**, lower premolar.

SYSTEMATIC PALEONTOLOGY

Lukeino Formation rodents.

The relatively small sample from the Kapcheberek locality yielded a minimum of four taxa of rodents. Two of these are nesomyines, *Dendromus* and *Steatomys*, and two are murines, *Saidomys* and *Arvicanthis*.

Family NESOMYIDAE Forsyth Major, 1897
Subfamily DENDROMURINAE Allen, 1939
Genus *DENDROMUS* A. Smith, 1829
DENDROMUS sp.
(Fig. 3A)

Referred material — Left M1, KNM-TH 19464, from the Kapcheberek locality, BPRP#76c, Lukeino Formation.

Description — Measurements are given in Table 2. Tooth terminology used here refers to two different systems: see Fig. 2 and Denys & Winkler (2015). This tiny tooth is longer than wide and heavily worn. There is a distinct low median anterior cusp nestled between the labial and lingual anterocones. The latter two cusps are roughly similar in size with the labial anterocone slightly larger and extending slightly further posteriorly than the lingual lobe. The protocone (t5) is the largest cusp; wear has caused it to contact both the lingual anterocone and the enterostyle (t4). The paracone (t6) is displaced posteriorly relative to the protocone. There is a large labiolingually compressed enterostyle (t4) posterolingual to the protocone. There is a short crest connecting the paracone and metacone (t9) and a shorter indistinct crest connecting the protocone and hypocone. A protoloph joins the protocone and paracone, and a metaloph joins the metacone and hypocone. A well-developed posterior cingulum is present, connecting the two posterior-most cusps. The tooth has three large roots: anterior, lingual, and posterior. Presence or absence of a labial rootlet is indeterminate.

Discussion — KNM-TH 19464 was mentioned by Mein and Pickford (2006) in association with two other specimens of *Dendromus* (an M1 and m1) recovered from their Kapsomin locality, Lukeino Formation. It is difficult to make detailed comparisons of the Kapsomin and Kapcheberek teeth based on the published image in Mein & Pickford (2006: Plate 1, 20), but the hypocone (t8) of the Kapsomin tooth appears proportionally larger relative to the metacone (t9), compared to their relationship on the Kapcheberek tooth. The Kapsomin tooth is slightly larger (1.54×0.91 mm) than that from Kapcheberek (1.46×0.81 mm). With such a small sample, the significance, if any, of those differences is unknown (for example, see the variability noted by Denys [1994] in size and morphology of fossil and extant *Dendromus*).

Dendromus is currently a widely distributed taxon in sub-Saharan Africa (e.g., Musser & Carleton, 2005; Voelker et al,

Table 2. Occlusal measurements (in mm) of Dendromurinae from the Kapcheberek and Kapsomin localities, Lukeino Formation, Kenya, and comparative fossil and extant taxa.

Taxon	Locality	Tooth position	N	Length	Width	M1 L/W
Dendromus sp.	Kapcheberek	LM1	1	1.46	0.81	1.80
Dendromus[a] sp. nov.	Kapsomin	LM1	1	1.54	0.91	
Dendromus sp.	Laetoli	LM1	1	1.92	1.13	1.70
D. mesomelas	Kenya	M1	5	1.81-2.35	1.01-1.19	1.74-2.01
D. mystacalis	Kenya	M1	2	1.93-2.00	0.96-1.04	1.92-2.01
D. melanotis	southern Africa	M1	11	1.61-1.82	0.92-1.05	1.60-1.90 X=1.75
S. minus	Kapcheberek	Lm1	1	1.71	1.08	-
S. minus[a]	Kapsomin?	m1	9 length 8 width	1.62-1.82 X=1.69	1.00-1.17 X=1.17	-
"K. minus"[b]	Ch'orora	m1	22	1.59-1.89 X=1.68	1.04-1.22 X=1.10	-
S. cf. *intermedius*[a]	Kapsomin?	m1	2	1.89-1.97	1.34-1.36	-
S. sp. indet.	Laetoli	Rm1	1	1.54	1.00	
S. minus	Kapcheberek	Rm2	1	1.22	1.12	-
S. minus[a]	Kapsomin?	m2	4	1.27-1.31 X=1.29	1.07-1.18 X=1.12	-
"K. minus"[b]	Ch'orora	m2	11	1.22-1.34 X=1.28	1.10-1.22 X=1.14	-
S. cf. *intermedius*[a]	Kapsomin?	Rm2	1	1.33	1.24	-

[a] Measurements from Mein & Pickford (2006)
[b] Measurements from Geraads (2001)

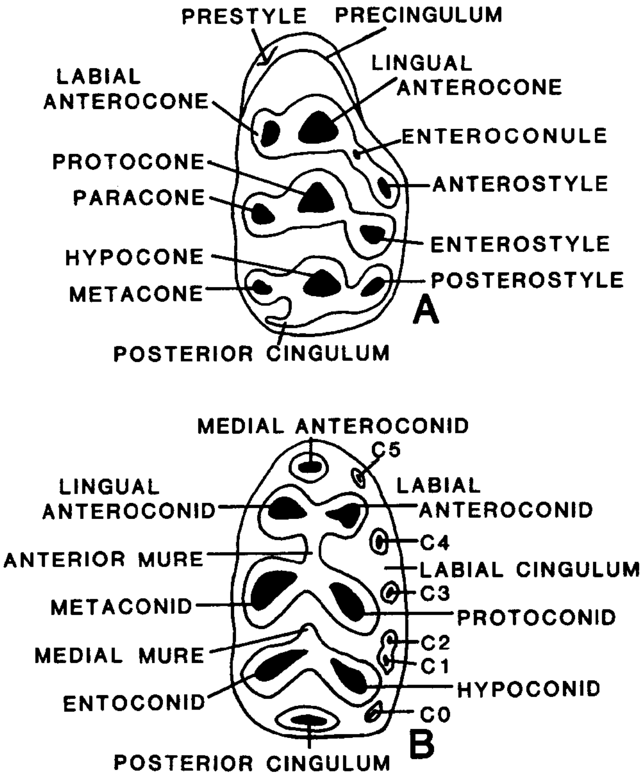

Figure 2. Murid rodent tooth terminology (from Jacobs, 1978) for A) upper right and B) lower right molars.

2021). KNM-TH 19464 was compared with five (*D. lovati*, *D. nyikae*, *D. melanotis*, *D. mesomelas*, and *D. mystacalis*) of the many extant species: it is distinct from these species primarily because the labial cusps are not strongly compressed labial-lingually as are those of the extant taxa. Among those taxa, the fossil *Dendromus* is most similar to *D. melanotis* based on its small size and relatively low length:width ratio (Table 2).

Denys (1987) partially summarizes the fossil record of *Dendromus* in eastern (Laetoli, and Olduvai, Tanzania) and southern Africa (Sterkfontein, Makapansgat, and Langebaanweg, South Africa; Langebaanweg ca. 5.2-5.0 Ma [Denys, 1994], Sterkfontein and Makapansgat date to later in the Pliocene), as well as a late Miocene record from Salobrena, Spain. Other southern African records include Gcwihaba C Hill, Botswana (similar age as Makapansgat based on faunal correlation; Pickford and Mein, 1988), Kromdraai (Pocock, 1987), Taung (Broom, 1948), and Cooper's Cave (1.4 Ma; Linchamps et al., 2023), South Africa. An isolated M2 of a large *Dendromus* is mentioned, but not described (Jaeger & Wesselman, 1976), from the Shungura Formation, lower Omo valley, Ethiopia. However, no dendromurines are reported in Wesselman's (1984) comprehensive study of the Omo micromammals. Mein et al. (2004) further summarized the fossil record of the genus, including reports from Namibia, Abu Dhabi, and Bolt's Farm, South Africa. Geraads (2001) considers two teeth from Ch'orora (8-10 Ma) to be aff. *Dendromus* sp. *Dendromus* is also reported (but not described) from Aramis, Ethiopia (4.4 Ma; Louchart et al., 2009).

Mein & Pickford (2006) briefly made comparisons of the Lukeino material to that of *D. denysae* from the late Miocene of Harasib, Namibia (Mein et al., 2004). A comparison is also made here of KNM-TH 19464 to the description and illustration of a less worn M1 (ARI 129) from Harasib. The teeth are similar overall with the following differences: the Harasib tooth 1) is larger in size (1.78×0.95 mm); 2) has a more distinct crest between t5 (protocone) and t8 (hypocone); 3) has a proportionally larger t8 (hypocone) versus the size of t9 (metacone); and 4) has a posterior cingulum that opens labially (although connection of that crest to t9 in KNM-TH 19464 may be a function of occlusal wear). The measurements in Mein et al. (2004: Table 4) for all remains of *D. denysae* are accidentally a duplication of those for another taxon. Mein & Pickford (2010) report *D.* cf. *denysae* from the late Miocene of Sheikh Abdallah, Egypt. The M1 from that site (n = 3; mean L = 1.75; mean W = 0.97) are also larger than those from Laetoli and they are described as having poorly developed crests between t5 (protocone) and t8 (hypocone) and between t6 (paracone) and t9 (metacone).

Compared to a cast of the M1 of the genus from Laetoli (Denys, 1987) and to observed individuals of some extant species, the Lukeino specimens (and *D. denysae*) lack strongly compressed labial cusps. This character may be primitive for the genus. Denys (1987) lists several characters of the Laetoli M1 to differentiate it from extant *Dendromus* and suggests the Laetoli species may also have characters primitive for the genus. These characters (orientation of the longitudinal groove, compression of the metacone and its connection to the paracone, presence of a crest between the protocone and hypocone, and a small, low, isolated enterostyle) are, however, within the range of variation observed in extant specimens. Measurements of the Laetoli tooth (Denys, 1987:127) are also within the range of variation seen in extant forms (Table 2). Thus, while the less compressed labial cusps of the Lukeino M1s appear primitive for the genus, the Laetoli *Dendromus* appears of more similar

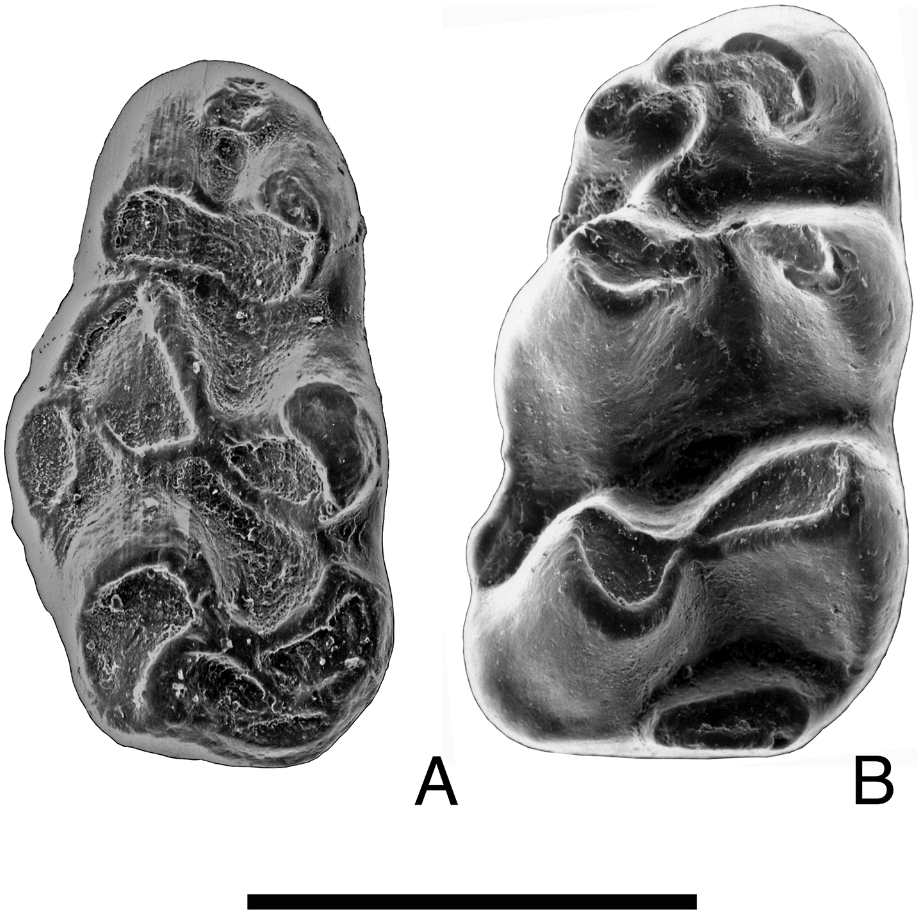

Figure 3. Dendromurine rodents from the Kapcheberek locality, Lukeino Formation, Kenya. A) *Dendromus* sp., left M1, KNM-TH 19464. B) *Steatomys minus*, left m1, KNM-TH 19467. Bar scale is 1 mm.

evolutionary grade as modern *Dendromus* compared to the Lukeino tooth.

Voelker et al. (2021) noted that the extant genus is widely distributed in sub-Saharan African and found in a variety of habitats 'ranging from tall grassland and savannah, to dense scrub, grassy wetlands and subalpine or alpine vegetation" and even Afrotropical lowland forests. *Dendromus melanotis* is found in habitats ranging from dry-grass savannas to montane forests but is most commonly present in fairly open dry savannas (Kingdon, 1974).

Genus *STEATOMYS* Peters, 1846
STEATOMYS MINUS Geraads, 2001
(Fig. 3B)

Referred material — Left m1, KNM-TH 19467; right incomplete m1 (anteroconid through the first row of major cusps), KNM-TH 19461; right incomplete m1 (missing the anteroconid), KNM-TH 19463; right m2, KNM-TH 19441; all from Kapcheberek, BPRP#76c, Lukeino Formation.

Description — Measurements of the complete Lukeino specimen (and the m2, TH-19441) are in Table 2. The m1 has a large medial anteroconid that extends labially as an anterior cingulum that contacts the protoconid. The valley between this cingulum and protoconid is deep. On KNM-TH 19467 (very lightly worn) the anteroconid is weakly bilobed with a larger lingual lobe and a much smaller labial lobe. There is another cuspid lateral to the labial lobe that continues as a cingulum to contact the protoconid. With occlusal wear, these multiple components of the anterior end of the tooth would likely fuse into a single structure. An anterior longitudinal crest (mure) runs obliquely posterolabially to join the labial lobe of the anteroconid with the protoconid. KNM-TH 19461 (more heavily worn) has a single anteroconid with a long labial cingulum that almost contacts the protoconid. On this specimen a wide median anterior longitudinal crest connects the anteroconid to the first row of major cusps. On both specimens, the first row of major cusps is only slightly oblique: the protoconid is slightly larger in size than the metaconid. The hypoconid and entoconid are large, with the hypoconid conical and the entoconid more transversely elongate. These latter two cusps are aligned obliquely, with the hypoconid posterior. There is a moderately developed ectostylid between the protoconid and hypoconid: this cuspid is indistinct on the more heavily worn KNM-TH 19463. A short indistinct posterior longitudinal crest connects the protoconid and hypoconid on KNM-TH 19467. The posterior cingulum is a well-developed flattened oval located toward the lingual side of the tooth. KNM-TH 19467 has a low weak posterolabial shelf on the hypoconid. This tooth has large anterior and posterior roots.

A slightly worn M2, KNM-TH 19441, is almost square in outline. The protoconid is slightly larger and more rounded than the transversely elongate metaconid. The elongate entoconid and larger and more rounded hypoconid are oriented obliquely, with the entoconid approaching the metaconid. The hypoconid is separated from the protoconid by a deep valley. There is a well-developed anterolabial cingulum; the cingulum originates from the metaconid and extends across the anterior two-thirds of the tooth. A prominent posterior cingulum is located posterolingually. There are large anterior and posterior roots.

Discussion — The Lukeino specimens were compared briefly with dentitions of extant *Steatomys*, including the species *S. pratensis*, *bocagei*, *caurinus*, and *parvus*. Taxonomy of modern *Steatomys* is complex and in need of revision (Coetzee, 1977; Musser & Carleton, 2005). Examination of extant specimens was informative regarding the extent of individual variation, which is important when considering the significance of character differences in small samples of fossil taxa. Characters such as the extent of bilobing of the anteroconid and development of the anterior cingulum of m1 are variable. All extant specimens examined had an ectostylid, and in most it was similar in size to that of KNM-TH 19467. All extant specimens also had a well-developed posterior cingulum on m1. Presence or absence of an anterior longitudinal crest on Recent material was generally indeterminate because *Steatomys* teeth wear quickly; of 17 extant individuals, one had a short anterior longitudinal crest, four probably lacked this crest, and 12 were indeterminate. An anterior longitudinal crest did not contact the protoconid on the extant specimens examined by Denys (1987). Presence of anterior (and posterior) longitudinal crests on KNM-TH 19467 is considered a primitive trait.

Mein & Pickford (2006) considered their sample of *Steatomys* from other localities in the Lukeino Formation to be most comparable to "*Dendromus*" [Gen. nov. "*K.*" Winkler] *minus* n. sp. and "*Dendromus*" [Gen. nov. "*K.*" Winkler] *intermedias* n. sp. from Ch'orora, Ethiopia (8-10 Ma; Geraads, 2001): they considered these Ch'orora species best referred to *Steatomys*. The Kapcheberek specimens are comparable in size to *S. minus* as recorded by Mein & Pickford (2006) and Geraads (2001) but are smaller than *Steatomys* cf. *intermedius* (Table 2). General morphology also seems comparable to *S. minus*, although the disposition of anterior and posterior longitudinal crests on m1 was unclear from the descriptions and photographs from the larger Lukeino sample examined by Mein & Pickford (2006). All three m1s illustrated by Geraads (2001: Plate 3, figs 14-16) have an anterior longitudinal crest, and one of the three also has a short posterior crest.

Other extinct species of *Steatomys* (*S. harasibensis*, *S. jaegeri*) were described by Mein et al. (2004) from Harasib, Namibia (ca. 10.5-9.5 Ma). Mein & Pickford (2010) also named *S. bartheli*, from Sheikh Abdallah, Egypt (ca. 11 Ma). These authors briefly compared those species to *S. minus*.

The Kapcheberek m1s were compared also with *Steatomys* sp. indet (including a cast of #79/A641.2; Denys, 1987) from Locality 6, Laetolil Beds, Laetoli, Tanzania (and see a measurement in Table 2). The Laetoli m1 is similar in overall morphology although slightly smaller in size than the Kapcheberek m1. Samples from both sites have distinct anterior longitudinal crests ("small distal crest" of Denys, 1987). The Laetoli specimen lacks an ectostylid and a posterior longitudinal crest). Development of the anterior cingulum of the Laetoli specimen is similar to that of KNM-TH 19461. Sample sizes from Kapcheberek and Laetoli are small, and the differences between the two samples may reflect individual or geographic variation and may not be of taxonomic significance.

There is a very small sample of *Steatomys* reported from Kanapoi, but these specimens have not yet been described (4.19 Ma; Manthi & Winkler, 2020). *Steatomys* has been reported from several Plio-Pleistocene sites in South Africa.

Steatomys cf. *S. pratensis* is known from Rodent Cave, Makapansgat Limeworks, and Cave of Hearths (de Graaff, 1960; Pocock, 1987). Pocock (1987) reported *Steatomys* sp. from Kromdraai A and B and from Sterkfontein. Linchamps et al. (2023) recorded *Steatomys* in their sample from Cooper's Cave, South Africa. *Steatomys* sp. or *Malacothrix* sp. is also known from Langebaanweg (ca. 6 Ma; Hendey, 1981), South Africa. Pickford and Mein (1988) reported *Steatomys* cf. *S. opimus* from Gcwihaba C Hill, Botswana.

Steatomys is currently widely distributed in sub-Saharan Africa. It is known from habitats ranging from subdesert to degraded forest or forest edge, but it is most commonly found in savannas (Swanepoel and Schlitter, 1978).

Family MURIDAE Illiger, 1815
Subfamily MURINAE Illiger, 1815
Genus *SAIDOMYS* James and Slaughter, 1974
SAIDOMYS ALISAE Mein & Pickford, 2006
(Fig. 4A)

Referred material — Incomplete right mandible with m1-m3 and the posterior aspect of the incisor, missing the anterior end of the jaw, ascending ramus and coronoid process, KNM-TH 18476; left m1, KNM-TH 19465; both from Kapcheberek, BPRP#76c, Lukeino Formation.

Description — Measurements of the Kapcheberek and Tabarin *Saidomys*, as well as comparative material, are given in Table 3.

The first lower molars have distinct cusps in three separate transverse chevrons separated by wide valleys. The lingual cusps are slightly larger than, and located slightly anterior to, the labial cusps. There is a weakly developed (i.e., in comparison to *Saidomys* from Tabarin) medial anteroconid connected to the lingual anteroconid. A distinct labial cingulum extends from the labial anteroconid to the prominent C1 adjacent to the hypoconid. The cingulum includes C4 attached to the labial anteroconid and a tiny C2 anterior to C1. The posterior cingulum is a distinct midline low flatted oval. KNM-TH 18476 has large anterior and posterior roots: presence or absence of other roots is indeterminate. KNM-TH 19465 has large anterior and posterior roots and a smaller lingual root: presence or absence of a labial root is indeterminate.

The second lower molar is almost square in outline and has two well-separated transverse chevrons. The labial cusps are slightly larger and displaced slightly posterior to the lingual cusps. There is a prominent conical labial anteroconid that has a narrow valley between it and the protoconid. A strong labial cingulum extends from the labial anteroconid to the hypoconid. This cingulum includes small accessory cusps: tiny C4, C2, and C1, and slightly larger C3. C1 is about half the size that it is on the m1s. The elongate posterior cingulum is about 30% wider than it is on the m1 of KNM-TH 18476. There are large anterior and posterior roots.

The third lower molar is triangular in outline with a labial anteroconid that is adjacent to the protoconid and about half the size of the labial anteroconid of m2. An anterior loph is slightly crescentic in orientation: it is formed by fusion of the metaconid and a slightly larger protoconid. There is a large elongate hypoconid that is connected to the metaconid by a very short crest. A very narrow low posterior cingulum is present on the posterolabial aspect of the tooth. There is a large posterior root and likely two large anterior roots.

Discussion — Morphology of the very limited remains of *Saidomys* from Kapcheberek fits well within the diagnosis and description of *S. alisae* from the Kapsomin locality, collected and described by Mein & Pickford (2006; KNM-TH 18476 was included in their "Other material"). The Kapcheberek specimens can be assigned to *S. alisae* based on the following similarities: 1) similar size (see Table 3); 2) m1 with a weak medial anteroconid (=anterior median tubercle) that is connected to the lingual anteroconid, labial cingulum extending from the labial anteroconid to C1 (=posterior accessory cusplet), presence of a distinct posterior cingulum (=posteroconid) developed as a flattened oval (2006: Plate 2, fig. 26); 2) m2 with distinct labial anteroconid, labial cingulum extending from the labial anteroconid to C1, and posterior cingulum larger than on m1; and 3) m3 with a distinct labial anteroconid. The m3 of KNM-TH 18476 lacks a posterior cingulum but does have a weak low stylar shelf on the posterolabial side of the tooth. On the m3 figured by Mein & Pickford (2006: Plate 2, fig. 28), there is a low median shelf on the posterior end of the tooth. Root development cannot be accurately compared for the two samples since the teeth on KNM-TH 18476 are embedded in the bone and TH 19465 lacks roots.

The five generally accepted species of *Saidomys* include: *S. natrunensis* from Wadi el Natrun, Egypt (James & Slaughter, 1974; Slaughter & James, 1979), *S. afarensis* from two localities in the Sidi Hakoma Member, Hadar Formation,

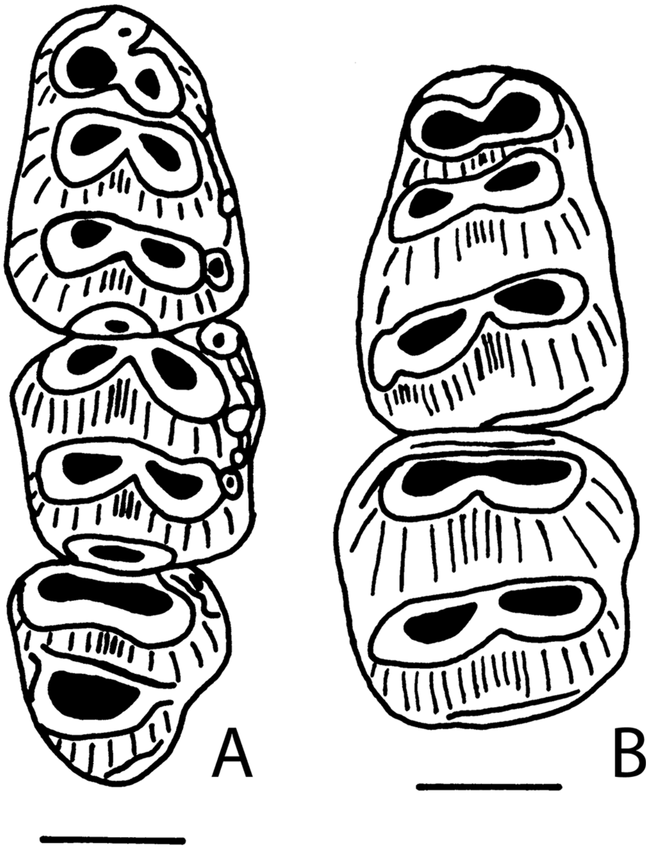

Figure 4. Murine rodents from the Kapcheberek locality, Lukeino Formation, Kenya. A) *Saidomys alisae*, right lower tooth row with m1-m3, KNM-TH 18476. B) *Arvicanthis* sp., left lower tooth row with m1-m2, KNM-TH 19462. Bar scale is 1 mm.

Ethiopia (Sabatier 1982), *S. afghanensis* (Sen 1983), from Pul-e Charkhi and Dawrankhel 14 and 15, Afghanistan, and *S. parvus* from Tanzania (Winkler, 1997). The chronologic range of the genus is from circa 6.5-2 Ma. Mein & Pickford (2006) made comparisons of *S. alisae* with these other species. Winkler (1997) discussed relationships among different species of *Saidomys* with respect to *S. parvus*. Small samples of *Saidomys* have also been reported from Lemudong'o (ca. 6 Ma; Manthi, 2007) and Kanapoi (4.19 Ma; Manthi, 2006; Manthi & Winkler, 2020), Kenya, as well as Aramis, Ethiopia (4.4 Ma; Louchart et al., 2009), but this material has not yet been described.

Genus *ARVICANTHIS* Lesson, 1842
ARVICANTHIS sp.
(Fig. 4B)

Referred material — Left incomplete mandible with m1, m2, the anterior end of the alveolus for m3, and the proximal portion of the coronoid process; KNM-TH 19462, BPRP #76c.

Description — Measurements of the Lukeino *Arvicanthis* and comparative material are given in Table 4. The specimen has wide molars with cusps elongated transversely. Labial and lingual cusps join to form transverse lophs.

The first lower molar has three separate transverse rows of cusps and lacks a medial anteroconid. C1 is present, moderate in size, and fused with the hypoconid. There are indistinct posterolabial spurs off the labial anteroconid and protoconid. A narrow posterior cingulum forms a shelf along the posterior end of the tooth. There is a large anterior root, one or two large posterior roots, and a smaller lingual root under the metaconid. Bulging of the base of the crown under the protoconid suggests a small labial root, but its presence is obscured by bone.

The second lower molar has two transverse chevrons formed by elongate cusps. There is a narrow anterior cingulum and a small labial anteroconid. C1 may be represented by a slight inflection of the enamel on the labial side of the hypoconid. A narrow posterior cingulum extends as a shelf along the posterior border of the tooth. The tooth has two anterior and two posterior roots. Presence of a labial root is obscured by bone.

Discussion — KNM-TH 19462 is assigned to *Arvicanthis* based primarily on the transverse orientation of the major rows of cusps on both m1 and m2, as well as the lack of a medial anteroconid on m1, reduced posterior cingula and poorly developed labial cingula on both teeth, and a reduced labial anteroconid on m2 (Misonne, 1969). Measurements of KNM-TH 19462 are within the size range seen in a small sample of extant *Arvicanthis* (Table 4).

Arvicanthis is presently a widespread and abundant taxon in savanna habitats. It ranges from south of the Sahara (although found along the Nile River) to the southern border of Zambia (Kingdon, 1974; Nowak, 1999; Monadjem et al., 2015). The sample from Lukeino is too small to assign to an extant species but the specimen appears distinct from several extinct taxa.

In East Africa *Arvicanthis primaevus* is known from Olduvai Bed I, Tanzania (Jaeger, 1976). *Arvicanthis primaevus* is diagnosed as smaller in size and having a simpler root

Table 3. Occlusal measurements (in mm) of *Saidomys alisae* from the Kapcheberek and Kapsomin localities, Kenya, and *Saidomys parvus* from the Tabarin locality, Kenya, and the Inolelo 1 locality, Tanzania.

	Length			Width		
Tooth & taxon	N	Mean	Observed range	N	Mean	Observed range
M1						
S. alisae[a]	-	-	-	-	-	-
S. alisae[b]	34	2.62	2.39-3.00	38	1.90	1.76-2.06
S. parvus[c]	4	2.58	2.50-2.65	3	2.04	2.00-2.12
S. parvus[d]	2	-	2.42-2.50	2	-	1.83-1.92
M2						
S. alisae[a]	-	-	-	-	-	-
S. alisae[b]	32	1.83	1.62-2.03	33	1.95	1.84-2.16
S. parvus[c]	2	-	2.06-2.12	2	-	1.88-2.00
S. parvus[d]	5	1.94	1.72-2.16	5	1.97	1.80-2.20
M3						
S. alisae[a]	-	-	-	-	-	-
S. alisae[b]	16	1.64	1.41-1.80	18	1.53	1.38-1.70
S. parvus[c]	1	-	1.88	2	-	1.62-1.65
S. parvus[d]	1	-	2.08	1	-	1.88
m1						
S. alisae[a]	2	-	2.36-2.41	2	-	1.59-1.71
S. alisae[b]	30	2.46	2.30-2.63	31	1.61	1.51-1.73
S. parvus[c]	1	-	2.67	1	-	1.83
S. parvus[d]	3	2.52	2.33-2.67	3	1.73	1.67-1.79
m2						
S. alisae[a]	1	-	1.82	1	-	1.76
S. alisae[b]	38	1.87	1.72-2.15	38	1.81	1.62-1.92
S. parvus[c]	2	-	1.92-2.04	2	-	1.88-2.04
S. parvus[d]	-	-	-	-	-	-
m3						
S. alisae[a]	1	-	1.65	1	-	1.59
S. alisae[b]	24	1.66	1.60-1.81	25	1.58	1.46-1.71
S. parvus[c]	3	-	1.71-1.82	3	-	1.59-1.71
S. parvus[d]	-	-	-	-	-	-

[a] *Saidomys alisae* from the Kapcheberek locality, Kenya
[b] *Saidomys alisae* from the Kapsomin locality, Kenya (Mein & Pickford, 2006)
[c] *Saidomys parvus* from the Tabarin locality, Kenya
[d] *Saidomys parvus* from the Inolelo 1 locality, Tanzania (Winkler, 1997)

pattern than extant *Arvicanthis*. Jaeger considered those characters primitive for the genus. Six specimens assigned to *Arvicanthis* sp. by Black and Krishtalka (1986) from Pleistocene deposits in the Koobi Fora Formation, east Lake Turkana, Kenya, are generally similar to *A. primaevus* in size and overall morphology of the lower teeth.

The Lukeino *Arvicanthis* is distinct from *A. primaevus* because the latter is smaller in size (Table 4), has posterior cingula as distinct cusps, has less transverse cusps, has a better developed C1 on m2, and eight of the nine m1s have a feeble anterior crest (mure) between the lingual anteroconid and metaconid. Presence of cuspate posterior cingula, an anterior crest on m1, and less transverse cusps, are plesiomorphic characters of *A. primaevus* relative to both the Lukeino specimen and extant *Arvicanthis.*

Arvicanthis sp. indet. is known from two upper molars from the Shungura Formation, Omo River valley, Ethiopia (3.03- >1.87 Ma; Wesselman, 1984). Wesselman (ibid) lists other Plio-Pleistocene reports of *Arvicanthis* from eastern, north, and southern Africa. Specimens from Olduvai Beds II and IV and Peninj (Denys, 1987), Tanzania, and from Garba IV, Ethiopia, are referred to extant taxa.

Jaeger (1975) described a new species, *A. arambourgi*, from Ternifine (middle Pleistocene), Algeria. Although comparable in size to the Lukeino jaw (Table 4), *A. arambourgi* has less transverse cusps, presence of an anterior crest (mure) on 42% (N = 36) of the m1s, and has a small cuspate posterior cingulum on at least one m2 (disposition of the posterior cingula on m1 and other m2s is uncertain).

Jaeger (1975) also named a new extinct subspecies of the extant, *A. niloticus*, from Irhoud Derbala Virage, Morocco, and Aïn Mefta, Algeria (one M1). *Arvicanthis niloticus irhoudae* was diagnosed as being 20% larger than *A. n. testicularis* (an extant subspecies) and having a simpler root pattern on M2 (Jaeger, 1975). He speculated that *A. n. irhoudae* may be ancestral to *A. arambourgi* because the former has a simpler root pattern on M2 and more isolated cusps. The validity of this subspecies needs to be reexamined. *Arvicanthis n. irhoudae* and the Lukeino teeth are overall quite similar. The single specimen (cast) of *A. n. irhoudae* examined differs in having a small medial anteroconid and larger lingual anteroconid on m1, and a better developed labial anteroconid and C1 on m2. An illustration of another m2 (Jaeger, 1975) shows a posterior cingulum developed as a moderate-sized cusp. These differences are likely within the range of individual variation seen in extant *Arvicanthis*. Individual variation in *A. n. irhoudae* is undescribed.

Tchernov (1968) mentioned (but did not describe or illustrate) *Arvicanthis ectos*, an extinct species from the Pleistocene of Israel. Jaeger (1976) stated that the upper toothrow of this species is referable to *Rattus*, but the lower toothrow corresponds to *Arvicanthis*. Size of the lower toothrow is not indicated. The specimen resembles *Arvicanthis* of modern grade based on transverse rows of cusps, lack of a medial anteroconid on m1, reduced labial cingula (only a small C1 on m1, a smaller C1 or just a cingulum on m2), and reduced posterior cingula on both m1 and m2. From occlusal morphology alone, the Israeli and Lukeino dentaries are of similar evolutionary grade, but detailed comparisons await a revision of the Israeli material.

Lavocat (1957, 1967) reported *Arvicanthis* (?) from Sterkfontein, South Africa. If substantiated, this is an important record, as the genus is not currently found in southern Africa (Kingdon, 1974; Nowak, 1999). However, there are no descriptions or illustrations of the specimen(s), and the genus is not included in faunal lists from Sterkfontein in de Graaff (1960) or Pocock (1987).

A partial maxilla, left and right mandibles and fragmentary postcrania of a single individual of an extinct species, *A. musisii,* were reported by Mein (1994) from the lower Pliocene of Uganda. *Arvicanthis musisii* is diagnosed by large size, and (in terms of m1 and m2) having: 1) an m1 with a connection between the lingual anteroconid and the metaconid (lacking in KNM-TH 19462) and a weak posterior cingulum (present as a cusp on *A. musisii* but as a low ridge on KNM-TH 19462); and 2) an m2 lacking a posterior cingular tubercle (an elongate low ridge is present along the posterior margin of the tooth on the drawing of m2 (Mein, 1994: Planche I.B). The m2 of KNM-TH 19462 also has a low posterior cingular ridge, but it is located posterolabially. Other differences (from comparison with the illustrated specimen in Mein [Mein, 1994: Planche I.B] include: on the Ugandan teeth: 1) on m1 anteroconids unequal in size (lingual is larger), while they are comparable in size on KNM-TH 19462; 2) the Ugandan specimen has a weaker C1 on m1; and 3) the m2 of the Ugandan specimen has an anterolabial cusp (only a weak crest on KNM-TH 19462) and a small C1 (absent on KNM-TH 19462). The m1 of *Arvicanthis musisii* is longer than that of KNM-TH 19462, but otherwise the size is comparable.

Manthi (2007) reported 10 dental elements (including upper and lower dentition) from Lemudong'o, Kenya (6 Ma), attributable to *Arvicanthis* sp., plus two assignable to cf. *Arvicanthis*. The remains are not illustrated, described or compared in detail. Manthi does note, however, that the material is comparable in size and morphology to that of extant *A. niloticus* and/or *A. abyssinicus*. Tooth morphology of an illustrated specimen from Lemudong'o, KNM-NK

Table 4. Measurements (in mm) of *Arvicanthis* sp. from the Kapcheberek locality, BPRP#76, Lukeino formation, Kenya, and comparative fossil and extant specimens.

Taxon	Locality	Length m1	Width m1	Length m2	Width m2
Arvicanthis sp.	BPRP#76	2.59	1.94	2.06	2.18
A. *musisii*[a]	Kazinga Channel, Uganda	2.92-2.96 N=2	1.98-2.03 N=2	1.99-2.01 N=2	2.18-2.19 N=2
A. primaevus[b]	Olduvai, Tanzania	2.15-2.33 N=8	1.47-1.65 N=8	1.56-1.63 N=4	1.56-1.65 N=4
A. sp.[c]	Lake Turkana, Kenya	2.21-2.25 N=2	1.47-1.55 N=2	1.47-1.81 N=3	1.50-1.70 N=3
A. arambourgi[d]	Ternifine, Algeria	2.56-2.95 X=2.76 N=36	1.69-2.01 X=1.89 N=36	1.85-2.07 X=1.98 N=31	1.91-2.16 X=2.03 N=31
A niloticus[e]	East & west Africa	2.46-3.00 N=4	1.77-2.25 N=4	1.77-2.00 N=4	1.92-2.58 N=4

[a] Measurements from Mein (1994)
[b] Measurements from Jaeger (1976)
[c] Measurements from Black & Krishtalka (1986)
[d] Measurements from Jaeger (1975)
[e] Extant specimens; specimen labels list them as subspecies *mordax*, *testicularis*, and *abyssinicus*

41089 (m1-m2; Manthi, 2007: fig. 4) is comparable to that of teeth of KNM-TH 19462. However, there are some differences in development of the labial cuspids on the Lukeino m2 (e.g., stronger C1 on KNM-NK 41089 than on that from Lukeino), although that may be attributable to individual variation. Measurements of the Lemudong'o teeth (Manthi, 2007: Table 1) are confusing as they are considerably lower than that for the extant and fossil *Arvicanthis* reported here (Table 4; e.g., m1 of the Lemudong'o averaging 1.7×1.1 mm). *Arvicanthis* is also reported (but not described) from Aramis, Ethiopia (4.4 Ma; Louchart et al., 2009).

In summary, the Lukeino *Arvicanthis* is one of the earlier records of the genus. For its geologic age, it, surprisingly, already possesses many derived characters of the genus such as large size, transverse cusp rows, lack of a medial anteroconid and connections between the anterior two toothrows on m1, posterior cingula developed only on m1 and m2, and reduction of other accessory cuspids. Although the sample size is very small, the Lukeino specimen appears more similar to extant *Arvicanthis* than it does to any adequately described extinct taxon. The possibility that this specimen was contamination from more recent sediments was considered, but its preservation matches that of other rodents from the Kapcheberek locality.

Chemeron Formation rodents.

Matrix from the Tabarin locality yielded a minimum of eight taxa of rodents. These include the sciurids *Heliosciurus* and *Paraxerus*, the deomyine *Tectonomys*, the murines cf. *Mus*, *Grammomys* or *Thallomys* sp., *Saidomys parvus*, and the thryonomyid, *Thryonomys*.

Family SCIURIDAE Hemprich, 1820
Subfamily XERINAE Osborn, 1910
Genus *HELIOSCIURUS* Trouessart, 1880
Cf. *HELIOSCIURUS* sp.
(Fig. 5A)

Referred material — Left p4, KNM-TH 19484, from Tabarin, BPRP#77a, Chemeron Formation.

Description — Occlusal measurements of the Tabarin sciurids are given in Table 5. The tooth is lightly worn and roughly ellipsoidal in outline. A protoconid and hypoconid are well-developed and about equal in height. The metaconid is the tallest cusp on the tooth. There is a distinct anteroconid separated by a sulcus from the protoconid and connected lingually to the metaconid. The protoconid and metaconid are connected by a short metalophid. An indistinct mesoconid is present on the ectolophid between the protoconid and

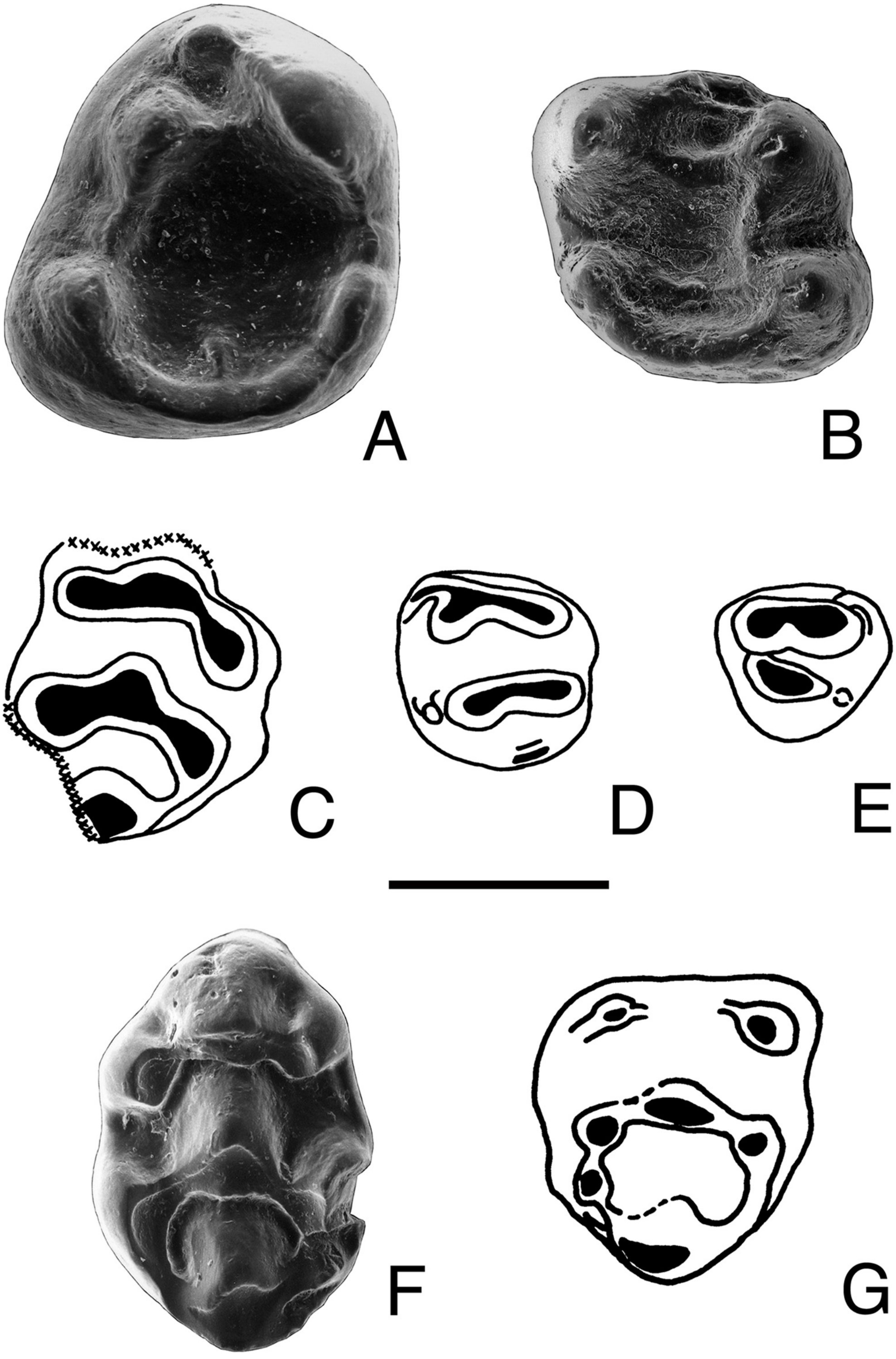

Figure 5. Sciurids (cf. *Heliosciurus*, *Paraxerus meini*), and murines (cf. *Mus*, *Grammomys* or *Thallomys*) from the Tabarin locality, Chemeron Formation, Kenya. A) cf. *Heliosciurus* sp., left p4, KNM-TH 19484. B) *Paraxerus meini*, right m1 or m2, KNM-TH 19473. C-E, cf. *Mus*, C), right M1, KNM-TH 19468, D) left m2, KNM-TH 19475, E) right m3, KNM-TH 19476. *Grammomys* or *Thallomys* sp. F) left M1, KNM-TH 22308, G) right M2, KNM-TH 19478. Bar scale is 1 mm.

Table 5. Occlusal measurements (in mm) of fossil sciurids from the Tabarin locality, Kenya, and comparative fossil and extant taxa.

Taxon	Specimen number	Locality	Tooth position	Length	Width
Cf. *Heliosciurus*	KNM-TH 19484	Tabarin, Kenya	Lp4	2.31	1.85
H. ruwenzorii	-	Extant, Congo	p4	2.00-2.08 N=3 X=2.03	1.71-2.00 N=3 X=1.69
H. gambianus	-	Extant, Congo	p4	1.77	1.69
H. rufobrachium	-	Extant, Ivory Coast	p4	2.15-2.31 N=5 X=2.21	2.15-2.46 N=5 X=2.26
Kubwaxerus pattersoni	KNM-LT 23087	Lothagam, Kenya	Rp4	2.44	2.06
Paraxerus meini	KNM-TH 19473	Tabarin, Kenya	Rm1 or m2	1.64	1.60
P. meini[a]	various	Laetoli, Tanzania	m1	1.67=1.90 N=6 X=1.77	1.57-1.76 N=6 X=1.68
			m2	1.71-1.82 N=5 X=1.75	1.71-1.90 N=5 X=1.80
P. ochraceus[b]	various	Omo, Ethiopia	m1 or m2	1.61-1.86 N=6 X=1.77	1.70-1.97 N=7 X=1.80

[a] Measurements from Denys (2011)
[b] Measurements from Wesselman (1984)

hypoconid. An entoconid is moderately developed and connected to the hypoconid by a posterolophid. A small mesostylid lies between the entoconid and metaconid. There is a weak hypoconulid just labial to the entoconid. The talonid basin is wide and relatively shallow. Short spurs extend toward its center from the metalophid and posterolophid. Root development is indeterminate.

Discussion — Among extant taxa, the Tabarin tooth is most similar to the exclusively African genus *Heliosciurus* (Sun Squirrels). The fossil tooth was compared with three of the six extant forms listed by Thorington & Hoffmann (2005), *Heliosciurus ruwenzorii vulcanius*, *H. gambianus rhodesiae*, and *H. rufobrachium rubricatus*, *coenosus* and *aubryi*. Amtmann (1975) lists 52 subspecies for these and notes that “too many subspecies are certainly recognized” for *H. gambianus* and *H. rufobrachium*. Taxonomy of the genus is extremely complicated, primarily because of the great variability in pelage color reflecting local conditions of temperature and moisture (Rosevear, 1969).

Major differences between the fossil and the extant taxa include: in the extant specimens (1) the distance between the protoconid and hypoconid is greater; (2) the labial side of the tooth between the protoconid and hypoconid slopes labially less steeply, and the ectolophid often has a lingually projecting spur; and (3) in many individuals of *H. gambianus* and some of *H. rufobrachium*, the hypoconid is proportionally larger and extends more labially. The major difference between the fossil and the extant taxa is in the development of the entoconid. The entoconid of the fossil is relatively small, distinct, and anteriorly placed. In the extant specimens of *Heliosciurus* examined, the entoconid is usually larger, less distinct, and extends farther posteriorly. A large and posteriorly placed entoconid, especially associated with a large hypoconid, gives a more triangular outline to many modern specimens. Differences in size between the Tabarin tooth and comparative material are generally one of proportion; the fossil is narrow for its length because of the relatively small hypoconid and entoconid. Root development is indeterminate.

The Tabarin cf. *Heliosciurus* tooth also shows similarities with an extinct giant squirrel, *Kubwaxerus pattersoni*, known only from the late Miocene (7.44-6.54 Ma), upper member of the Nawata Formation, at Lothagam, Kenya (Cifelli et al., 1986; Winkler, 2003). The Tabarin specimen was compared with casts of two specimens mentioned by Winkler (2003), but not yet described. The two taxa differ in: 1) in KNM-TH 19484 the anteroconid does not contact the protoconid while in *Kubwaxerus pattersoni* the anteroconid is present as an anterior cingulum that contacts the protoconid; 2) the entoconid of KNM-TH 19484 is located relatively more anteriorly; 3) the talonid basin of KNM-TH 19484 is relatively wider; and 4) *Kubwaxerus pattersoni* is larger, with the smaller of two specimens (KNM-LT 23087) 5-10% larger than the Tabarin tooth.

Sun squirrels are exclusively African and are found from the west to east coasts from about 17° N to 20° S Latitude (Rosevear, 1969). Rosevear describes them (in West Africa) as typically inhabiting dense woodland, “fringing forest and remnant patches, as well as of secondary farm regrowth within the high forest zone itself.” Amtmann (1975) notes that *H. ruwenzorii* occurs in forests between 1600 to 2400 m, *H. gambianus* in savanna woodland and secondary forest (“more of an open woodland animal,” Rosevear, 1969; has a “general but not exclusive preference for drier habitats,” Kingdon, 1974), and *H. rufobrachium* in rain forests (“more of a closed forest animal,” Rosevear, 1969; it may occupy relatively dry habitats in East Africa according to Kingdon, 1974). The presence of *Heliosciurus* in the Tugen Hills fossil record is consistent with a savanna woodland, woodland, or dense forest habitat.

Genus *PARAXERUS* Forsyth Major, 1893
PARAXERUS MEINI Denys, 2011
(Fig. 5B)

Referred material — Right m1 or m2, KNM-TH 19473, from Tabarin, BPRP#77a, Chemeron Formation.

Description — Based on size comparison with the material from Laetoli, Tanzania (Table 5), KNM-TH 19473 is likely an m2. The Tabarin tooth is essentially square in occlusal outline with transverse crests and bunodont cusps. A ridge with multiple very small supplementary cuspids connects the metaconid to the anteroconid. There is a distinct metalophid, which is slightly concave posteriorly. The ectolophid is also distinct and slightly curved: a mesoconid may be present but is very indistinct. A low transverse entolophid connects the entoconid to the anterior part of the hypoconid. There are a few indistinct supplementary cuspids on the entolophid. There is also a long, posteriorly concave, posterolophid: this lophid lacks any supplementary cusps. Root development is indeterminate.

Discussion — The Tabarin *Paraxerus* is assigned to *P. meini*, described from the Upper Laetolil (3.8-ca.3.4 Ma) and Upper Ndolanya Beds (2.7-2.6 Ma), Laetoli, Tanzania (Denys, 1987 as *Paraxerus* sp. indet.; Denys, 2011). Comparisons of the Tabarin specimen with the Laetoli material were based on two casts (LAET-76, 4170 and 4178) as well as published illustrations and descriptions in Denys (2011). Assignment of the Tabarin tooth to *P. meini* is based on the tooth being of small size with bunodont cusps, presence of supplementary cuspids, a distinct ectolophid and a transverse entolophid directly connected to the anterior part of the hypoconid. In contrast to the Laetoli specimens, TH 19473 lacks supplementary cusps on the posterolophid. The ectolophid of the Laetoli material is described as longitudinal, but it is curved on at least one specimen (LAET 76-4178), comparable to the curvature seen on the Tabarin tooth. Denys noted the presence of a mesoconid on the ectolophid: on the two casts, the cusp appears to be lacking on the m1s, but is present on an m2. Wesselman (1984) described multiple isolated teeth of *P. ochraceus* (an extant species) from the Shungura Formation, Omo River Valley (Members B, C; 3.03-2.08 Ma) of Ethiopia. He noted the specimens from Omo were generally similar to those from Laetoli, except for some differences in tooth size. Denys (2011) also noted that the Omo material was quite similar in morphology to *P. meini* from Laetoli.

Early records of *Paraxerus* are from Lemudong’o, Kenya (Manthi, 2007; ca. 6 Ma) and Kanapoi, Kenya (Manthi, 2006; Manthi & Winkler, 2020; 4.19 Ma). The Lemudong’o record is a single isolated Lp4 (KNM-NK 44920). Based on the published image (Manthi, 2007: Fig. 10), and as noted by Denys (2011), the tooth lacks an ectolophid, a characteristic feature of the genus. The specimen also does not appear to have an entolophid. The Lemudong’o tooth does have similarities to the other sciurid from Tabarin, KNM-TH 19484: comparable small size, protoconid and metaconid close with an anteroconid between them, wide talonid basin, and relatively anterior entoconid. For now, it is recommended that the Lemudong’o tooth be re-examined before being definitively assigned to *Paraxerus*. Manthi (2006) reported a mandible (KNM-KP 46313) from Kanapoi as *Paraxerus*.

However, Manthi and Winkler (2020) consider all sciurids from Kanapoi to pertain to *Xerus*. Pending assignment of the Lemudong'o specimen, the Tabarin *Paraxerus* would be the oldest record of the genus from Africa.

Paraxerus, the African Bush Squirrel, is found exclusively in Africa. Thorington and Hoffman (2005) include 11 species in the genus. *Paraxerus ochraceus* is the only species currently found in the study area. It includes five (Kingdon, 1974) to eight (Amtmann, 1975) subspecies, which occur in a wide variety of wooded habitats. Nowak (1999: 1279) notes that the genus *Paraxerus* is currently "found in forests, plantations, and other areas where there are trees."

Family MURIDAE Illiger, 1815
Subfamily DEOMYINAE Lyddeker, 1889
Genus *TECTONOMYS* Winkler, 1997
TECTONOMYS AFRICANUS Winkler, 1997

Referred material — Right M1, KNM-TH 18477, holotype, from Tabarin, BPRP#77a, Chemeron Formation.

Description — The tooth (figured in Winkler, 1997: Fig. 4A; Winkler, 2002: Fig. 2c; Denys & Winkler, 2015: Fig. 7.3) is relatively elongate. Cusps in the longitudinal midline (lingual anterocone, protocone, and hypocone) are the largest. An anterostyle is slightly displaced posteriorly relative to the rest of the anterior chevron and is strongly compressed labio-lingually. The large lingual anterocone is situated transverse to the smaller labial anterocone. Projecting posterolabially from the labial anterocone is an elongate spur. A precingulum and stylar cusps are lacking. Cusps of the middle chevron are transverse with the paracone and enterostyle only slightly posterior to the protocone. The enterostyle is slightly oblique to the protocone and paracone. The paracone and enterostyle are rounded and similar in size. The posterior chevron includes a transversely elongate hypocone and a smaller more rounded metacone. These two cusps are at the same transverse level. The hypocone is lingual relative to the median location of the lingual anterocone and protocone. A posterostyle is lacking. The posterior cingulum is well developed, semi-lunar in shape, and posteriorly connects the hypocone to the metacone, enclosing an ellipsoidal basin. Chevrons of the tooth are separated by deep transverse valleys and the cusps of each chevron are separated by shallow wide valleys. There are three large roots: anterior, posterior, and lingual.

Discussion — *Tectonomys africanus* is based on a holotype from Tabarin and a hypodigm of two M1s and seven M2s from Inolelo 1, Ibole Member, Manonga Valley, Tanzania (Winkler, 1997). The Manonga Valley specimens date to the late Miocene or early Pliocene (ca. 6-4 Ma) based on overall faunal correlation, or to the early Pliocene using only the rodents. Teeth of *Tectonomys* are large, brachydont, and relatively elongate. The M1 is characterized by a posteriorly displaced anterostyle, cusps in the middle chevron oriented transverse to one another, an elongate lingually placed hypocone at the same transverse level as the metacone, a very strong posterior cingulum, and three roots. The phylogenetic relationships of *Tectonomys* were discussed in Winkler (1997) and Denys & Winkler (2015). *Tectonomys* was originally considered within Murinae (Winkler, 1990, 1997) but placed later within Deomyinae (Winkler, Denys & Avery, 2010; Denys & Winkler, 2015).

Subfamily MURINAE Illiger, 1815
Genus *MUS* Linneaus, 1758
cf. *MUS* sp.
(Fig. 5)

Referred material — Right incomplete M1, KNM-TH 19468 (width ~1.06 mm); left m2, KNM-TH 19475 (1.02× 1.00 mm); right m3, KNM-TH 19476 (0.94×0.72 mm). All from Tabarin, BPRP#KO77a, Chemeron Formation.

Description — These teeth are small and brachydont. The M1 (Fig. 5C) is missing the anterior end of the tooth and the posterolabial corner including the metacone and part of the hypocone. An anterior chevron consists of a smaller labial anterocone closely opposed to and transversely aligned with a larger lingual anterocone. The anterostyle is lightly compressed and is displaced posteriorly at about 70^{o} to the rest of the chevron. The middle chevron has a large protocone, and a paracone and enterostyle that are roughly similar in size and only slightly smaller than the protocone. The enterostyle is not compressed: it is displaced posteriorly relative to the rest of the chevron. The anterostyle and enterostyle are notably less compressed labiolingually compared to the condition observed in *Acomys*. There is a large inflated hypocone with the enamel on its lingual side thickened slightly. A short indistinct crest connects the hypocone to the enterostyle. A posterostyle is lacking. Presence of a posterior cingulum and the number of roots is indeterminate.

The m2 (Fig. 5D) is trapezoidal in shape and tapers posteriorly. There are two lophs formed by the protoconid and metaconid anteriorly, and the hypoconid and entoconid posteriorly. The major labial cusps are slightly larger than, and located a little posterior to, the major lingual cusps. An anterolabial cusp is elongate and connected by wear to the protoconid. This cusp is considerable smaller than that seen in *Acomys*. There is a labial cingulum between the protoconid and hypoconid which includes a small C1 adjacent to the hypoconid. The posterior cingulum is low and elongate connecting the posterior two cusps and enclosing a circular basin. There are large anterior and posterior roots.

An m3 (Fig. 5E) is triangular with the apex posterior. The larger protoconid and smaller metaconid are fused through wear to form a transverse loph. There is a low, moderately developed anterolabial cingulum. The hypoconid is large with its lingual side tilted anteriorly. A weak indentation on its anterior side demarcates an indistinct entoconid that is fused to the hypoconid. C1 is low, indistinct, and adjacent to the hypoconid. A large posterior root and one or two anterior roots are present.

Discussion — These specimens are similar to *Mus* in their small size, presence of a posteriorly displaced anterostyle and enterostyle on M1, and a strongly trapezoidal outline to m2. In extant *Mus*, however, the anterostyle tends to be more compressed labiolingually and the m3 tends to be more reduced in length relative to m2. The oldest known African records of *Mus* are from Lissasfsa, Morocco (Mio-Pliocene: Geraads, 1998), and Aramis, Ethiopia (Louchart et al., 2009). The large sample from Lissasfsa (around 150 teeth) was assigned to a new extinct species, *M. ique*. Compared to the very small sample from Tabarin, the m2 and m3 of *M. ique* (the Tabarin M1 is quite incomplete) are smaller, and from the photographs (Geraads, 1998: Fig. 12.4, 7, 8), the lophs on m2 are more oblique and there is a distinct posterior cingulum, and the m3 is proportionally longer. The Aramis material has not yet been described.

Some other African fossil records of *Mus* are from just over 3 Ma at Hadar (Sabarier, 1982) and the Omo Valley (Wesselman, 1984), Ethiopia, as well as the Plio-Pleistocene of the Maghreb, North Africa (e.g., Jaeger, 1975). Wesselman (1984) summarizes other fossil African records of *Mus*.

Presence of an anterolabial cingulum (or labial anteroconid) on the Tabarin m3 is a primitive character seen in the extinct genus *Progonomys* (a sister taxon to *Mus*) and at least some fossil *Mus* (i.e., *Mus auctor* from Pakistan [5.7 Ma, Jacobs, 1978], and some *Mus petteri* from Olduvai, Tanzania [Jaeger, 1978]). Development of this cingulum on *M. ique* is uncertain (likely very small or lacking). There are no m3s of the *Mus* from Hadar or Omo. The anterolabial cingulum is lacking in extant *Mus*. It is observed on some *Acomys* (pers. comm. C. Denys).

Genus *GRAMMOMYS* Thomas, 1915 or *THALLOMYS* Thomas, 1920

GRAMMOMYS or *THALLOMYS* sp.

(Fig. 5)

Referred material — Left M1, KNM-TH 22308 and right M2, KNM-TH 19478; both from BPRP#77a.

Description — Measurements of the Tabarin specimens and comparative material are given in Table 6. The first upper molar (Fig. 5F) is rounded in occlusal outline and has distinct cusps. The midline cusps (lingual anterocone, protocone, and hypocone) are the largest. The anterior chevron has conical cusps. The labial anterocone is relatively small and located close to the lingual anterocone. The anterostyle is slightly larger than the labial anterocone and is posterior to the rest of the chevron. A precingulum and prestyles are lacking. The middle chevron is slightly concave posteriorly. A rounded paracone (broken) is slightly posterior to the protocone. The enterostyle is similar in size to the paracone but is less rounded and located more posteriorly. The paracone and enterostyle are separated from the protocone by short crests. The posterior chevron includes a very large conical hypocone and smaller conical metacone (broken) situated anterolabially. The metacone is connected to the paracone and hypocone by short crests. The posterostyle is reduced to a long crest connecting the hypocone to the enterostyle. There is a weak posterior cingulum. There are large anterior and posterolabial roots, two closely spaced lingual roots (the most anterior is the larger), and a smaller labial root.

The second upper molar (Fig. 5G) is wide anteriorly and tapers posteriorly. There is a large conical anterostyle and a much smaller labial anterocone. The labial anterocone is joined to the protocone by a very low crest. The large protocone is connected to a smaller paracone and enterostyle by short crests. The latter two cusps are conical and located slightly posterior (especially the enterostyle) to the protocone. A

Table 6. Measurements (in mm) of *Grammomys* or *Thallomys* sp. from Tabarin, Kenya, as well as representative fossil and extant taxa.

Taxon	Locality	Length M1	Width M1	Length M2	Length M2
Grammomys or *Thallomys* sp.	Tabarin, Kenya	1.92	1.33	1.43	1.36
Grammomys dolichourus[a]	various	1.81-2.27 X=2.03 N=14	1.22-1.50 X=1.38 N=14	1.26-1.65 X=1.43 N=15	1.22-1.50 X=1.36 N=15
Grammomys cometes	Various (N=5)	1.89-2.31 X=2.13	1.36-1.52 X=1.44	1.43-1.62 X=1.50	1.39-1.50 X=1.44
Thallomys loringi	Various (N=7)	2.28-2.56 X=2.45	1.61-1.71 X=1.66	1.61-1.89 X=1.79	1.57-1.73 X=1.68
Thallomys quadrilobatus[b]	Olduvai, Tanzania	2.23-2.59 X=2.41 N=16	1.58-1.78 X=1.67 N=16	1.52-1.75 X=1.62 N=8	1.53-1.72 X=1.63 N=8
Thallomys jaegeri[c]	Omo, Ethiopia	2.06-2.08 N=2	1.35-1.38 N=2	1.46-1.54 N=4	1.34-1.40 N=4
Thallomys laetolilensis[d]	Laetoli, Tanzania	2.05-2.42 X=2.18 N=11	1.40-1.67 N=1.54 N=13	1.55-1.68 N=1.61 N=7	1.50-1.62 N=1.57 N=6

[a] Includes *G. dolichourus discolor*, *G. d. lutosus*, and *G. d. polionops*
[b] Measurements from Jaeger (1976)
[c] Measurements from Wesselman (1984)
[d] Measurements from Denys (1987)

short crest extends between the very large hypocone and smaller, conical, more anteriorly placed metacone. A short crest connects the metacone to the paracone. The posterostyle is represented by a long crest connecting the hypocone to the enterostyle. A weak posterior cingulum is present. The root pattern is indeterminate.

Discussion — One of the most distinctive characters of KNM-TH 18481 and 19478 is presence of a strong ridge connecting the hypocone to the enterostyle, which represents the posterostyle. This (along with overall morphology including stephanodonty between the middle and posterior chevrons, a weak posterior cingulum, and five roots on M1) is consistent with assignment to one of two extant genera, *Grammomys* or *Thallomys* (Davis, 1972; Misonne, 1974). The strength of the connection between the enterostyle and hypocone is more like *Grammomys*, but within the range of individual variation in *Thallomys*. The fossils are excluded from *Thamnomys* because that taxon has a distinct posterostyle and a reduced metacone (Davis, 1972; Misonne, 1974).

The Tabarin teeth were compared with two species (four subspecies) of extant *Grammomys* and with one species of *Thallomys* (sensu Misonne, 1974). From comparison of occlusal and root morphology of M1 and M2, and from published descriptions of the two genera [which state that they differ in pelage, bullae, and development of the anteroconid on m1 (Misonne, 1974)], the fossils cannot be confidently assigned to one genus or the other. The M1 and M2 of comparative specimens of *Thallomys* are longer and wider than those of *Grammomys* (and larger than the fossils; Table 6), but this difference by itself is not enough to warrant generic distinction of the fossils. Extant comparative specimens of *Thallomys* and *Grammomys* have similar length:width ratios for M1 and M2 (1.48 for M1 and 1.04-1.06 for M2). Another Tabarin M1 is proportionally wider (L/W for M1 = 1.36) compared to the extant specimens, but the significance of this is uncertain. The Tabarin teeth differ from extant taxa in that the ridge connecting the hypocone and metacone on both the fossil M1 and M2 is short. This ridge is appreciably longer on 93% (N = 20) of the M2s of extant *Grammomys*. Ridge length is similar (50%) or longer (50%) on the M1s of *Grammomys* and on M1s and M2s of *Thallomys*.

Grammomys and *Thallomys* are known from the Plio-Pleistocene of southern and eastern Africa (summarized in Denys, 1999). De Graaff (1981) reported *Grammomys* cf. *G. dolichurus* and *Thallomys* cf. *T. paedulcus* from Makapansgat (about 3.3 Ma; Denys, 1999) and Kromdraai, South Africa. Broom (1948) described an extinct species, *Thallomys debruyni*, from Taung (about 2.5 Ma; Denys, 1999), South

Africa. This taxon is based on a single specimen, the anterior two-thirds of a skull with the molars "broken off." Taxonomic assignment of this specimen needs confirmation. *Thallomys* and *Grammomys* are reported from Aigames II (1-2 Ma; *Thallomys*) and Berg Aukas I (~13 Ma; *Grammomys*), Namibia (Conroy et al., 1992). This material has not been described. Denys (1999) also noted late Pliocene-early Pleistocene records of *Thallomys* from Humpata Level 2, Leba, Angola, and *Grammomys* from Sterkfontein and Swarkkrans, South Africa. *Thallomys* has also been reported from Cooper's Cave, South Africa (1.4 Ma; Linchamps et al., 2023).

Thallomys laetolilensis was reported from the Upper Laetolil Beds, Laetoli, Tanzania (Denys, 1987, 2011). Denys also described an incomplete mandible of *Thallomys* cf. *T. laetolilensis* from the Upper Ndolanya Beds of Laetoli. Considering only the upper dentition, Denys (1984) distinguished the Laetoli material from *Grammomys* primarily on the absence of a posterostyle on *Thallomys* and on the Laetoli fossils. However, both of these taxa (personal observation) usually have the posterostyle represented by a small cusp or a ridge between the enterostyle and hypocone, although it is usually more prominent in *Grammomys*.

The specimens from Tabarin differ from *T. laetolilensis* in two derived characters. The Tabarin teeth seem to have a stronger ridge between the enterostyle and hypocone and the M1 has five roots (*T. laetolilensis* has four). The Tugen Hills M1 is close to the size range of *T. laetolilensis*, but the M2 is smaller (Table 6).

Wesselman (1984) described *Thallomys quadrilobatus* (Omo Member F, 2.08 and Member G, 1.98 Ma) and a new species of *Thallomys*, *T. jaegeri* (Member B, 3.03 and Member C, 2.48 Ma), from small samples of isolated teeth from the Omo River valley, Ethiopia. *Thallomys jaegeri* is basically similar in morphology to, but significantly smaller than, *T. quadrilobatus* (Table 6). Although similar in size (Table 6), the Tabarin specimens differ from *T. jaegeri* in having an extra root on M1. The posterior cingula on the Tabarin M1 and M2 are weak (derived condition), while those of *T. jaegeri* are described as well developed (Wesselman, 1984).

The type of the extinct species *Thallomys quadrilobatus* is from Olduvai Beds I and II, Tanzania (1.8-1.75 Ma, Jaeger, 1976). In addition to the Omo River Valley record (Wesselman, 1984), the species is also known from the Koobi Fora Formation, East Turkana, Kenya (Plio-Pleistocene, Black and Krishtalka, 1986) and the Peninj Site, West Natron, Tanzania (Denys, 1987). This species is similar in size and overall morphology (including five roots on M1) to an extant species *Thallomys paedulcus*, however, *T. quadrilobatus* differs in a number of minor characters including having an M1 with the labial anterocone closer to the lingual anterocone (Jaeger, 1976). Contra Black and Krishtalka (1986), extant *T. paedulcus* does have a posterior cingulum on M1, but it is weakly developed. Jaeger (1976) noted that extant east and South African populations of *T. paedulcus* have a number of differences, and that *T. quadrilobatus* is most similar, and probably ancestral to, the southern African populations. *Thallomys quadrilobatus* lacks a posterostyle according to Jaeger (1976), but it has distinct crests between the enterostyle and hypocone.

Grammomys or *Thallomys* from Tabarin is distinct from *T. quadrilobatus* in being noticeably smaller (Table 6). The two taxa share the synapomorphy of five roots on M1 and differ from *T. laetolilensis*, which has a primitive pattern of four roots.

Jaeger (1976) tentatively referred a small M1 and partial mandible with m1-m3 from Olduvai Middle Bed I to *Grammomys*. Contra Jaeger (1976), a cast of the M1 shows a connection between the enterostyle and hypocone. Minor differences between that material and the Tabarin teeth are probably within the range of individual variation seen in modern populations.

Denys (1987) suggested that *T. laetolilensis* is ancestral to *T. quadrilobatus* based on the former's smaller size (primitive), weaker stephanodonty (primitive), and less elongate anterior four major cusps on m1. The derived root pattern of the geologically younger *T. quadrilobatus* also suggests this relationship. Wesselman (1984) suggested that *T. jaegeri* (from Omo localities dated 3.08-2.48 Ma) may be ancestral to *T. quadrilobatus* (from Omo localities dated 2.08-1.98 Ma). Differences between these taxa from Omo localities include *T. jaegeri* having less stephanodonty (primitive), more robust posterior cingula on M1 and M2 (primitive), less developed posterior cingulum on m1, and four roots on M1 (primitive). Affinities of the Tabarin specimens are difficult to evaluate because of the small sample size and questionable generic assignment. However, the synapomorphy of five roots on M1 suggests a closer relationship with both Olduvai taxa [*T. quadrilobatus* and especially the smaller taxon, *Grammomys* sp. indet.].

Mein & Pickford (2006) established a new genus, *Lukeinomys*

(*L. cheptumoae*), from a small sample from Kapsomin, Lukeino Formation. They suggested it "could be ancestral to" (Mein & Pickford, 2006: pg 208) the *Thallomys*-*Grammomys* group and noted that it differed from that group by the presence of archaic characters such as the absence of stephanodonty between the paracone (t6) and metacone (t9) and a simpler root pattern. On the Tabarin teeth, the presence of stephanodonty between the paracone and metacone as well as an M1 with five roots (*L. cheptumoae* has four) precludes assignment of the Tabarin teeth to *L. cheptumoae*. Mein & Pickford (2006: p. 208) noted they have new collections of material from Tabarin (unpublished) that includes lower molars and that these specimens lack the sharp chevroning they observe in *Thallomys*, but which is lacking in *Grammomys*. Thus, they consider their Tabarin specimens to pertain to *Grammomys*. They also consider *T. laetolilensis* (Denys, 1987) to pertain to *Grammomys* for this reason. Since lower molars are unavailable in the collection described here, this character cannot be evaluated.

Thallomys is currently found in East Africa in acacia bush and woodland habitats where it lives almost exclusively in acacia trees (Kingdon, 1974). Species of *Grammomys* are found in habitats ranging from wet forests to tall grass and secondary scrub (Kingdon, 1974). Members of both genera are adept climbers.

Genus *SAIDOMYS* James and Slaughter, 1974
SAIDOMYS PARVUS Winkler, 1997
(Fig. 6)

Referred material — Left M1s, KNM-TH 18479, -18480, -19486; right M1s, KNM-TH 18478, KNM-TH 19470; left M2s, KNM-TH 18482, -19482, -19466; right M2, KNM-TH 18484 (incomplete); left M3s, KNM-TH 18483 (incomplete), 30591 (incomplete); right M3, KNM-TH 19472; left m1, KNM-TH 19465; right m1, KNM-TH 19471; left m2, KNM-TH 19488; right m2, KNM-TH 19469; left m3, KNM-TH 18487; right m3s, KNM-TH 18485, -18486; incomplete right mandible with m1-m3, KNM-TH 18476. All from Tabarin, BPRP#77a, Chemeron Formation.

Description — Measurements of the Tabarin *Saidomys parvus* as well as comparative material are given in Table 3.

First upper molar — First upper molars are broad in occlusal outline (Fig. 6A). The first two chevrons are fairly symmetrical with respect to the longitudinal axis of the tooth. The first chevron consists of a large lingual anterocone and smaller labial anterocone and anterostyle. The latter two cusps are approximately equal in size and almost transversely aligned with the lingual anterocone. There is a precingulum on three of four specimens; it extends all along the anterior side of the lingual anterocone. The precingulum may contact the labial anterocone (KNM-TH 18479) or both the labial anterocone and anterostyle (KNM-TH 18480). A small labial prestyle is present on KNM-TH 18478. The middle chevron includes a large protocone (similar in size to the lingual anterocone) and slightly smaller paracone and enterostyle. The latter two cusps are similar in size and located slightly posterior to the protocone. A large hypocone is somewhat elongate transversely and connected to a smaller anteriorly placed metacone. A short posterior cingulum is present on all five specimens. The posterostyle is lacking but may be represented by a thickening of the enamel. A short crest connects the enterostyle and hypocone on three of four specimens. Large anterolabial and posterolabial, two fused lingual, and a small labial root are present.

Second upper molars are broad anteriorly and taper posteriorly (Fig. 6B). Anteriorly, the teeth have a small conical labial anterocone and a conical anterostyle which is at least twice the size of the labial anterocone. The middle row of cusps includes a large protocone and smaller posteriorly placed paracone and enterostyle. The hypocone is the largest cusp. It is connected to a much smaller anteriorly placed metacone. A distinct posterostyle is absent, but enamel on the lingual side of the hypocone is thickened. There is a short crest connecting (or almost connecting) the enterostyle and hypocone. A posterior cingulum is vestigial on the two specimens where this area is preserved. Root pattern is indeterminate.

The third upper molars are wide anteriorly and taper posteriorly, and are noticeably longer than wide (Fig. 6C). There is a large anterostyle and a much smaller labial anterocone. The enterostyle is large (compared to the protocone and paracone) and transversely elongate. A short low lingual cingulum connects the anterostyle and enterostyle. The hypocone is large and transversely elongate; it is connected to a smaller conical metacone. A posterostyle is lacking. The posterior cingulum is also absent but, there is a low indistinct posterior stylar shelf. The root pattern is indeterminate.

Part of the lower incisor and mandible is preserved on KNM-TH 18476. The incisor is ungrooved and in cross-section is shaped like a flattened oval. The indistinct

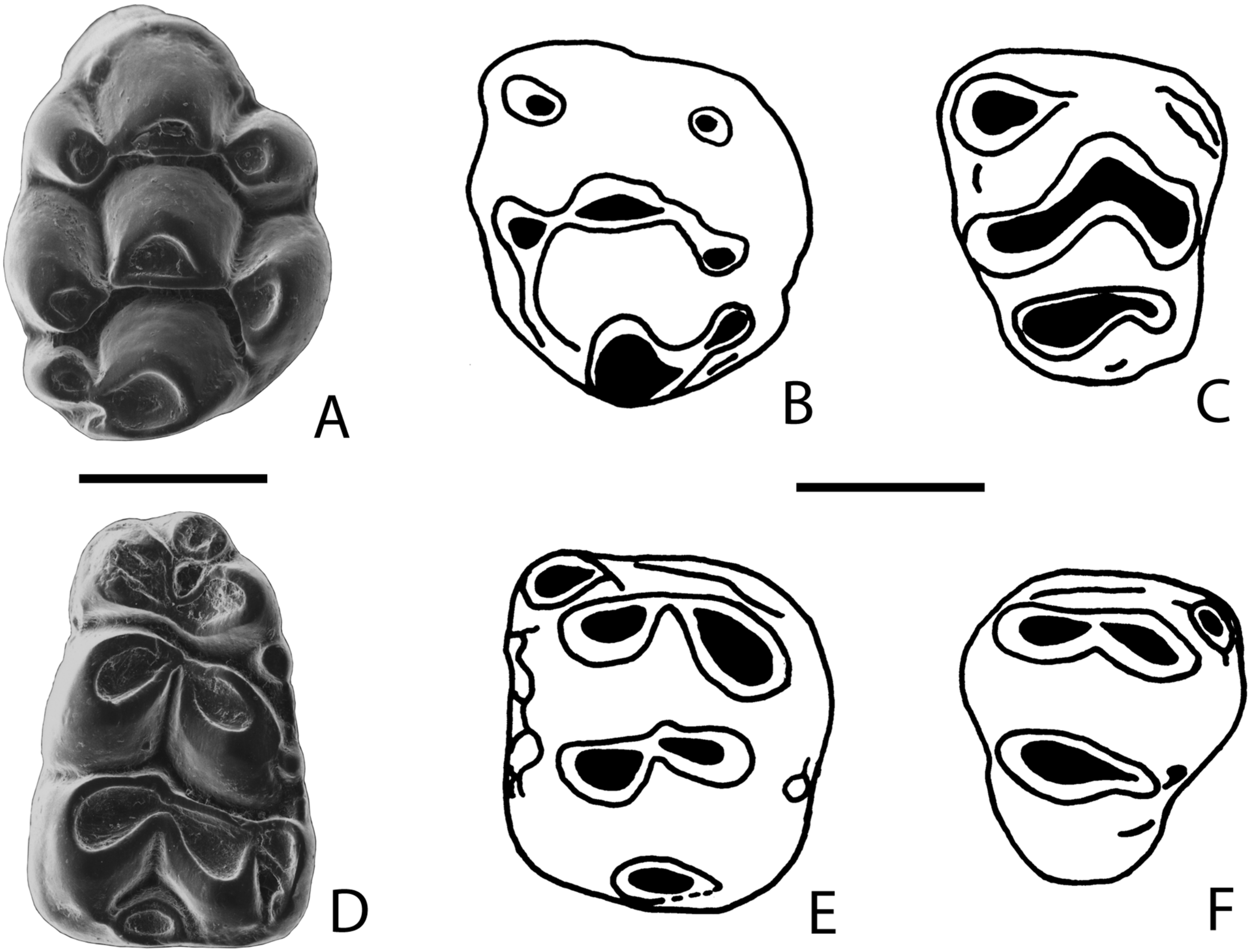

Figure 6. *Saidomys parvus* from the Tabarin locality, Chemeron Formation, Kenya. A) right M1, KNM-TH 18478, B) left M2, KNM-TH 18482, C) left M3, KNM-TH 18483, D) right m1, KNM-TH 19471, E) left m2, KNM-TH 19488, F) right m3, KNM-TH 18485. Both bar scales are 1 mm. The scale on the left is for the scanning electron photomicrographs: that on the right is for the drawings.

posterior end of the mental foramen is preserved. It is located anterior to and under M1. The masseteric crest is strong and does not reach the mental foramen.

Both lower first molars have moderate occlusal wear. Their major cusps are arranged in three transverse rows, separated by moderately deep furrows (Fig. 6D). The labial cusps are located slightly posterior to, and are a little smaller than, the lingual cusps. There is a large medial anteroconid, nestled between the lingual and labial anteroconids: on KNM-TH 19481 it is more closely associated with the lingual anteroconid. The posterior cingulum is a small, somewhat flattened oval. A labial cingulum includes a well-developed C1: on KNM-TH 19481 this cingulum also includes small C2 and C4. On KNM-TH 19481 there is only a very small C3 in addition to C1. There are large anterior and posterior roots (the posterior formed by two fused roots), as well as a small labial root and smaller lingual root.

Second lower molars are almost square to rectangular in outline and have two rows of cusps (protoconid, metaconid, and hypoconid, entoconid) separated by a furrow (Fig. 6E). The labial cusps are oriented somewhat posterior to the lingual cusps. A small labial anteroconid is present. KNM-TH 19488 has a low distinct anterior cingulum along most of the anterior side of the tooth. This cingulum is faint on KNM-TH 19469, which also has a tiny accessory conule anterolingual to the labial anteroconid. The posterior cingulum is as described for M1. There is a low cingulum between the metaconid and entoconid on KNM-TH 19488; this cingulum is absent on KNM-TH 19469. Both specimens have a posterior spur off the labial anteroconid. On KNM-TH 19469 (which is more heavily worn) C1 is similar in size to the labial anteroconid and in contact with the hypoconid. On KNM-TH 19488 an accessory labial cuspule is about half the size of the labial anteroconid and is not in contact with the hypoconid. Root development is indeterminate.

Third lower molars are triangular in outline and are formed primarily by three cusps (protoconid, metaconid, hypoconid; Fig. 6F). Along the anterior side of the tooth is a small labial anteroconid and a long low anterior cingulum. A chevron is formed by the protoconid and metaconid, which are similar in size. These two cusps are distinct but they are almost completely fused on KNM-TH 18486. This chevron is separated by a deep furrow from the large hypoconid which forms the apex of the triangle. On KNM-TH 18485 and -18487, C1 is present and fused with the hypoconid. KNM-TH 18486 lacks C1 but has a small labial cingulum between the metaconid and hypoconid. A reduced posterior stylar shelf is present on KNM-TH 18486 and along the posteriolabial side of KNM-TH 18485 but is lacking on KNM-TH 18487. Two anterior and one posterior roots are present.

Discussion — Morphology and size of the Tabarin *Saidomys* fits well within the diagnosis and description of *S. parvus* from the Inoleleo 1 and Shoshamagai 2 (tentatively referred specimen) localities, Ibole Member, Manonga Valley, Tanzania (Winkler, 1997). The age of this material is considered as late Miocene/early Pliocene based on overall faunal correlation or early Pliocene based on faunal correlation using only the rodents.

The sample sizes are limited for the two populations: this is especially true for the Manonga sample, which does not include m2 or m3. The following differences for the other teeth between the two samples were noted: 1) M1 – the Manonga sample (n = 2) has a weaker posterior cingulum (Tabarin sample n = 5); 2) M3 – the single Manonga specimen has a small conical posterior cingulum versus an indistinct shelf seen in this area on the single Tabarin tooth. Also, on the Manonga tooth the metacone and hypocone appear more similar in size (although fused from heavy occlusal wear) compared to the smaller metacone and larger hypocone on the less worn Tabarin tooth; and 3) m1 – three of four Manonga m1s have a conical posterior cingulum compared to the flattened ovals observed on the two Tabarin teeth. However, those three Manonga m1s have light occlusal wear and the more worn specimen with heavier wear has a flattened oval more similar to the m1s from Tabarin. Both populations have strong labial cingula with a distinct c1, but there is variable development of other cingular cusps even within each population.

As noted for *S. alisae*, Winkler (1997) made comparisons of *S. parvus* with *S. natrunensis*, *S. afarensis*, and *S. afghanensis*. Mein & Pickford (2006) made comparisons of *S. alisae* with *S. parvus* from Tanzania. One of the major differences they noted (and this applies also to *S. parvus* from Tabarin) is that *S. alisae* has an m1 with a weak medial anteroconid (=anterior median tubercle) compared to a larger one (sometimes more centrally located) on *S. parvus*.

Family THRYONOMYIDAE Pocock, 1922
Genus *THRYONOMYS* Fitzinger, 1867
THRYONOMYS sp.

Referred material — Incomplete right upper M1 or M2, KNM-TH 19483, from Tabarin, BPRP#77a. Right lower incisor, KNM-TH 13628, from Tabarin c (specimen not described here). Both from the Chemeron Formation.

Description and discussion — If complete, this specimen would be roughly square in occlusal outline. It consists of the area anterolingual to a diagonal line running from the anterolabial corner to the posterolingual corner. The roots are not preserved. Minimum measurements are 3.42 mm length by 3.42 mm width. Extremely heavy wear has obscured all surface features except for a wide lingual reentrant that extends anterolabially almost half-way across the tooth.

The Tabarin tooth is assigned to *Thryonomys* based on size and morphology including the transverse orientation of the anterior end of the tooth, relatively compressed lophs, and extent of the lingual reentrant. The tooth is, however, too incomplete for specific comparisons or assignment. A small (labiolingual width 4.0 mm) left upper incisor (KNM-LT 26734) of *Thryonomys* was recovered from BPRP#75A (Sagatia locality). An autapomorphy of *Thryonomys* is the presence of three grooves on the upper incisor. On this specimen, the three grooves are distributed relatively equally (of the two extant genera, more similar to the pattern seen in *T. gregorianus*; see Kingdon, 1974: pg. 696; Denys, 2011).

Thryonomys sp. is known from the Pleistocene Kapthurin Formation, Baringo District (Denys, 1999; McBrearty, 1999).

A right upper incisor of *Thryonomys* from the Kapthurin Formation has three grooves in the pattern seen in extant *T. swinderianus* (grooves concentrated on the lingual side of the tooth making the lateral most ridge distinctly larger than the others).

Thryonomys has been reported from several sites in East Africa (see discussion in Denys, 2011). Some of the oldest records of the genus are from Lemudong'o, Kenya (6 Ma, material not yet fully described; Manthi, 2007) and the late Miocene (5.7 Ma) of the Middle Awash, Ethiopia (Wesselman et al., 2009). It should be noted that the Middle Awash material, assigned to an extinct species, *T. asakomaae*, has an upper incisor with two grooves (as observed in the extinct genera *Paraulacodus* and *Protohummus* [Wesselman et al., 2009; Kraatz et al., 2013]).

Thryonomys is currently represented in Africa by two species (Kingdon, 1974). *Thryonomys gregorianus* is found in moist savannas from northern Cameroon to the East African coast. The generally larger *T. swinderianus* is more widely distributed in sub-Saharan Africa. It is essentially semi-aquatic and is associated with reed beds and grassy areas. Both species are dependent on a permanent source of water.

CONCLUSIONS

The rodents described in this paper augment our knowledge of late Miocene/early Pliocene faunas in East Africa, and the origins of some extant African rodent genera. The sample from the Kapcheberek locality (5.9-5.7 Ma) is very small, but it complements the larger sample published by Mein & Pickford (2006), which is derived primarily from their Kapsomin locality. Three of the four taxa from the Kapcheberek collection described here were also collected by Mein & Pickford (2006): *Dendromus*, *Steatomys minus* and *Saidomys alisae*. Mein & Pickford (2006) do not report *Arvicanthis*, but multiple specimens of that genus were found (not yet formally described) from the 6 Ma Lemudong'o locality, Kenya (Manthi, 2007). The Kapcheberek and Lemudong'o reports of *Arvicanthis* are some of the earliest for this genus. The Kapcheberek rodents described in the present paper suggest the presence of a savanna habitat ca. 5.9-5.7 Ma. Based on the overall small mammal fauna from the Kapsomin locality, Mein & Pickford (2006) suggested the presence of well-wooded to forested habitats, in addition to some relatively more open habitats.

Rodents from the Tabarin locality (4.5-4.4 Ma) reported here are more abundant and diverse than those from Kapcheberek. Significantly, the fauna includes some of the earliest records of several extant African rodent genera (*Paraxerus*, and either *Grammomys* or *Thallomys*). If cf. *Heliosciurus* is referrable to *Heliosciurus*, it may be the earliest record of this genus in Africa. The rodents from the Tabarin locality are suggestive of a woodland habitat in this area in the early Pliocene.

ACKNOWLEDGMENTS

This manuscript is dedicated to my dissertation supervisor and colleague, Lou Jacobs, who has provided many years of encouragement, support, patience, and friendship. Financial support was generously provided by the Institute for the Study of Earth and Man and the Roy M. Huffington Department of Earth Sciences, Southern Methodist University, the Geological Society of America, and Sigma Xi. Collection study grants were courtesy of the Smithsonian Institution, Washington, D.C., and the American Museum of Natural History, New York. I thank the government of the Republic of Kenya for research permission and the staff of the Nairobi National Museum (in particular the late K. Cheboi), Nairobi, Kenya, for their assistance. This study benefitted from discussions with the late A. Hill. Dwight Deuring (formerly with SMU) assisted with the photomicrographs. D. Winkler generously prepared the figures for the manuscript. I thank Yuong-Nam Lee for the kind invitation to contribute to this volume, and for his suggestions to improve the manuscript. The manuscript benefited from constructive reviews by L. Flynn and C. Denys. This research was in partial fulfillment for a Doctorate in Philosophy in Geology at Southern Methodist University, Dallas, Texas, under the supervision of Louis Jacobs.

LITERATURE CITED

Amtmann, E. (1975). Family Sciuridae. In J. Meester & H. W. Setzer (Eds.), *The Mammals of Africa, an Identification Manual* (pp. 1–12). Smithsonian Institution Press.

Bishop, W. W. & Pickford, M. H. L. (1975). Geology, fauna and palaeoenvironments of the Ngorora Formation, Kenya Rift Valley. *Nature*, 254, 185–192.

Black, C. C. & Krishtalka, L. (1986). Rodents, bats, and insectivores from the Plio-Pleistocene sediments to the east of Lake Turkana, Kenya. *Natural History Museum of Los Angeles County, Contributions in Science*, 372, 1–15.

Broom, R. (1948). Some South African Pliocene and Pleistocene mammals. *Annals of the Transvaal Museum*, 21, 1–38.

Cifelli, R. L., Ibui, A. K., Jacobs, L. L., & R. Thorington, Jr., W. (1986). A giant tree squirrel from the late Miocene of Kenya. *Journal of Mammalogy*, 67, 274–283.

Coetzee, C. G. (1977). Genus *Steatomys*. In J. Meester & H. W. Setzer (Eds.), *The Mammals of Africa, an Identification Manual* (pp. 1–4). Smithsonian Institution Press.

Conroy, G. C., Pickford, M., Senut, B., Van Couvering, J., & Mein, P. (1992). *Otavipithecus namibiensis*, first Miocene hominoid from southern Africa, Nature, 356, 144–148.

de Graaff, G. (1960). A preliminary investigation of the mammalian microfauna in Pleistocene deposits of caves in the Transvaal system. *Palaeontologia Africana*, 7, 59–118.

de Graaff, G. (1981). *The Rodents of Southern Africa*. Butterworths and Company.

Deino, A., Tauxe, L. L., Hill, A., & Monaghan, M. (2002). ^{40}Ar/^{39}Ar geochronology and paleomagnetic stratigraphy of the Lukeino and lower Chemeron succession at Tabarin and Kapcheberek, Tugen Hills, Kenya. *Journal of Human Evolution*, 42 (1–2), 117–140.

Denys, C. (1987). Fossil rodents (other than Pedetidae) from Laetoli. In M. D. Leakey & J. M. Harris (Eds.), *Laetoli: a Pliocene site in northern Tanzania* (pp. 118–170). Oxford University Press.

Denys, C. (1987). Micromammals from the West-Natron Pleistocene deposits (Tanzania). Biostratigraphy and Paleoecology. *Sciences Géologiques, Bulletin*, 40(1–2), 185–201.

Denys, C. (1994). Nouvelles espèces de *Dendromus* (Rongeurs, Muroidea) à Langebaanweg (Pliocene, Afrique du Sud): consèquences stratigraphiques et paléoécologiques. *Palaeovertebrata*, 23(1–4), 153–176.

Denys, C. (1999). Of mice and men: evolution in east and South Africa during Plio-Pleistocene times. In T. G. Bromage & F. Schrenk (Eds.), *African Biogeography, Climate Change and Human Evolution* (pp. 226–252). Oxford University Press.

Denys, C. (2011). Chapter 2. Rodents. In T. Harrison (Ed.). Paleontology and Geology of Laetoli: Human Evolution in Context. Volume 2: Fossil Hominins and the Associated Fauna. *Vertebrate Paleobiology and Paleoanthropology Series* (pp. 15–53). Springer Dordrecht.

Denys, C. & Winkler, A. (2015). Advances in integrative taxonomy and evolution of African murid rodents: how morphological trees hide the molecular forest. In P. G. Cox & L. Hautier (Eds.), *Evolution of the Rodents, Advances in Phylogeny, Functional Morphology and Development* (pp. 186–220). Cambridge University Press.

Flynn, L. J., Jacobs, L. L., & Sen, S. (1983). La diversité de *Paraulacodus* (Thryonomyidae, Rodentia) et des groupes apparentés pendant le Miocène. *Annales de Paléontologie*, 69, 355–366.

Flynn, L. J., Jacobs, L. L., & Lindsay, E. H. (1985). Problems in muroid phylogeny: relationship to other rodents and origin of major groups. In W. P. Luckett & J. -L. Hartenberger (Eds.), *Evolutionary relationships among rodents, a multidisciplinary analysis* (pp. 589–616). NATO ASI Series A, Life Sciences Vol. 92.

Geraads, D. (1998). Rongeurs du Mio-Pliocène de Lissasfa (Casablanca, Maroc). *Geobios*, 31, 229–245.

Geraads, D. (2001). Rongeurs du Miocène superiéur de Ch'orora, Ethiopie: Murinae, Dendromurinae et conclusions. *Palaeovertebrata*, 30, 89–109.

Hendey, Q. B. (1981). Palaeoecology of the late Tertiary fossil occurrences in E Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. *Annals of the South African Museum*, 84, 1–104.

Hill, A. (1985). Early hominid from Baringo, Kenya. *Nature*, 315, 222–224.

Hill, A. (1999). The Baringo Basin, Kenya: from Bill Bishop to BPRP. In P. Andrews & P. Banham (Eds.), *Late Cenozoic Environments and Hominid Evolution: a Tribute to Bill Bishop* (pp. 85–97). Geological Society.

Hill, A. (2002). Introduction. Paleoanthropological research in the Tugen Hills, Kenya. *Journal of Human Evolution*, 42, 1–10.

Hill, A., Curtis, G., & Drake, R. (1986). Sedimentary stratigraphy of the Tugen Hills, Baringo, Kenya. In L. E. Frostick, R. W. Renaut, I. Reid, & J. J. Tiercelin (Eds.), *Sedimentation in the African Rifts* (pp. 285–295). Geological Society of London, Special Publication No. 25.

Hill, A., Behrensmeyer, K., Brown, B., Deino, A., Rose, M., Saunders, J., Ward, S., & Winkler, A. (1991). Kipsaramon: a lower Miocene hominoid site in the Tugen Hills, Baringo District, Kenya. *Journal of Human Evolution*, 20, 67–75.

Jacobs, L. L. (1978). Fossil rodents (Rhizomyidae & Muridae) from Neogene Siwalik deposits, Pakistan. *Museum of Northern Arizona Press, Bulletin Series*, 52, 1–103.

Jaeger, J. -J. (1975). *Les Muridae (Mammalia, Rodentia) du Pliocène et du Pléistocène du Maghreb: Origine, évolution, données biogéographiques et paléoclimatiques* [Unpublished doctoral dissertation]. Université des Sciences et Techniques du Languedoc.

Jaeger, J. -J. (1976). Les rongeurs (Mammalia, Rodentia) du Pléistocène Inférieur d'Olduvai Bed I, Ière Partie: les muridés. In R. J. G. Savage & S. C. Coryndon (Eds.), *Fossil Vertebrates of Africa, Volume 4* (pp. 57–120). Academic Press.

Jaeger, J. -J., & Wesselman, H. B. (1976). Fossil remains of micromammals from the Omo Group deposits. In Y. Coppens, F. C. Howell, G. L. Isaac, & R. E. F. Leakey (Eds.), *Earliest man and environments in the Lake Rudolf Basin* (pp. 351–360). University of Chicago Press.

Jaeger, J. -J., Tong, H., Buffetaut, E., & Ingavat, R. (1985). The first fossil rodents from the Miocene of northern Thailand and their bearing on the problem of the origin of the Muridae. *Revue de Paléobiologie*, 4, 1–7.

James, G. T. & Slaughter, B. H. (1974). A primitive new middle Pliocene murid from Wadi el Natrun, Egypt. *Annals of the Geological Survey of Egypt*, 4, 333–362.

Kingdon, J. (1974). *East African Mammals: an Atlas of Evolution in Africa. Volume IIB (Hares and Rodents).* University of Chicago Press.

Kraatz, B. P., Bibi, F., Hill, A., & Beech, M. (2013). A new fossil thryonomyid from the Late Miocene of the United Arab Emirates and the origin of African cane rats. *Naturwissenschaften*, 100, 437–449. DOI 10.1007/s00114-013-1043-4

Lavocat, R. (1957). Sur l'âge des faunes de rongeurs des grottes à Australopithèques. In J. D. Clark (Ed.), *Proceedings 3rd Pan-African Congress on Prehistory* (pp. 133–134). Chatto and Windus.

Lavocat, R. (1967). Les microfaunes du quaternaire ancient d'Afrique orientale et austral. In W. W. Bishop & D. D. Clark (Eds.), *Background to Evolution in Africa* (pp. 67–72). University of Chicago Press.

Linchamps, P., Stoetzel, E., Cornette, R., Denys, C., Hanon, R., Maringa, N., Matthews, T., & Steininger, C. (2023). Fossil micromammals and the palaeoenvironments of the *Paranthropus robustus* site of Cooper's Cave. *Historical Biology.* DOI:10.1080/08912963. 2023.2196677

Louchart, A., Wesselman, H., Blumenschine, R. J., Hlusko, L. J., Njau, J. K., Black, M. T., Asnake, M., & White, T. D. (2009). Taphonomic, avian, and small-vertebrate indicators of *Ardipithecus ramidus* habitat. *Science*, 326, 66e1–66e4. DOI: 10.1126/science. 1175823

Manthi, F. Y. (2006). *The Pliocene micromammalian fauna from Kanapoi, northwestern Kenya, and its contribution to understanding the environment of Australopithecus anamensis* [Unpublished doctoral dissertation]. University of Cape Town.

Manthi, F. K. (2007). A preliminary review of the rodent fauna from Lemudong'o, southwestern Kenya, and its implication to the late Miocene paleoenvironments. *Kirklandia*, 56, 92–105.

Manthi, F. K. & Winkler, A. J. (2020) Rodents and other terrestrial small mammals from Kanapoi, north-western Kenya. *Journal of Human Evolution*, 140. DOI: 10.1016/j.jhevol.2019.102694.

McBrearty, S. (1999). The archaeology of the Kapthurin Formation. In P. Andrews & P. Banham (Eds.), *Late Cenozoic Environments and Hominid Evolution: a Tribute to Bill Bishop* (pp. 143–156). Geological Society.

Mein, P. (1994). Micromammifères du Miocène superiéur et du Pliocène du Rift Occidental, Ouganda. In B. Senut & M. Pickford (Eds.), *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire* (pp. 187–193). Vol. II: Palaeobiology. Orléans, CIFEG Occasional Publication 1994/29.

Mein, P. & Pickford, M. (2006). Late Miocene micromammals from the Lukeino Formation (6.1 to 5.8 Ma), Kenya. *Bulletin Mensuel Société Linnéenne de Lyon*, 75(4), 183–223.

Mein, P. & Pickford, M. (2004). Vallesian rodents from Sheikh Abdallah, Western Desert, Egypt. *Historical Biology*, 22, 224–259.

Mein, P., Pickford, M., & Senut, B. (2004). Late Miocene micromammals from the Harasib karst deposits, Namibia. Part 2b - Cricetomyidae, Dendromuridae and Muridae, with an addendum on the Myocricetodontinae. *Communs geol. Surv. Namibia*, 13, 43–61.

Misonne, X. (1969). African and Indo-Australian Muridae, evolutionary trends. *Musee Royal de l'Afrique Centrale Annales, Serie 8, Sciences Zoologiques*, 172:1–219.

Misonne, X. (1974). Part. 6. Order Rodentia In J. Meester & H. W. Setzer (Eds.), *The Mammals of Africa, an Identification Manual* (pp. 1–39). Smithsonian Institution Press.

Monadjem, A., Taylor, P. J., Denys, C., & Cotterill, F. P. D. (2015). *Rodents of Sub-Saharan Africa, a Biogeographic and Taxonomic Syntheses*. De Gruyter.

Musser, G. G. & M. D. Carleton. (2005). Superfamily Muroidea. In D. E. Wilson & A. M. Reeder (Eds.), *Mammal Species of the World, A Taxonomic and Geographic Reference*, 3rd Edition, Vol. 2 (pp. 894–1531). John Hopkins University Press.

Nowak, R. M. (1999). *Walker's Mammals of the World. 6th Edition*. The Johns Hopkins University Press.

Pickford, M. H. L. 1975. *Stratigraphy and palaeoecology of five late Cainozoic formations in the Kenya Rift Valley* [Unpublished doctoral dissertation]. University of London.

Pickford, M. (1978). Stratigraphy and mammalian palaeontology of the late-Miocene Lukeino Formation, Kenya. In W. W. Bishop (Ed.), *Geological Background to Fossil Man* (pp. 263–278). Scottish Academic Press.

Pickford, M. & Mein, P. (1988). The discovery of fossiliferous Plio-Pleistocene cave fillings in Ngamiland, Botswana. *Comptes rendus des séances de l'Académie des Sciences* 307, Série 2, 1681–1686.

Pickford, M. H. L., Johanson, D. C., Lovejoy, C. O., White, T. D., & Aronson, J. L. (1983). A hominoid humeral fragment from the Pliocene of Kenya. *American Journal of Physical Anthropology*, 60, 337-346.

Pickford, M., Senut, B., Gommery, D., & Kipkech, J. (2022). New Pliocene hominid fossils from Baringo County, Kenya. *Fossil Imprint*, 78(2), 451–488.

Pocock, T. N. (1987). Plio-Pleistocene fossil mammalian microfauna of southern Africa - a preliminary report including description of two new fossil muroid genera (Mammalia: Rodentia). *Palaeontologia Africana*, 26, 69–91.

Robinson, P. & Black, C. C. (1973). A small Miocene faunule from near Testour, Beja gouvernorat, Tunisia. *Annales des Mines et de la Géologie, Tunis*, 26, 445–449.

Rosevear, D. R. (1969). *The Rodents of West Africa*. British Museum (Natural History).

Sabatier, M. (1982). Les rongeurs du site Pliocène a hominidés de Hadar (Ethiopie). *Palaeovertebrata*, 12, 1–56.

Sen, S. (1983). Rongeurs et lagomorphes du gisement pliocène de Pul-e Charkhi, bassin de Kabul, Afghanistan. *Bulletin du Museum National d'Histoire Naturelle, série 5, section C*, 1, 33–74.

Senut, B., Pickford, M., Mein, P., Conroy, G., & Couvering, J. V. (1992). Discovery of 12 new Late Cainozoic fossiliferous sites in palaeokarsts of the Otavi Mountains, Namibia. *Comptes rendus des séances de l'Académie des Sciences* 314, Série 2, 727–733.

Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., & Coppens, Y. (2001). First hominid from the Miocene (Lukeino formation, Kenya). *Comptes rendus des séances de l'Académie des Sciences* 332, Série 2, 137–144.

Slaughter, B. H. & James, G. T. (1979). *Saidomys natrunensis*, an arvicanthine rodent from the Pliocene of Egypt. *Journal of Mammalogy*, 60, 421–425.

Swanepoel, P. & D. A. Schlitter. (1978). Taxonomic review of the fat mice (Genus *Steatomys*) of West Africa (Mammalia: Rodentia). *Bulletin of Carnegie Museum of Natural History*, 6, 53–76.

Tchernov, E. (1968). *Succession of rodent faunas during the upper Pleistocene of Israel*. Verlag Paul Parey.

Thorington, R. W. & Hoffmann, R. S. (2005). Family Sciuridae. In D. E. Wilson & A. M. Reeder (Eds.), *Mammal Species of the World, A Taxonomic and Geographic Reference*, 3rd Edition, Vol. 2 (pp. 754–818). John Hopkins University Press.

Voelker, G., Huntley, J. W., Bryia, J., Denys, C., Sumbera, R., Demos, T. C., Lavrenchenko, L., Nicolas, V., Gnoske, T. P., & Kerbis Peterhans, J. C. (2021). Molecular systematics and biogeographic history of the African climbing-mouse complex (*Dendromus*). *Molecular Phylogenetics and Evolution*, 161. doi.org/10.1016/j.ympev.2021.107166

Ward, S. & Hill, A. (1987). Pliocene hominid partial mandible from Tabarin, Baringo, Kenya. *American Journal of Physical Anthropology*, 72, 21–37.

Ward, S., Brown, B., Hill, A., Kelley, J., & Downs, W. (1999). *Equatorius*: a new hominoid genus from the Middle Miocene of Kenya. *Science* 285, 1382–1386.

Wesselman, H. B. (1984). The Omo micromammals, systematics and paleoecology of early man sites from Ethiopia. *Contributions to Vertebrate Evolution*, 7, 1–219.

Wesselman, H. B., Black, M. T., & Asnake, M. (2009). Chapter 5. Small mammals. In Y. Haile-Selassie & G. WoldeGabriel (Volume Eds.),

T. D. White (Series Ed.), *Ardipithecus kadabba in Africa: Miocene Evidence from the Middle Awash, Ethiopia* (pp. 105–134). University of California Press.

Winkler, A. J. (1990). *Systematics and biogeography of Neogene rodents from the Baringo District, Kenya* [Unpublished doctor dissertation]. Southern Methodist University.

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. (1994). The middle/upper Miocene dispersal of major rodent groups between southern Asia and Africa. In Y. Tomida, C. Li, & T. Setoguchi (Eds.), *Rodent and Lagomorph Families of Asian Origins and Diversification. National Science Museum Monographs No. 8* (pp. 173–184). National Science Museum, Tokyo.

Winkler, A. J. (1997). Systematics, paleobiogeography, and paleoenvironmental significance of rodents from the Ibole Member, Manonga Valley, Tanzania. In T. Harrison (Ed.), *Neogene Paleontology of the Manonga Valley, Tanzania: A Window into East African Evolution* (pp. 311–332). Plenum Press.

Winkler, A. J. (2002). Neogene paleobiogeography and East African paleoenvironments: contributions from the Tugen Hills rodents and lagomorphs. *Journal of Human Evolution*, 42(1–2), 237–256. DOI: 10.1006/jhev.2001.0501

Winkler, A. J. (2003). Rodents and lagomorphs from the Miocene and Pliocene of Lothagam, Northern Kenya. In M. G. Leakey & J. Harris (Eds.), *Lothagam: The Dawn of Humanity in Eastern Africa* (pp. 169–198). Columbia University Press.

Winkler, A. J., Denys, C., & Avery, D. M. (2010). Chapter 17. Rodentia. In L. Werdelin & W. J. Sanders (Eds.), *Cenozoic Mammals of Africa* (pp. 262–304). University of California Press.