A PRELIMINARY REVIEW OF THE RODENT FAUNA FROM LEMUDONG'O, SOUTHWESTERN KENYA, AND ITS IMPLICATION TO THE LATE MIOCENE PALEOENVIRONMENTS

FREDRICK KYALO MANTHI
Department of Palaeontology
National Museums of Kenya
fkyalo@hotmail.com

ABSTRACT

Fossil remains of rodents from Lemudong'o, southwestern Kenya, have been studied to understand the taphonomy of the faunal assemblage, and to interpret the paleoenvironment from which the fauna derived. Skeletal representation, breakage patterns, evidence of etching on the incisors, and the body size of the rodents suggest that the material was a predator assemblage that accumulated *in situ*, and that a small owl, and most probably a barn owl, would have been responsible. The fossil rodents recovered from the site suggest that at around 6 Ma, the environment at Lemudong'o and the surrounding area was a mosaic of open grasslands/woodlands (dry savanna), riverine forests, and flood plains. Elements of aridity and sandy substrates were also a common feature at Lemudong'o. Overall, the higher numbers of Murinae relative to Gerbillinae in the Lemudong'o faunal sample suggest that the paleoenvironment in the area would have been more mesic than xeric.

Introduction

For a long time, paleontologists paid minimal attention to the study of small-mammal remains, and interpretations of past ecosystems centered primarily on macrofauna. However, since Andrews' (1990) landmark report on the agency of accumulation of small-mammal remains and the taphonomic processes that affect these remains, the study of small-mammal remains has continued to receive increasing attention. Following these studies, there is a general consensus that the majority of small-mammal faunal assemblages result, respectively, from pellets and scats accumulated by avian raptors and by small carnivorous mammals (e.g., Mellett, 1974; Dodson and Wexlar, 1979; Korth, 1979; Andrews and Evans, 1983; Kemp and Calburn, 1987; Avery, 1988; Andrews, 1990; Fernandez-Jalvo et al., 1998).

It is significant that among the vertebrates, small mammals have a number of attributes that render their remains valuable for ecological studies. For instance, unlike the highly mobile macrofauna, most small mammals, including rodents, usually have very specific habitat requirements, and are therefore sensitive indicators of environmental contexts (Coe, 1972; Jaeger and Wesselman, 1976; Wesselman, 1984, 1995; Black and Krishtalka, 1986; Delany, 1986; Avery, 1990, 1992; Denys, 1996; Winkler, 2002; Lyons, 2003; Smoke and Stahl, 2004). The utility of small-mammal remains as paleoenvironmental proxies is further amplified by the fact that small-bodied species tend to occur in high population densities, have shorter life-spans, and their remains potentially contribute more individuals and carcasses per year (Potts, 1982; Badgley et al., 1998; Reitz and Wing, 1999; Xijun and Zhuding, 2002; Vermeij and Herbert, 2004). In addition, even though predation may result in the concentration of small-mammal remains in areas far-away from where the animals lived (Mellett, 1974; Steyn, 1982, 1984; Kemp and Calburn, 1987; Andrews, 1990; Taylor, 1994), small mammals, like their large mammal counterparts, naturally tend to die in the areas where they live (Wolff, 1981). If not transported to a great distance, therefore, small-mammal remains have potential to reveal the habitat/s which the once living species occupied (Wolff, 1981). Inevitably, analysis of micromammalian assemblages such as the one from Lemudong'o has increasingly become one of the most widespread modes of palaeoecological analysis (e.g., Avery, 1982, 2001, 2002; Wesselman, 1984, 1995; Denys, 1985; Andrews, 1989; Dauphin et al., 1994; Winkler, 1997; Kovarovic et al., 2002; Manthi, 2006).

Studies by workers such as Avery (2001, 2002) have attempted to integrate both taphonomic and taxonomic inquiries in the reconstruction of the taphonomic history of micromammalian faunas as well as the paleoecosystems from which the faunas originated. The primary purpose of this paper is to apply the

Figure 1. Hill slope on which the rodent fauna is found, with the speckled tuff evidently visible.

above techniques on rodent fossil remains from Lemudong'o with the aim of shedding some light on the taphonomic history of the fauna as well as inferring the late Miocene paleoenvironment from which the fauna derived. Although no hominins have been discovered at Lemudong'o to date, it is hoped that the rodent fauna will make a contribution to the understanding of the environmental conditions during the Late Miocene, a period considered critical to the evolutionary history of early hominins (e.g., Andrews and Humphrey, 1999).

Material and Methods

The presence of microfauna at Lemudong'o was noted in 2001, following a test sieving that was carried out to establish whether or not the sediments contained microfauna. During the test sieving, the sediments proved to be rich with microfauna including rodents, and this prompted further sieving and investigation (L. Hlusko, personal communication). Sediments were sieved through a 1.0-mm mesh and hand-picked for microfauna, after which the fauna was taken to the National Museums of Kenya in Nairobi for further investigation.

The rodent material under investigation was obtained from Lemudong'o Locality 1 (LEM 1), and was collected during several field seasons beginning from 2001. The fauna derives from an outcrop of coarse alluvial deposits with interstratified tuffs. The speckled tuff, in particular (Figure 1), which incises the dome

that characterizes Lemudong'o Area 7, has yielded the bulk of the small mammals (Ambrose, Kyule, and Hlusko, 2007), including the rodents, as well as other terrestrial vertebrates such as colobines, carnivores, bovids, hyracoids, and equids (e.g., Ambrose et al., 2003; Ambrose, Bell, et al., 2007). Dates obtained from the four tuffs that bracket the fossiliferous horizons at Lemudong'o indicate an age span of 6.12 to 6.08 Ma (Deino and Ambrose, 2007).

During the study of the Lemudong'o rodents, skeletal elements were observed under a microscope under a magnification of up to 20×. The identifiable elements were assigned to taxonomic groups and subsequently accessioned. Although not confined to them, the assignment of skeletal elements to taxonomic groups was carried out on the jaws. This was because of the large proportion of isolated teeth and also because this has been the standard practice in the identification of small mammals (e.g., Avery, 1990, 1999). Attempts were, however, made to assign a considerable number of isolated teeth to taxonomic groups. Molars were also measured to help identify closely related taxa. In this exercise, lengths of the molars were taken on the lingual side, and widths were taken across the widest dimension of the teeth (e.g., Wesselman, 1984). It is noteworthy that, because of the rare associations between postcranial and cranial or dental material, the assignment of postcranial material to genus and/or species is seldom reliable, a situation often compounded by body size

overlap between taxonomically close species within the same faunal assemblage (e.g., Gagnon, 1997; Alemseged, 2003).

In this initial study of the Lemudong'o rodents, attempts were also made to establish the taphonomic processes that have influenced the faunal assemblage. A taphonomic analysis was therefore carried out on the incisors and the long bones. The analysis of the incisors focused at investigating the extent of predator digestion on the incisors, whereas the analysis of the long bones was undertaken with a view to providing some insight into the effect of breakage on the faunal assemblage (e.g., Andrews, 1990; Fernandez-Jalvo et al., 1998). Because of the involvement of the author in sorting the 2001 sample, the taphonomic analysis was confined to this material.

Following Manthi (2002), the Lemudong'o incisors were separated into five categories depending on their degree of etching. Category 1 incisors are those that have no visible evidence of etching, whereas Category 2 incisors are those that exhibit slight etching and pitting of the enamel surface, and etching has not penetrated the dentine. For Category 3 incisors, etching is not much greater than Category 2 but has made slight penetration into the dentine. Category 4 incisors show more extensive area of etching and in some areas there is total removal of the enamel, and areas underlying the dentine are etched. The last category (Category 5) includes incisors whose enamel has been completely removed and the dentine is extensively etched.

As clearly outlined in Andrews (1990) and further amplified in Manthi (2002), the relatively abundant long bones namely, humeri, ulnae, femora, and tibiae were investigated for breakage. These bones were separated into four categories, namely, complete, proximal, shaft, and distal, and the proportion of each category counted. To further understand the extent of taphonomic bias on skeletal representation, all the other postcranial elements were counted (e.g., Korth, 1979; Andrews and Jenkins, 2000).

In the reconstruction of the microhabitats represented by the Lemudong'o rodents, ecological aspects of the fauna were used with due regard for the influence of taphonomic processes such as the differential preservation of fossil bones and taxa. Ecological considerations were based on the present-day microhabitats and characteristics of the genera represented at Lemudong'o.

Conventions and Abbreviations

The full accession number for the Lemudong'o specimens, which are housed at the National Museums of Kenya in Nairobi, begins with the prefix KNM-NK (short-form for Kenya National Museum, and Narok, the district from where the fauna came). Additionally, the following abbreviations appear in the descriptions and lists of the specimens:

max.	maxilla
mand.	mandible
M	molar
I	incisor
upp.	upper
frag.	fragment
w/	with

Dental abbreviations follow the convention of superscript numbers indicating maxillary teeth and lower case numbers indicating mandibular teeth.

Figure 2. *Acomys* sp. indet., KNM-NK 42315, left mandibular fragment w/ M_{1-2}.

Systematic Descriptions and Discussions

In all, nine distinct genera were identified from the Lemudong'o faunal samples, and among these, murinae genera ($n = 8$) dominate over the gerbils ($n = 1$). The abundance of murinae rodents is exemplified particularly by the presence of a fairly large number of specimens assignable to *Arvicanthis* (19%) and *Mastomys* (13%). Although only represented by *Tatera* and a few other specimens assignable to Gerbillinae, gerbils are also a key component of the Lemudong'o fauna, as indicated by the relatively high numbers of specimens attributable to *Tatera*, which comprise 21% of the total number of specimens. It is noteworthy that there is poor representation of relatively larger species, as only two elements ascribable to *Thryonomys* and four sciurids represent these.

Order RODENTIA Bowdich, 1821
Family MURIDAE Gray, 1821
Subfamily MURINAE Illiger, 1815
Genus *ACOMYS* Geoffroy, 1838
ACOMYS species indeterminate
Figure 2

Referred material

KNM-NK 42315, left mand. frag. w/ M_{1-2} and KNM-NK 46243, left mand. frag. w/ M_{1-2}. Also, an additional specimen, KNM-NK 46253 (left M_1), has been ascribed to cf. *Acomys*.

Discussion

On the basis of the dental morphology, including the cusp pattern, two elements (KNM-NK 42315 and KNM-NK 46243) have been ascribed to *Acomys* (e.g., Figure 2) and a further isolated molar has been attributed to cf. *Acomys*. The size (see also Table 1) and the cusp pattern of the molars of KNM-NK 42315 and KNM-NK 46243 compares fairly well with that of the extant *Acomys percivali*. Although there appear to be minor differences in the size and the cusp pattern of the isolated molar ascribed to KNM-NK 46253, overall, the morphology of the molar also resembles that of the contemporary *A. percivali*.

The evolutionary history of the genus *Acomys* has for a long time remained an issue of great debate (Denys, 1990; Chevret et al., 1993; Denys et al., 1994). This phenomenon may be attributed to the generally poor representation of members of this genus in the fossil record, as well as the difficulty in separating members of *Acomys* from murines such as *Mastomys* and *Uranomys* (Denys, 1990; Denys et al., 1994). Nonetheless, *Acomys* has been reported from a number of sites including the Early Pliocene deposits at Langebaanweg (Denys, 1990) and the Upper Pliocene deposits of

Table 1. Measurements (in mm) of selected dental elements of murine taxa in the Lemudong'o fossil small-mammal fauna (measurement error $\pm$ 0.1 mm).

KNM-NK	Family	Genus, species	Element	Length	Width
41046	Sciuridae	*Xerus* sp.	P^4	1.6	1.5
			M^1	1.4	2
41049	Muridae	*Mastomys* sp.	M_1	1.1	0.9
			M_2	0.7	0.9
			M_3	0.6	0.7
41083	Muridae	*Arvicanthis* sp.	M_1	1.7	1
41087	Muridae	*Tatera* sp.	M_1	2	1.4
			M_2	1.2	1.3
41088	Muridae	*Lemniscomys* sp.	M_2	1.1	1.2
			M_3	1.1	1.1
41089	Muridae	*Arvicanthis* sp.	M_1	1.7	1.2
			M_2	1.1	1.2
41096	Muridae	cf. *Mastomys*	M_1	1.5	0.9
			M_2	0.9	1
			M_3	0.7	0.8
41106	Muridae	*Tatera* sp.	M_1	1.7	1.2
41107	Murinae		M_1	1.2	0.9
41127	Murinae		M_1	1.1	1.1
41128	Muridae	cf. *Arvicanthis*	M^1	1.7	1.1
41232	Muridae	*Arvicanthis* sp.	M_1	1.7	1.2
			M_2	1.2	1.2
42315	Muridae	*Acomys* sp.	M_1	1.2	0.9
			M_2	0.6	0.8
42335	Sciuridae	*Xerus* sp.	P_4	1.5	1.6
42360	Muridae	*Mastomys* sp.	M^1	2	1.1
44815	Muridae	cf. *Saidomys*	M_1	1.6	1.1
			M_2	1.1	1.2
			M_3	1	0.9
44830	Muridae	cf. *Arvicanthis*	M^1	1.8	1.1
			M^2	1.1	1
44832	Muridae	cf. *Aethomys*	M_2	1.1	1.2
			M_3	1	1
44856	Muridae	*Lemniscomys* sp.	M_1	1.4	0.9
			M_2	1	0.9
44858	Muridae	*Mastomys* sp.	M_2	0.9	1
			M_3	0.6	0.8
44920	Sciuridae	*Paraxerus* sp.	P_4	1.5	1.5
44921	Muridae	*Aethomys* sp.	M^1	1.6	1.3
45907	Muridae	*Mastomys* sp.	M_1	1.4	0.9
			M_2	1.2	0.9
			M_3	0.6	0.7
45934	Thryonomyidae	*Thryonomys* sp.	M_1	2	1.7
45945	Thryonomyidae	*Thryonomys* sp.	M_1	1.5	1.2
			M_2	1.5	1.4
45946	Muridae	*Arvicanthis* sp.	M_1	1.6	1.1
			M_2	1	1.3
			M_3	1.1	1.2
45947	Muridae	*Arvicanthis* sp.	M^1	1.9	1.3
			M^2	1	1.2
			M^3	0.9	0.9
46232	Muridae	*Tatera* sp.	M_2	1	1.3
46234	Muridae	*Tatera* sp.	M_1	1.9	1.4
46235	Muridae	*Arvicanthis* sp.	M^1	1.5	1.4
46236	Muridae	*Arvicanthis* sp.	M_1	1.7	1.2
46237	Muridae	*Tatera* sp.	M^1	1.9	1
46238	Muridae	*Tatera* sp.	M_1	1.7	1.2
46239	Muridae	*Arvicanthis* sp.	M_1	1.6	1.1
46240	Muridae	cf. *Saidomys*	M^1	1.5	1.4
46241	Muridae	*Tatera* sp.	M_1	1.7	1.3
46242	Muridae	*Arvicanthis* sp.	M_1	1.6	1.1
46243	Muridae	*Acomys* sp.	M_1	1	0.6
			M_2	0.6	0.6
46244	Muridae	*Tatera* sp.	M^2	1	1.2
46245	Murinae		M_1	1.5	1
46246	Muridae	*Arvicanthis* sp.	M^1	2	1.4
46247	Muridae	*Mastomys* sp.	M^1	1.5	1.1
46248	Muridae	*Tatera* sp.	M_2	1	1.2
46249	Muridae	*Mastomys* sp.	M_1	1.2	0.9
46250	Muridae	*Mastomys* sp.	M^1	1.4	1.1
46251	Muridae	*Tatera* sp.	M_1	1.6	1.3
46252	Muridae	*Tatera* sp.	M_1	1.9	1.3
46253	Muridae	cf. *Acomys*	M_1	1	0.6
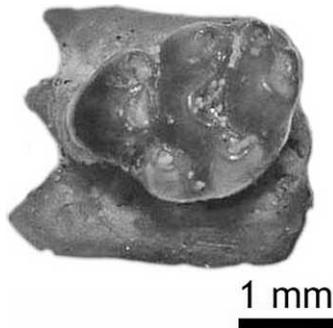
Figure 3. *Aethomys* sp. indet., KNM-NK 44921, left M^1 in maxillary fragment.

the Shungura Formation (Wesselman, 1984). The presence of *Acomys* at Lemudong'o is one of the earliest occurrences of this rodent in the fossil record.

Genus *AETHOMYS* Thomas, 1915
AETHOMYS species indeterminate
Figure 3

Referred material

KNM-NK 44921 (left M^1 in max. frag.). An additional specimen, KNM-NK 44832 (right mand. frag. w/ M_{2-3}), has been identified as cf. *Aethomys*.

Discussion

Aethomys is represented at Lemudung'o by two fragmented jaws, whose dental elements are, however, very well preserved. The general morphology as well as the occlusal surface of KNM-NK 44921 (Figure 3) resembles that of *Aethomys lavocati* from Olduvai Bed 1 (e.g., Fernandez-Jalvo et al., 1998). While the occlusal surfaces and the general morphology of the molars of KNM-NK 44832 (right mand. frag. w/ M_{2-3}) correlate with that of, for instance, *A. lavocati* from Olduvai Bed 1, the M_2 of the Lemudong'o specimen broadens slightly on the anterior end.

Although *Aethomys* is reasonably well represented in the Plio-Pleistocene fossil record of East Africa (Wesselman, 1984; Black and Krishtalka, 1986; Fernandez-Jalvo et al., 1998), it is less common in the lower Pliocene fossil record (e.g., Manthi, 2006). As at Lemudong'o, *Aethomys* is represented largely by isolated molars in the upper Pliocene deposits of the Omo (Jaeger and Wesselman, 1976; Wesselman, 1984). Prior to the discovery of *Aethomys* at Lemudong'o, the earliest record of members of this genus had been reported from the Lower Pliocene deposits at Langebaanweg (Denys, 1999; Matthews, 2004).

Figure 4. *Arvicanthis* sp. indet., KNM-NK 41089, right mandibular fragment w/ M_{1-2}.

Figure 5. *Mastomys* sp. indet., KNM-NK 41049, right mandibular fragment w/ $I–M_3$.

Genus *ARVICANTHIS* Lesson, 1842
ARVICANTHIS species indeterminate
Figure 4

Referred material

KNM-NK 41083, left mand. frag. w/ M_1; KNM-NK 41089, right mand. frag. w/ M_{1-2}; KNM-NK 41232, left mand. frag. w/ M_{1-2}; KNM-NK 45946, right mand. w/ $I-M_3$; KNM-NK 45947, right max. w/ M^{1-3}; KNM-NK 46235, left M^1; KNM-NK 46236, right M_1; KNM-NK 46239, left mand. frag. w/ M_1; KNM-NK 46242, left M_1 and KNM-NK 46246, left M^1, are attributed to *Arvicanthis* sp. KNM-NK 41128, right M^1 and KNM-NK 44830, right max. frag. w/ M^{1-2} are assigned to cf. *Arvicanthis*. The anterior end of the M^1 of KNM-NK 44830 is slightly more elongated than that of the typical members of this genus, including the extant *Arvicanthis abyssinicus*, but the size and the cusp pattern of the M^2 correlates well with that of members of this genus.

Discussion

Ten elements are attributed to *Arvicanthis*, while two elements have been ascribed to cf. *Arvicanthis*. Generally, although the incomplete nature of the jaws is evident, the teeth are in good condition, and their sizes and morphology exhibit close resemblance to those of the contemporary *Arvicanthis niloticus* and/ or *A. abyssinicus*. Figure 4, for instance, represents KNM-NK 41089, a mandible whose molars are very well preserved and are characterized by high and more inclined tubercles.

Fossil remains attributable to *Arvicanthis* have been reported in different Plio-Pleistocene sites, including the Omo (Wesselman, 1984, 1995) and Koobi Fora in Kenya (Black and Krishtalka, 1986). It is interesting to note that *Arvicanthis* has also been reported from the Lukeino Formation (Kenya), which dates between 5.9 and 5.7 Ma (Winkler, 2002). According to Winkler (2002), the Lukeino specimens represent the earliest record of this extant African genus (Winkler, 2002). Dated at 6 Ma it is conceivable that the *Arvicanthis* record from Lemudong'o possibly derives from a population that was contemporaneous with the Lukeino one.

Genus *MASTOMYS* Thomas, 1915
MASTOMYS species indeterminate
Figures 5–6

Referred Material

KNM-NK 41049, right mand. w/ $I–M_3$; KNM-NK 42360, right max. frag. w/ M^1; KNM-NK 44858, right mand. frag. w/ I and M_{2-3}; KNM-NK 45907, right mand. w/ $I–M_3$; KNM-NK 46247, right M^1; KNM-NK 46249, left M_1 in mand. frag. and KNM-NK 46250, left M^1, have all been identified as *Mastomys* sp. indet.

Figure 6. *Mastomys* sp. indet., KNM-NK 42360, right maxillary fragment w/ M^1.

Figure 7. *Lemniscomys* sp. indet., KNM-NK 41088, left mandibular fragment w/ $M_{2–3}$.

Further, KNM-NK 41096 (right mand. frag. w/ $M_{1–3}$) has been assigned to cf. *Mastomys*. This is because, even though the cusp pattern and the morphology of the $M_{2–3}$ of this specimen compares very well with those of the fossil and extant members of *Mastomys*, including the contemporary *M. natalensis*, the anterior end of the fossil M_1 is slightly more elongated than that of the typical members of this genus.

Discussion

The recent past has witnessed numerous assessments of the *Praomys* complex which comprises four genera namely, *Praomys*, *Mastomys*, *Myomys*, and *Hylomyscus* (Lecompte, Granjon, and Denys, 2002). This has been necessitated by the debate that has for a long time surrounded the systematics of members of this group (e.g., Kingdon, 1974; Lecompte, Granjon, and Denys, 2002; Lecompte, Granjon, Peterhans, et al., 2002). Based on the morphology of the dental elements, seven of the Lemudong'o specimens were ascribed to *Mastomys* sp. indet., and a further one element identified as cf. *Mastomys* sp. indet. Among the lower dentition, *Mastomys* at Lemudong'o is best represented by KNM-NK 41049 (Figure 5), a virtually complete right mandible whose molars exhibit very minimal wear on the occlusal surface.

Among the upper dentition, the presence of *Mastomys* at Lemudong'o is best represented by KNM-NK 42360 (Figure 6), which exhibits a long incisor foramen that ends after the prelobe of the M^1, a feature associated with members of this genus (C. Denys, personal communication). A right maxilla fragment with a low crowned M^1 and a portion of the zygomatic process, the characters (including the size) of this tooth generally resemble those of the contemporary *Mastomys natalensis*. As also the case with *Mastomys minor* from the Omo, Ethiopia (Wesselman, 1984), the first cusp (t1) of KNM-NK 42360 is broadly separated from the central cusp (t2) and runs from the back along the lingual side of the tooth. Overall, although some of the molars attributed to *Mastomys* exhibit light occlusal wear, they are generally well preserved.

Genus *LEMNISCOMYS* Trouessart, 1881
LEMNISCOMYS species indeterminate
Figure 7

Referred Material

KNM-NK 41088, left mand. frag. w/ $M_{2–3}$ and KNM-NK 44856, left mand. w/ I–M_3.
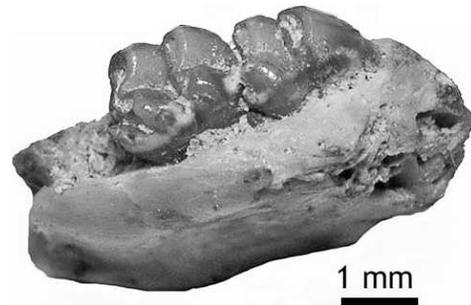
Discussion

Two dental elements have been assigned to *Lemniscomys* sp. indet. The molars of KNM-NK 41088 are complete and do not show any evidence of wear, and generally resemble those of the modern-day *Lemniscomys griselda*. Of note are the transverse shallow valleys that separate the laminae of M_2 from each other. On the other hand, however, the cusp pattern of KNM-NK 41088 (Figure 7) exhibits some resemblance to that of the extant *Arvicanthis abyssinicus*, although the molars of the Lemudong'o specimen are smaller in size. The molars of KNM-NK 44856 are all complete but show a substantial amount of wear on the occlusal surface. The cusp pattern and the wear on the occlusal surface resemble that exhibited by the modern-day *Lemniscomys striatus*.

Genus cf. *SAIDOMYS* James and Slaughter, 1974
Figure 8

Referred Material

KNM-NK 44815, right mand. w/ $M_{1–3}$; KNM-NK 46233, right M^2; and KNM-NK 46240, left M^1 are ascribed to cf. *Saidomys*.

Discussion

Three dental elements have been attributed to cf. *Saidomys* (e.g., Figure 8). This is because although the general morphology of these elements resembles that of the members of the *Arvicanthis* division, which includes the genera *Arvicanthis*, *Lemniscomys*, as well as the extinct *Saidomys* (Musser, 1987; Denne Reed, personal communication), the cusps of the Lemudong'o specimens are more conical than, particularly, those of the members of the genera *Arvicanthis* and *Lemniscomys*. Unlike the case with *Arvicanthis* and *Lemniscomys*, deep valleys separate the cusps of particularly the M^1 of the Lemudong'o cf. *Saidomys*. Further, although the

Figure 8. cf. *Saidomys*, KNM-NK 46240, left M^1.

molars of KNM-NK 44815 exhibit some occlusal wear, and parts of the occlusal surface are covered by matrix, their size and morphology compares well with those of LT 24201 (left mandible w/ I–M_3) from the Late Miocene site of Lothagam, Kenya, which has also been assigned to *Saidomys* (Winkler, 2003). By and large, the overlap in the morphological characteristics among the members of the *Arvicanthis* division makes it difficult to discriminate *Saidomys* from other members of this division (Musser, 1987; D. Reed, personal communication).

Remains of *Saidomys* are relatively common in a number of Late Miocene to Late Pliocene sites of East Africa, as well as the Early Pliocene of Afghanistan (Sabatier, 1982; Winkler, 1997, 2002, 2003). In East Africa, these sites include the Kenyan sites of Lothagam (Winkler, 2003) and Tabarin (Winkler, 2002), which are to the north of Lemudong'o, as well as Tanzania's Manonga Valley (Winkler, 1997).

Despite the occurrence of *Saidomys* in numerous sites in both Africa and Asia, the area of origin of members of this genus is uncertain, but is more likely to have been in southern Asia (Winkler, 1997). The Tertiary record of *Saidomys natrunensis* from Wadi el Natrun in Egypt is one of earliest members of this genus and the entire *Arvicanthis* division in Africa (James and Slaughter, 1974; Wesselman, 1984). The presence of *Saidomys* in Egypt may be attributed to the intercontinental dispersal and faunal interchange between southern Asia and Africa during the later part of the late Miocene. According to Winkler (2002), this faunal interchange is also demonstrated by the presence of *Mus* in both southern Asia and Africa during the late Miocene and early Pliocene. The presence of *Saidomys* at Lothagam and the larger Turkana Basin may suggest that this basin served as a biogeographic corridor (e.g., Wesselman, 1995) through which this genus and others would have dispersed to other areas including Lemudong'o. This dispersal corridor would have included the Kenyan Baringo Basin in which *Saidomys* has also been found (Winkler, 2002), and is situated several hundred kilometers to the north of Lemudong'o. According to Musser (1987), however, before an Asian-northeastern African linkage during Pliocene is accepted as a reality, species associated with *Saidomys*, both extinct and extant (e.g., *Arvicanthis* and *Lemniscomys*), should be carefully restudied, particularly considering the overlap in the morphological characteristics among the teeth (Wesselman, 1984; Musser, 1987).

<center>Subfamily MURINAE
Genus and species indeterminate</center>

Referred Material

KNM-NK 40998, left mand. w/ I and alveoli of M_{1-3}; KNM-NK 41050, left and right pre-max. w/ incisors; KNM-NK 41085, right upp. I; KNM-NK 41107, right mand. frag. w/ I–M_1; KNM-NK 41127, left mand. w/ I–M_1; KNM-NK 41448, left mand. w/ I and alveoli of M_{1-3}; KNM-NK 44857, right upp. I; KNM-NK 46245, left M_1.

Discussion

For various reasons including lack of dentition (particularly molars) in some of the jaws, eight dental elements have been ascribed to Murinae gen. and sp. indet. The assignment of these elements to Murinae rather than Gerbillinae was based on either the morphology of the teeth or the alveoli pattern (for those elements lacking dentition) which is typical to that of the murinae rodents.

Figure 9. *Tatera* sp. indet., KNM-NK 41087, right mandibular fragment w/ M_{1-2}.

<center>Subfamily GERBILLINAE Gray, 1825
Genus *TATERA* Lataste, 1882
TATERA species indeterminate
Figure 9</center>

Referred Material

KNM-NK 41087, right mand. frag. w/ M_{1-2}; KNM-NK 41106, right M_1; KNM-NK 41449, right mand. w/ I and alveoli of M_{1-3}; KNM-NK 42295, left M^1; KNM-NK 46232, right M_2; KNM-NK 46234, left M_1 in mand. frag.; KNM-NK 46237, left M^1; KNM-NK 46238, left M_1; KNM-NK 46241, left M_1; KNM-NK 46244, right M^2; KNM-NK 46248, right M_2; KNM-NK 46251, left M_1 and KNM-NK 46252, left M_1.

Discussion

Thirteen dental elements have been identified as *Tatera* sp. indet. The presence of *Tatera* at Lemudong'o may best be explained by KNM-NK 41087 (Figure 9). Despite their remarkably large size, the molars of this specimen clearly display the typical *Tatera* and generally gerbil morphology in which the cusps of M_1 and M_2 are arranged into respectively three and two broad transverse laminae (e.g., Wesselman, 1984; Flynn et al., 2003). Of further note in KNM-NK 41087 are the broad lophs that characterize the molars, as well as the wear on the occlusal. Overall, it is noteworthy that gerbils can be recognized without much difficulty using the dentition since the cusps of the first and second molars of *Tatera* (both upper and lower) are generally arranged into transverse laminae, which are inclined backwards.

Members of the genus *Tatera* have been recorded from a number of Late Miocene as well as Pliocene sites of East Africa including the Tugen Hills (e.g., Winkler, 2002), Laetoli (Denys, 1987), and Hadar (e.g., Sabatier, 1982).

<center>Subfamily GERBILLINAE
Genus and species indeterminate</center>

Referred Material

KNM-NK 41086, left mand. frag. w/ I and alveolus of M_1, has been identified as Gerbillinae. Additional material, KNM-NK 41070, left and right pre-max. w/ incisors, has been attributed to cf. Gerbillinae.

Discussion

Although no molars are intact in KNM-NK 41086, the mandible fragment and the incisor are very well preserved. The
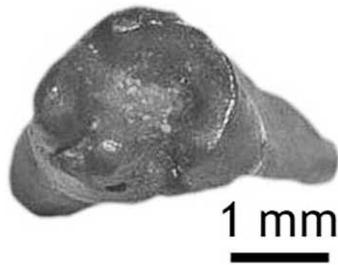
Figure 10. *Paraxerus* sp. indet., KNM-NK 44920, left P_4.

Figure 11. *Xerus* sp. indet., KNM-NK 41046, left maxillary fragment w/ P^4–M^1.

alveolar pattern of the M_1 is typical of that of the gerbils, and was used to assign this specimen to the Gerbillinae group. KNM-NK 41070 has lost all the molars and the assignment of this specimen to cf. Gerbillinae was based on the grooves on the incisors.

Family MURIDAE
Genus and species indeterminate

Referred Material

KNM-NK 41101, right edentulous mand. frag.; KNM-NK 44831, right mand. frag. w/ I.

Discussion

KNM-NK 41101 is broken at the inferior border, and lacks dentition. KNM-NK 44831 is also broken at the inferior border and, although it lacks any of the molars, a large part of the incisor is still intact.

Family SCIURIDAE Gray, 1821
Genus *PARAXERUS* Forsyth Major, 1893
PARAXERUS species indeterminate
Figure 10

Referred Material

KNM-NK 42311, right pre-mandibular frag. w/ I; KNM-NK 44920, left P_4.

Discussion

The pre-mandibular fragment ascribed to KNM-NK 42311 is broken at the inferior border. Although the incisor in this mandible fragment exhibits very minimal corrosion which is confined to the dentine, its preservation is good. The preservation of KNM-NK 44920 (Figure 10) is also good, and the P_4 shows very minimal wear. The size and morphology of this specimen resemble that of the contemporary *Paraxerus palliatus*. Of note is that, compared with the lower molar from Tabarin, Kenyan (Winkler, 2002), the size of KNM-NK 44920, in spite of being a premolar, is larger than that of the Tabarin specimen. Further comparison between the Lemudong'o specimen (KNM-NK 44920) with *Vulcanisciurus africanus* (left mand. w/ P_4–M_3) from Rusinga, Kenya (e.g., Lavocat, 1978) reveals that although the general morphology and occlusal surfaces of the two specimens show a lot of resemblance, the Lemudong'o specimen is slightly larger in size. It should, however, be noted that among *Paraxerus*, size alone is not particularly helpful in identifying members of this genus as most of the species under this genus are very variable in their sizes (Wesselman, 1984).

Paraxerus has been reported from a number of sites, including the Late Miocene deposits of the Middle Awash in Ethiopia (Haile-Selassie et al., 2004) as well as the Pliocene beds at Laetoli (Denys, 1987). It is significant that, although the *Paraxerus* specimen from Tabarin (dated to 4.5–4.4 Ma) was originally believed to represent the earliest record of this extant African genera (Winkler, 2002), the Middle Awash material (dated between 5.8 and 5.2 Ma) and the Lemudong'o material are to date the earliest known evidence of this sciurid.

Genus *XERUS* Ehrenberg, 1833
XERUS species indeterminate
Figure 11

Referred Material

KNM-NK 41046, left max. frag. w/ P^4–M^1; and KNM-NK 42335, right P_4.

Discussion

The preservation of all the teeth is good, and the teeth show very minimal wear. The morphology of the dentition, particularly that of KNM-NK 41046 (Figure 11) compares well with the contemporary unstriped ground squirrel, *Xerus rutilus*; although in a number of respects (including the general morphology of the dentition) the specimen also resembles the contemporary red-legged sun squirrel, *Heliosciurus rufobrachium*. A comparison between KNM-NK 42335, right P_4, and a left P_4 attributed to the fossil sun squirrel, *Heliosciurus*, from Tabarin (Winkler, 2002), however, reveals that the size of the latter is smaller than that of the former. On the whole, little is known about the variability of the fossil *Xerus* species particularly because of their paucity in the fossil record (Denys et al., 2003). This situation is further compounded by the fact that both the fossil *Xerus* and *Paraxerus* are virtually indistinguishable from modern species, a phenomenon which suggests that a stasis would have occurred in these taxa (Wesselman, 1984).

Genus cf. *XERUS*

Referred Material

KNM-NK 45798, left upp. I.

Figure 12. *Thryonomys* sp. indet., KNM-NK 45945, left mandible w/ I and M_{1-2}.

Discussion

This isolated incisor is about 80% complete, and although some moderate corrosion is evident on the dentine, there is no visible corrosion on the enamel.

Family THRYONOMYIDAE Pocock, 1922
Genus *THRYONOMYS* Fitzinger, 1867
THRYONOMYS species indeterminate
Figure 12

Referred Material

KNM-NK 45934, right mand. w/ I and M_2; KNM-NK 45945, left mand. w/ I and M_{1-3}.

Discussion

KNM-NK 45934 is broken at the posterior end and therefore lacks the ascending ramus. The inferior border and the tip of the incisor are also partly broken. The M_2 is complete and shows very minimal wear. The general morphology of the incisor and the M_2 in KNM-NK 45934 resembles that of the dental elements of KNM-LT 22998 (*Paraphiomys chororensis*, right mandible with incisor, dP_4, M_{1-3}) from the early Pliocene site of Lothagam (Winkler, 2003), although the former appears to be slightly smaller in size.

KNM-NK 45945 is largely embedded in matrix (Figure 12). The tip of the incisor is broken and, although the molars are complete, they show some occlusal wear. A comparison between KNM-NK 45945 and the Lothagam specimen mentioned above suggests that, although the teeth of the former specimen are smaller in size, there seems to be a close resemblance in the general morphology of the dentition of the two specimens.

Taphonomy

Breakage is quite high among the Lemudong'o rodents, and this is strongly suggested by the substantial number of incomplete

Table 2. Breakage patterns of the long bones from the 2001 sample.

	Humeri	Ulnae	Femora	Tibiae
Complete	0	0	0	0
Proximal	0	21	19	0
Shaft	3	16	0	26
Distal	18	0	4	35

Table 3. Number of identified specimens (NISP).

Skeletal element	%
Isolated molars	18.7
Isolated incisors	22.5
Scapulae	0.6
Humeri	2.42
Ulnae	4.3
Radii	1.3
Innominates	0.5
Vertebrae	13.6
Femora	2.7
Tibiae	7.0
Astragali	1.6
Calcanea	2.0
Podials	0.35
Metapodials	8.7
Phalanges	13.9
TOTAL NISP	866

cranial and postcranial elements. Although vertebrae and phalanges occur in relatively large numbers, isolated teeth are by far the most abundant elements (Tables 1 and 3). The large numbers of isolated teeth are suggestive of high breakage among the jaws (Andrews, 1990). Among the long bones, there is a bias for the more durable and robust portions of the bones, as strongly indicated by the relatively higher numbers of the distal humeri, proximal femora, distal tibiae, and proximal ulnae (Table 2). The differential representation of skeletal elements at Lemudong'o should be treated as an artifact of predation (damage and loss caused by the predator/s), damage inflicted by diagenetic processes (e.g., during compaction of sediments), breakage during the recovery process, and generally the differential survivability of skeletal elements (Korth, 1979; Andrews, 1990; Fernandez-Jalvo and Andrews, 1992; Coard and Dennell, 1995; Coard, 1999). As an example, the high numbers of either the distal or proximal ends of the long bones may be explained by the robusticity and hence durability of these portions of the bones, which enhances their survivability against many taphonomic processes (Andrews, 1990; Andrews and Jenkins, 2000; Manthi, 2002).

On the whole, because elements such as the vertebrae and phalanges are easily transported (Behrensmeyer, 1978; Korth, 1979; Frostick and Reid, 1982), their high proportions among the Lemudong'o rodent remains (13.6% and 13.9%, respectively) as reported in Table 3, suggest that the fauna was buried *in situ*. Furthermore, although teeth are moved last by, for instance, currents (Winkler, 1983), the abundance of molars (18.7%) at Lemudong'o further supports the hypothesis that the fauna accumulated *in situ*, and that breakage among the jaws occurred within the primary area of accumulation. It can therefore be concluded that the Lemudong'o small-mammal remains represent

Table 4. Etching on the Lemudong'o lower rodent incisors.

Lower incisors		Upper incisors	
Etching category	%	Etching category	%
1	63	1	61
2	33	2	32.2
3	4.2	3	6.8
Total NISP	48	Total NISP	59

in situ accumulations that, after their accumulation, would only have been moved a few meters, if at all, before their burial. Over time, however, erosion exposed the bones to surface transport, as well as detection and collection by the workers.

The agency of accumulation

The condition of fossil material can provide evidence of intervening processes before and after burial and, together with the percentage representation of skeletal elements, can help establish the source of faunal assemblages (Korth, 1979; Andrews, 1990). For instance, assemblages resulting from predation by either birds or mammals, or both, tend to have a high representation of skeletal elements, and may exhibit evidence of etching (caused during digestion) on elements such as the incisors and the articular ends of long bones. On the other hand, because alluvial processes tend to disperse micromammalian elements rather than concentrate them (Denys, 1997; Flynn et al., 1998), a bone assemblage that has been subjected to alluvial processes often has a low percentage body part representation and one or two elements in abundance (Korth, 1979, p. 275; Andrews, 1990).

Because nearly all skeletal elements are represented in the Lemudong'o sample, and in fairly considerable numbers (Table 3), it is believed that predators were responsible for the accumulation of the assemblage (e.g., Avery, 1982, 1988; Andrews, 1990). Among the predators of small mammals, the likelihood that small carnivorous mammals accumulated the Lemudong'o fauna is ruled out by several factors, including the fact that, through consumption and digestion, these predators cause considerable damage and loss to the bones of their prey (Andrews and Evans, 1983; Andrews, 1990). Furthermore, small carnivorous mammals cause a substantial amount of etching (Andrews, 1990), a phenomenon not evident among the incisors investigated for etching (Table 4). Likewise, analyses done on diurnal raptors' pellets (e.g., Dodson and Wexlar, 1979) have yielded very few micromammalian bones. This is largely because during consumption (including dismemberment and digestion), diurnal raptors cause considerable destruction to the bones of their prey (Dodson and Wexlar, 1979; Andrews, 1990). Further, although most diurnal raptors prey on micromammals, their generally mobile existence makes them less potential accumulators of micromammalian bones (e.g., Steyn, 1982). Studies have also shown that diurnal raptors prey on larger prey species whose representation among the Lemudong'o rodent faunal sample is negligible. In South Africa, for instance, the most common animals appearing in martial-eagle roosts are Cape hares, *Lepus capensis* (e.g., Cruz-Uribe and Klein, 1998).

Among the owls, the body sizes of the rodent species in the Lemudong'o sample do not suggest the involvement of large owls such as the Cape eagle owl (*Bubo capensis capensis*) and the giant eagle owl (*Bubo lacteus*) in the accumulation of the fauna. This is largely because these owls feed primarily on larger prey species including mole rats, red hyraxes, scrub hares, red rock hares, and springhares, which are rare among the Lemudong'o fauna (e.g., Steyn, 1982, 1984; Kemp and Calburn, 1987). Although the relatively high diversity of rodent genera may implicate the spotted eagle owl, the candidacy of this owl in the accumulation of the Lemudong'o fauna is called into question by, among other factors, the tendency of the owl to use various nest sites (Steyn 1982), and therefore not accumulating large clusters of pellets.

It is interesting that the Lemudong'o rodents comprise largely species whose modern counterparts weigh below 150 g (Kingdon,

1974). Among the owls, the barn owl, which is predominantly associated with the accumulation of most micromammalian assemblages, is known to take prey weighing up to 150 g. Further, the barn owl causes minimal etching, breakage, and loss to the bones of its prey (Kemp and Calburn, 1987; Avery, 1988, 1990, 2002; Andrews, 1990; Taylor, 1994), features that are evident among the Lemudong'o faunal remains. The fact that most of the species represented in the sample including *Paraxerus*, *Lemniscomys*, *Arvicanthis*, and *Tatera* are either diurnal or crepuscular (Kingdon, 1974; Wesselman, 1984; Delany, 1986; Fernandez-Jalvo et al., 1998) whereas the barn owl is largely nocturnal may be explained by the behaviour of the barn owl to also hunt during overcast days (Steyn, 1982). In addition, because the large size and diurnal habits of sciurids (including *Xerus*) make them an uncommon prey for virtually all owls, it is likely that the sciurids at Lemudong'o may have been captured by either small carnivorous mammals or diurnal raptors (Kingdon, 1997).

By and large, the possibility that several predators may have been involved in the accumulation of the Lemudong'o rodent fauna may not completely be ruled out. This is true particularly considering that, among the owls, for instance, the barn owls and the spotted eagle owls take a broad range of prey species, although the latter tends to take larger mammalian and avian prey, and causes considerable damage to the bones of its prey than the former (Grindley et al., 1973; Steyn, 1982; Dean, 1989; Andrews, 1990; Avery, 2002).

Paleoenvironment

The environmental interpretations drawn from the Lemudong'o rodents are based on the use of modern analogues, and the assumption that ecological requirements and/or behaviour have remained constant for both the rodents and the accumulating agency (e.g., Avery, 1982). It is significant that predators generally hunt within a certain range of the area in which they occur. As an example, the barn owl has been reported to hunt up to a maximum of 16 km from its roost site (e.g., Kemp and Calburn, 1987). Assuming that the Lemudong'o rodent fauna accumulated by way of predation and is an *in situ* assemblage, it is, therefore, possible to determine the local environment for this site as provided by the rodents.

The Lemudong'o rodent fauna includes taxa that are known to occur in varied microhabitats, suggesting a mosaic of biotopes in the area some 6 Ma. Open vegetation and/or dry savanna, grassland/woodland environments, as well as flood plains would have been significant features of the Lemudong'o area. This is suggested by the abundance of dental elements ascribable to *Tatera* and *Arvicanthis*, as well as the presence of *Acomys* in the sample. Arid environments are suggested by *Tatera* and *Acomys*, with the latter being an indicator of environments characterized by lava gravel flats and generally rocky grounds, sandy valleys, dry savanna woodlands, dry *Acacia* and scrub, and dry grasslands (Walker et al., 1964; Coe, 1972; Kingdon, 1974; Happold, 1975; Reed, 2003). Sandy substrates as well as sandy grasslands are also suggested by *Tatera*, which prefers such environments where they build elaborate burrows (e.g., Coe, 1972; Kingdon, 1974; Wesselman, 1984; Black and Krishtalka, 1986; Fernandez-Jalvo et al., 1998; Antoñanzas and Bescós, 2002; Winkler, 2002). In the Kenyan South Turkana area, Coe (1972) also found *Tatera* to be associated with *Salvadora* thickets along the edges of the alluvial flats bordering the Kerio River. In view of this, mesic grasslands and/or open flood-plains would have existed in the Lemudong'o area, a proposal also supported by the presence at the site of

Lemniscomys. Species of the genus *Lemniscomys* are associated with open and mesic savanna/grassy environments, as well as savanna grasslands characterized by pockets of bushes and tree cover (Delany, 1972; Kingdon, 1974; Wesselman, 1984).

Further support for the presence of bushes and/or woodlands in a savanna grassland environment comes from the presence of *Mastomys*, *Paraxerus*, and *Aethomys*. Even though species of *Mastomys* occur in a very wide range of environments, this genus is associated with savannas and woodlands, whereas members of the genus *Paraxerus* are common in low-level vegetation and shade set in savanna environments (Kingdon, 1974, 1997). While *Aethomys* species exhibit some variation in habitat preference, this genus is generally associated with more or less closed microhabitats, including dry savanna woodlands, *Acacia* savanna and scrub, and dry grasslands (e.g., Kingdon, 1974; Wesselman, 1984; Reed, 2003).

In further support of grassy environments at Lemudong'o is the extinct *Saidomys*, which although its habitats are difficult to determine (Winkler, 2002, 2003), has grazinglike dental morphology suggestive of a preference for grassy environments (Denys, 1999). Moreover, in spite of the doubt cast on the assignment of the Lemudong'o sciurids to *Paraxerus* and/or *Xerus*, the presence of *Xerus* at Lemudong'o lends further support to the argument that dry savanna/woodlands and soft grounds suitable for burrowing existed in the area. This is because members of the genus *Xerus* are known to inhabit the ecotone between thickets and grasslands (Coe, 1972; Kingdon, 1974; Wesselman, 1984; Denys et al., 2003).

Conclusions

The Lemudong'o rodent remains represent an *in situ* assemblage which probably has a predation origin. Although it is possible that several predators may have contributed in the accumulation of the rodents, it is more likely that one of the small owls (e.g., the barn owl) would have played a key role in the accumulation of the assemblage. Further, even though transportation of the small-mammal assemblage from its primary area of deposition appears to be minimal, it is evident that post-depositional taphonomic processes (including the process of diagenesis) modified the original assemblage that accumulated and was subsequently exposed to surface collection.

The Lemudong'o rodent fauna comprises taxa that prefer different but often overlapping microhabitats. These include riverine thickets, woodlands, and grasslands, all set in a largely savanna environment. This feature has also been reported virtually throughout the Lake Turkana basinal succession, where the fossil small mammals represented at any one level comprise a mixture of species associated with mesic conditions (riverine forests, savanna woodlands, and moist savanna) and species associated with xeric conditions such as dry savanna grasslands, *Acacia* scrub, and semi-desertic grassland (e.g., Black and Krishtalka, 1986; Feibel et al., 1991; Manthi, 2006). Because Gerbillinae as a group is an indicator of open conditions, while Murinae are typically considered to be more abundant in closed environments (Dauphin et al., 1994; Denys et al., 1996), the higher representation of taxa allied to the latter group at Lemudong'o suggest that forested and mesic micro-environments dominated over open grassland/woodland habitats. By and large, except for the extinct *Saidomys*, all the rodent genera from Lemudong'o are extant, and these provide some of the earliest appearances of the genera in Africa.

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