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KIRTLANDIA®

GEOLOGY AND PALEONTOLOGY OF LEMUDONG'O, KENYA

(Continued on back)

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HISTORY OF PALEONTOLOGICAL RESEARCH IN THE NAROK DISTRICT OF KENYA

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ABSTRACT

The geology of the Narok District of southern Kenya was first studied in the 1960s. From 1994 through 2005 more extensive paleontological and geological research was conducted on a series of late Miocene sediments of the Lemudong'o Formation in the region of Lemudong'o Gorge and Enamankeon where the Ntuka and Narok Rivers merge to form the Uaso Ngiro River. Numerous paleontological sites have been located, however all but one are poorly fossiliferous. The exception is the site of Lemudong'o Locality 1, near the village of Enkorika. Here we describe the geological and paleontological research that has been performed in the entire project area, with detailed information about the paleontology at Lemudong'o Locality 1.

Introduction

A small section of the western margin of the Gregory Rift Valley in the southern Narok District of Kenya (Figure 1), spanning approximately 60 km from north to south, may be one of the last areas of the Kenya Rift with terminal Miocene sedimentary formations to be systematically explored by geologists and paleontologists. Because sites dating to this time span are particularly scarce in Africa, this region provides important clues to the diversity of environments present during the time when hominids emerged in Africa, and can contribute to a refined geochronology and tephrastratigraphy of eastern Africa. The geologic and paleontological importance of this area is discussed in detail by Ambrose, Bell, et al. (2007). The history of research conducted in this district as of January 2005 is briefly summarized in this chapter. Localities are indicated in **boldface** when first described.

Previous Research

J. B. Wright (1967) conducted the first systematic geological research in the southern Narok District for the Geological Survey of Kenya between February and August of 1959. In less than seven months of fieldwork, Wright was able to produce a remarkably thorough report and a detailed and accurate geological map of the region, especially considering the size of the area (½ degree of latitude and longitude square). Wright reported a deeply stratified sequence of sediments, ashes and tuffs, in part waterlain, representing three overlapping paleolake basins. He estimated these to be of Pleistocene age. The deposits crop out over an area extending 30 km from north to south in the survey area, and are best exposed in the deeply incised valleys of the lower reaches of the Siyiapei, Narok, and Ntuka Rivers, which all converge on the Uaso Ngiro River. The Uaso Ngiro River flows south of Wright's survey area, and exposes additional outcrops of stratified

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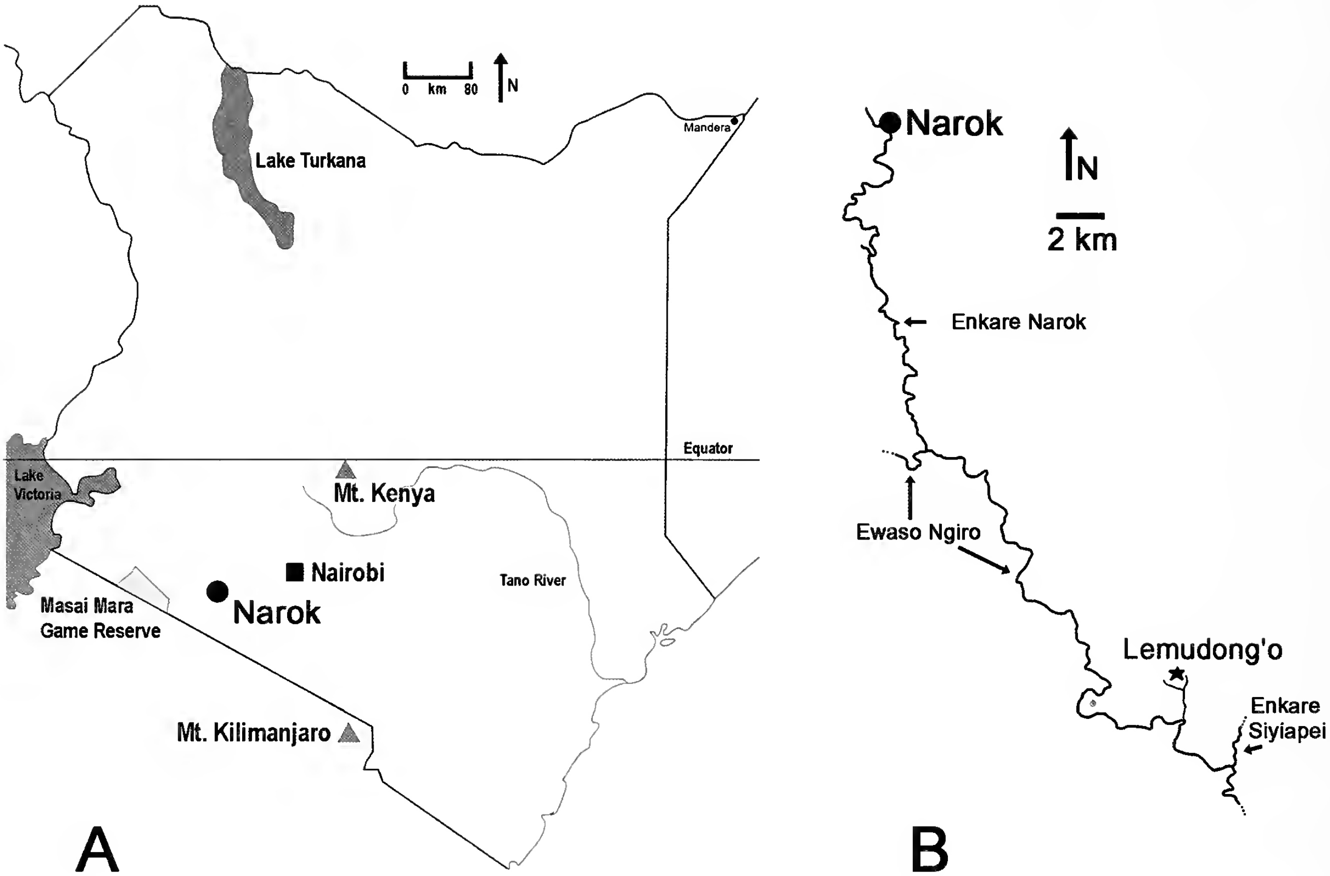

Figure 1. A, map of Kenya. B, finer-scale map showing the location of Lemudong'o relative to Narok.

sediments and volcanic tephra. Wright did not report vertebrate fossils, but he collected a number of flakes throughout this region, and a phonolite handaxe in the northern end of his survey area.

The potential for paleontological and archaeological research in this region was first recognized in 1976 by Waibel and McDonough during a survey of obsidian sources for the University of Massachusetts at Boston archaeological research project (Bower et al., 1977). Waibel and McDonough reported nine fossil localities in stratified sediments of the Ntuka River, approximately 5 km upstream from the confluence with the Uaso Ngiro River. Taxa collected included oryx, Cape buffalo, warthog, and zebra. Two archaeological sites with fossils were also identified in the Ntuka valley, one of which was possibly Early Stone Age (Sangoan). A K/Ar date of 4.4 ± 0.2 Ma was obtained on a welded tuff unconformably underlying the fossil-bearing sediments. A second tuff stratified within a sequence of pumices, waterlain ashes, and silts interbedded with channel deposits, collected 1 km upstream from the confluence of the Ntuka and the Olonganaiyo River, produced a K/Ar date of 3.0 ± 0.1 Ma. Waibel and McDonough concluded their brief report by noting the fossils and artifacts that they recovered may have come from the oldest of Wright's three paleolake basins, and that this region had potential for further geological and archaeological research.

Stanley Ambrose and Robert Blumenschine made a very brief visit to the Olonganaiyo River in December 1981. Fossil equid teeth were observed in a stratified series of late Quaternary fluvial and alluvial deposits in the first outcrop upstream from the confluence with the Ntuka River.

The Kenya Power and Lighting Corporation began to implement plans for the Amala Development Project in 1991, which involves construction of a series of three hydroelectric dams on the Uaso Ngiro River (Gereta et al., 2002). Surveyors and engineers were active in this region for a decade. As of 2001 the project has been put on hold, but if completed, it will flood virtually all of the late Neogene sedimentary exposures and fossil-bearing sites, as well as many archaeological sites in this region.

Current Research

In June 1994, Stanley Ambrose, David Kyule and Michael Noll visited the Ntuka region to revisit the sites reported by Waibel and McDonough and assess the potential for future research. Several late Quaternary archaeological and fossil sites were discovered in the Ntuka River Valley (Kyule et al., 1997). Joel Ole Raen, a local resident from Enaramatishoreki, guided us to Lemudong'o Gorge, near the Masai village of Enkorika (Figures 1 and 2). Well-preserved fossil bones and teeth were observed eroding from the outcrops in the vicinity of a cave eroded in the claystones of Wright's second paleolake. They collected a few diagnostic fossils, including a *Nyanzachoerus syrticus* third molar (Suidae, Artiodactyla) and a sample of tuff for dating. This site was designated GvJh15 in the Standardized African Site Enumeration System (SASES) (Nelson, 1971).

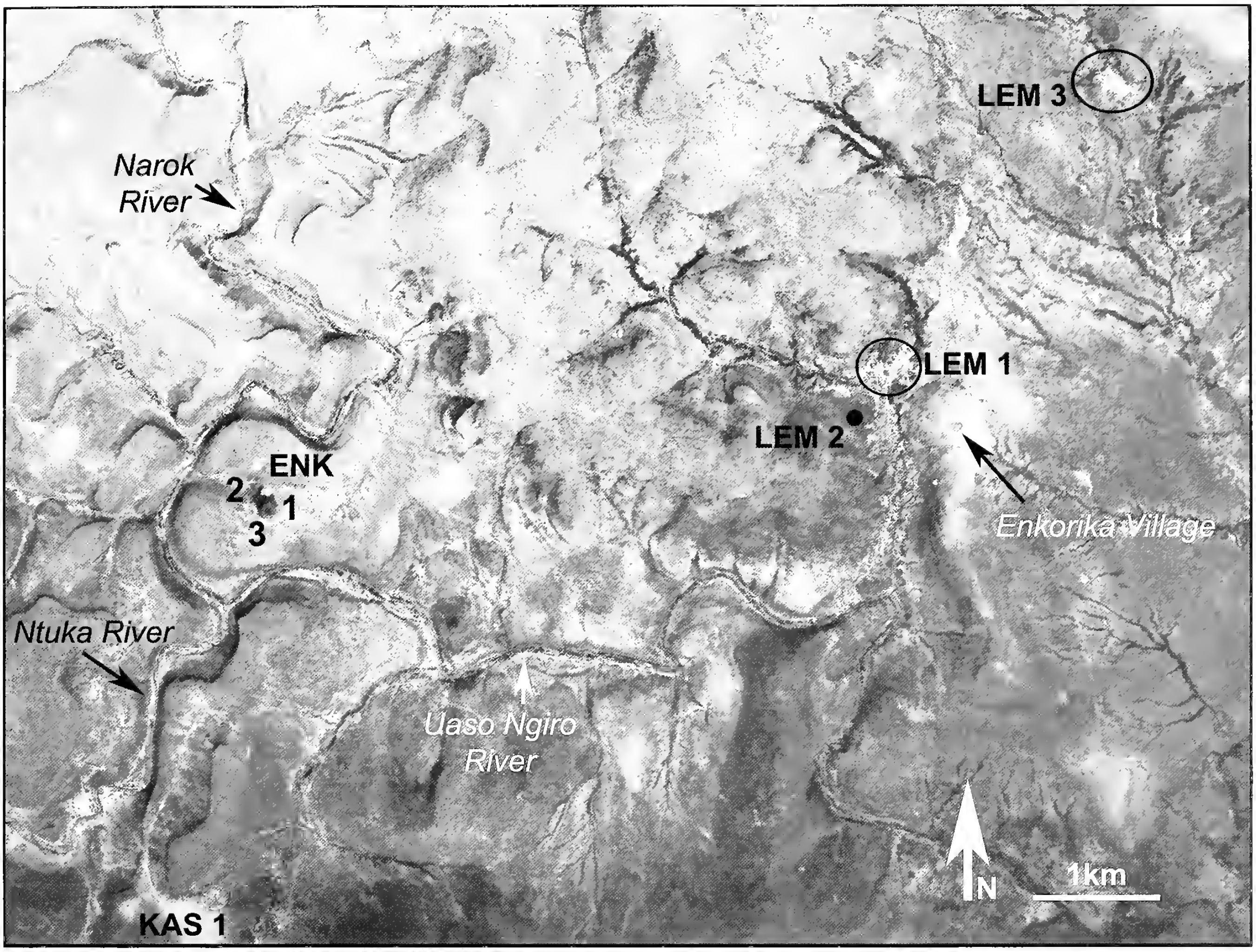

Figure 2. Aerial photograph showing the geography of the correlated late Miocene localities in the Narok District of Kenya. KAS 1 = Kasiolei Locality 1; LEM = Lemudong'o localities; ENK = Enamankeon. Scale is approximate.

Throughout this report we refer to this site as **Lemudong'o Locality 1 (LEM 1)** (01° 18.170 S, 35° 58.762 E; GPS elevation ~ 1,593 m). The team returned for additional survey of this region in July 1995 and 1999, collecting a total of 271 specimens.

A second sedimentary exposure in the Lemudong'o Gorge, approximately 0.5 km downstream from the main exposures at LEM 1 was identified in 1999, and designated as GvJh32. **Lemudong'o Locality 2 (LEM 2)** (01° 17.98 S, 35° 56.04 E) has only yielded one specimen, an associated pair of Elephantidae molars (Saegusa and Hlusko, 2007), but preserves a longer sedimentary sequence with well-stratified volcanic ashes that spans the main fossil horizon at LEM 1. Four tephra samples were collected, and three were submitted for radiogenic-argon dating, all of which date to ~6.0 Ma (Ambrose et al., 2003; Deino and Ambrose, 2007).

Lemudong'o Locality 3 (LEM 3) (01° 17.228 S, 35° 59.470 E; GPS elevation 1,646 m) was also identified in 1994 and designated as GvJh25. The local name for this exposure is Emparkutet Enkoreroi. This is a wide, shallow exposure of claystones overlying yellow-brown lacustrine silts with an interstratified reworked gray cindery ash, underlain by fluvial sands and fine gravels, located ~3 km northeast of LEM 1. A few undiagnostic bone fragments were observed eroding from the upper claystones. We collected four lightly rolled fossilized cercopithecid and bovid teeth from the basal sands. These specimens are not included in the faunal descriptions of the late Miocene sediments of the Narok District as this outcrop has not yet been geologically correlated with the LEM 1 sequence.

Sparse, mainly undiagnostic fossils were also observed eroding from paleosols and claystones within the long sedimentary sequences of two prominent flat-topped hills, named Enamankeon and Ol Doinyo Siloma, which lie on the east and west sides of the Uaso Ngiro River, respectively, near its confluence with the Ntuka River. These dispersed localities (described below) were not given SASES numbers. A small number of undiagnostic fossils were also observed in paleosols, waterlain silts and ashes stratified below plateau trachyte lavas at a locality called the Enaramatishoreki Depression (Wright, 1967, plate IVa), west of the Enaramatishoreki settlement. Its stratigraphic position within Wright's three paleolakes sequence is unknown. On the north side of the lower reaches of the Leshota Gorge east of Enaramatishoreki, a few undiagnostic longbone fragments were collected at a locality that was designated GvJi2. The stratified sequence at Leshota is at least 150-m thick, and is exposed in very steep outcrops for at least 15 km south of Leshota along the west side of the lower Uaso Ngiro valley. These deposits belong to the oldest paleolake.

Survey around the initially recognized sites (Lemudong'o and Enamankeon), and a 2002–2004 systematic survey of sediment exposures identified with ASTER satellite imagery and aerial photographs, led to the discovery of nine additional paleontological sites, mainly within this second paleolake formation, which is formally defined as the Lemudong'o Formation by Ambrose, Nyamai, et al. (2007). These are briefly described below.

Enamankeon (East) Locality 1 (ENK 1) (01° 18.568 S, 35° 56.774 E; GPS elevation ~1628 m), is located on the east side of the flat-topped hill after which the locality is named. The top of the hill is formed by a ~14-m-thick series of resistant yellow water-lain tuffs (Yellow Tuff) capped by a thick gray welded tuff (Gray Ignimbrite). These two tuffs cap most of the stratigraphic sequences at the fossiliferous localities of the second paleolake in this region. The sparsely fossiliferous claystones and sandstones are stratified below a thick, poorly consolidated gray tuff (Gray Tuff) that forms a prominent cliff around the entire perimeter of Enamankeon and above a blue-gray tuff. The gray tuff may correlate with the uppermost gray tuff at LEM 2 (Ambrose, Nyamai, et al., 2007).

Enamankeon (West) Locality 2 (ENK 2) (01° 18.500 S, 35° 56.570 E; GPS elevation ~ 1634 m) lies on the west side of the hill. This locality comprises a conformable depositional sequence of ~65 meters of interbedded claystones and sands with three possible tufa horizons. It unconformably overlies a very thick sequence of gray welded tuffs and phonolite lava. The sequence is sparsely fossiliferous from the second tufa to below the Gray Tuff. Two specimens were collected from the second tufa (an artiodactyl proximal femur and a carnivore distal femur). A hippopotamid mandible is embedded in a large block of carbonate cemented sandstone in the second tufa and large mammal long bones are nearby (exact location: 01° 18.505 S, 35° 56.568 E; elevation ~1633 m). The second tufa is stratigraphically below ENK 1 and 3 but is part of the same conformable depositional sequence.

Enamankeon (Southwest) Locality 3 (ENK 3) (01° 18.599 S, 35° 56.605 E; GPS elevation ~1642 m) is an approximately 50 m^2 exposure of claystones on the southern part of the west side of Enamankeon. Three specimens were collected, two carnivores and one cercopithecid primate from "popcorn"/sandy clays ~9 m below the aforementioned poorly consolidated Gray Tuff.

Entapot Enchoro Locality 1 (ENE 1) (01° 17.992 S, 35° 57.114 E; GPS elevation ~1613 m) is an exposure of brown mudstones with a sand lens outcropping for approximately 50 m^2. Five specimens were collected: three bovids, one colobine, and one carnivore. The age of this locality is uncertain although it is overlain by the Yellow Tuff and Gray Ignimbrite and is therefore most likely late Miocene as well.

Kapor Locality 1 (KAP 1) (01° 17.980 S, 36° 13.098 E; elevation ~1435 m) is restricted to the basalt cobble lag of the Kapor River. Only one bovid horn core was collected. This area is ~26 km east of Lemudong'o and is stratigraphically distinct. Its stratigraphic position relative to Lemudong'o is unknown but probably much younger.

Kasiolei Locality 1 (KAS 1) (01° 19.78 S, 35° 56.47 E; elevation ~1653 m) is composed of an approximately 20 m^2 exposure of pink/brown sediments with some root casts. The fossils are covered in carbonate. This locality is stratified within a sequence highly similar to that at Enamankeon below the poorly consolidated Gray Tuff. There are also a few fragments of fossilized bone and an equid tooth on the north side of Kasiolei as well. We did not collect this specimen but its location is 01° 19.577 S, 35° 56.327 E; GPS elevation ~1679 m.

Mpopong Locality 1 (MPO Loc 1) (01° 19.198 S, 35° 55.125 E; GPS elevation ~1685 m) consists of an outcrop of red sediments below a welded tuff. Four specimens were collected including an owl pellet, bovids (left maxillary fragment and mandibular right molar with surrounding alveolar bone), and a cercopithecid humeral shaft fragment. The age and stratigraphic position of this locality relative to other sites is uncertain.

Olodoo Kulapunyi Locality 1 (OLO Loc 1) (01° 18.925 S, 35° 55.341 E; GPS elevation ~1689 m) is composed of approximately 30 m^2 area of exposed sediment from which 12 specimens were collected from a carbonate horizon with sand, pebbles, and fossils cemented together. A carnivore skeleton was collected. This specimen is subfossilized and needs significant preparation. The age and stratigraphic position of this locality relative to other sites is also uncertain; a Pleistocene age seems likely.

Siloma Locality 1 (SIL 1) (01° 17.736 S, 35° 56.281E; elevation ~1658 m) is located north of Entapot where light brown sediments are exposed. Two bovid fossils covered in carbonate were collected. This locality is stratified within a sequence similar to that at Enamankeon below the poorly consolidated Gray Tuff.

None of these sites yielded significant or numerous fossil material. The three Enamankeon localities and KAS 1 and SIL 1 are stratigraphically related to LEM 1 and 2 (Ambrose, Nyamai, et al., 2007). Therefore, fossils collected from these sites are included in the descriptions of the Narok late Miocene fauna. The other five sites require further investigation to determine their age. Therefore, these fossils are not yet described but are listed in Appendix 1.

Research at Lemudong'o Locality 1

The most fossiliferous site in the Narok District identified to date is LEM 1 (see Appendix 1 for list of specimens). After the initial 1994 survey, this site was visited briefly on 11 July 1998, 20 June 1999, and 3 July 2000, with staff from the Palaeontology and Archaeology Divisions of the National Museums of Kenya in Nairobi. Additional fossils were collected, including a partial mandible of the proboscidean genus *Anancus* (KNM-NK 41502).

Intensive paleontological research at LEM 1 was undertaken from 2001 to 2004 under the lead of Leslea Hlusko. A 100% collection strategy was employed following that used at the sedimentologically similar sites at Aramis in Ethiopia (White, 2004). Only specimens diagnostic of order (or more specific) were collected from LEM 2 and other penecontemporaneous sites (ENK 1, 2, and 3, and KAS 1).

Systematic measurements of partial stratigraphic sections were made at LEM 1 and 2 in July 2002 with Martin A. J. Williams. More complete stratigraphic sections were measured with Chris Nyamai, Eliud Mathu and Justus Muragwa from the Geology Department at the University of Nairobi in July 2004 and January 2005. These latter sections sampled most strata for petrographic and geochemical analyses and correlations between outcrops. The geological findings are reported in more detail elsewhere (Ambrose, Nyamai, et al., 2007).

The lateral variation in sediments at LEM 1 is outlined below in the descriptions of the collection areas. All of the fossils come from an 8-m-thick sequence of mudstones, sands and gravels stratified above yellow lacustrine silts (Figures 3–4). The sequence (Figure 4) represents a small shallow lake (Stratum 1) that receded, forming a beach or delta (Stratum 2), and then an

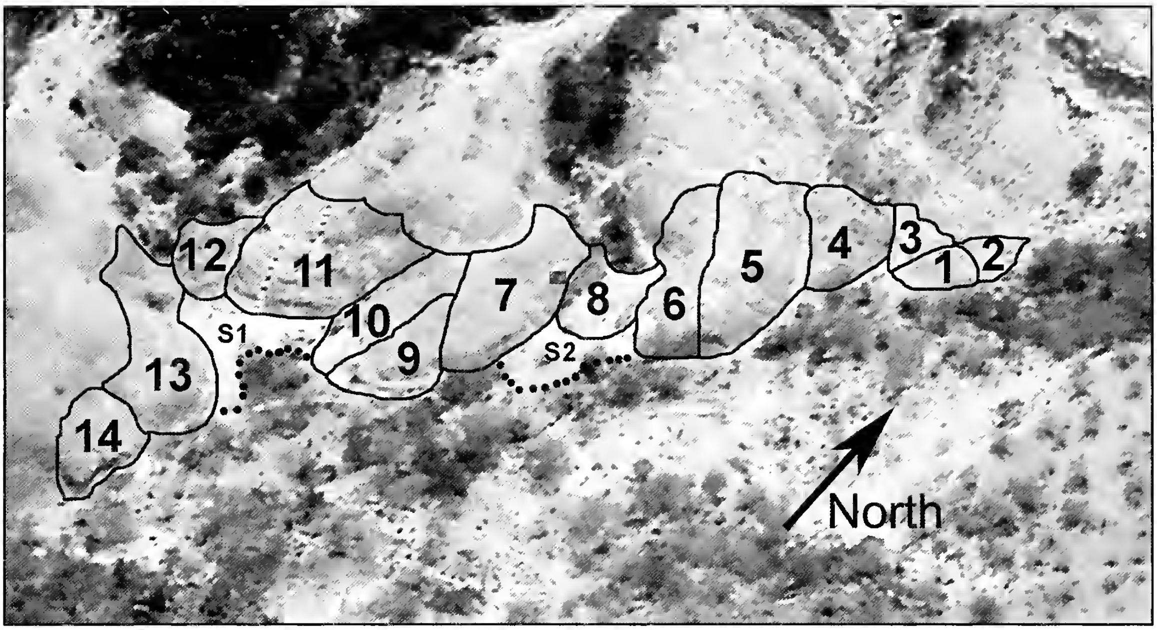

Figure 3. Aerial photograph showing the collection areas of Lemudong'o Locality 1. S1 = sieving area 1; S2 = sieving area 2. See text for details.

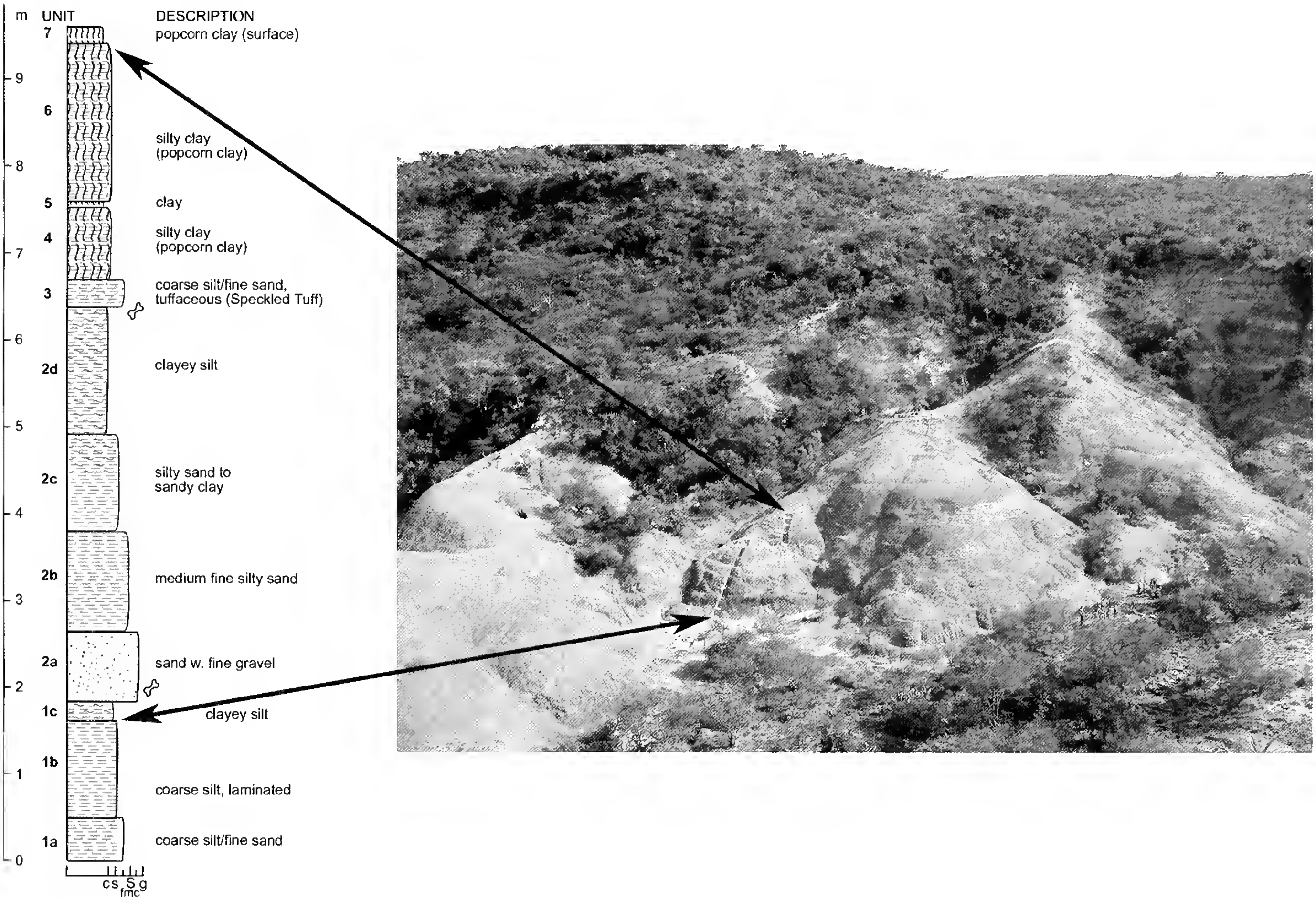

Figure 4. Photograph of LEM 1 taken from the eastern side of the Lemudong'o Gorge beside the stratigraphic column (see Ambrose, Nyamai, et al., 2007 for a more detailed diagram). There is a person standing in sieving area 2 for scale.

intermittently flooded muddy lake margin zone (Strata 4–7). The speckled tuff (Stratum 3), dated to 6.084 Ma (Ambrose et al., 2003; Deino and Ambrose, 2007), lies approximately 5 m above the lacustrine silts (Figure 4). The lowest 2–3 m of the fossiliferous sequence comprises mainly sands and gravels (Stratum 2), whereas the upper portion of the fossiliferous section is dominated by mudstones and cracking claystones (Strata 4–7). In collection area 9 the basal sands contain a shallow channel or depression filled with a lens of dark green, fine-grained dense tuff.

At LEM 1, all plant and animal fossil material was collected systematically: the field crew crawled along the small lobes of the outcrop shoulder to shoulder within 14 collection areas defined by erosional microtopography and stratigraphy (Figure 3). Although the sediments extend beyond these areas, those outcrops are virtually sterile. Meave Leakey oversaw the collection in 2000, providing descriptions of specimen provenience that were translated to the areas defined in 2001. Working from the bottom of the erosional fan of each slope, specimens were collected such that stratigraphic provenience could be determined for scattered specimens and to ensure that all recoverable pieces of broken specimens were recovered.

The fossils within the cracking claystones are typically highly fragmentary but with very little to no evidence of pre-depositional weathering. Only specimens that were identifiable to family were provided with a National Museum of Kenya specimen number (all are preceded by KNM-NK). All other material is held in "bulk" bags with the catalogued Narok collection in the Division of Palaeontology at the National Museum of Kenya in Nairobi.

Our 100% collection strategy enabled the recovery of microfauna and fragmentary specimens that were then reassembled, and provided information on the rejuvenation of exposed fossils from year to year. The most complete and larger specimens were collected in the first few years (i.e., 1995–2000); fewer, and primarily smaller, specimens were collected in later years, with the exception of the erosional basins that were partially sieved, as described further below. Collection of specimens identifiable to family level declined from 382 in 2001 to 109 in 2004. This follows expectations given the nature of fossiliferous-sediment erosional rates (White, 2004).

Brief descriptions of the collection areas within LEM 1 follow. Areas 1–3 yielded highly weathered and large bone fragments in the first year of 100% collection and virtually no fossil material in subsequent years. Only one specimen from these three areas was given a catalogue number.

Area 4 yielded a mix of fossil material, some with preservation similar to fossils found in the sandstones (typically weathered and stained black and green) and others with preservation reminiscent of the mudstones (typically unweathered and pale gray, brown and/or pink). All fossils collected from the southern side of the Area 4 hill are from the mudstones.

Areas 5, 7, 13, and 14 consist mainly of claystone sediments. All fossils from these localities are from the claystones and Speckled Tuff unless noted as gully wash from sediments higher in the stratigraphic section. Areas 13 and 14 are quite steep. A proboscidean mandible (KNM-NK 41502) was collected from the poorly-consolidated lower sands in the steep, rapidly-eroding southern edge of Area 14.

Area 6 primarily consists of claystones. However, at the southwestern edge there is an outcrop of the underlying sands. Area 8 is a small hill with claystones at the top and sands at the bottom. Area 9 is mostly claystones with an outcrop of the underlying sands at the base of the hill (the southern edge).

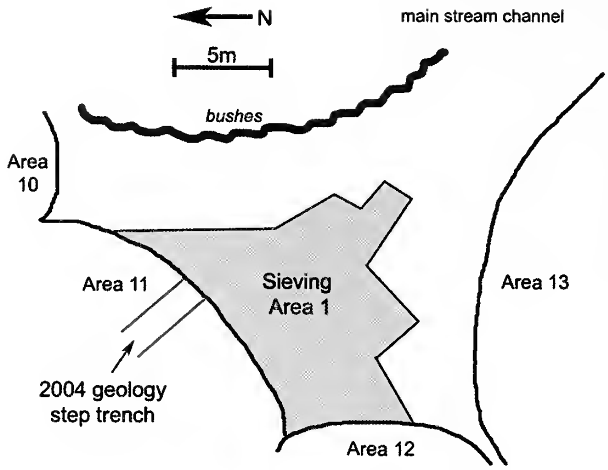

Figure 5. Diagram of sieving area 1, including areas sieved between 2001 and 2004. See text for details.

The speckled tuff is more consolidated in Area 7. In this section it contains a significant number of micromammal fossils (indicated by a small gray box in Figure 3). The majority of the Lemudong'o micromammal collection is from this Area. In 2001 approximately 2 m^2 of the lag surface on the hill and the gully separating Areas 7 and 8 was dry sieved with a 0.5-cm screen. The material that passed through this screen was wet sieved with a series of fine mesh screens to recover isolated micromammal teeth and bone fragments. The material from this sieving is housed in the Division of Palaeontology at the National Museum of Kenya in Nairobi with the rest of the Narok collection. The type specimen of *Paracolobus* sp. nov. (KNM-NK 44770; Hlusko, 2007) was recovered *in situ* immediately below this horizon, 1 m to the south.

Between the basal yellow silts and speckled tuff the claystones in Areas 10 and 11 are interbedded with sand and fine gravel horizons. The type specimen of *Plesiogulo botori* was found *in situ* in these sands of Area 10 (KNM-NK 41420; Haile-Selassie et al., 2004). Many fragments of large mammalian postcrania had eroded from these sands, and were also found in the gully that separates the two collection areas. These large, indeterminate specimens were not collected but rather consolidated in a rock-ringed circle in Area 11 to the east of the 2004 geological step trench (seen in Figures 3 and 6). The slope of this hill is very steep.

The sediments of Area 12 are predominately claystones but have some contamination from above. This is a relatively non-fossiliferous section.

LEM 1 is characterized by steeply sloping exposures with significant erosional gullies that drain into the main channel of the Lemudong'o Gorge. The outcrops are eroding rapidly. In the southern part of the site there is a basin that is approximately 225 m^2 where water and sediments from the steep slopes of collection Areas 10–13 pool prior to spilling into the main drainage. Each year we sieved a section of these recently re-deposited fossiliferous sediments through 0.5-cm screens to recover fossils that had eroded in previous years. The sediments were removed in ~1-m^2 units to the top of the underlying lacustrine silts. The removed sediment was deposited in a pile surrounded by a ring of stones on the other side of the gully.

Over the four years, almost half (~120 m^2) of the modern silts in this basin were removed (Figure 5). The extent of the sieving

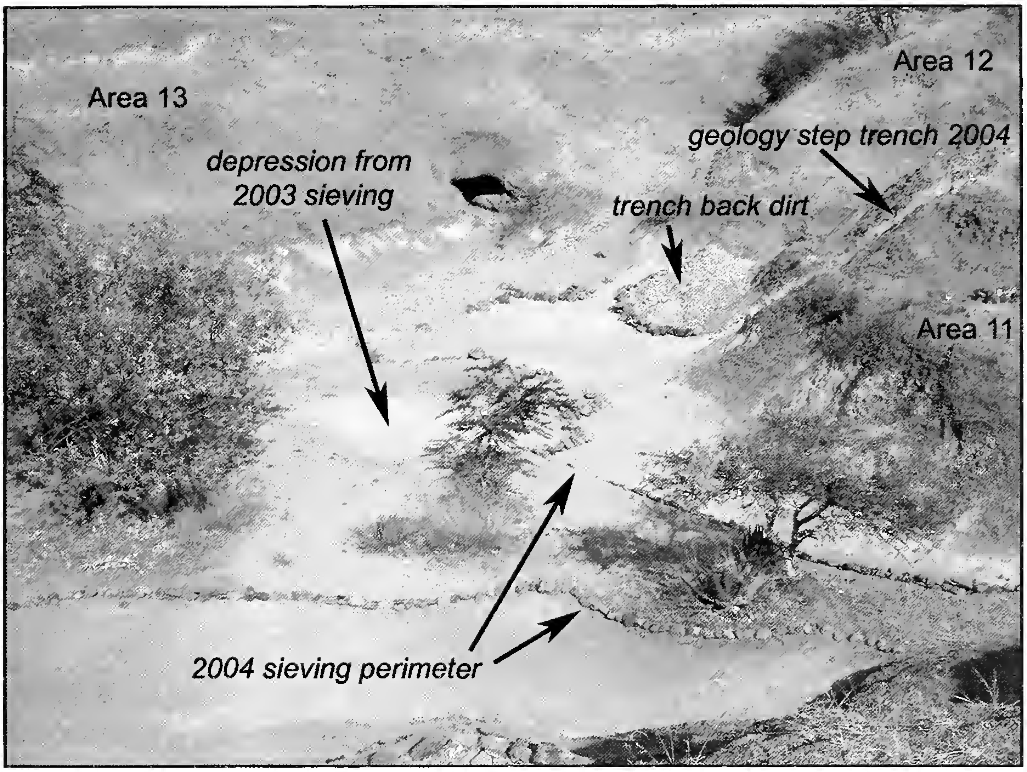

Figure 6. Photograph taken from the top of the Area 9 slope in 2004. This shows the extent of the 2004 sieving area 1 operation, as well as the fill depression from the earlier years' sieving. Stones outline the walls of the sieving area, as well as demarcate the back dirt from digging the extensive 2004 geological trench in Area 11. The ring of stones around the large indeterminate long bones can be seen in Area 11. See text for more details.

operation was marked with large rocks (Figure 6). A total of 110 taxonomically diagnostic specimens (i.e., identifiable to family level) were recovered and catalogued from sieving area 1 using this technique.

The sand horizon and gully lag from the catchment for Areas 6–8 (sieving area 2, Figure 3) were also sieved. By clearing this area to the top of the yellow lacustrine silts, 73 specimens were recovered and cataloged. The shallow sand horizon exposed at the base of Area 10 was similarly removed and sieved, recovering 11 catalogued specimens.

In total, 1268 specimens from LEM 1 were catalogued and deposited in the Division of Palaeontology at the National Museum of Kenya in Nairobi. Although the preservation of the fossils from the claystones is quite distinct from that of the sands and fine gravels (as described previously), we chose to take a conservative approach and do not designate stratigraphy based on preservation except in a few instances (Appendix 1). Therefore, just over half of the collection does not have secure stratigraphic provenience, as many specimens were collected in the first few years before exact horizons were recorded at the time of collection, or because they come from a mixed collection area (such as sieving area 1).

The faunas associated with the two fossil horizons are distinct. The 625 specimens stratigraphically provenienced to the speckled tuff and claystones are dominated by cercopithecoid primates and small bovids, with a large number of hyracoids, carnivores, and lagomorphs. Birds and snakes are also found in these sediments. The microfauna is significant, but underrepresented, given that the microbreccia in Area 7 has not yet been as extensively sieved/excavated.

The sands and fine gravels yielded 21 specimens, including hippopotamids, suids, bovids, mustelid, hyaenid, equids, and cercopithecids. The proboscidean mandible KNM-NK 41502 also came from this horizon (Saegusa and Hlusko, 2007). The implications of these differing faunal compositions are discussed by Ambrose, Bell, et al. (2007).

Intensive paleontological research at LEM 1 is currently in a hiatus. However, we revisit the site annually to check the outcrops for newly exposed significant fossils.

Summary

A detailed geological study of the Narok District has only recently begun (Ambrose, Nyamai, et al., 2007). This study, in conjunction with the last decade of archaeological and paleontological research, is yielding significant insights into the late Miocene of the region (Ambrose et al., 2003; Ambrose, Bell, et al., 2007), as well as the Pleistocene and early human occupation (Kyule et al., 1997; Ambrose, 2002). From the field work conducted to date, the Narok District is clearly a region that will prove to be of paleoanthropological interest for years to come.

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Appendix 1. Catalogued fossils from the Narok District of Kenya.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
36563	PPX	1995	LEM 1	na		Aves					
36940	R.SCA	1995	LEM 1	na		Aves	Galliformes	Phasianidae		*Phasianus* (cf.)	
36960	PHX	1999	LEM 1	na		Aves					
36966	SCA	1999	LEM 1	na		Aves					
40898	HUM shaft + ungual PHX	2000	LEM 1	Area 7	*	Aves					
41004	R.CMC (prox.)	2001	LEM 1	Area 7	*	Aves	Falconiformes	Acciptridae			
41068	FEM (dist.)	2001	LEM 1	Area 7	*	Aves					
41126	TPX	2001	LEM 1	Area 7	*	Aves					
41244	RAD (prox.)	2001	LEM 1	Area 4, claystones	*	Aves					
41255	R.SCA	2001	LEM 1	Area 6	*	Aves	Galliformes	Phasianidae		*Phasianus* (cf.)	
41406	FEM (shaft frag.)	1999	LEM 1	na		Aves (cf.)					
41476	ungual PHX + ungual PHX (prox.)	2001	LEM 1	Area 6	*	Aves					
41489	R.ULN (dist.)	2001	LEM 1	Area 6	*	Aves	Strigiformes	Strigidae (cf.)			
41490	MTT	2001	LEM 1	Area 4, claystones	*	Aves (cf.)					
41501	MTT V	2001	LEM 1	Area 4, claystones	*	Aves (cf.)					
42280	postcranial frag.	2002	LEM 1	Area 5, claystones	*	Aves					
42291	PHX	2002	LEM 1	Area 5, claystones	*	Aves					
42349	2 PHXs	2002	LEM 1	Area 13, claystones	*	Aves (cf.)					
42355	PHX	2002	LEM 1	Area 13, claystones	*	Aves					
42377	TPX	2002	LEM 1	sieving area 1		Aves					
42391	TPX	2002	LEM 1	sieving area 1		Aves					
44764	IPX (prox. frag.)	2003	LEM 1	Area 4, claystones	*	Aves (cf.)					
44781	TPX	2003	LEM 1	Area 5, claystones	*	Aves					
44801	pedal PHX	2003	LEM 1	Area 6 (gulley, on pebble/sand side)		Aves	Falconiformes (cf.)				
44809	postcranial frag.	2003	LEM 1	Area 9	*	Aves					
44810	TBT	2003	LEM 1	Area 9	*	Aves					
44811	PHX	2003	LEM 1	Area 9	*	Aves					
44820	TBT (dist. frag.)	2003	LEM 1	Area 5, claystones	*	Aves					
44851	TPX	2003	LEM 1	Area 5, claystones	*	Aves					
44855	postcranial frag.	2003	LEM 1	East side of main gulley		Aves					
45768	TBT	2004	LEM 1	Area 5, 3 m from top of hill, near gulley, brown mudstones	*	Aves					
45799	TAR	2004	LEM 1	Areas 9/10 boundary, 1/2 m > speckled tuff	*	Aves					
45831	TPX	2004	LEM 1	sieving area 1		Aves					
45938	TBT	2004	LEM 1	sieving area 2		Aves					
36507	R.AST	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36513	FIB	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36522	L.MTP (dist.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36523	MTP (a and b)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36524	R.HUM (dist.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36525	L.HUM (dist.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36526	R.&L.TIB (dist.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36527	L.FEM (prox.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36529	R.CAL	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36530	L.NAV	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36531	R.MAN w/m2-3	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Boselaphini		
36532	R.AST	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36533	R.AST	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36535	R.AST	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
36536	R.NAV	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36538	OCC	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36562	R.+L.MAN w/m2-3 + m1 (frags.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
36565	L.MAN w/erupting m2	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
36566	L.HOR frag.	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Neotragini	*Madoqua*	
36567	R.MAN w/p4-m1	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36569	L.MAN w/m1-m2	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
36570	L.MAN w/p4-m1	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36576	L.M3	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
36579	R.m3	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36580	R.MAN w/dp3-4	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Tragelaphini (cf.)		
36582	L.p3	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36583	DENT (frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36865	R.RAD (dist.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36867	HOR frag.	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Boselaphini		
36868	R.M1or2	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Tragelaphini (cf.)		
36869	L.m2	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36870	L.M3	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
36871	L.m1or2	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
36872	MPT (dist. frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36873	R.M2	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
36874	TIB (dist.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36877	RAD (dist.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36878	AST	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36879	R.m1	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
36880	R.MAX w/P4 + M1 (frags.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36881	R.M3	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36882	R.MAN (frag.) w/m1 or 2 unerupted	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
36883	L.MAX (frag.) w/M3 erupting	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Tragelaphini (cf.)		
36884	UNC	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36885	R.MAN (edent. frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36886	L.MAN (edent. frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36887	FIB	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36888	R.M1	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini (cf.)		
36938	R.MAN w/p1-2	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36942	M frag.	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36946	L.RAD (dist.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36948	TAR	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36949	R.LUN	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36950	PHXs + SPD	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36952	MTP (prox.)	1995	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
36963	PPX		LEM 1	na		Mammalia	Artiodactyla	Bovidae			
38311	L.m3	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Boselaphini		
38314	R.MAN w/dp4-m2	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
38316	L.P4	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
40862	MAN w/p4 + half m	2000	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
40863	MAN (edent. frag.)	2000	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
40864	M (frag.)	2000	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae	Aepycerotini		

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
40865	MAG + UNC	2000	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
40866	L.M3	2000	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae	Aepycerotini		
40867	CAR	2000	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
40868	R.+L.p3s	2000	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
40869	I	2000	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
40872	MAN w/m3	2000	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
40873	PHX (prox. frag.)	2000	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
40874	TPX	2000	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
40883	FIB	2000	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae			
40884	FIB	2000	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae			
40886	RAD (prox.)	2000	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae			
40893	TAR	2000	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
40896	MAX (frag.)	2000	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
40899	TPX	2000	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
40902	PPX, IPX, TAR	2000	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
40903	VER atlas (frag.)	2000	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
40904	immature PPX + PHX (frag.)	2000	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
40905	FIB	2000	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
40906	TPX	2000	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
40913	RAD (prox.)	2000	LEM 1	Area 9/10		Mammalia	Artiodactyla	Bovidae			
40916	assoc. M + P + frags.	2000	LEM 1	Area 9/10		Mammalia	Artiodactyla	Bovidae	Boselaphini		
40918	PHX	2000	LEM 1	Area 9/10		Mammalia	Artiodactyla	Bovidae			
40919	I	2000	LEM 1	Area 9/10		Mammalia	Artiodactyla	Bovidae			
40920	L.M1or2	2000	LEM 1	Area 9/10		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
40985	TPX	2000	LEM 1	Area 9/10		Mammalia	Artiodactyla	Bovidae			
40986	MTP (frag.)	2000	LEM 1	Area 9/10		Mammalia	Artiodactyla	Bovidae			
40987	TAR (a and b)	2000	LEM 1	Area 9/10		Mammalia	Artiodactyla	Bovidae			
40988	PHX (dist. frag.)	2000	LEM 1	Area 9/10		Mammalia	Artiodactyla	Bovidae			
40989	MAX (frag.) + M	2000	LEM 1	Area 9/10		Mammalia	Artiodactyla	Bovidae			
40996	P	2001	LEM 1	Area 4, claystones	*	Mammalia	Artiodactyla	Bovidae			
40999	I	2001	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae			
41005	SCA	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41010	MAN (edent. frag.)	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41011	NAV	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41012	AST	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41015	MAN (frag., condyle)	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41016	half M	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41019	PHX	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41021	I	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41023	M (frag.)	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41026	HOR (frag.)	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41027	TPX	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41029	HUM (dist.)	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41031	PHX (prox. frag.)	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41032	UNC	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41034	VER axis	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41035	R.M (frag.)	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41038	TIB (dist. epiphysis)	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41039	MTP (prox.)	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41040	TPX	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41044	TPX	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
41045	MAN (frag.) w/2 ms	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae	Aepycerotini (cf.)		
41054	M	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41055	MAN (frag.) w/half m	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41057	MAN (edent. frag.)	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41060	half M	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41067	P	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41071	TAR	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41072	TAR	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41074	TPX	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41076	P	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41077	CAL	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41112	SES	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41117	TAR	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41120	PHX (dist. frag.)	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41121	MAN (edent. frag.)	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
41129	HOR	2001	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae			
41130	MAN (condyle)	2001	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae			
41131	CAL (frag.)	2001	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae			
41132	R.MAN w/m1-2	2001	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41134	HUM (dist.)	2001	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae			
41135	R.m (frag.)	2001	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41136	M (frag.)	2001	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae			
41137	MAN (edent. frag.)	2001	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae			
41138	PHX (dist. frag.)	2001	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae			
41142	AST	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
41143	CAL	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
41144	TIB (dist.)	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
41145	MAN (edent. frag.)	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
41146	CAL	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
41148	NAV	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
41155	TAR	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
41156	R.M (frag.)	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae	Tragelaphini (cf.)		
41157	TPX	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
41158	SPD	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
41160	NAV	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
41167	CUN	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
41170	HOR + CRA (frags.)	2001	LEM 1	sands from South side of main gulley		Mammalia	Artiodactyla	Bovidae			
41173	R.m3 (frag.)	2001	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae	Tragelaphini (cf.)		
41178	TAR	2001	LEM 1	Area 14, claystones	*	Mammalia	Artiodactyla	Bovidae			
41179	IPX	2001	LEM 1	Area 14, claystones	*	Mammalia	Artiodactyla	Bovidae			
41180	TPX	2001	LEM 1	Area 14, claystones	*	Mammalia	Artiodactyla	Bovidae			
41181	MAN (condyle)	2001	LEM 1	Area 14, claystones	*	Mammalia	Artiodactyla	Bovidae			
41184	assoc. R.P4 + L.M1-2 (frags.)	2001	LEM 1	Area 14, claystones	*	Mammalia	Artiodactyla	Bovidae	Aepycerotini (cf.)		
41185	L.MAN w/p3-m2 + R.p2-3 + R.m1or2	2001	LEM 1	Area 11, mudstones	*	Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41187	PPX	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41188	PPX	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41189	MTP (dist. frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41192	TAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41193	CAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41194	UNC	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
41195	CAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41197	MTP (dist.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41198	TPX	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41199	M (frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41200	ULN (prox.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41201	MTP (prox.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41202	MTP (dist.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41203	MTP (dist.)	2001	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
41204	AST	2001	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
41205	AST	2001	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
41206	PHX (prox. frag.)	2001	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
41209	R.p3-4	2001	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
41219	R.p4 (frag.)	2001	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
41220	PHX (dist. frag.)	2001	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
41221	CAR	2001	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
41224	HUM (dist.)	2001	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
41228	FEM (dist.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Artiodactyla	Bovidae			
41230	CAL (frag.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Artiodactyla	Bovidae			
41246	TPX	2001	LEM 1	Area 4, claystones	*	Mammalia	Artiodactyla	Bovidae			
41247	R.i1	2001	LEM 1	Area 4, claystones	*	Mammalia	Artiodactyla	Bovidae			
41248	TAR	2001	LEM 1	Area 4, claystones	*	Mammalia	Artiodactyla	Bovidae			
41249	NAV (frag.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Artiodactyla	Bovidae			
41256	M	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41258	R.m3 (frag.)	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41264	R.+L.p3	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae	Aepycerotini (cf.)		
41274	VER axis	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41275	L.M1	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae	Tragelaphini (cf.)		
41276	HOR (frag.)	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41277	TPX	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41278	MTP (dist. frag.)	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41290	TAR	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41291	TAR	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41292	PHX (dist. frag.)	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41293	L.i	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41297	VER cervical	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41299	AST	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41300	PPX	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41311	TPX	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41312	TAR	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41313	TAR	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41314	TAR	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41315	TAR	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41324	TPX (frag.)	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
41335	M (frag.)	2001	LEM 1	Area 11		Mammalia	Artiodactyla	Bovidae			
41336	M (frag.)	2001	LEM 1	Area 11		Mammalia	Artiodactyla	Bovidae	Neotragini	*Madoqua*	
41337	HOR (frags.)	2001	LEM 1	Area 11		Mammalia	Artiodactyla	Bovidae			
41338	R.p4	2001	LEM 1	Area 11		Mammalia	Artiodactyla	Bovidae			
41339	TPX	2001	LEM 1	Area 11		Mammalia	Artiodactyla	Bovidae			
41340	L.i	2001	LEM 1	Area 11		Mammalia	Artiodactyla	Bovidae			
41341	TAR	2001	LEM 1	Area 11		Mammalia	Artiodactyla	Bovidae			
41342	TPX (prox. frag.)	2001	LEM 1	Area 11		Mammalia	Artiodactyla	Bovidae			
41343	L.m (frag.)	2001	LEM 1	Area 11		Mammalia	Artiodactyla	Bovidae	Tragelaphini (cf.)		

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
41344	SCA (frag.)	2001	LEM 1	Area 11		Mammalia	Artiodactyla	Bovidae			
41345	TPX	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41346	CAL	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41347	MTP (dist. frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41348	AST	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41349	L.HOR (frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini	*Aepyceros*	*premelampus* (aff.)
41350	SCA (frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41351	R.m3 (frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41355	R.M1-3	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini (cf.)		
41356	L.M2+3	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41357	L.m1or2	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41358	R.m3	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41361	R.MAN w/p3 + dp4 + m1	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41365	MTP (dist.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41366	MTP (prox.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41367	CAL	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41368	R.m1or2	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41369	L.MAN w/m1-3	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41371	HOR (frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41372	R.+L.M1or2	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Boselaphini		
41373	R.P4	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41374	L.p4	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41378	AST	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41379	MAN (frag., condyle)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41380	TPX	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41382	SCA (frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41384	TIB (dist.) + AST	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41385	TAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41386	CAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41387	NAV	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41388	MTC (frags.) (a + b)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41389	MTP (dist. frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41390	NAV	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41391	TAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41392	TAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41393	TAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41394	TAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41395	TAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41396	TAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41397	TAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41398	AST	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41401	M (frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41402	PHX (dist. frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41403	MTP (dist. frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41404	MAN (edent. frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41409	TAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41416	PHX (dist. frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41423	R.TIB (prox.)	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41425	CAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41430	CAR	1999	LEM 1	na		Mammalia	Artiodactyla	Bovidae			
41436	HOR (frag.)	2001	LEM 1	Area 12		Mammalia	Artiodactyla	Bovidae			

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
41437	M	2001	LEM 1	Area 12		Mammalia	Artiodactyla	Bovidae			
41438	TAR	2001	LEM 1	Area 12		Mammalia	Artiodactyla	Bovidae			
41439	AST	2001	LEM 1	Area 12		Mammalia	Artiodactyla	Bovidae			
41452	HOR + CRA (frags.)	2001	LEM 1	Area 6, mudstones	*	Mammalia	Artiodactyla	Bovidae	Boselaphini		
41464	AST	2001	LEM 1	Area 4, claystones	*	Mammalia	Artiodactyla	Bovidae			
41470	CAR	2001	LEM 1	Area 6	*	Mammalia	Artiodactyla	Bovidae			
42255	FIB	2002	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae			
42262	MAN (edent. frag.)	2002	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae			
42264	TPX	2002	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae			
42267	PHX (dist. frag.)	2002	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae			
42268	PHX (prox. frag.)	2002	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae			
42271	TPX (frag.)	2002	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae			
42301	PHX (prox. frag.)	2002	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
42304	P	2002	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
42310	M	2002	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
42321	assoc. craniodental + postcranial elements	2002	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
42322	AST	2002	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
42323	AST	2002	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
42324	R.M (frag.)	2002	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
42326	PHX (dist. frag.)	2002	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
42329	FIB	2002	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
42330	TAR	2002	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
42334	ULN (prox.)	2002	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
42337	TIB (dist.)	2002	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae			
42338	R.m1	2002	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
42339	CAL	2002	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae			
42345	L.MAN w/p (frag.)	2002	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
42348	HOR (frag.)	2002	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
42350	R.M (frag.)	2002	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae	Aepycerotini (cf.)		
42361	P	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
42362	R.m3 (frag.)	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
42363	M	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
42371	L.M1or2	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae	Tragelaphini (cf.)		
42378	AST	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
42379	L.m3	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
42380	M	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
42381	L.M3	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
42382	R.MAN w/m1 (frag.)	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae	Aepycerotini (cf.)		
42383	P	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
42393	AST	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
42394	CUN	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
44747	TEM (frag.)	2003	LEM 1	upslope in gulley above Area 7		Mammalia	Artiodactyla	Bovidae			
44765	HOR (frag.)	2003	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
44768	L.M (frag.)	2003	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
44777	LUN	2003	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae			
44797	OCC condyle	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
44798	L.MAN w/dp4-m1	2003	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae	Aepycerotini		
44802	MTT + AST + NAV	2003	LEM 1	Area 11 in situ, mudstones < Speck Tuff	*	Mammalia	Artiodactyla	Bovidae			

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
44817	immature postcranial elements (vertebrae, tarsals) and unerupted P	2003	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
44835	L.m1or2	2003	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae	Aepycerotini		
44839	L.m3 (frag.)	2003	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae			
44854	TAR	2003	LEM 1	East side of main gulley		Mammalia	Artiodactyla	Bovidae			
44897	R.M1or2	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
44898	R.M1	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
44899	R.M1	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae	Aepycerotini (cf.)		
44900	L.m3 (frag.)	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
44901	R.m1	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
44902	R.m3	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae	Neotragini	*Madoqua*	
44903	R.m3 (frag.)	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
44904	R.p4	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
44905	CUN	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
44906	CUN	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
44907	RAD (prox.)	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
44925	NAV	2002	LEM 1	Area 11		Mammalia	Artiodactyla	Bovidae			
45761	TPX	2004	LEM 1	Area 4, south side of hill, 1/2 m from top	*	Mammalia	Artiodactyla	Bovidae			
45769	TAR	2004	LEM 1	Area 5, 3 m from top of hill, near gulley, brown mudstones	*	Mammalia	Artiodactyla	Bovidae			
45771	TAR	2004	LEM 1	Area 6, brown mudstones 10 cm above sands	*	Mammalia	Artiodactyla	Bovidae			
45772	L.HOR (frag.)	2004	LEM 1	Area 8, sands	x	Mammalia	Artiodactyla	Bovidae	Tragelaphini	*Tragelaphus*	
45774	AST	2004	LEM 1	Area 7, east most point, in the sands at the top	x	Mammalia	Artiodactyla	Bovidae			
45776	TPX	2004	LEM 1	Area 7, just below microbreccia	*	Mammalia	Artiodactyla	Bovidae			
45785	TAR	2004	LEM 1	Area 8, sands	x	Mammalia	Artiodactyla	Bovidae			
45787	TAR	2004	LEM 1	Area 5, mudstones above sands	*	Mammalia	Artiodactyla	Bovidae			
45790	L.p4	2004	LEM 1	Area 11, sands 1 m > yellow silts	x	Mammalia	Artiodactyla	Bovidae			
45793	R.M3	2004	LEM 1	Area 7/9, sands	x	Mammalia	Artiodactyla	Bovidae	Aepycerotini		
45794	TIB (dist.)	2004	LEM 1	Area 7, speckled tuff	*	Mammalia	Artiodactyla	Bovidae			
45810	TAR	2004	LEM 1	Area 5, mudstones just below speckled tuff	*	Mammalia	Artiodactyla	Bovidae			
45811	R.i	2004	LEM 1	Area 5, mudstones just below speckled tuff	*	Mammalia	Artiodactyla	Bovidae			
45819	R.p	2004	LEM 1	Area 5, mudstones 3 m above speckled tuff	*	Mammalia	Artiodactyla	Bovidae			
45820	R.i	2004	LEM 1	Area 5, mudstones 3 m above speckled tuff	*	Mammalia	Artiodactyla	Bovidae			
45821	R.MAN w/p2-m3	2004	LEM 1	Area 14, claystones	*	Mammalia	Artiodactyla	Bovidae	Tragelaphini (cf.)		
45824	L.MAN w/m1 (frag.)	2004	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
45825	AST	2004	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
45830	TPX	2004	LEM 1	sieving area 1		Mammalia	Artiodactyla	Bovidae			
45833	L.MAX w/M1 (frag.)	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
45836	R.MAN (edent. frag.)	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae			
45837	R.p	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae			
45838	TPX	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae			
45840	R.m3	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae	Tragelaphini (cf.)		
45844	TAR	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae			

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
45845	TAR	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae			
45848	L.p3	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
45859	L.p3	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
45900	P	2004	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae			
45902	L.p	2004	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae			
45911	TPX	2004	LEM 1	Area 14, claystones	*	Mammalia	Artiodactyla	Bovidae			
45920	M	2004	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae			
45929	P	2004	LEM 1	Area 7, speckled tuff	*	Mammalia	Artiodactyla	Bovidae			
45931	P	2004	LEM 1	Area 14, claystones	*	Mammalia	Artiodactyla	Bovidae			
45937	R.m1or2	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae			
45939	dm	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae			
45941	M	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae			
45942	M	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae			
45944	L.p	2004	LEM 1	sieving area 2		Mammalia	Artiodactyla	Bovidae			
45948	TAR	2004	LEM 1	Area 7, speckled tuff	*	Mammalia	Artiodactyla	Bovidae			
45954	CUN	2004	LEM 1	sieving, sands Area 10		Mammalia	Artiodactyla	Bovidae			
41063	LUN	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae (cf.)			
41064	NAV	2001	LEM 1	Area 7	*	Mammalia	Artiodactyla	Bovidae (cf.)			
41139	CAR	2001	LEM 1	Area 10		Mammalia	Artiodactyla	Bovidae (cf.)			
41163	PIS	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae (cf.)			
41499	LUN	2001	LEM 1	Area 4, claystones	*	Mammalia	Artiodactyla	Bovidae (cf.)			
42250	LUN	2002	LEM 1	Area 4, claystones	*	Mammalia	Artiodactyla	Bovidae (cf.)			
42277	LUN	2002	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae (cf.)			
42293	LUN	2002	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Bovidae (cf.)			
42327	LUN	2002	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae (cf.)			
42328	LUN	2002	LEM 1	Area 8		Mammalia	Artiodactyla	Bovidae (cf.)			
42357	LUN	2002	LEM 1	Area 13, claystones	*	Mammalia	Artiodactyla	Bovidae (cf.)			
36501	I	1995	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
36503	p4 (frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
36504	M (frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
36506	m (frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
36537	i (frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
36875	P (frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
36876	M (frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
36936	IPX	1995	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae			
36964	c		LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
36965	p1 (frag.)		LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
38315	M (frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
38317	M (frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
40857	P + M (frags.)	2000	LEM 1	Area 6, sands	x	Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
40858	PPX or IPX	2000	LEM 1	Area 6, sands	x	Mammalia	Artiodactyla	Hippopotamidae			
40887	PHX (dist. frag.)	2000	LEM 1	Area 5, claystones	*	Mammalia	Artiodactyla	Hippopotamidae			
40915	m (frag.)	2000	LEM 1	Area 9/10		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
41140	CAR	2001	LEM 1	Area 10		Mammalia	Artiodactyla	Hippopotamidae			
41141	CUN	2001	LEM 1	Area 10		Mammalia	Artiodactyla	Hippopotamidae			
41147	m1or2 (frag.)	2001	LEM 1	Area 8		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
41176	TPX	2001	LEM 1	Area 9		Mammalia	Artiodactyla	Hippopotamidae			
41190	SES	1999	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae			
41352	m (frags.)	1999	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
41353	R.P1,D2,M1	1999	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
41354	R.d4	1999	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae	Hippopotaminae		
41364	TIB (dist.)	1999	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae			

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
41426	CAR	1999	LEM 1	na		Mammalia	Artiodactyla	Hippopotamidae			
41461	PHX (dist. frag.)	2001	LEM 1	Area 4		Mammalia	Artiodactyla	Hippopotamidae			
45823	AST	2004	LEM 1	Area 11, sands 4 m > yellow silts	x	Mammalia	Artiodactyla	Hippopotamidae			
36512	P1	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36561	L.m2 (frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36564	R.m2	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36568	R.+L.m3 (frags.)	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus*
36571	R.M2	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36572	L.I1-2 + R.I3	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36573	L.m1	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
36574	p3 germ	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
36584	L.dp4	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
36585	L.m3	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus*
36862	dc	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36863	MTP	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36864	MTP (prox.)	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36931	M germ	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36937	ULN (prox.)	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36943	L.c (frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36945	p3 germ	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36953	SCA	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36954	P (frag.)	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
36956	VER axis	1995	LEM 1	na		Mammalia	Artiodactyla	Suidae			
38318	R.NAV	1999	LEM 1	na		Mammalia	Artiodactyla	Suidae			
38319	LUN	1999	LEM 1	na		Mammalia	Artiodactyla	Suidae			
38321	AST	1999	LEM 1	na		Mammalia	Artiodactyla	Suidae			
41362	R.p3	1999	LEM 1	na		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
41376	L.MTC I-III + PHX	1999	LEM 1	na		Mammalia	Artiodactyla	Suidae			
41377	RAD (prox.)	1999	LEM 1	na		Mammalia	Artiodactyla	Suidae			
41408	C	1999	LEM 1	na		Mammalia	Artiodactyla	Suidae			
41417	m3 (frag.)	1999	LEM 1	na		Mammalia	Artiodactyla	Suidae			
41435	L.m2	2001	LEM 1	geological trench on south side of main gulley, SW of Area 13		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
41462	L.i1, L.p1, R.dp4, R.+L.m1	1999	LEM 1	na		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
42344	M (frags.)	2002	LEM 1	Area 11		Mammalia	Artiodactyla	Suidae			
42370	R.I1	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
42385	L.i1 + R.p2	2002	LEM 1	sieving area 1		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
44760	R.di2	2003	LEM 1	Area 11		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
44793	C	2003	LEM 1	Area 6 (cobbles and sands)	x	Mammalia	Artiodactyla	Suidae			
44794	P	2003	LEM 1	Area 12		Mammalia	Artiodactyla	Suidae			
44803	L.MAN (frag.) w/p4-m3	2003	LEM 1	Area 6, sands	x	Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus*
44887	L.m2	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
44888	R.m1	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
44889	R.di1	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
44890	L.p4	2003	LEM 1	sieving area 1		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
45783	R.M3	2004	LEM 1	Area 8, sands	x	Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus*
40990	R.p1	2000	LEM 1	Area 9/10		Mammalia	Artiodactyla	Suidae		*Nyanzachoerus*	*syrticus* (cf.)
41183	assoc. MAN deciduous dentition	2001	LEM 1	Area 14, claystones	*	Mammalia	Artiodactyla	Suidae			
36508	L.C	1995	LEM 1	na		Mammalia	Carnivora				
36518	L.C + R.c	2002	LEM 1	Area 13, claystones	*	Mammalia	Carnivora	Mustelidae	Guloninae	*Plesiogulo*	*botori*

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
36577	R.MAN w/p2-p4, alveolus of p1 + c	1995/ 2001	LEM 1	Area 7	*	Mammalia	Carnivora	Herpestidae	Herpestinae	*Herpestes*	
36578	R.MAN (frag.) w/p3-4	1995	LEM 1	na		Mammalia	Carnivora	Viverridae	Viverrinae	*Genetta*	sp. indet. "x"
36581	R.MAN w/p4-m1 + m2 roots	1995	LEM 1	na		Mammalia	Carnivora	Viverridae	Viverrinae	*Genetta*	sp. indet. "x"
36595	R.MAN w/p + m alveoli	1995	LEM 1	na		Mammalia	Carnivora	Viverridae	Viverrinae	*Genetta*	sp. indet. "y"
36596	MTP (dist.)	1995	LEM 1	na		Mammalia	Carnivora				
36597	R.MAN (edent. frag.)	1995	LEM 1	na		Mammalia	Carnivora	Viverridae			
36598	R.MAN w/p4 + p3, m1 roots	1995	LEM 1	na	x	Mammalia	Carnivora	Hyaenidae		*Hyaenictis*	*hendeyi*
36892	L.MAN (frag.) w/p3	1995	LEM 1	na		Mammalia	Carnivora	Herpestidae	Herpestinae	*Helogale*	
36926	R.c root + MAN symph.	1995	LEM 1	na		Mammalia	Carnivora	Viverridae			
36927	L.MAN (frag.) w/p alveoli	1995	LEM 1	na		Mammalia	Carnivora	Viverridae	Viverrinae	*Genetta*	sp. indet. "y"
36928	L.C	1995	LEM 1	na	x	Mammalia	Carnivora	Felidae	Machairodontinae	*Lokotunjailurus*	*emageritus*
36929	MAX w/P4	1995	LEM 1	na		Mammalia	Carnivora	Viverridae			
36951	FEM (shaft)	1995	LEM 1	na		Mammalia	Carnivora (cf.)				
36955	L.MAN w/c root	1995	LEM 1	na		Mammalia	Carnivora	Viverridae			
36957	MAN (frag.)	1995	LEM 1	na		Mammalia	Carnivora	Viverridae			
36959	RAD (dist.)		LEM 1	na		Mammalia	Carnivora				
38310	R.MAN (frag.) w/p3	1999	LEM 1	na		Mammalia	Carnivora	Viverridae	Viverrinae	*Genetta*	sp. indet. "y"
40888	ULN (prox.)	2000	LEM 1	Area 5, claystones	*	Mammalia	Carnivora (cf.)				
40890	MAN (edent. frag.)	2000	LEM 1	Area 4/5, claystones	*	Mammalia	Carnivora				
41008	P	2001	LEM 1	Area 7	*	Mammalia	Carnivora				
41053	p1	2001	LEM 1	Area 7	*	Mammalia	Carnivora	Canidae	Caninae	*Eucyon*	*intrepidus* (aff.)
41056	CAL	2001	LEM 1	Area 7	*	Mammalia	Carnivora (cf.)				
41082	M	2001	LEM 1	Area 7	*	Mammalia	Carnivora				
41095	M	2001	LEM 1	Area 7	*	Mammalia	Carnivora				
41097	C	2001	LEM 1	Area 7	*	Mammalia	Carnivora				
41099	P	2001	LEM 1	Area 7	*	Mammalia	Carnivora				
41114	R.MAN (edent. frag.)	2001	LEM 1	Area 7	*	Mammalia	Carnivora	Herpestidae	Herpestinae	*Helogale*	
41123	PHX (prox. frag.)	2001	LEM 1	Area 7	*	Mammalia	Carnivora				
41149	c	2001	LEM 1	Area 8		Mammalia	Carnivora				
41174	FEM (prox.)	2001	LEM 1	Area 9		Mammalia	Carnivora				
41233	1	2001	LEM 1	Area 4, claystones	*	Mammalia	Carnivora				
41241	HUM (dist.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Carnivora				
41242	MTP (prox.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Carnivora				
41243	AST	2001	LEM 1	Area 4, claystones	*	Mammalia	Carnivora				
41245	MTP (prox.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Carnivora				
41253	TPX	2001	LEM 1	Area 6	*	Mammalia	Carnivora				
41263	TIB (dist.)	2001	LEM 1	Area 6	*	Mammalia	Carnivora				
41273	L.i	2001	LEM 1	Area 6	*	Mammalia	Carnivora				
41284	R.M1	2001	LEM 1	Area 6	*	Mammalia	Carnivora	Canidae	Caninae	*Eucyon*	*intrepidus* (aff.)
41285	L.m1	2001	LEM 1	Area 6	*	Mammalia	Carnivora	Canidae	Caninae	*Eucyon*	*intrepidus* (aff.)
41287	FEM (prox.)	2001	LEM 1	Area 6	*	Mammalia	Carnivora				
41288	ULN (prox.)	2001	LEM 1	Area 6	*	Mammalia	Carnivora				
41298	C (frag.)	2001	LEM 1	Area 6	*	Mammalia	Carnivora				
41330	MTT (dist. frag.) + 3 MTT (prox. frags.)	2001	LEM 1	Area 6	*	Mammalia	Carnivora				
41331	TPX	2001	LEM 1	Area 6	*	Mammalia	Carnivora				
41381	R.ULN (prox.)	1999	LEM 1	na		Mammalia	Carnivora				
41414	TPX	1999	LEM 1	na		Mammalia	Carnivora				

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
41420	R.CRAN + TEMP frag. + R.P3-M1 + L.P3-M2	1999/ 2004	LEM 1	Area 11, sands 2 m > yellow silts	x	Mammalia	Carnivora	Mustelidae	Guloninae	*Plesiogulo*	*botori*
41424	P	1999	LEM 1	na		Mammalia	Carnivora				
41427	HUM (dist.)	1999	LEM 1	na		Mammalia	Carnivora				
41433	R.C	1999	LEM 1	na		Mammalia	Carnivora				
41442	c	2001	LEM 1	Area 12		Mammalia	Carnivora				
41485	C	2001	LEM 1	Area 5, claystones	*	Mammalia	Carnivora				
42247	MAN (edent. frag.)	2002	LEM 1	Area 4		Mammalia	Carnivora				
42266	CAL	2002	LEM 1	Area 5, claystones	*	Mammalia	Carnivora				
42269	R.m1 (frag.)	2002	LEM 1	Area 5, claystones	*	Mammalia	Carnivora	Felidae	Felinae	*Leptailurus* (cf.)	
42286	MTT (dist.)	2002	LEM 1	Area 5, claystones	*	Mammalia	Carnivora				
42287	PHX	2002	LEM 1	Area 5, claystones	*	Mammalia	Carnivora				
42302	MAN (edent. frag.)	2002	LEM 1	Area 7	*	Mammalia	Carnivora				
42309	R.MAX w/M2 + M3	2002	LEM 1	Area 7	*	Mammalia	Carnivora				
42319	R.MAN (edent. frag.)	2002	LEM 1	Area 7	*	Mammalia	Carnivora	Herpestidae	Herpestinae	*Herpestes*	
42320	R.MAN (frag.) w/m alveoli	2002	LEM 1	Area 7	*	Mammalia	Carnivora	Viverridae	Viverrinae	*Genetta*	sp. indet. "y"
42358	PAT	2002	LEM 1	sieving area 1		Mammalia	Carnivora (cf.)				
42384	C (frag.)	2002	LEM 1	sieving area 1		Mammalia	Carnivora	Felidae			
44783	p (frag.)	2003	LEM 1	Area 5, claystones	*	Mammalia	Carnivora				
44818	TPX	2003	LEM 1	Area 8		Mammalia	Carnivora				
44822	M1	2003	LEM 1	Area 5, claystones	*	Mammalia	Carnivora				
44852	RAD (prox.)	2003	LEM 1	upslope in gulley above Area 7		Mammalia	Carnivora	Felidae			
44915	i	2003	LEM 1	sieving area 1		Mammalia	Carnivora				
45773	FEM (prox.)	2004	LEM 1	Area 8, sands	x	Mammalia	Carnivora				
45780	L.M1	2004	LEM 1	Area 7, just below microbreccia	*	Mammalia	Carnivora	Procyonidae	Simocyoninae	*Simocyon*	
45788	ULN (prox.)	2004	LEM 1	Area 11, mudstones 6 m > yellow silts	*	Mammalia	Carnivora				
45791	TPX	2004	LEM 1	Area 11, sands 2 m > yellow silts	x	Mammalia	Carnivora				
45802	R.p4	2004	LEM 1	Area 7, speckled tuff	*	Mammalia	Carnivora	Herpestidae	Herpestinae	*Ichneumia*	*albicauda* (aff.)
45822	R.ULN (prox.)	2004	LEM 1	Area 7, speckled tuff	*	Mammalia	Carnivora				
45828	IPX	2004	LEM 1	sieving area 1		Mammalia	Carnivora (cf.)				
45832	L.MAN w/p3-4	2004	LEM 1	sieving area 2		Mammalia	Carnivora	Felidae	Felinae	*Metailurus*	*major*
45834	PAT	2004	LEM 1	sieving area 2		Mammalia	Carnivora				
45835	m1	2004	LEM 1	sieving area 2		Mammalia	Carnivora				
45863	P3 (frag.)	2004	LEM 1	sieving area 2		Mammalia	Carnivora	Felidae	Felinae	*Metailurus*	*major*
45864	M	2004	LEM 1	sieving area 2		Mammalia	Carnivora				
45867	R.I1	2004	LEM 1	sieving area 2		Mammalia	Carnivora				
45881	C	2004	LEM 1	sieving area 2		Mammalia	Carnivora				
45882	C	2004	LEM 1	sieving area 2		Mammalia	Carnivora				
45883	C	2004	LEM 1	sieving area 2		Mammalia	Carnivora				
45884	MAN (edent. frag.)	2004	LEM 1	sieving area 2		Mammalia	Carnivora				
45890	RAD	2004	LEM 1	sieving area 2		Mammalia	Carnivora				
45891	MTP	2004	LEM 1	sieving area 2		Mammalia	Carnivora				
45924	C	2004	LEM 1	Area 13, claystones	*	Mammalia	Carnivora (cf.)				
45925	dm	2004	LEM 1	Area 7	*	Mammalia	Carnivora (cf.)				
45930	C	2004	LEM 1	Area 14, claystones	*	Mammalia	Carnivora (cf.)				
45933	P	2004	LEM 1	Area 14, claystones	*	Mammalia	Carnivora (cf.)				
45951	L.i	2004	LEM 1	sieving, sands Area 10		Mammalia	Carnivora				
36517	I		LEM 1	Area 5, top of hill	*	Mammalia	Hyracoidea	Procaviidae			
36534	L.MAN w/p4-m2	1995	LEM 1	na		Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
36539	CAL	1995	LEM 1	na		Mammalia	Hyracoidea	Procaviidae			
36575	R.MAN w/p2-m2	1995	LEM 1	na		Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
36934	MAN w/m	1995	LEM 1	na		Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
40907	MAN (edent. frag.)	2000	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
40909	I1	2000	LEM 1	Area 9/10		Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
40910	C	2000	LEM 1	Area 9/10		Mammalia	Hyracoidea	Procaviidae			
40993	R.MAN w/m3	2001	LEM 1	Area 4, claystones	*	Mammalia	Hyraeoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
41006	MAN (edent. frag.) w/ symphysis	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
41042	M	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41043	M	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41047	M	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41080	R.FEM (dist.)	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41090	M	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41091	M	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41098	M	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41100	M	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41102	C frag.	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41103	m	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41104	M	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41108	M	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41109	M (frag.)	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41110	M	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41115	MAN (edent. frag.)	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41116	R.+L.MAN (edent. frag.)	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41125	M	2001	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
41152	M	2001	LEM 1	Area 8		Mammalia	Hyracoidea	Procaviidae			
41153	associated dentition	2001	LEM 1	Area 8		Mammalia	Hyracoidea	Procaviidae			
41215	C	2001	LEM 1	Area 4, claystones	*	Mammalia	Hyracoidea	Procaviidae			
41231	M	2001	LEM 1	Area 4, claystones	*	Mammalia	Hyracoidea	Procaviidae			
41235	IPX	2001	LEM 1	Area 4, claystones	*	Mammalia	Hyracoidea	Procaviidae			
41240	MAN (edent. frag.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Hyracoidea	Procaviidae			
41250	C	2001	LEM 1	Area 4, claystones	*	Mammalia	Hyracoidea	Procaviidae			
41259	M	2001	LEM 1	Area 6	*	Mammalia	Hyracoidea	Procaviidae			
41262	C (frag.)	2001	LEM 1	Area 6	*	Mammalia	Hyracoidea	Procaviidae			
41266	M	2001	LEM 1	Area 6	*	Mammalia	Hyracoidea	Procaviidae			
41267	M	2001	LEM 1	Area 6	*	Mammalia	Hyracoidea	Procaviidae			
41268	half M	2001	LEM 1	Area 6	*	Mammalia	Hyracoidea	Procaviidae			
41269	L.M3	2001	LEM 1	Area 6	*	Mammalia	Hyracoidea	Procaviidae			
41270	P	2001	LEM 1	Area 6	*	Mammalia	Hyracoidea	Procaviidae			
41289	R.MAN w/p2-3	2001	LEM 1	Area 6	*	Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
41303	M	2001	LEM 1	Area 6	*	Mammalia	Hyracoidea	Procaviidae			
41304	R.+L.MAN w/L.M3	2001	LEM 1	Area 6	*	Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
41418	M	1999	LEM 1	na		Mammalia	Hyracoidea	Procaviidae			
41432	L.FEM (prox. shaft)	1999	LEM 1	na		Mammalia	Hyracoidea	Procaviidae			
41454	C	2001	LEM 1	na		Mammalia	Hyracoidea	Procaviidae			
41460	L.I1 (frag.)	2001	LEM 1	na		Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
41465	M (frag.)	2001	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
41466	M (frag.)	2001	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
41467	L.FEM (dist.)	2001	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
41472	ULN (dist.)	2001	LEM 1	Area 6	*	Mammalia	Hyracoidea	Procaviidae			

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
41488	M	2001	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
42257	R.I1	2002	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
42259	RAD (prox.)	2002	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
42272	R.HUM (dist.)	2002	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
42282	Ms	2002	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
42283	I	2002	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
42300	L.M3	2002	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
42305	M	2002	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
42306	CAL	2002	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
42313	M	2002	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae			
42331	M	2002	LEM 1	Area 8		Mammalia	Hyracoidea	Procaviidae			
42336	RAD (prox.)	2002	LEM 1	Area 10		Mammalia	Hyracoidea	Procaviidae			
42351	M	2002	LEM 1	Area 13, claystones	*	Mammalia	Hyracoidea	Procaviidae			
42374	C	2002	LEM 1	sieving area 1		Mammalia	Hyracoidea	Procaviidae			
42375	C	2002	LEM 1	sieving area 1		Mammalia	Hyracoidea	Procaviidae			
42395	L.MAN w/m1 + m2 roots	2002	LEM 1	sieving area 1		Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
44776	L.HUM (dist.)	2003	LEM 1	Area 7	*	Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
44787	C	2003	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
44796	C	2003	LEM 1	Area 10		Mammalia	Hyracoidea	Procaviidae			
44804	MAX/MAN (frags.) w/7 teeth	2003	LEM 1	Area 8		Mammalia	Hyracoidea	Procaviidae		*Dendrohyrax*	*validus* (cf.)
44805	C	2003	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
44807	M	2003	LEM 1	Area 9	*	Mammalia	Hyracoidea	Procaviidae			
44825	M	2003	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
44849	HUM (dist.)	2003	LEM 1	Area 8		Mammalia	Hyracoidea	Procaviidae			
44850	R.i	2003	LEM 1	Area 8		Mammalia	Hyracoidea	Procaviidae			
44891	HUM (dist.)	2003	LEM 1	sieving area 1		Mammalia	Hyracoidea	Procaviidae			
44909	MTC II1 (prox.)	2003	LEM 1	sieving area 1		Mammalia	Hyracoidea	Procaviidae			
44910	PAT	2003	LEM 1	sieving area 1		Mammalia	Hyracoidea	Procaviidae			
44911	PAT	2003	LEM 1	sieving area 1		Mammalia	Hyracoidea	Proeaviidae			
44912	ULN (prox)	2003	LEM 1	sieving area 1		Mammalia	Hyracoidea	Procaviidae			
44918	M	2003	LEM 1	sieving area 1		Mammalia	Hyracoidea	Procaviidae			
44919	M	2003	LEM 1	sieving area 1		Mammalia	Hyracoidea	Procaviidae			
45777	MAN (edent. frag.)	2004	LEM 1	Area 7, just below microbreccia	*	Mammalia	Hyracoidea	Procaviidae			
45779	RAD (prox.)	2004	LEM 1	Area 7, just below microbreccia	*	Mammalia	Hyracoidea	Procaviidae			
45786	i	2004	LEM 1	Area 6, mudstones above sands	*	Mammalia	Hyracoidea	Procaviidae			
45795	assoc. postcrania	2004	LEM 1	Area 7, speckled tuff	*	Mammalia	Hyracoidea	Procaviidae			
45796	M	2004	LEM 1	Area 9, speckled tuff	*	Mammalia	Hyracoidea	Procaviidae			
45807	R.MAX (frag.) w/M	2004	LEM 1	Area 6, mudstones 1 m above speckled tuff	*	Mammalia	Hyracoidea	Procaviidae			
45808	R.m	2004	LEM 1	Area 5, mudstones, 1 m above speckled tuff	*	Mammalia	Hyracoidea	Procaviidae			
45812	L.M3	2004	LEM 1	Area 5, mudstones 1/2 m above yellow silts	*	Mammalia	Hyracoidea	Procaviidae			
45870	C	2004	LEM 1	sieving area 2		Mammalia	Hyracoidea	Procaviidae			
45871	L.m	2004	LEM 1	sieving area 2		Mammalia	Hyracoidea	Procaviidae			
45872	L.m	2004	LEM 1	sieving area 2		Mammalia	Hyracoidea	Procaviidae			
45873	L.m	2004	LEM 1	sieving area 2		Mammalia	Hyracoidea	Procaviidae			
45874	L.m	2004	LEM 1	sieving area 2		Mammalia	Hyracoidea	Procaviidae			
45875	R.m	2004	LEM 1	sieving area 2		Mammalia	Hyracoidea	Procaviidae			
45876	R.m	2004	LEM 1	sieving area 2		Mammalia	Hyracoidea	Procaviidae			

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
45877	L.M	2004	LEM 1	sieving area 2		Mammalia	Hyracoidea	Procaviidae			
45878	L.M	2004	LEM 1	sieving area 2		Mammalia	Hyracoidea	Procaviidae			
45879	R.M	2004	LEM 1	sieving area 2		Mammalia	Hyracoidea	Procaviidae			
45880	R.m	2004	LEM 1	sieving area 2		Mammalia	Hyracoidea	Procaviidae			
45885	I	2004	LEM 1	sieving area 2		Mammalia	Hyracoidea	Procaviidae			
45904	R.m	2004	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
45905	L.m	2004	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
45906	L.M	2004	LEM 1	Area 5, claystones	*	Mammalia	Hyracoidea	Procaviidae			
45910	R.Ms (2)	2004	LEM 1	Areas 9/10 boundary; speckled tuff	*	Mammalia	Hyracoidea	Procaviidae			
45918	M	2004	LEM 1	Areas 9/10 boundary; speckled tuff	*	Mammalia	Hyracoidea	Procaviidae			
45949	ULN (prox.)	2004	LEM 1	sieving, sands Area 10		Mammalia	Hyracoidea	Procaviidae			
45781	VER	2004	LEM 1	Area 7, just below microbreccia	*	Mammalia	Hyracoidea (cf.)				
41009	MAN (edent. frag.)	2001	LEM 1	Area 7	*	Mammalia	Insectivora				
41041	MAN (edent. frag.)	2001	LEM 1	Area 7	*	Mammalia	Insectivora				
41079	MAN (edent. frag.)	2001	LEM 1	Area 7	*	Mammalia	Insectivora				
42373	MAN (frag.) w/2 teeth	2002	LEM 1	sieving area 1		Mammalia	Insectivora				
44816	L.MAN w/c	2003	LEM 1	Area 9	*	Mammalia	Insectivora				
36939	R.MAX w/P2-4	1995	LEM 1	na		Mammalia	Lagomorpha	Leporidae		*Alilepus*	
36961	R.TIB (dist.)	1995	LEM 1	na		Mammalia	Lagomorpha	Leporidae			
36962	L.CAL (frag.)	1995	LEM 1	na		Mammalia	Lagomorpha	Leporidae			
40876	R.+L.HUM (dist.) + RAD (prox.)	2000	LEM 1	Area 6	*	Mammalia	Lagomorpha	Leporidae			
40895	L.CAL	2000	LEM 1	Area 7	*	Mammalia	Lagomorpha	Leporidae			
40901	PHX	2000	LEM 1	Area 7	*	Mammalia	Lagomorpha				
40917	OCX (frag.)	2000	LEM 1	Area 9/10		Mammalia	Lagomorpha	Leporidae			
40991	L.TIB (dist.)	2001	LEM 1	Area 2		Mammalia	Lagomorpha	Leporidae			
40997	Tooth	2001	LEM 1	Area 4, claystones	*	Mammalia	Lagomorpha				
41001	R.TIB (dist.) + NAV	2001	LEM 1	Area 5, claystones	*	Mammalia	Lagomorpha	Leporidae			
41003	L.FEM (prox. epiphysis)	2001	LEM 1	Area 7	*	Mammalia	Lagomorpha	Leporidae			
41025	R.TIB (dist.)	2001	LEM 1	Area 7	*	Mammalia	Lagomorpha	Leporidae			
41065	PPX hindlimb	2001	LEM 1	Area 7	*	Mammalia	Lagomorpha	Leporidae			
41078	M	2001	LEM 1	Area 7	*	Mammalia	Lagomorpha	Leporidae			
41254	I	2001	LEM 1	Area 6	*	Mammalia	Lagomorpha				
41323	R.+L.AST (frags.)	2001	LEM 1	Area 6	*	Mammalia	Lagomorpha	Leporidae			
41478	CAL (frag.)	2001	LEM 1	Area 6	*	Mammalia	Lagomorpha	Leporidae			
41486	FEM (prox.)	2001	LEM 1	Area 5, claystones	*	Mammalia	Lagomorpha	Leporidae			
41493	MTP (dist. frag.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Lagomorpha	Leporidae			
42249	PHX (dist. frag.)	2002	LEM 1	Area 4, claystones	*	Mammalia	Lagomorpha				
42253	L.CUB	2002	LEM 1	Area 4, claystones	*	Mammalia	Lagomorpha	Leporidae			
42265	R.AST	2002	LEM 1	Area 5, claystones	*	Mammalia	Lagomorpha	Leporidae			
42290	L.CAL (frag.)	2002	LEM 1	Area 5, claystones	*	Mammalia	Lagomorpha	Leporidae			
42292	M	2002	LEM 1	Area 5, claystones	*	Mammalia	Lagomorpha	Leporidae			
42299	L.p3	2002	LEM 1	Area 7	*	Mammalia	Lagomorpha	Leporidae			
42307	R.HUM (dist.)	2002	LEM 1	Area 7	*	Mammalia	Lagomorpha				
42317	PHX (dist. frag.)	2002	LEM 1	Area 7	*	Mammalia	Lagomorpha				
42356	R.AST	2002	LEM 1	Area 13, claystones	*	Mammalia	Lagomorpha	Leporidae			
42368	P3 + M1-2	2002	LEM 1	sieving area 1		Mammalia	Lagomorpha	Leporidae			
44763	L.HUM (dist.)	2003	LEM 1	Area 4, claystones	*	Mammalia	Lagomorpha	Leporidae			
44772	L.FEM (dist.)	2003	LEM 1	Area 7	*	Mammalia	Lagomorpha	Leporidae			
44773	L.FEM (dist.)	2003	LEM 1	Area 7	*	Mammalia	Lagomorpha	Leporidae			
44780	MAX (frag.)	2003	LEM 1	Area 7	*	Mammalia	Lagomorpha				
44812	1	2003	LEM 1	Area 9	*	Mammalia	Lagomorpha				

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
44813	IPX	2003	LEM 1	Area 9	*	Mammalia	Lagomorpha	Leporidae			
44824	PPX	2003	LEM 1	Area 5, claystones	*	Mammalia	Lagomorpha	Leporidae			
45764	1	2004	LEM 1	Area 4, south side of hill, 1/2 m from top	*	Mammalia	Lagomorpha				
45801	m	2004	LEM 1	Area 7, speckled tuff	*	Mammalia	Lagomorpha	Leporidae			
45803	TIB (dist.)	2004	LEM 1	Area 7, speckled tuff	*	Mammalia	Lagomorpha				
45935	PHX	2004	LEM 1	sieving area 2		Mammalia	Lagomorpha				
45936	AST	2004	LEM 1	sieving area 2		Mammalia	Lagomorpha				
36500	R.M2	1995	LEM 1	na		Mammalia	Perrissodactyla	Rhinocerotidae			
36505	L.M3	1995	LEM 1	na		Mammalia	Perrissodactyla	Rhinocerotidae			
36510	M (frag.)	1995	LEM 1	na		Mammalia	Perrissodactyla	Rhinocerotidae			
36511	R.M2	1995	LEM 1	na		Mammalia	Perrissodactyla	Rhinocerotidae			
36866	M (frag.)	1995	LEM 1	na		Mammalia	Perrissodactyla	Equidae			
36935	L.M (frag.)	1995	LEM 1	preservation matches sands	x	Mammalia	Perrissodactyla	Equidae		*Eurygnathohippus*	*feibeli* (cf.)
38312	R.M3	1999	LEM 1	preservation matches sands	x	Mammalia	Perrissodactyla	Equidae		*Eurygnathohippus*	*feibeli* (cf.)
38320	TAL	1999	LEM 1	na		Mammalia	Perrissodactyla	Rhinocerotidae			
40994	L.p4	2001	LEM 1	Area 4		Mammalia	Perrissodactyla	Equidae		*Eurygnathohippus*	*feibeli* (cf.)
41218	M (frag.)	2001	LEM 1	Area 13, claystones	*	Mammalia	Perrissodactyla	Rhinocerotidae			
41302	M (frag.)	2001	LEM 1	Area 6	*	Mammalia	Perrissodactyla	Rhinocerotidae			
41359	P	1999	LEM 1	na		Mammalia	Perrissodactyla	Rhinocerotidae			
41360	MTP (dist.)	1999	LEM 1	na		Mammalia	Perrissodactyla	Rhinocerotidae			
41375	R.p4 (frag.)	1999	LEM 1	na		Mammalia	Perrissodactyla	Equidae		*Eurygnathohippus*	*feibeli* (cf.)
41431	Tooth (frag.)	1999	LEM 1	na		Mammalia	Perrissodactyla	Rhinocerotidae			
41453	MTT (prox.)	2001	LEM 1	Area 11		Mammalia	Perrissodactyla	Rhinocerotidae			
42279	M (frag.)	2002	LEM 1	Area 5, claystones	*	Mammalia	Perrissodactyla	Rhinocerotidae			
44926	m (frag.)	2002	LEM 1	Area 11 (NOT in situ)		Mammalia	Perrissodactyla	Equidae			
36502	L.m1or2	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae		large taxon
36514	R.MAN (p3-m3)	1995/ 2000	LEM 1	Area 6, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		small taxon
36515	R.MAN w/i1, c, m1-2, L.MAN w/i1-p3, m2-3, L.MAX w/P3-M3	1995/ 2000	LEM 1	Area 6, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae	*Paracolobus*	*enkorikae*
36516	L.MAX w/P3-M3	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae		small taxon
36519	L.HUM (dist.)	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae			
36521	L.MAX w/P3-M3	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae		
36528	R.ULN (prox.)	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae			
36540	L.HUM (dist.)	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae			
36541	L.ULN (frag.)	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae			
36542	L.ULN (prox.)	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae			
36543	MAN w/Ldp3-m1	1995/ 2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
36544	R.M3	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae			
36545	L.RAD (prox.)	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae			
36546	L.MAN w/dm2-m1 + m2 in crypt	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae		
36547	R.CAL	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae			
36550	MAX w/R.C-P3 + L.M1-3	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae		small taxon
36551	L.c (female)	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae			
36552	L.i2	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae		
36553	R.MAN w/dp4 + m1	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae		
36555	MAN dentition w/L.p3-4, R.p3-m1, probably assoc. w/NK 36502	1995/ 2004	LEM 1	Area 9	*	Mammalia	Primate	Cercopithecidae	Colobinae		large taxon

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
36558	m (frag.)	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae		
36559	R.m1or2	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae		
36560	R.HUM (dist.)	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae			
36586	L.MAX w/broken C root, P3-4 + M2-3	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae	*Paracolobus*	*enkorikae*
36587	R.+L.MAN w/dentition	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae	*Paracolobus*	*enkorikae*
36932	L.ULN (prox.)	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae			
36933	R.MAX w/roots I1-I2	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae		
36941	R.MAN w/i2	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae		
36944	RAD (prox. shaft)	1995	LEM 1	na		Mammalia	Primate	Cercopithecidae			
36958	MTT shaft (R III)		LEM 1	na		Mammalia	Primate	Cercopithecidae			
38308	L.c	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae			
38309	R.C	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae			
40859	RAD (prox.) + VER (frag.)	2000	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
40860	L.dP4	2000	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		
40861	L.m1or2	2000	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		
40870	L.I	2000	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		
40877	RAD (dist.)	2000	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
40878	VER caudal	2000	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
40880	R.+L.PAT + FEM (dist.)	2000	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
40882	R.M	2000	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
40885	L.MAN w/m2	2000	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae	*Paracolobus*	*enkorikae*
40889	FEM (prox.)	2000	LEM 1	Area 4/5, claystones	*	Mammalia	Primate	Cercopithecidae			
40891	FEM (prox.)	2000	LEM 1	Area 4/5, claystones	*	Mammalia	Primate	Cercopithecidae			
40894	VER caudal	2000	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
40900	R.MAX (frag.) w/I1-2, C + P3 alveoli (juvenile)	2000	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
40911	TEM (frag.)	2000	LEM 1	Area 9/10		Mammalia	Primate	Cercopithecidae			
40912	CAR	2000	LEM 1	Area 9/10		Mammalia	Primate	Cercopithecidae			
40914	PAT	2000	LEM 1	Area 9/10		Mammalia	Primate	Cercopithecidae			
40992	L.NAV	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae			
41000	assoc. p + m	2001	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41007	R.P4	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41013	IPX	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41014	half M	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41017	PHX (dist. frag.)	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41018	TIB (prox. epiphysis)	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41020	half m	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41028	R.HUM (dist.)	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41030	L.P4	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41033	M (frag.)	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41051	R.c	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41058	half m	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41059	RAD (prox. epiphysis)	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41061	VER (frag.)	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41062	TPX	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41066	MTC V (prox.)	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41073	half M	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41075	L.c	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41081	PHX (prox. frag.)	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41094	M (frag.)	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
41111	MTC III or IV (prox.)	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41122	PHX (prox. frag.)	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41124	PHX (dist. frag.)	2001	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
41150	L.m3	2001	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
41151	L.M	2001	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
41159	R.ZYG	2001	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae			
41161	m (frag.)	2001	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
41162	M (frag.)	2001	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
41164	MAN (edent. frag.)	2001	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae			
41165	ZYG (frag.)	2001	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae			
41168	MAN (edent. frag.)	2001	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae			
41169	R.HUM (dist.)	2001	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
41171	i (very worn)	2001	LEM 1	from stream bed on south side of main gulley		Mammalia	Primate	Cercopithecidae			
41172	L.i1	2001	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
41175	FEM (prox.)	2001	LEM 1	Area 9		Mammalia	Primate	Cercopithecidae			
41177	RAD (dist.)	2001	LEM 1	Area 14, claystones	*	Mammalia	Primate	Cercopithecidae			
41182	assoc. dentition	2001	LEM 1	Area 14, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41186	OCX	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae			
41196	L.HUM (dist.)	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae			
41207	ULN (dist.)	2001	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae			
41208	PAT	2001	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae			
41210	R.c	2001	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae			
41211	R.+L.i1	2001	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41212	L.c	2001	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae			
41213	L.dP3	2001	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41214	L.m1or2	2001	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41216	L.M1or2	2001	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41217	R.LM1or2	2001	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41222	PHX (dist. frag.)	2001	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae			
41225	R.p4	2001	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae			
41234	R.MAN w/dp4	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41236	L.I	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41237	C (frag.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae			
41238	L.m1or2	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41239	L.I1	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41257	L.FEM (prox.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41260	L.m3	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41261	M (frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41279	M (frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41280	L.m1or2	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41281	R.M3	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41282	R.m3 (frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41283	R.C	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41286	L.C	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41294	PAT	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41295	L.HUM (dist.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41296	i (frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41301	R.MAN (frag.) w/m2-3	2001	LEM 1	Area 4, gulley		Mammalia	Primate	Cercopithecidae	Colobinae	*Paracolobus*	*enkorikae*
41305	R.+L.MAN (frag.) w/ R.m2-3 + L.p4-m2	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		small taxon
41307	R.ULN (prox.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
41308	R.ULN (prox.) + RAD	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41309	L.CUB	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41310	L.EXT	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41317	R.TIB (dist.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41318	R.FRO (frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41319	R.HUM (dist.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41320	OCC (frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41321	R.MAX (frag.) w/P4-M3 + isolated L.M2 + L.C	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		small taxon
41322	L.I1	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		
41325	MTT (dist. frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41326	MTT (dist. frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41327	PHX (dist. frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41328	VER caudal	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41332	MTP (shaft frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41333	VER caudal (frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41334	PHX (dist. frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41370	L.C	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae			
41383	SCA glenoid (frag.)	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae			
41405	L.CAL	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae			
41407	HUM (dist. shaft frag.)	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae			
41410	RAD (prox.)	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae			
41411	RAD (prox.)	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae			
41412	L.HUM (dist.)	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae			
41413	R.HUM (dist.)	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae			
41419	L.MAX w/P3-M2 roots	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae	Colobinae		
41441	L.I1	2001	LEM 1	Area 12		Mammalia	Primate	Cercopithecidae	Colobinae		
41443	L.c	2001	LEM 1	Area 12		Mammalia	Primate	Cercopithecidae			
41444	R.I1	2001	LEM 1	Area 12		Mammalia	Primate	Cercopithecidae	Colobinae		
41445	R.M1or2	2001	LEM 1	Area 12		Mammalia	Primate	Cercopithecidae	Colobinae		
41463	L.C	1999	LEM 1	na		Mammalia	Primate	Cercopithecidae			
41471	MTT III (prox. frag.)	2001	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
41487	TPX	2001	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
41491	RAD (prox.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae			
41492	L.HUM (dist.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae			
41494	PPX (prox. frag.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae			
41495	IPX	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae			
41496	PPX	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae			
41497	L.MTT V (prox.)	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae			
41500	L.MTT III + IV	2001	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae			
42248	R.i1	2002	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
42256	R.i2	2002	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
42258	R.c	2002	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
42260	L.M1+2 (frags.)	2002	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
42261	RAD (prox. epiphysis)	2002	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
42263	P	2002	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
42273	HUM (dist.)	2002	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
42274	PHX	2002	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
42275	L.M	2002	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
42276	MAN w/L.i1, R.p3-m3	2002	LEM 1	Area 5 top of hill	*	Mammalia	Primate	Cercopithecidae	Colobinae	*Paracolobus*	*enkorikae*
42278	VER axis	2002	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
42284	R.MAN w/dm1, m1 + m2 erupting	2002	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
42288	IPX	2002	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
42294	IPX	2002	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
42297	PAT	2002	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
42308	MTT (dist.)	2002	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
42312	L.dm1	2002	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
42325	R.p4	2002	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
42332	MAN (edent. frag.)	2002	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae			
42333	I	2002	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
42341	R.i2	2002	LEM 1	Area 10		Mammalia	Primate	Cercopithecidae	Colobinae		
42342	TPX	2002	LEM 1	Area 10		Mammalia	Primate	Cercopithecidae			
42343	L.P3	2002	LEM 1	Area 10		Mammalia	Primate	Cercopithecidae	Colobinae		
42346	assoc. L.I1-RC + M1	2002	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae	*Paracolobus*	*enkorikae*
42347	R.m1or2	2002	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		large taxon
42352	L.I	2002	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
42353	R.dM2	2002	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
42354	L.p3	2002	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
42359	L.p4	2002	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
42364	R.M3	2002	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
42365	R.i1	2002	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
42366	L.i2	2002	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
42367	PPX	2002	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae			
42372	R.C (frag.)	2002	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae			
42376	assoc. P4-M2	2002	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae	*Paracolobus*	*enkorikae*
42386	L.m3	2002	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
42387	L.m1	2002	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
42388	R.+L.C (frags.)	2002	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae	*Paracolobus*	*enkorikae*
42389	AST	2002	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae			
42392	R.C	2002	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae			
44761	R.c	2002	LEM 1	na		Mammalia	Primate	Cercopithecidae			
44762	R.i2	2003	LEM 1	Area 4, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
44766	R.HUM (dist.)	2003	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae			
44767	IPX	2003	LEM 1	Area 13, claystones	*	Mammalia	Primate	Cercopithecidae			
44769	L.c (male)	2003	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
44770	MAN w/c frag., L.p3-m3, R.c, R.m1-3 + isolated L.I1-2, L.M1, R.I2-M1	2003	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae	*Paracolobus*	*enkorikae*
44774	L.I1	2003	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
44775	R.p3	2003	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
44779	i root (frag.)	2003	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
44782	L.CAL	2003	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
44784	I (frag.)	2003	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
44785	IPX	2003	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
44788	MTT (prox. frag.)	2003	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
44790	R.i2	2003	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		
44791	R.AST	2003	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			
44792	R.M3	2003	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae	Colobinae		
44799	TPX	2003	LEM 1	Area 6	*	Mammalia	Primate	Cercopithecidae			

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
44800	L.MAN w/di1, dm1-2, m1 in crypt, gonial angle, ascending ramus, condyle + coronoid process	2003	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
44808	dm2	2003	LEM 1	Area 9	*	Mammalia	Primate	Cercopithecidae	Colobinae		
44814	R.p3 or 4 (frag.)	2003	LEM 1	Area 9	*	Mammalia	Primate	Cercopithecidae	Colobinae		
44819	MTP (dist. frag.)	2003	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
44821	dm2	2003	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
44823	L.dM1	2003	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae	Colobinae		
44828	EXT	2003	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
44836	L.HUM (dist. shaft)	2003	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
44837	RAD (shaft)	2003	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae			
44840	R.m3	2003	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
44841	R.M3	2003	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
44842	L.M1or2	2003	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
44843	L.I1 (frag.)	2003	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
44844	I (frag.)	2003	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
44845	L.I	2003	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
44846	L.C (female)	2003	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae			
44847	L.c (female)	2003	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae			
44848	L.i2	2003	LEM 1	Area 8		Mammalia	Primate	Cercopithecidae	Colobinae		
44853	R.i2	2003	LEM 1	East side of main gulley		Mammalia	Primate	Cercopithecidae	Colobinae		
44859	R.c (frag.)	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae			
44860	L.c	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		large taxon
44861	R.dc	2002	LEM 1	Area 9		Mammalia	Primate	Cercopithecidae			
44863	R.M3 (frag.)	2002	LEM 1	Area 9		Mammalia	Primate	Cercopithecidae	Colobinae		
44864	R.m3	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44865	L.m1or2	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44866	R.+L.m3s (antimeres)	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae	*Paracolobus*	*enkorikae*
44867	R.p3	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		large taxon
44868	L.p4	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		large taxon
44870	R.p3	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae	*Paracolobus*	*enkorikae*
44871	L.m1or2	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44872	R.I1	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44873	R.I1	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44874	L.i1	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44875	L.i2	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44876	R.i2	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44877	L.m1or2	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44878	R.i2	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44879	L.i2	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44880	L.i1 (very worn)	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44881	R.dm2	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44882	P3	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44883	L.dM2	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44884	L.C (frag.)	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae			
44885	L.HUM (dist.)	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae			
44886	L.CAL	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae			
44908	RAD (prox.)	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae			
44923	dm	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
44924	L.i2	2003	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
45762	IPX	2004	LEM 1	Area 4, south side of hill, 1/2 m from top	*	Mammalia	Primate	Cercopithecidae			
45763	IPX	2004	LEM 1	Area 4, south side of hill, 1/2 m from top	*	Mammalia	Primate	Cercopithecidae			
45766	PPX	2004	LEM 1	Area 5, 3 m from top of hill, near gulley, brown mudstones	*	Mammalia	Primate	Cercopithecidae			
45770	PPX	2004	LEM 1	Area 5, 3 m from top of hill, near gulley, brown mudstones	*	Mammalia	Primate	Cercopithecidae			
45782	MAN (edent. frag.)	2004	LEM 1	Area 8, sands	x	Mammalia	Primate	Cercopithecidae			
45784	R.I	2004	LEM 1	Area 8, sands	x	Mammalia	Primate	Cercopithecidae	Colobinae		
45792	L.SCA (frag.)	2004	LEM 1	Area 7/9, sands	x	Mammalia	Primate	Cercopithecidae			
45797	R.m1or2	2004	LEM 1	Arca 9, speckled tuff	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45805	L.M	2004	LEM 1	Area 6, mudstones above sands	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45806	R.i2	2004	LEM 1	Area 6, mudstones above sands	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45809	L.dP4	2004	LEM 1	Area 5, mudstones at level of speckled tuff	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45813	R.i1	2004	LEM 1	Area 5, mudstones 1/2 m > yellow silts	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45814	L.m1or2	2004	LEM 1	Area 5, mudstones 2 m above speckled tuff	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45815	L.m3	2004	LEM 1	Area 5, mudstones 3 m above speckled tuff	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45816	R.M1or2	2004	LEM 1	Area 5, mudstones 3 m above speckled tuff	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45817	TPX	2004	LEM 1	Area 5, mudstones 3 m above speckled tuff	*	Mammalia	Primate	Cercopithecidae			
45826	L.m3	2004	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
45829	R.M1or2	2004	LEM 1	sieving area 1		Mammalia	Primate	Cercopithecidae	Colobinae		
45839	L.c	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae			
45841	IPX	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae			
45842	IPX	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae			
45843	IPX	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae			
45846	L.I2	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45847	L.i1	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45849	R.m1or2	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45850	R.m1or2	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45851	R.m1or2	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45852	L.M1or2	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45853	R.P4	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45854	L.i1	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45855	R.P4	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45856	L.M	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45857	L.M	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45858	R.m1or2	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopitheeidae	Colobinae		
45860	L.m1or2	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45861	R.M3	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45862	L.P4	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45865	L.P3	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45866	R.m1or2	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45868	L.c	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae			
45869	L.C	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae			
45886	L.dp4	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
45887	L.dc	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae			
45888	L.dc	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae			
45889	L.p3	2004	LEM 1	sieving area 2		Mammalia	Primate	Cercopithecidae	Colobinae		
45901	L.c	2004	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
45903	L.c	2004	LEM 1	Area 5, claystones	*	Mammalia	Primate	Cercopithecidae			
45908	L.M3	2004	LEM 1	Area 9		Mammalia	Primate	Cercopithecidae	Colobinae		
45909	R.M1or2	2004	LEM 1	Area 11, 8 m > yellow silts	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45912	R.MAN (edent. frag.)	2004	LEM 1	Area 14, claystones	*	Mammalia	Primate	Cercopithecidae			
45913	L.M1or2	2004	LEM 1	Area 13, 3 m>yellow silts	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45914	R.i1	2004	LEM 1	Areas 9/10 boundary; speckled tuff	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45915	L.di1 + L.dc + L.dp4	2004	LEM 1	Areas 9/10 boundary; speckled tuff	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45916	R.p4	2004	LEM 1	Areas 9/10 boundary; speckled tuff	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45917	R.m1or2	2004	LEM 1	Areas 9/10 boundary; speckled tuff	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45919	L.m1or2	2004	LEM 1	Area 11, 12 m >yellow silts	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45921	L.m1or2	2004	LEM 1	Area 10, 8 m>yellow silts	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45922	R.P4	2004	LEM 1	Area 10, 3 m>yellow silts	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45923	L.M1or2	2004	LEM 1	Area 10, 6 m>yellow silts	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45926	L.dp4	2004	LEM 1	Area 7	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45932	L.p3	2004	LEM 1	Area 14, 7 m>yellow silts	*	Mammalia	Primate	Cercopithecidae	Colobinae		
45953	MTP (prox.)	2004	LEM 1	sieving, sands Area 10		Mammalia	Primate	Cercopithecidae			
45958	MAN (edent.)	2004	LEM 1	sieving, sands Area 10		Mammalia	Primate	Cercopithecidae			
45959	R.MTC V	2004	LEM 1	sieving, sands Area 10		Mammalia	Primate	Cercopithecidae			
41133	M (frag.)	2001	LEM 1	Area 10		Mammalia	Proboscidea				
41227	M (frag.)	2001	LEM 1	Area 4		Mammalia	Proboscidea				
41502	L. MAN w/m3 (frag.)	1999	LEM 1	preservation matches sands	x	Mammalia	Proboscidea	Gomphotheriidae		*Anancus*	*kenyensis*
36588	R.CAL	1995	LEM 1	na		Mammalia	Rodentia				
36589	L.P4	1995	LEM 1	na		Mammalia	Rodentia	Hystricidae		*Xenohystrix*	
36590	R.M	1995	LEM 1	na		Mammalia	Rodentia	Hystricidae		*Xenohystrix*	
36893	I	1995	LEM 1	na		Mammalia	Rodentia	Hystricidae		*Hystrix*	
40995	R.MAN (frag.)	2001	LEM 1	Area 4 (from sands)	x	Mammalia	Rodentia				
40998	L.MAN frag. w/ broken I + m1-3 alveoli	2001	LEM 1	Area 4		Mammalia	Rodentia	Muridae	Murinae		
41002	I (frag.)	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Hystricidae		*Hystrix*	
41022	FEM (prox.)	2001	LEM 1	Area 7	*	Mammalia	Rodentia				
41024	OCX	2001	LEM 1	Area 7	*	Mammalia	Rodentia				
41046	MAX (frag.) w/P4-M1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Sciuridae	Sciurinae	*Xerus*	
41048	MAN	2001	LEM 1	Area 7	*	Mammalia	Rodentia				
41049	R.MAN w/i-m3	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Mastomys*	
41050	L.+R. pre-MAX w/Is	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae		
41052	L.M (frag.)	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Hystricidae		*Xenohystrix*	
41069	MAN (frag.) w/m	2001	LEM 1	Area 7	*	Mammalia	Rodentia				
41070	L.+ R. pre-MAX w/Is	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae (cf.)		
41083	MAN (frag.) w/m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Arvicanthis*	
41084	MAN (frag.) w/m	2001	LEM 1	Area 7	*	Mammalia	Rodentia				
41085	R.I	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae		
41086	L.MAN (frag.) w/i+m alveolus	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae		
41087	R.MAN (frag.) w/m1-2	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	
41088	L.MAN (frag.) w/m2-3	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Lemniscomys*	
41089	MAN (frag.) w/m1-2	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Arvicanthis*	
41092	bulk isolated incisors	2001	LEM 1	Area 7	*	Mammalia	Rodentia				

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
41093	bulk postcrania	2001	LEM 1	Area 7	*	Mammalia	Rodentia				
41096	MAN (frag.) w/m1-3	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Mastomys* (cf.)	
41101	R.MAN (edent. frag.)	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae			
41106	R.m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	
41107	MAN (frag.) w/broken i+m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae		
41127	L.MAN w/i-m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae		
41128	R.M1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Arvicanthis* (cf.)	
41232	L.MAN w/m1-2	2001	LEM 1	Area 4		Mammalia	Rodentia	Muridae	Murinae	*Arvicanthis*	
41306	MAN (edent. frag.)	2001	LEM 1	Area 6	*	Mammalia	Rodentia				
41448	L.MAN w/i+m1-3 alveoli	2001	LEM 1	Area 12		Mammalia	Rodentia	Muridae	Murinae		
41449	R.MAN w/i+m1-3 alveoli	2001	LEM 1	Area 12		Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	
42281	L.dm1	2002	LEM 1	Area 5, claystones	*	Mammalia	Rodentia				
42295	L.M1	2002	LEM 1	Area 5, claystones	*	Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	
42296	M3	2002	LEM 1	Area 6	*	Mammalia	Rodentia				
42303	MAN (edent. frag.)	2002	LEM 1	Area 7	*	Mammalia	Rodentia				
42311	R.MAN (frag.) w/i	2002	LEM 1	Area 7	*	Mammalia	Rodentia	Sciruidae	Sciurinae	*Paraxerus*	
42315	L.MAN (frag.) w/m1-2	2002	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Acomys*	
42316	MAX (edent. frag.)	2002	LEM 1	Area 7	*	Mammalia	Rodentia				
42335	R.p4	2002	LEM 1	Area 7	*	Mammalia	Rodentia	Sciruidae	Sciurinae	*Xerus*	
42360	MAX (frag.) w/M1	2002	LEM 1	sieving area 1		Mammalia	Rodentia	Muridae	Murinae	*Mastomys*	
44771	L.M3	2003	LEM 1	Area 7	*	Mammalia	Rodentia	Hystricidae		*Xenohystrix*	
44778	CAL	2003	LEM 1	Area 7	*	Mammalia	Rodentia				
44815	R.MAN w/m1-3	2003	LEM 1	Area 9	*	Mammalia	Rodentia	Muridae	Murinae	*Saidomys* (cf.)	
44830	R.MAX w/M1-2	2003	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Arvicanthis* (cf.)	
44831	R.MAN (frag.) w/i	2003	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae			
44832	R.MAN w/m2-3	2003	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Aethomys* (cf.)	
44834	L.MAN (frag.) w/i	2003	LEM 1	Area 7	*	Mammalia	Rodentia				
44856	L.MAN w/i-m3	1995	LEM 1	na		Mammalia	Rodentia	Muridae	Murinae	*Lemniscomys*	
44857	R.I	1995	LEM 1	na		Mammalia	Rodentia	Muridae	Murinae		
44858	R.MAN w/i+m2-3	1995	LEM 1	na		Mammalia	Rodentia	Muridae	Murinae	*Mastomys*	
44892	i	2003	LEM 1	sieving area 1		Mammalia	Rodentia	Hystricidae		*Atherurus*	
44893	i	2003	LEM 1	sieving area 1		Mammalia	Rodentia	Hystrieidae		*Atherurus*	
44894	cheek tooth (frag.)	2003	LEM 1	sieving area 1		Mammalia	Rodentia	Hystricidae			
44895	cheek tooth (frag.)	2003	LEM 1	sieving area 1		Mammalia	Rodentia	Hystricidae			
44896	R.M	2003	LEM 1	sieving area 1		Mammalia	Rodentia	Hystricidae		*Hystrix*	
44920	L.p4	2003	LEM 1	sieving area 1		Mammalia	Rodentia	Sciuridae	Sciurinae	*Paraxerus*	
44921	L.MAX w/M1	2003	LEM 1	sieving area 1		Mammalia	Rodentia	Muridae	Murinae	*Aethomys*	
44922	MAX (frag.) w/is	2003	LEM 1	sieving area 1		Mammalia	Rodentia				
45767	RAD (dist.)	2004	LEM 1	Area 5, 3 m from top of hill, near gulley, brown mudstones	*	Mammalia	Rodentia				
45778	MAN w/i1	2004	LEM 1	Area 7, just below microbreccia	*	Mammalia	Rodentia				
45798	L.I	2004	LEM 1	Areas 9/10 boundary, 1/2 m > speckled tuff	*	Mammalia	Rodentia	Sciruidae	Sciurinae	*Xerus* (cf.)	
45907	R.MAN w/i-m3	2004	LEM 1	Area 7, speckled tuff	*	Mammalia	Rodentia	Muridae	Murinae	*Mastomys*	
45934	R.MAN w/i+m2	2004	LEM 1	Area 14, claystones	*	Mammalia	Rodentia	Thryonomyidae		*Thryonomys*	
45945	L.MAN w/i1-m2	2004	LEM 1	sieving area 2		Mammalia	Rodentia	Thryonomyidae		*Thryonomys*	
45946	R.MAN w/i1-m3	2004	LEM 1	sieving area 2		Mammalia	Rodentia	Muridae	Murinae	*Arvicanthis*	
45947	R.MAX w/M1-3	2004	LEM 1	sieving area 2		Mammalia	Rodentia	Muridae	Murinae	*Arvicanthis*	
46232	R.m2	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
46233	R.M2	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Saidomys* (cf.)	
46234	L.m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	
46235	L.M1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Arvicanthis*	
46236	R.m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Arvicanthis*	
46237	L.M1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	
46238	L.m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	
46239	L.MAN w/m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Arvicanthis*	
46240	L.M1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Saidomys* (cf.)	
46241	L.m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	
46242	L.m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Arvicanthis*	
46243	L.MAN w/m1-2	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Acomys*	
46244	R.M2	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	
46245	L.m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae		
46246	L.M1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Arvicanthis*	
46247	R.M1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Mastomys*	
46248	R.m2	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	
46249	L.m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Mastomys*	
46250	L.M1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Mastomys*	
46251	L.m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	
46252	L.m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Gerbillinae	*Tatera*	
46253	L.m1	2001	LEM 1	Area 7	*	Mammalia	Rodentia	Muridae	Murinae	*Acomys* (cf.)	
36509	C (frag.)	1995	LEM 1	na		Mammalia					
40881	RAD (dist.)	2000	LEM 1	Area 6	*	Mammalia					
40908	HUM (dist.)	2000	LEM 1	Area 7	*	Mammalia					
41118	PHX	2001	LEM 1	Area 7	*	Mammalia					
41119	TAR	2001	LEM 1	Area 7	*	Mammalia					
41154	C	2001	LEM 1	Area 8		Mammalia					
41166	MAN (condyle)	2001	LEM 1	Area 8		Mammalia					
41265	RAD (dist.)	2001	LEM 1	Area 6	*	Mammalia					
41316	PHX	2001	LEM 1	Area 6	*	Mammalia					
41428	VER caudal	1999	LEM 1	na		Mammalia					
41429	VER caudal	1999	LEM 1	na		Mammalia					
41434	Tooth root	1999	LEM 1	na		Mammalia					
41446	CAR	2001	LEM 1	Area 12		Mammalia					
41450	P	2001	LEM 1	Area 12		Mammalia					
41451	P	2001	LEM 1	Area 12		Mammalia					
41479	MTT V (prox.)	2001	LEM 1	Area 4, claystones	*	Mammalia					
41498	PAT	2001	LEM 1	Area 4, claystones	*	Mammalia					
42251	PHX (dist. frag.)	2002	LEM 1	Area 4, claystones	*	Mammalia					
42254	RAD (dist.)	2002	LEM 1	Area 4, claystones	*	Mammalia					
42289	PHX	2002	LEM 1	Area 5, claystones	*	Mammalia					
42298	PHX (dist. frag.)	2002	LEM 1	Area 6	*	Mammalia					
42318	MTP (prox.)	2002	LEM 1	Area 7	*	Mammalia					
42340	PHX	2002	LEM 1	Area 10		Mammalia					
42369	PHX	2002	LEM 1	sieving area 1		Mammalia					
42390	PHX	2002	LEM 1	sieving area 1		Mammalia					
44786	PAT	2003	LEM 1	Area 5, claystones	*	Mammalia					
44789	PAT	2003	LEM 1	Area 5, claystones	*	Mammalia					
44795	TAR	2003	LEM 1	Area 10		Mammalia					
44826	IPX	2003	LEM 1	Area 5, claystones	*	Mammalia					
44827	IPX	2003	LEM 1	Area 5, claystones	*	Mammalia					
44862	IPX (frag.)	2002	LEM 1	Area 9		Mammalia					

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
44913	RAD (prox.)	2003	LEM 1	sieving area 1		Mammalia					
44914	PPX	2003	LEM 1	sieving area 1		Mammalia					
44916	CAL	2003	LEM 1	sieving area 1		Mammalia					
44917	MAN (edent. frag.)	2003	LEM 1	sieving area 1		Mammalia					
45818	PPX	2004	LEM 1	Area 5, mudstones 3 m above speckled tuff	*	Mammalia					
45927	VER	2004	LEM 1	Area 7	*	Mammalia					
45943	R. MAN (edent. frag.)	2004	LEM 1	sieving area 2		Mammalia					
45950	ULN (prox.)	2004	LEM 1	sieving, sands Area 10		Mammalia					
45952	RAD (prox.)	2004	LEM 1	sieving, sands Area 10		Mammalia					
42314	Spine	2002	LEM 1	Area 7	*	Pisces					
36889	Carapace (frag.)	1995	LEM 1	na		Reptilia	Chelonia				
36890	Tooth	1995	LEM 1	na		Reptilia	Crocodylia				
36891	Tooth	1995	LEM 1	na		Reptilia	Crocodylia				
36947	PHX	1995	LEM 1	na		Reptilia	Crocodylia				
38313	VER	1999	LEM 1	na		Reptilia					
40892	VER (n=7)	2000	LEM 1	Area 4/5, claystones	*	Reptilia	Serpentes				
40897	VER	2000	LEM 1	Area 7	*	Reptilia	Serpentes	(Coluboidea)			
41105	MAN (frag.)	2001	LEM 1	Area 7	*	Reptilia					
41113	VER	2001	LEM 1	Area 7	*	Reptilia	Serpentes				
41191	Tooth	1999	LEM 1	na		Reptilia	Crocodylia				
41226	VER	2001	LEM 1	Area 13, claystones	*	Reptilia	Serpentes		Pythoninae (cf.)		
41229	VER	2001	LEM 1	Area 4, claystones	*	Reptilia	Serpentes				
41251	MAN (frag.)	2001	LEM 1	Area 4, claystones	*	Reptilia					
41329	VER	2001	LEM 1	Area 6	*	Reptilia	Serpentes		Pythoninae (cf.)		
41363	VER cervical	1999	LEM 1	na		Reptilia	Serpentes		Pythoninae		
41399	Carapace (frag.)	1999	LEM 1	na		Reptilia	Chelonia				
41400	Carapace (frag.)	1999	LEM 1	na		Reptilia	Chelonia				
41415	VER (frag.)	1999	LEM 1	na		Reptilia	Serpentes		Pythoninae		
41440	VER	2001	LEM 1	Area 12		Reptilia	Serpentes		Pythoninae		
41484	Tooth	2001	LEM 1	S side of main gulley, edge of stream channel W of main locality		Reptilia	Crocodylia				
42252	PHX	2002	LEM 1	Area 4, claystones	*	Reptilia					
42270	TPX	2002	LEM 1	Area 5, claystones	*	Reptilia					
42285	PHX	2002	LEM 1	Area 5, claystones	*	Reptilia	Crocodylia				
44829	VER	2003	LEM 1	Area 5, claystones	*	Reptilia	Serpentes		Pythoninae		
44833	jaw frag w/2 teeth	2003	LEM 1	Area 7	*	Reptilia					
44838	postcranial element	2003	LEM 1	Area 7	*	Reptilia					
45765	VER	2004	LEM 1	Area 4, 1/4 m down slope, mudstone/clay	*	Reptilia	Serpentes				
45775	CRA	2004	LEM 1	Area 7, just below microbreccia	*	Reptilia					
45800	FEM (prox.)	2004	LEM 1	Area 11, west side of hill, 10 m > yellow silts, found near top of geol trench in mudstones	*	Reptilia					
45804	VER	2004	LEM 1	Area 7, speckled tuff	*	Reptilia					
45928	VER	2004	LEM 1	Area 7	*	Reptilia					
45940	VER	2004	LEM 1	sieving area 2		Reptilia					
45955	VER	2004	LEM 1	sieving, sands Area 10		Reptilia					
45956	VER	2004	LEM 1	sieving, sands Area 10		Reptilia					
45957	VER	2004	LEM 1	sieving, sands Area 10		Reptilia					
41252	IPX	2001	LEM 1	Area 4, claystones	*	(Vertebrate)					

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
41447	indet	2001	LEM 1	Area 12		Vertebrate					
41468	PHX	2001	LEM 1	Area 5, claystones	*	Vertebrate					
41469	indet	2001	LEM 1	Area 6	*	Vertebrate					
41473	CAR	2001	LEM 1	Area 6	*	Vertebrate					
41474	CAR	2001	LEM 1	Area 6	*	Vertebrate					
41475	MTP (dist.)	2001	LEM 1	Area 6	*	Vertebrate					
41477	PHX	2001	LEM 1	Area 6	*	Vertebrate					
41480	TIB (prox.)	2001	LEM 1	Area 4, claystones	*	Vertebrate					
41481	TAR	2001	LEM 1	Area 4, claystones	*	Vertebrate					
41482	ULN (prox.)	2001	LEM 1	Area 4, claystones	*	Vertebrate					
41483	PHX	2001	LEM 1	Area 4, claystones	*	Vertebrate					
44742	TPX	2003	ENE 1	brown sediments		Mammalia	Artiodactyla	Bovidae			
44743	Ms	2003	ENE 1	top of sand lens between pink and brown sediments		Mammalia	Artiodactyla	Bovidae			
44744	L.p3	2003	ENE 1	brown sediments		Mammalia	Primate	Cercopithecidae	Colobinae		
44745	M	2003	ENE 1	top of sands just below brown sediments		Mammalia	Artiodactyla	Bovidae			
44746	C (frag.)	2003	ENE 1	sand lens at base of brown sediments		Mammalia	Carnivora				
41455	R.+L.MAN (frag.) w/ m1-2, m3 erupting	2001	ENK 1	brown mudstone below sandstone		Mammalia	Artiodactyla	Bovidae	Aepycerotini		
41456	R. MAN (frag.) w/m3	2001	ENK 1	brown mudstone below sandstone		Mammalia	Artiodactyla	Bovidae			
41457	R.TIB + CAL + AST + 2 MTTs + PHXs + L.CUB + MTT (frag.)	2001	ENK 1	brown mudstone below sandstone		Mammalia	Lagomorpha	Leporidae			
41458	L.HOR + VER (frags.)	2001	ENK 1	base of the gray sands		Mammalia	Artiodactyla	Bovidae		*Aepyceros*	*premelampus* (aff.)
41459	L.M3	2001	ENK 1	gully bottom below sands and mudstones		Mammalia	Artiodactyla	Bovidae	Tragelaphini (cf.)		
42243	L.dm2	2002	ENK 1	stream channel at level of sands		Mammalia	Primate	Cercopithecidae	Colobinae		
42244	L.MTT	2002	ENK 1	sands		Mammalia	Artiodactyla	Hippopotamidae			
42245	R.MAN (frag.) w/m1+2	2002	ENK 1	red silts above tuff (ignimbrite)		Mammalia	Artiodactyla	Bovidae			
42246	HOR (frag.)	2002	ENK 1	red silts above tuff (ignimbrite)		Mammalia	Artiodactyla	Bovidae			
44748	AST	2003	ENK 1	top of sand conglomerate		Mammalia	Artiodactyla	Bovidae			
44749	IPX	2003	ENK 1	gully bottom at level of brown mudstones		Mammalia	Artiodactyla	Bovidae			
44750	L.m1or2	2003	ENK 1	brown mudstones		Mammalia	Primate	Cercopithecidae	Colobinae		
44751	TIB (prox.)	2003	ENK 1	gully bottom at level of brown mudstones		Mammalia					
44752	TIB (dist.)	2003	ENK 1	gully bottom at level of brown mudstones		Mammalia	Artiodactyla	Bovidae			
44753	L.p3 + m (frag.)	2003	ENK 1	brown mudstones near 44750		Mammalia	Primate	Cercopithecidae	Colobinae		
44754	TPX	2003	ENK 1	brown mudstones		Mammalia	Proboscidae				
44755	MTC (3/4 frag.)	2003	ENK 1	brown mudstones		Mammalia	Carnivora	Felidae			
44756	TIB (dist.)	2003	ENK 1	brown mudstones		Mammalia	Primate	Cercopithecidae			
44757	R.MAN (frag.) w/m1-3	2003	ENK 1	brown mudstones		Mammalia	Artiodactyla	Bovidae			
44758	R.RAD + ULN	2003	ENK 1	brown mudstones		Mammalia	Primate	Cercopithecidae			
44759	IPX	2003	ENK 1	brown mudstones		Mammalia	Artiodactyla	Bovidae			
45789	L.MTT III (prox)	2004	ENK 1	sands interbedded w/mudstones, near top of mudstone horizon		Mammalia	Carnivora	Felidae	Machairodontinae	*Lokotunjailurus*	*emageritas* (aff.)
45827	TIB (prox.)	2004	ENK 1	sands interbedded w/mudstones, near top of mudstone horizon		Mammalia	Carnivora				

Appendix 1. Continued.

Sp no.	Skeletal element and side	Year	Locality	Provenience	n	Class	Order	Family	Subfamily or tribe	Genus	Species
45892	HOR	2004	ENK 1	sands at base of EK, > gray mudstones		Mammalia	Artiodactyla	Bovidae			
45893	L.M	2004	ENK 1	brown mudstones, gulley bottom near 44758		Mammalia	Artiodactyla	Bovidae	Bovini		
45899	PPX	2004	ENK 1	sands > gray mudstones		Mammalia	Artiodactyla	Bovidae			
45894	L.FEM (prox.)	2004	ENK 2	calcified sandstone		Mammalia	Artiodactyla	Suidae (cf.)			
45898	FEM (dist.)	2004	ENK 2	top of calcified sandstone		Mammalia	Carnivora (cf.)				
45895	CAL	2004	ENK 3	gravely gray sands		Mammalia	Carnivora (cf.)				
45896	R. FEM (prox.)	2004	ENK 3	gravely gray sands		Mammalia	Carnivora	Felidae	Machairodontinae	*Lokotunjailurus*	*emageritas* (aff.)
45897	HUM (dist.)	2004	ENK 3	gravely gray sands		Mammalia	Primate	Cercopithecidae			
44739	HOR	2003	KAP 1	gulley bottom		Mammalia	Artiodactyla	Bovidae			
42397	R.m3 + TIB (dist.)	2002	KAS 1	white carbonates		Mammalia	Primate	Cercopithecidae	Colobinae		
42398	MAN (edent. frag.)	2002	KAS 1	white carbonates		Mammalia	Artiodactyla	Bovidae			
42399	M3	2002	KAS 1	white carbonates		Mammalia	Artiodactyla	Bovidae			
42400	MAX (edent. frag.)	2002	KAS 1	white carbonates		Mammalia	Carnivora				
42396	R.m2 (frag.)	2002	LEM 2	yellow sands with basalt cobbles on top, above yellow silts		Mammalia	Proboscidea	Elephantidae			
36591	R.m3	1995	LEM 3	na		Mammalia	Primate	Cercopithecidae	Colobinae		
36592	L.P4	1995	LEM 3	na		Mammalia	Artiodactyla	Bovidae			
36593	L.dP4	1995	LEM 3	na		Mammalia	Primate	Cercopithecidae	Colobinae		
36594	R.M3	1995	LEM 3	na		Mammalia	Primate	Cercopithecidae	Colobinae		
44734	L.MAX (frag.)	2003	MPO 1	reddish sediments < welded tuff		Mammalia	Artiodactyla	Bovidae			
44735	R.m w/alveolar bone	2003	MPO 1	reddish sediments < welded tuff		Mammalia	Artiodactyla	Bovidae			
44736	HUM shaft (frag.)	2003	MPO 1	reddish sediments < welded tuff		Mammalia	Primate	Cercopithecidae			
44737	owl pellet	2003	MPO 1	reddish sediments < welded tuff		Mammalia	Rodentia				
44723	SKU + postcranial elements	2003	OLO 1	red sediments w/carb nod		Mammalia	Carnivora				
44724	L.MAN (frag.)	2003	OLO 1	red sediments w/carb nod		Mammalia	Artiodactyla	Bovidae			
44725	SKU + HOR	2003	OLO 1	red sediments w/carb nod		Mammalia	Artiodactyla	Bovidae			
44726	M	2003	OLO 1	red sediments w/carb nod		Mammalia	Artiodactyla	Bovidae			
44727	M (frag.)	2003	OLO 1	red sediments w/carb nod		Mammalia	Perrissodactyla	Equidae			
44728	SKU	2003	OLO 1	red sediments w/carb nod		Mammalia	Artiodactyla	Bovidae			
44729	ULN (prox.)	2003	OLO 1	red sediments w/carb nod		Mammalia	Primate	Cercopithecidae			
44730	MAX w/P4-M3	2003	OLO 1	red sediments w/carb nod		Mammalia	Artiodactyla	Bovidae			
44731	MAX w/2 ms	2003	OLO 1	red sediments w/carb nod		Mammalia	Artiodactyla	Bovidae			
44732	MAX w/2 ms	2003	OLO 1	red sediments w/carb nod		Mammalia	Artiodactyla	Bovidae			
44733	SKU w/HOR (big)	2003	OLO 1	red sediments w/carb nod		Mammalia	Artiodactyla	Bovidae			
44738	MTP	2003	OLO 1	red sediments w/carb nod		Mammalia	Artiodactyla	Bovidae			
44740	ULN	2003	SIL 1	pink/brown re-worked ash (sediments)		Mammalia	Artiodactyla	Bovidae			
44741	OCX	2003	SIL 1	pink/brown re-worked ash (sediments)		Mammalia	Artiodactyla	Bovidae			

All specimen numbers are preceded by KNM-NK. "Year" denotes year of collection. Locality abbreviations and proveniences are defined in the text. See Appendix 2 for skeletal element key. "n" = horizon at LEM 1 (* = mudstones/claystones, x = underlying sands). "carb nod" = carbonate nodules.

Appendix 2. Skeletal-element key.

Side is indicated by a preceding R. or L.
(frag.)/(frags.) = fragment/fragments
(edent. frag.) = edentulous fragment
assoc. = associated
prox. = proximal
dist. = distal

PHX	phalanx
PPX	proximal phalanx
IPX	intermediate phalanx
TPX	terminal phalanx
MTT	metatarsal (position indicated by roman numeral)
MTC	metacarpal (position indicated by roman numeral)
MTP	metapodial
CRA	cranium
OCC	occipital
TEM	temporal
ZYG	zygomatic
HOR	horn core
MAN	mandible
MAX	maxilla
I/i	incisor (max/man), position indicated by number
C/c	canine (max/man)
P/p	premolar (max/man), position indicated by number
M/m	molar (max/man), position indicated by number
d	denotes a deciduous tooth
VER	vertebra
SCA	scapula
HUM	humerus
RAD	radius
ULN	ulna
OCX	os coxae
FEM	femur
FIB	fibula
TIB	tibia
PAT	patella
TAR	tarsal
CAR	carpal
AST	astragalus
TAL	talus
CAL	calcaneus
NAV	navicular
UNC	unciform
LUN	lunar
CUB	cuboid
CUN	cuneiform
PIS	pisiform
MAG	magnum
SPD	scaphoid
CMC	carpometacarpus
TBT	tibiotarsus
EXT	external cuneiform
SES	sesamoid

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THE PALEOECOLOGY AND PALEOGEOGRAPHIC CONTEXT OF LEMUDONG'O LOCALITY 1, A LATE MIOCENE TERRESTRIAL FOSSIL SITE IN SOUTHERN KENYA

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ABSTRACT

The Lemudong'o Formation in the Narok District of Kenya comprises a 135-m-thick series of predominantly lacustrine and lake basin margin sedimentary rocks with interstratified primary and reworked tuffs. The formation, deposited ~6 Ma, records deposition within the second of three sequential lake basins created by tectonic and volcanic activity on the western margin of the southern Rift Valley of Kenya. These sedimentary paleobasins are exposed in the vicinity of the confluence of three rivers cutting steep cliffs into rugged, vegetated terrain. Over 1200 fossils of terrestrial vertebrates have been recovered from the site of Lemudong'o Locality 1 (LEM 1), which was formed at the edge of a shallow lake fed by slow-moving streams. Much like smaller Rift Valley lake basins in Kenya today, the Lemudong'o lake margin probably supported a mosaic of habitats ranging from closed riparian woodland to grassland and swamps.

There are two fossiliferous horizons at LEM 1, clayey sands and gravels and overlying mudstones. Although the mudstones yielded the majority of the fossil material, there are significant faunal differences between the two horizons. The mudstone assemblage consists of taxa whose modern representatives primarily prefer relatively closed environments such as riparian forests, as well as many species that prefer open woodland to wooded grasslands. The sandstone assemblage samples fauna from a wider range of habitats. This contrast in taxonomic composition suggests that the mudstone and sandstone horizons sample a lakeshore environment that was varying through time. The apparent shift in habitat preferences of the fauna is consistent with the geological and geomorphological evidence for a mosaic of closed to open habitats that characterize rapidly variable rift-valley lake basins in mesic climatic regimes.

One of the salient characteristics of these assemblages is the complete absence of fish, and the paucity of large mammals and reptiles, such as hippos, crocodiles, and larger bovid species that would be expected at the edge of lake basins fed by large rivers. Modern central rift-valley lake basins that are fed by small streams vary widely in size and salinity in response to climate change, and occasionally dry out completely. They do not contain fish and crocodiles, and only one has a substantial hippo population. These modern rift-valley lakes may therefore provide an analog to the depositional environment of Lemudong'o.

The LEM 1 fossil assemblage is also unusual because it is dominated by small mammalian taxa, including numerous rodents, small colobine monkeys, hyracoids, and a diversity of viverrid and other carnivores. Given the lack of evidence for fluvial transport in the main fossil horizon, the biased size composition, and the significant carnivore damage on the bones, we interpret this site to represent an accumulation of carcasses by several avian and small mammalian carnivores. This paleoecological and paleogeographic reconstruction is discussed relative to penecontemporaneous fossil sites in Africa.

Introduction

Lemudong'o Locality 1 (LEM 1) exposes 6 million-year-old sedimentary rocks, volcaniclastic rocks, and primary tuffs deposited within the second of three late Neogene paleolake basins reconstructed by Wright (1967) in the Ewaso Ngiro and Siyabei River valleys (Ambrose, Nyamai et al., 2007; Deino and Ambrose, 2007). Paleoanthropological research has been conducted in this region since 1994 (Ambrose, Kyule, and Hlusko, 2007). Here we provide a reconstruction of the paleoecological and depositional environments in the area of LEM 1 within the Lemudong'o paleolake basin, combining preliminary geological research with more in-depth paleontological studies that are published in detail in this issue of *Kirtlandia* (Bernor, 2007; Boisserie, 2007; Darwent, 2007; Head and Bell, 2007; Hlusko, 2007a and 2007b; Hlusko and Haile-Selassie, 2007; Hlusko et al., 2007; Howell and Garcia, 2007; Manthi, 2007; Pickford and Hlusko, 2007; Saegusa and Hlusko, 2007; Stidham, 2007).

Paleolandscape of the Lemudong'o Formation

The three main types of rift-valley sedimentary basins include large, deep, fresh-water basins (such as Lakes Tanganyika and Malawi), closed basins supplied by very large river systems (such as Lake Turkana) and smaller closed basins (Frostick and Reid, 1990; Tiercelin, 1990). The Lemudong'o basin may have been of the third general rift-basin type, a small half-graben on the western margin of the nascent eastern (Gregory) Rift Valley, which is exemplified by the Baringo and Bogoria basins in the north-central Rift Valley of Kenya. Although a fault named the Naitiami Fault (Wright, 1967; Crossley, 1979) that may have formed such a half-graben is recognized south of this paleobasin, the hypothesized fault scarps that should have bounded this basin have not yet been identified. The Lemudong'o paleobasin lies above the western margin of the Rift Valley, so it may have more closely resembled rift-margin plateau basins such as the modern Amboseli basin or the Olduvai Gorge paleobasin (Hay, 1976).

Although Baringo and Bogoria may provide useful modern analogs for the geology and geomorphology of Lemudong'o, they are located within a comparatively hot and arid segment of the northern/central Kenya Rift Valley. The Naivasha and Nakuru/Elementeita basins in the central Rift Valley of Kenya, where rainfall is higher, may provide more appropriate ecological analogs for the Lemudong'o paleobasin.

Volcanic eruptions and tectonic activity along rift-valley margins often block drainages, forming small lakes with limited catchment areas. Such closed-basin lake levels will fluctuate rapidly in response to variations in rainfall, evaporation, seepage, stream flow, and groundwater recharge. Water loss will primarily result from evaporation, and as such, water quality can change quickly from fresh to saline and/or alkaline in response to short and long term variation in rainfall. Fossil preservation is favored by such rapid sedimentation in closed lake basins (Hay, 1976; Frostick and Reid, 1990; Tiercelin, 1990; Pickford, 1994).

Within the lake-margin zone, where sedimentation is rapid and subaerial exposure of sediments is intermittent, soil horizons will be weakly developed, and easily eradicated by large-mammal trampling and other agents of bioturbation. Such fine-grained sediments are usually classified as claystones and mudstones, similar to those seen in the Lemudong'o Formation, and represent shallow lakes, swamps, or frequently inundated floodplains. Paleosol carbonates are rare in such wet environments, but fossils of terrestrial species may be common. Again, this is similar to what we find at LEM 1 and more widely within the Lemudong'o Formation (Ambrose, Nyamai et al., 2007).

Because such rift-valley lakes can vary rapidly from fresh to highly alkaline, and occasionally dry out completely, fish populations are not able to establish and populations of crocodiles and hippopotamuses are limited. Therefore, the absence of these animals does not always indicate that water was not present, or rather, a lake could well have existed in the area that did not support such aquatic faunal elements.

Transgressive and regressive shorelines are marked by horizons of well-sorted sands and fine gravels. Where ephemeral or seasonal streams flow into a lake, deltaic fans of coarse-grained sands and gravels would be juxtaposed with fine-grained lake silts and clays. Depending on elevation and distance from the permanently inundated basin center, and the frequency of inundation, lake-margin microhabitats may span the continuum from bare sediment and open grass to woodland and dense groundwater-fed riparian forest. Gallery forest and woodlands may also occur where slow-moving streams meander across relatively flat lake-margin zones.

The fauna preserved at LEM 1 suggests that these late Miocene sediments captured such a relatively closed environment. The sedimentology suggests that this environment was associated with an ephemeral rift-valley lake system.

Structural Geology and Sedimentary Environments of the Lemudong'o Formation

Based on the distribution of waterlain sedimentary rocks and volcaniclastic strata, Wright (1967, p. 31) reconstructed the minimum extent of the Lemudong'o paleolake basin, which he called the "first Uaso Ngiro lake," as >16 km from north to south and >8 km from east to west (Figure 1). The south shore of the lake was partly bounded by a prominent hill of erosion-resistant Archaean metamorphic rocks called Ol Doinyo Oborosoit ("hill of white rocks" in the Masai language). The western margin of the lake was bounded by lava flows and sedimentary rocks. The eastern and northern margins are poorly exposed and not well-defined. The Oletugathi Ridge lies east of the Ewaso Ngiro River and parallels the north/south-trending Enkorika Fault. Eroded basalts underlying the Lemudong'o Formation may have formed a line of low hills within the paleobasin during the earliest phases of basin sedimentation.

Horizontal bedding suggests syn- or post-depositional uplift and tilting of the Lemudong'o Formation was insignificant in most of the localities in the center and west side of the paleobasin. However, the elevation of the top of the Lemudong'o Formation is 60–70m lower in the Lemudong'o area. The normal N-S trending Enkorika Fault, a major post-depositional structure, defines the east side of the Lemudong'o Gorge (Wright, 1967), and a smaller E-W trending fault at the north end of LEM 1 may have dropped strata belonging to the youngest paleolake episode (Wright's Siyiapei Lake) to the level of the Lemudong'o Formation. We suspect this block is down-faulted because the east side of the paleobasin lies closest to the modern Rift Valley, and faulting has shifted toward the modern rift axis over time (Birt et al., 1997).

The Lemudong'o Formation is formally named and described elsewhere (Ambrose, Nyamai et al., 2007). The formation is exposed at several localities dispersed over an area of more than 1250 km^2, shown in part in Figure 1. The formation records three main phases of sedimentation in the paleobasin. Phase 1 is represented by a sedimentary sequence dominated by siltstones, mudstones, and sandstones. Phase 2 consists of paleosols in the basin center, and fluvial and alluvial sedimentary rocks on the eastern margin of the basin. Phase 3 comprises mostly waterlain tuffs and siltstones, with a gray ignimbrite welded tuff capping the formation. Thus, the sequence represents a cycle of wetter, drier, and then wetter depositional environments. Vertebrate fossils are most abundant in the upper half of sedimentary phase 1, which is therefore the focus of our discussion.

The Lemudong'o paleolake formed on a deeply eroded and undulating land surface of Neoproterozoic gneiss (Oldoinyo Oborosoit) and early Miocene lavas and ignimbrites, as observed by elevation changes at the basal contact of the late Miocene section. In particular, we note the 65 m of relief observed in the top of the basal gray welded ignimbrite at Enamankeon Locality 2 (ENK 2), and the Oletugathi Ridge, where Lemudong'o Formation exposures lie unconformably on eroded lavas. Although the paleotopography of the Lemudong'o sedimentary basin floor may have been carved in part by streams and rivers, fluvial deposits have not been observed at the base of most of the sedimentary sequences studied. Speculatively, sedimentary depositional rates may have been rapid in the topographic lows

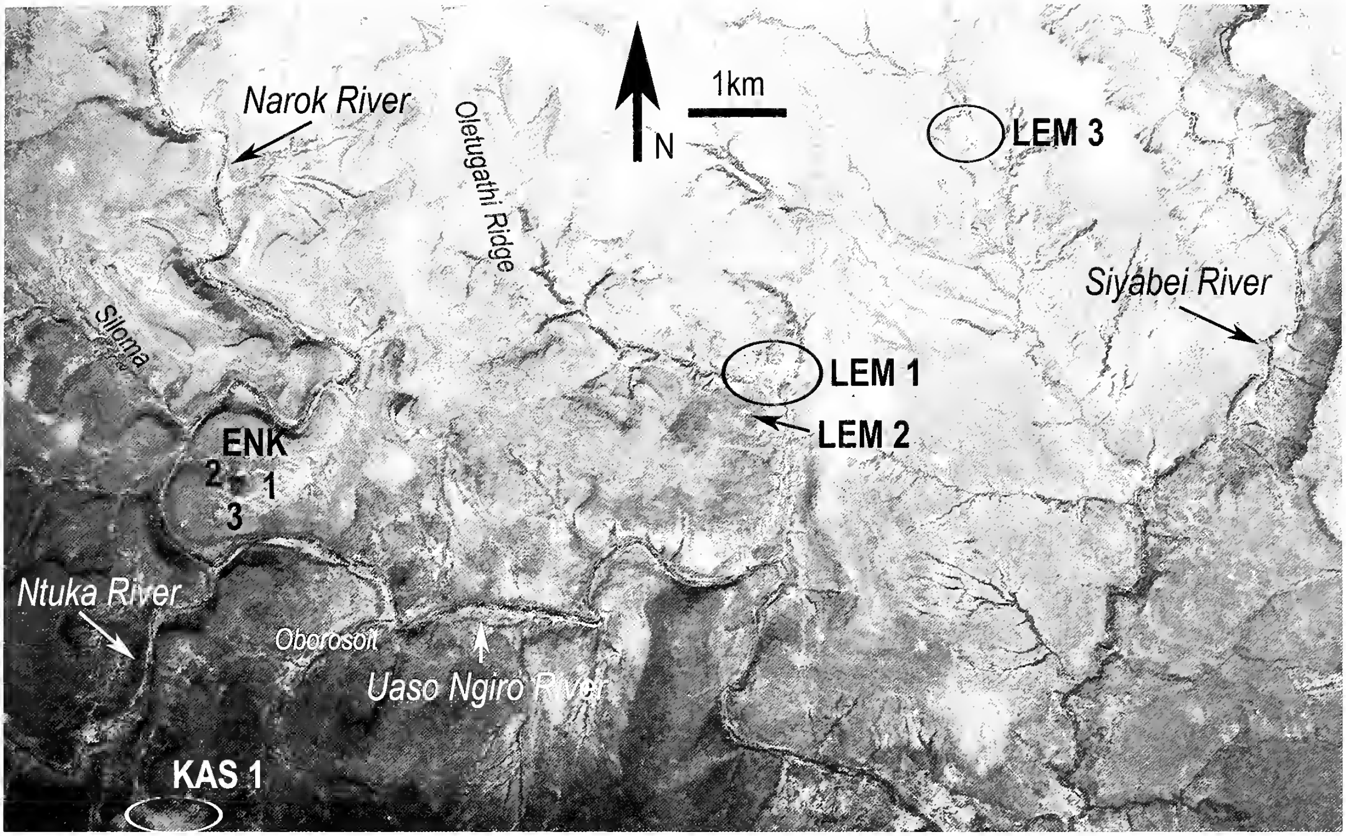

Figure 1. Aerial photograph showing the geography of the correlated late Miocene localities that expose sediments of the Lemudong'o Formation in the Narok District of Kenya. KAS 1 = Kasiolei Locality 1; LEM = Lemudong'o Localities; ENK = Enamankeon Localities. Scale is approximate. Figure is modified from Ambrose, Nyamai et al. (2007).

filled during this period, so despite the substantial thickness of the section (up to 65 m), the phase 1 sedimentation episode may have been brief. This complex paleotopography may have supported a diverse range of semi-aquatic and terrestrial floral microhabitats.

As sedimentation progressed, previously isolated small sedimentary loci such as those at ENK 2 and Kasiolei (KAS 1) may have coalesced into larger basins, forming the more continuously traceable beds of claystones, mudstones, and volcaniclastic units of the later stages of phase 1 accumulation, and the paleosols, alluvium, laminated siltstones, and tuffs of phases 2 and 3 in the upper 70 m of the Lemudong'o Formation.

Depositional Environments of LEM 1

The main fossil horizons at LEM 1 are relatively high in the sequence of phase 1 mudstone deposits (Figure 2). They are comprised predominantly of mudstones and claystones, with thin, discontinuous beds of poorly sorted coarse sandstones. Sediments above the fossil-bearing levels grade into phases 2 and 3 of the wider paleobasin sedimentary sequence.

At LEM 1, deposition begins with mudstones and claystones, representing a lake-margin environment (Figure 2, unit 1). Only the top meter of this bed is exposed in LEM 1. However, at Lemudong'o Locality 2 (LEM 2) it is over 20-m thick, and contains three tuffs dated to 6.09 to 6.12 Ma (Ambrose et al., 2003; Deino and Ambrose, 2007). Yellow laminated lacustrine silts (unit 2), representing deep-water deposits of a larger lake, overlie the basal mudstones. Clayey sands and imbricated, fine, well-sorted sandy gravels, fining upward to mudstones, overlay these lacustrine silts (units 3 and 5). These coarse sediments are fossiliferous sands and comprise the lower of the two fossil-bearing horizons at LEM 1. These sands may reflect a regressive beach shoreline or a small stream delta. The imbricated gravels could also reflect fluvial deposition, but stream-channel features such as cross-bedding and channel margins are lacking. A lens of green, fine-grained tuff within the coarse lower clayey sands (unit 4) may be a channel fill, but the tuff may have filled a small depression in the lake margin.

The overlying fine-grained clayey mudstones (unit 6) contain the majority of the fossils described from LEM 1 (Table 1), and the speckled tuff (unit 7), dated to 6.08 Ma (Deino and Ambrose, 2007). Sediments above the speckled tuff (units 10–13) gradually change from clays and silts to poorly sorted sands, reflecting predominantly alluvial/colluvial deposition, perhaps from a nearby fault scarp or upland. These coarse-grained sediments mark the onset of phase 2 basin-wide sedimentation. The yellow tuff and gray ignimbrite (units 14 and 15), cap the LEM 1 and 2 sequences, marking the last major expansion and termination of phase 3 basin-wide sedimentation of the Lemudong'o Formation lake. Trachyte lava (unit 18) lies

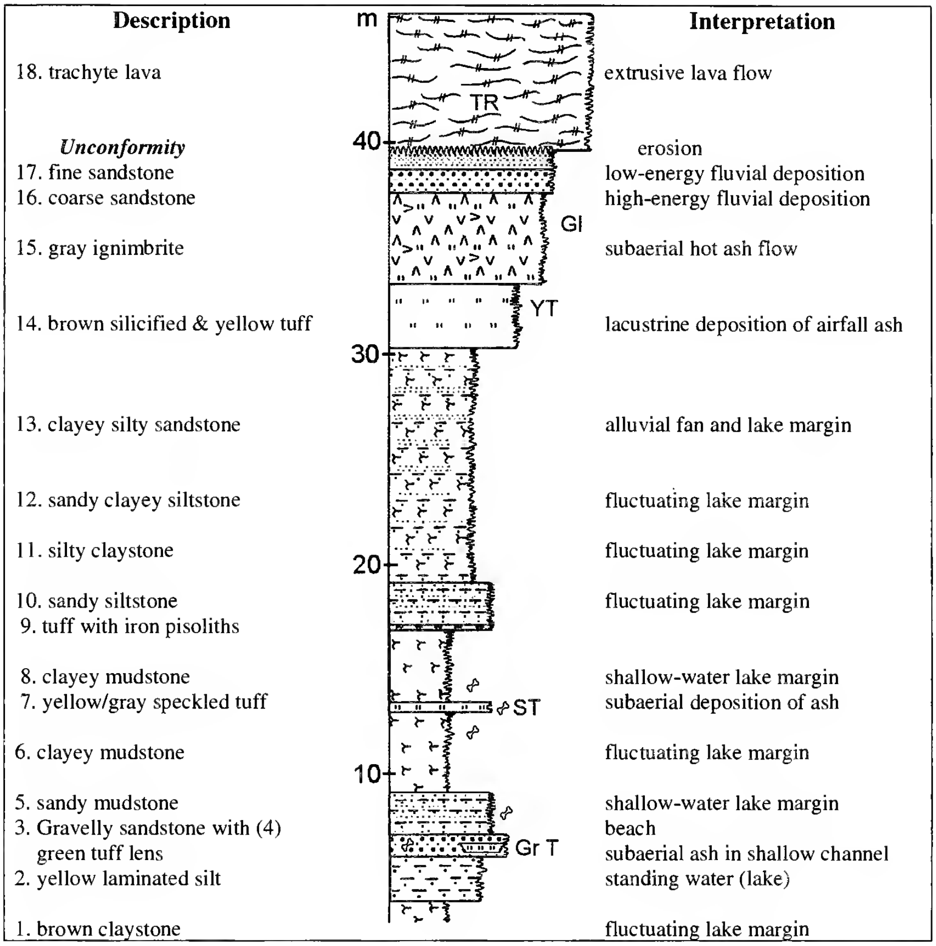

Figure 2. Stratigraphic column for Lemudong'o Locality 1 South (GvJh15) paleontological site, Narok area, southwest Kenya. Locality is at 1°18′1″ S, 35°58′44″ E, at an elevation of 1648 m. Abbreviations: TR, trachyte lava; GI, gray ignimbrite; YT, yellow tuff; ST, speckled tuff; GrT, green tuff.

unconformably (units 16–17) above the gray ignimbrite, which defines the upper boundary of the Lemudong'o Formation in the Lemudong'o Gorge.

Lateral facies variations in depositional subenvironments are pronounced within LEM 1. For example over a horizontal distance of approximately 100 m, the yellow lacustrine silts vary in thickness from two to six meters from east to west. This lacustrine silt bed is prominent and well defined at LEM 1, and it dips 3° east, toward the present Rift Valley, but thins at LEM 2 and thickens again in the lower Lemudong'o Gorge. These laminated silts are exposed only within the Lemudong'o Gorge localities. The beach/delta sands (Figure 2, units 3 and 5) and gravels at LEM 1 vary in thickness from 0.1 to ~2 m along the N/S axis of the gorge, disappearing completely near the northern limits of the outcrop, and thickening rapidly toward the south end of the main collection area. These coarse deposits contain fossils of predominantly large mammals, with more aquatic species, including crocodiles and hippos.

Sediments above and lateral to this beach (Figure 2, units 6–8) grade from clayey and sandy siltstones to claystones (collectively mudstones), reflecting low energy deposition in a swampy, fluctuating lake margin zone. Modern exposed surfaces of the dark gray, green and dark gray-brown claystones form deep cracks when dry, and are mantled by spheroidally weathered rounded peds, typically 1–3 cm in diameter informally referred to as "popcorn clays" (Richard Hay, personal communication, 1995). Dark, drab colors indicate deposition in predominantly wet or frequently inundated anoxic lake-margin environments, and bentonitic ("waxy") clays often indicate alkalinity (Hay, 1976). These silts and clays contain exclusively terrestrial-vertebrate fossils and seeds of the forest tree *Celtis zenkeri* (Ambrose et al., 2003).

Sediments above the speckled tuff coarsen upward from waxy, silty and sandy claystones to poorly sorted silts, sands and fine sandy gravels (units 10–13), most likely reflecting a distal alluvial/colluvial fan depositional environment. These coarse deposits lack fossils. At Enamankeon West (Figure 1 ENK Locality 2) this position in the stratigraphic section contains an ~11-m-thick series of paleosols with vertebrate fossils. This may have been a period of greater aridity, lower vegetation density and higher rates of erosion.

The alluvial sediments at LEM 1 are overlain by poorly exposed claystones and mudstones (uppermost unit 13), reflecting a return to a fluctuating lake-margin environment before lacustrine deposition of the yellow tuff (unit 14). At Enamankeon a thick bed of lacustrine silts beneath the yellow tuff reflects a larger lake, and probably wetter climate during paleobasin sedimentation phase 3. No significant fossils have been observed in phase 3 sediments.

The geological and geomorphological evidence presented above suggests that the main fossil locality of LEM 1 occupies a position on the eastern margin of the Lemudong'o Formation paleobasin. The habitat preferences of the modern counterparts of the tree and vertebrate fossil species suggests that predominantly forest habitats characterized the paleolake margin zone during the main period of fossil accumulation at Lemudong'o. The fossils probably accumulated in riparian gallery forests near the fluctuating margin of the paleolake. The vertebrate fossil evidence is discussed in the following section.

Vertebrate Paleontological Approaches to Paleoenvironmental Reconstruction

Andrews (1996), Bobe and Eck (2001), and Reed (2002) have provided useful reviews of the objectives, methods and limitations of paleoenvironmental reconstruction based primarily on mammalian fossil communities and their modern analogs. Paleoecological reconstructions based on vertebrate faunal assemblages are inherently less accurate and imprecise because of the mobility and wide range of habitat preferences of many species. The ecology and habitat preferences of modern species are usually assumed to be the same as those of fossil representatives of the same species, genera or families. However, their adaptations may have evolved and changed during the Neogene (Solounias and Dawson-Saunders, 1988; Andrews, 1996; Sponheimer et al., 1999). This becomes an important consideration when the fossil assemblages are older and species are less closely related to their extant relatives. Members of extinct lineages, such as sabre-toothed felids and megaherbivores, may have influenced community structure in ways that we can never fully appreciate from studies of modern ecosystems. Moreover, niche shifts in extant lineages may have occurred in response to extinctions of lineages with no modern counterparts, and in response to competition with immigrant species. Therefore modern species cannot be assumed uncritically to be living fossils that can be used as exact analogs for members of ancient faunal communities unless their ecological attributes can be independently demonstrated to be similar by functional morphology, dental microwear and/or stable isotope analyses (Solounias and Dawson-Saunders, 1988; Sponheimer et al., 1999).

Taxon-free methods of environmental reconstruction based on ecomorphological attributes, including body size, locomotor anatomy, substrate preference, and dietary adaptation (Andrews et al., 1979; Kappelman, 1988; Legendre, 1991; Andrews, 1996; Reed, 2002; DeGusta and Vrba, 2003; Haile-Selassie et al., 2004b; DeGusta and Vrba, 2005) may overcome some of the limitations of taxon-based referential models. Multidisciplinary approaches using analog species, ecomorphology, macro- and micropaleontology, geology, geomorphology, and soil and fossil stable isotope geochemistry (Cerling et al., 1997; Williams et al., 1998; Retallack, 2001; Cerling et al., 2003) are therefore the preferred approach for paleoenvironmental reconstructions as they provide crosschecks to individual methods.

Correlation with global climatic records (DeMenocal and Bloemendal, 1995) provides an additional source of evidence for reconstructing environments. However, correlation requires precise and accurate geochronology, and the role of local geological influences must also be considered, especially in tectonically active rift-valley settings (Hill, 1987). Here we summarize the results of

Table 1. Faunal List, Lemudong'o Locality 1 mudstones (NISP = 600).

- Aves
  - Galliformes
    - Phasianidae
  - Falconiformes
    - Acciptridae
  - Strigiformes
    - Strigidae (cf.)
- Mammalia
  - Insectivora
  - Primates
    - Cercopithecidae
      - Colobinae
        - *Paracolobus enkorikae*
        - large species
        - small species
  - Rodentia
    - Hystricidae
      - *Atherurus* sp.
      - *Hystrix* sp.
      - *Xenohystrix* sp.
    - Muridae
      - Gerbillinae
        - *Tatera* sp.
      - Murinae
        - *Acomys* sp.
        - *Aethomys* sp.
        - *Arvicanthis* sp.
        - *Lemniscomys* sp.
        - *Mastomys* sp.
        - *Saidomys* sp.
    - Sciuridae
      - Sciurinae
        - *Paraxerus* sp.
        - *Xerus* sp.
    - Thryonomyidae
      - *Thryonomys* sp.
  - Hyracoidea
    - Procaviidae
      - *Dendrohyrax validus* (cf.)
  - Lagomorpha
    - Leporidae
  - Carnivora
    - Canidae
      - *Eucyon* aff. *intrepidus*
    - Felidae
      - *Leptailurus* sp.
    - Mustelidae
      - *Plesiogulo botori*
    - Procyonidae
      - *Simocyon* sp.
    - Herpestidae
      - *Helogale* sp.
      - *Herpestes* sp.
      - *Ichneumia* aff. *albicauda*
    - Viverridae
      - *Genetta* sp. 'Y'
- Perissodactyla
  - Rhinocerotidae
- Artiodactyla
  - [1]Suidae
  - [2]Hippopotamidae
  - Bovidae
    - Aepycerotini
      - *Aepyceros* aff. *A. premelampus*
    - Boselaphini
    - Neotragini
      - *Madoqua* sp.
    - cf. Tragelaphini
- Reptilia
  - Crocodylia
  - Serpentes
    - Colubroidea
    - Pythoninae

[1] represented by an associated set of deciduous teeth

[2] represented by one fragmentary specimen

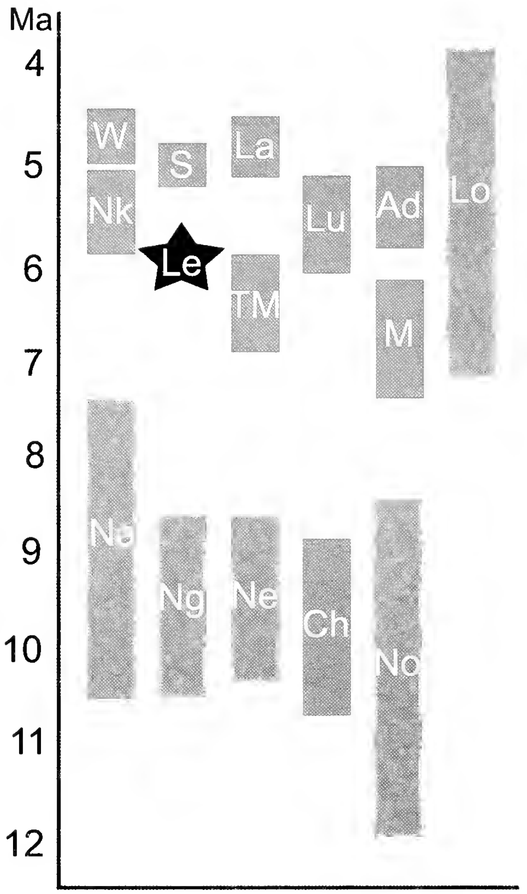

Figure 3. Temporal distribution of African late Miocene and early Pliocene paleontological sites, after Haile-Selassie et al. (2004a). Key: Ad = Adu-Asa; Ch = Chorora; La = Langebaanweg; Le = Lemudong'o; Lo = Lothagam; Lu = Lukeino; M = Mpesida; Na = Nakali; Ne = Namurungule; Ng = Ngeringerowa; Nk = Nkondo; No = Ngorora; S = Sahabi; TM = Toros-Menalla; W = Wembere-Manonga.

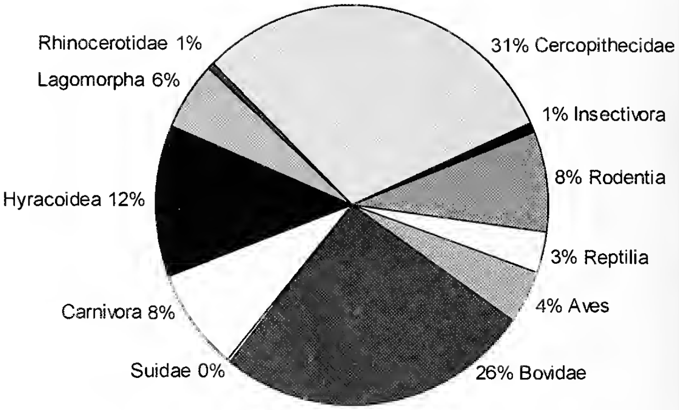

Figure 4. Pie chart of taxonomic representation in the mudstones of LEM 1, based on NISP = 600.

multiple independent studies for reconstructing the local environment of the LEM 1 fauna, using both taxon-based and taxon-free methods.

LEM 1 Vertebrate Fauna

Only terrestrial vertebrate fossils and a few crocodile and hippopotamus teeth were found at LEM 1. Although the assemblage consists primarily of highly fragmentary specimens, given the rarity of mammal-dominated fossil sites of this age, these fossils provide important insights to the evolution of terrestrial animals in the late Miocene of Africa. Figure 3 shows the temporal position of the Lemudong'o Formation relative to other late Miocene to early Pliocene African fossil sites.

The Lemudong'o and other Narok fossils are described in detail elsewhere (Bernor, 2007; Boisserie, 2007; Darwent, 2007; Head and Bell, 2007; Hlusko, 2007a and 2007b; Hlusko and Haile-Selassie, 2007; Hlusko et al., 2007; Howell and Garcia, 2007; Manthi, 2007; Pickford and Hlusko, 2007; Saegusa and Hlusko, 2007; Stidham, 2007). Table 1 lists taxa represented in the mudstone horizon, identified by collection location and/or distinctive preservation (number of identifiable specimens, NISP = 600). Taxonomic proportions are shown in Figure 4. Table 2 lists the fauna from the underlying sandstone (NISP = 21), and Table 3 presents a composite list, including specimens whose provenience to horizon is not certain, as well as those specimens included in Tables 1 and 2 (NISP = 1245). These fossil assemblages derive from strata that lie between tuffs with indistinguishable radiometric ages of 6.084 ± 0.018 and 6.087 ± 0.013 Ma (Deino and Ambrose, 2007), and so were deposited in a short interval of geologic time.

Reptilia

A few crocodylid teeth have been recovered from the sandstone horizon, however the most common reptiles found at LEM 1 are Serpentes. Unfortunately, only serpent vertebral elements were recovered limiting the alpha taxonomy of the material. However, these specimens indicate that Pythoninae and a colubroid snake were present (Head and Bell, 2006). In 2004 we found a partial skull of a Chamaeleonidae (Figure 5).

Aves

LEM 1 has yielded skeletal remains of an eagle, an owl, and possibly a pheasant (Stidham, 2007). The eagle is large, possibly similar to a fish eagle. The owl is approximately the size of *Asio flammeus* and *Strix woodfordi*. Additionally, two specimens are morphologically quite similar to modern pheasants, although this is a tentative designation given the fragmentary nature of the specimens. The avifauna of LEM 1 is predominately terrestrial and similar to Eurasian taxa, as has been noted for other contemporaneous and penecontemporaneous sites (Stidham, 2007). The lack of aquatic birds is relatively unusual, although this may be a result of the small sample size or a lack of fish for them to feed on in the aquatic environment, rather than from the absence of a local water source. The presence of an eagle and an owl most likely suggests proximity to appropriate roosting sites and indicates that carnivorous birds were present in the area, perhaps accounting for some of the bone accumulation.

Insectivora

Five edentulous or fragmentary insectivore mandibles have not yet been described.

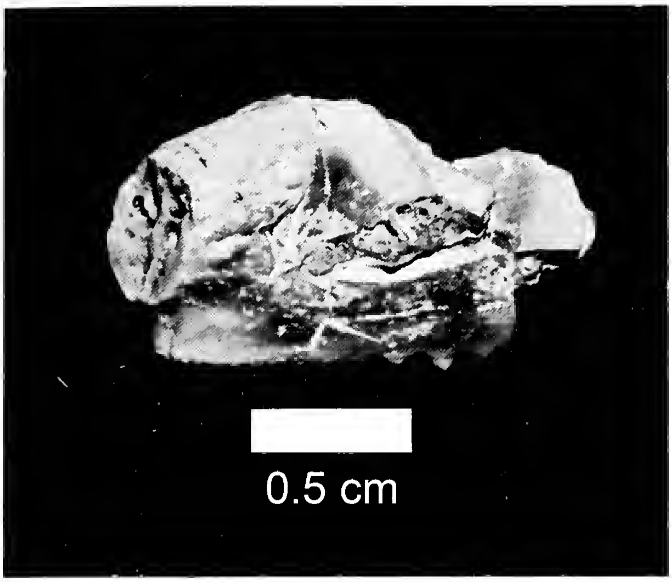

Figure 5. Partial skull of a Chamaeleonidae from Lemudong'o Locality 1 (KNM-NK 45775).

Primates

To date, only cercopithecoid primates have been found at LEM 1. Cercopithecoids comprise a large proportion of the total assemblage (~31% of the mudstone assemblage), sampling at least three taxa. This assemblage is unusual compared to other late Miocene/early Pliocene African sites, except for, perhaps, the Kapsomin site at Lukeino, Kenya (Pickford and Senut, 2001), in that all specimens identifiable to subfamily belong to Colobinae (Hlusko, 2007b). The best represented is a new species *Paracolobus enkorikae* that is much smaller than other known species of *Paracolobus*, approximately 7–8 kg in estimated body weight (based on dental metrics from Hlusko, 2007b, and regressions from Delson et al., 2000). There are a few teeth from a larger colobine (approximately the size of a small *Parapapio*) and several jaws of a much smaller colobine (similar in size to *Prohylobates tandyi*). Associated postcranial elements of *Paracolobus enkorikae* suggest that this colobine was dedicated to an arboreal habitus. Although other contemporaneous sites have yielded colobines (Pickford and Senut, 2001; Vignaud et al., 2002; Leakey and Harris, 2003), they lack the species diversity seen at LEM 1. Slightly younger assemblages in the Middle Awash and Lothagam (Leakey and Harris, 2003; Haile-Selassie et al., 2004b) include a wider range of taxa within the Cercopithecinae.

Rodentia

Ninety-three rodent specimens were recovered from LEM 1. These represent two families of hystricomorphs: Hystricidae (*Atherurus*, *Hystrix*, and *Xenohystrix*) and Thryonomyidae (*Thryonomys*); two families of sciuromorphs: Muridae (Gerbillinae: *Tatera*; and Murinae: *Acomys*, *Aethomys*, *Arvicanthis*, *Lemniscomys*, *Mastomys*, and *Saidomys*), and Sciuridae (*Paraxerus* and *Xerus*) (Hlusko, 2007a; Manthi, 2007). The hystricids, or porcupines, are quite diverse, sampling all three genera known to live or have lived in Africa (Hlusko, 2007a). This is similar to the diversity of hystricids found at the western margin Adu-Asa Formation localities in Ethiopia (Haile-Selassie et al., 2004b), although LEM 1 predates the western margin sediments by at least 200,000 years. The small rodent fauna is quite diverse although the taxa derive primarily from more mesic habitats (Manthi, 2007).

Table 2. Faunal List, Lemudong'o Locality 1 sandstone (NISP = 21).

- Aves
  - Indeterminate
- Mammalia
  - Primates
    - Cercopithecidae
      - Colobinae
  - Rodentia
  - Hyracoidea
  - Carnivora
    - Felidae
      - *Lokotunjailurus emageritus*
    - Hyaenidae
      - *Hyaenictis* aff. *hendeyi*
    - Mustelidae
      - *Plesiogulo botori*
  - Proboscidea
    - Gomphotheriidae
      - *Anancus kenyensis*
  - Perissodactyla
    - Equidae
      - *Eurygnathohippus* cf. *E. feibeli*
  - Artiodactyla
    - Bovidae
      - Aepycerotini
      - Tragelaphini
        - *Tragelaphus*
  - Hippopotamidae
    - Hippopotaminae
  - Suidae
    - *Nyanzachoerus syrticus*
- Reptilia
  - Crocodylia
    - Indeterminate

Lagomorpha

No lagomorph specimens have yet been recovered from the sandstones. Based on known provenience and preservation, all of the lagomorph specimens appear to derive from the mudstones at LEM 1. One maxillary fragment was recovered, which has been tentatively assigned to the genus *Alilepus* within the Leporidae. All of the remaining specimens, primarily postcranial, are also attributed to Leporidae, making this one of the earliest occurrences of leporids in Africa (Darwent, 2007).

Carnivora

The carnivore assemblage is fragmentary but quite diverse (Howell and Garcia, 2007). Seven families are represented: Canidae, Felidae, Herpestidae, Hyaenidae, Mustelidae, Procyonidae, and Viverridae. The specimens from the mudstones are primarily small (Table 1) and include at least two species of *Genetta* within the Viverridae and three genera of Herpestidae. The larger carnivores are typically found in the sandstones, including a mustelid, *Plesiogulo botori*, the type specimen of which comes from LEM 1 (Haile-Selassie et al., 2004a).

Proboscidea

Only one elephantoid specimen has been recovered from LEM 1, a mandibular fragment of *Anancus kenyensis* from the

Table 3. Faunal List, Lemudong'o Locality 1 composite (NISP = 1245).

- Aves
  - Galliformes
    - Phasianidae
      - *Phasianus* (cf.)
  - Falconiformes
    - Acciptridae
  - Strigiformes
    - Strigidae (cf.)
- Mammalia
  - Insectivora
  - Primates
    - Cercopithecidae
      - Colobinae
        - *Paracolobus enkorikae*
        - large species
        - small species
  - Rodentia
    - Hystricidae
      - *Atherurus* sp.
      - *Hystrix* sp.
      - *Xenohystrix* sp.
    - Muridae
      - Gerbillinae
        - *Tatera* sp.
      - Murinae
        - *Acomys* sp.
        - *Aethomys* sp.
        - *Arvicanthis* sp.
        - *Lemniscomys* sp.
        - *Mastomys* sp.
        - *Saidomys* sp.
    - Sciuridae
      - Sciurinae
        - *Paraxerus* sp.
        - *Xerus* sp.
    - Thryonomyidae
      - *Thryonomys* sp.
  - Hyracoidea
    - Procaviidae
      - *Dendrohyrax validus* (cf.)
  - Lagomorpha
    - Leporidae
      - *Alilepus* sp.
  - Carnivora
    - Canidae
      - *Eucyon* aff. *intrepidus*
    - Mustelidae
      - *Plesiogulo botori*
    - Procyonidae
      - *Simocyon* sp.
    - Herpestidae
      - *Helogale* sp.
      - *Herpestes* sp.
      - *Ichneumia* aff. *albicauda*
    - Viverridae
      - *Genetta* sp. 'X'
      - *Genetta* sp. 'Y'
    - Hyaenidae
      - *Hyaenictis* aff. *hendeyi*
    - Felidae
      - *Lokotunjailurus emageritus*
      - *Leptailurus* sp.
      - *Metailurus major*
  - Proboscidea
    - Gomphotheriidae
      - *Anancus kenyensis*
  - Perissodactyla
    - Equidae
      - *Eurygnathohippus* cf. *E. feibeli*
    - Rhinocerotidae

Table 3. continued

  - Artiodactyla
    - Suidae
      - *Nyanzachoerus syrticus*
    - Hippopotamidae
      - Hippopotaminae
    - Bovidae
      - Aepycerotini
        - *Aepyceros* aff. *A. premelampus*
        - cf. *Aepyceros*
      - Boselaphini
      - Neotragini
        - *Madoqua* sp.
      - Tragelaphini
        - *Tragelaphus* sp.
- Reptilia
  - Chelonia
  - Crocodylia
  - Serpentes
    - Colubroidea
    - Pythoninae

sandstone. An unusual mandibular molar that may represent a new elephantid taxon has been recovered from nearby LEM 2 (Saegusa and Hlusko, 2007).

Hyracoidea

A large proportion of the mudstone assemblage is attributable to the Hyracoidea. Specimens identifiable below the superfamily level are small and most similar to the genus *Dendrohyrax*, the extant arboreal tree hyrax (Pickford and Hlusko, 2007).

Perissodactyla

Very few perissodactyl specimens are present in the LEM 1 assemblage. Four very weathered and rolled equid cheek teeth assigned to *Eurygnathohippus* cf. *E. feibeli* were recovered from the sandstone horizon (Bernor, 2007). There are also three isolated rhinocerotid teeth (two upper molars and a premolar), a talus, a metapodial that is similar to but much larger than *Diceros* (S. Cote, personal communication, 2006), and several molar fragments that could not be serially identified (see Ambrose, Kyule, and Hlusko, 2007; Appendix 1). Three of these rhinocerotid specimens were definitely from the mudstones and the others were collected in the first few years before exact horizon was noted for each specimen.

Artiodactyla

The Artiodactyla assemblage consists of fossils attributable to the bovid, hippopotamid and suid families. As with the entire assemblage, these specimens are quite fragmentary, but they indicate the presence of at least four bovid tribes, one species of suid, and a large hippopotamid at LEM 1. Aepycerotini (*Aepyceros* aff. *A. premelampus*), Boselaphini and Neotragini have been recovered from the mudstones, and *Tragelaphus* sp. has been found in the underlying sandstones (Hlusko et al., 2007). Ecomorphological analysis of the bovid astragali and phalanges demonstrate a lack of open habitat forms in the assemblage, indicating that LEM 1 samples forest and/or light cover habitats (DeGusta and Vrba, 2003, 2005; Hlusko et al., 2007). The suid *Nyanzachoerus syrticus* is also represented, but primarily in the sandstone horizon (Hlusko and Haile-Selassie, 2007). Hippopotamid specimens are uncommon at LEM 1 and are usually recovered as only isolated dental fragments from the sandstone horizon (Boisserie, 2007).

Ecology of Extant Related Taxa

Animal habitat preferences are to certain degrees flexible, although some taxa appear to maintain their habitat preferences consistently, even over several million years (Andrews, 1996). Therefore, extrapolations of paleoenvironment can be made by cautiously interpreting extant habitat preferences to extinct members of the same genera, or in some instances, families. Taxa with restricted ecological ranges are more useful in this endeavor than are more catholic taxa. Geraads (1994, p. 222) argues that paleoecological reconstructions are best made by considering only one family, due to taphonomic biases introduced through accumulation and diagenesis. However, all taxonomic levels are affected to different degrees by these processes. Fossil vertebrate assemblages may reflect accumulation by a variety of agents from a mosaic of nearby habitats whose characteristics and proximity can be best assessed by understanding taphonomic effects on all of the recovered fossil taxa, as well as their habitat preferences. Below, we will discuss some of the more relevant and diagnostic taxa that have been recovered from LEM 1.

Although few taxonomic groups provide an irrefutable paleoecological signal, there are trends within a faunal list, as the majority of genera may be suggestive of the same range of local habitats. Habitat preferences discussed below are from Nowak (1991) and Haltenorth and Diller (1980) except where noted. In the case of LEM 1, the strongest local habitat signal is for the presence of gallery forest and woodland trees in the mudstone levels, with woodland and somewhat more open habitats nearby. The lower sandstone fossils accumulated or were redeposited in a proximal lake-shore habitat, and reflect a relatively broader range of habitats. We focus our paleoecological discussion on the dominant mudstone assemblage.

Within the mudstones, several taxa require trees for roosting or nesting, or spend a majority of their time in an arboreal habitus. For example, owls and eagles often require trees in which to roost (Stidham, 2007). Of the reptiles recovered from LEM 1, the partial Chamaeleonidae skull suggests the presence of trees, as almost all extant chameleons are arboreal and found primarily in trees (Vitt et al., 2003, p. 49). The postcrania of *Paracolobus enkorikae*, the medium-sized and dominant colobine monkey, resemble those of extant arboreal colobines (Hlusko, 2007b). Extant *Dendrohyrax* have been described as sharing a niche with colobine monkeys and they shelter in cavities of partially dead trees (Milner and Harris, 1999a, b). *Dendrohyrax arboreus* in South Africa also prefer to shelter in partially rotted trees with multiple cavities (Gaylard and Kerley, 2001). Additionally, extant *Dendrohyrax* spend approximately 90% of their time in trees (Milner and Harris, 1999a, b; Gaylard and Kerley, 2001). Although they are found throughout tropical forests in Africa, the ranges of modern tree hyraxes and colobus monkeys extend into outlier patches of continuous canopy woodlands and riparian forests within mesic savanna environments. Within the rodent fauna, extant *Atherurus*, the brush-tailed porcupine, is only found in forests (Kingdon and Howell, 1993, p. 232), and provides the strongest faunal evidence for a closed forest habitat at LEM 1. The extinct large porcupine *Xenohystrix* has also been interpreted as forest-dwelling (Maguire, 1978, p. 144).

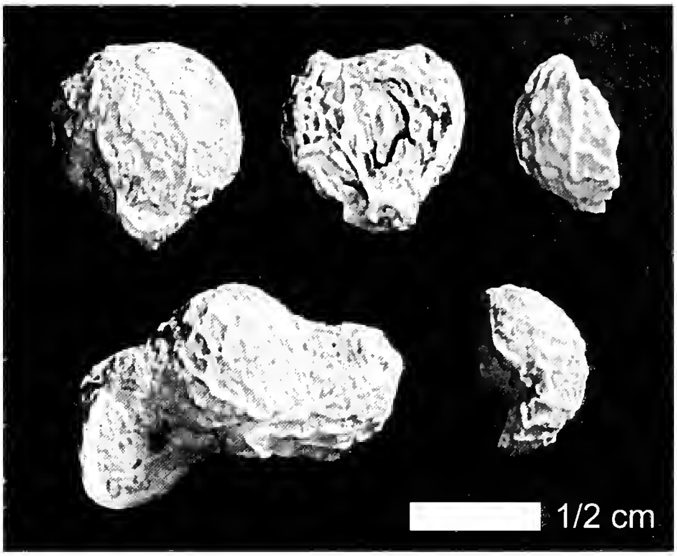

Figure 6. Fossil seeds of *Celtis zenkeri*, from the speckled tuff. Identified by C. Kabuye at the East African Herbarium.

Fossil seeds of *Celtis zenkeri* (Ulmacae) occur in the speckled tuff at Lemudong'o (Figure 6). This tree species is currently found in rain forests at elevations between 250 and 1200 m in equatorial Africa east as far as Tanzania, and western Uganda (Polhill, 1966). It provides strong evidence for a closed canopy woodland or forest during deposition of the mudstones contemporary with the speckled tuff and microfauna breccia (Ambrose et al., 2003; Ambrose, Kyule, and Hlusko, 2007). *Thryonomys* and *Arvicanthis* suggest mesic to wet highland savanna habitats. None of the recovered small rodent specimens represent rainforest endemics.

The LEM 1 bovids are dominated by *Aepyceros* aff. *A. premelampus*, which is a small impala. The preferred habitats of modern impala are grassy woodlands to wooded grasslands near water. Tragelaphine bovids such as the lesser kudu (*Tragelaphus imberbis*) inhabit predominantly arid thicket and scrub as well as gallery forests. Bushbuck (*T. scriptus*) occupies predominantly wetter savanna woodland, bush and forest habitats, often sharing habitats with colobus monkeys and tree hyrax, and is almost always found near water. Sitatunga (*T. spekei*) prefer swampy habitats with tall grass and reeds, forests and gallery forests, and nyala (*T. angasi*) prefer non-swampy thicket, bush, savanna woodland and gallery forest. Small tragelaphines at most late Miocene sites are similar to lesser kudu and nyala in size and may have been similar in their ecological requirements (WoldeGabriel et al., 1994; Pickford and Senut, 2001; Haile-Selassie et al., 2004b). However they could resemble bushbuck or sitatunga in their diet and habitat preferences. Bushbuck and especially sitatunga-like tragelaphines would provide stronger evidence for closed tropical forests in the late Miocene. Carbon and oxygen-isotope analysis of their tooth enamel and limb-bone ecomorphological analysis could help resolve this question. Dik-dik (*Madoqua*), which are present at LEM 1, inhabit a wide range of dry bush to mesic woodland habitats.

An ecomorphological analysis of the bovid astragali and phalanges is consistent with the species-based habitat reconstruction. The results clearly indicate that open habitat forms are not represented in this assemblage, and suggest the presence of forest and/or light cover (Hlusko et al., 2007).

However, the mudstone assemblage does contain some taxa that are indicative of relatively more open habitats. Several taxa, including *Tatera* (gerbils), *Aethomys*, *Arvicanthis*, *Xerus* (African ground squirrel), *Thryonomys* (cane rats), leporids, and aepycerotine bovids, indicate more open environments such as grassy woodlands, wooded grassland savanna and dry bush. *Tatera* prefers dry sandy soil for its burrows. The dry-habitat taxa *Acomys* and *Madoqua* both rely on brush for concealment but do not require access to a permanent source of water. Although *Eurygnathohippus* is an extinct equid lineage, its cursorial limb morphology indicates open habitat preferences, and its mesowear suggests a grazing adaptation (Bernor, 2007). The rarity and poor preservation of this hipparionine in the LEM 1 assemblage suggests that such open habitats were relatively far from the paleolake margin zone.

Several taxa from the mudstone assemblage are less habitat specific. The African bush squirrel genus *Paraxerus* includes a diverse range of species, only one of which is restricted to moist tropical forests. Modern viverrid carnivores are equally diverse, and occupy a spectrum of wet forests to dry bush habitats, so their catholic habitat preferences render them less informative for habitat reconstruction. Extant suids occur in a wide range of habitats including dense rainforest, swamps, gallery forest savanna woodlands, thickets and bush near water, but not in open grasslands. Carbon isotope analysis of *Nyanzachoerus syrticus* from Lothagam shows it consumed a substantial amount of C_4 grasses (Harris and Cerling, 2002; Cerling et al., 2003).

Taphonomy of LEM 1

As described above and in detail elsewhere (Ambrose, Nyami et al., 2007), there are two fossil horizons at LEM 1: 1) an upper mudstone and bioturbated tuff (the speckled tuff), and 2) underlying sandstone. The fossils from the sandstone horizon are typically rolled and abraded, and enamel is often manganese-stained. The number of identifiable specimens is small compared to the mudstones, comprising only ~3% of the total LEM 1 assemblage. Most of the fossils from LEM 1 derive from the upper mudstone horizon (~97%). These fossils demonstrate no evidence of fluvial transport, and sedimentation appears to have occurred in a frequently inundated distal lake margin zone. The high clay content of the mudstones causes extensive shrinking and swelling of the sedimentary matrix within and encasing the fossils, and results in intense fragmentation of the fossils during erosion. We focus our paleoecological discussion primarily on this upper horizon since fossils from the mudstones dominate the assemblage. However, it is important to keep in mind that there are two sedimentary facies that represent different time periods of the same lake-basin system, although radiometric dating indicates these layers were probably deposited closely in time.

A remarkable characteristic of the LEM 1 mudstone faunal assemblage is the rarity of large animals in comparison to other fossil assemblages such as Lothagam (Leakey and Harris, 2003). Most of the larger and more durable specimens recovered, such as the *Anancus* mandible and *Nyanzachoerus* molars, derive from the sandstone. As such, many of the large animals often found in lakeshore habitats, such as hippopotamids and crocodylids, are quite rare in this assemblage. This skewed representation and the high frequency of small animals that are usually biased against during deposition and diagenesis suggests that the assemblage may not fully sample one local habitat or ecology, or it may indicate the absence of these large aquatic terrestrial vertebrates during the time of mudstone deposition.

The largely unweathered and unpatinated surfaces of the majority of bones from the mudstone horizon indicate rapid burial. The primary taphonomic agents for accumulation and modification of the relatively larger taxa in the mudstone assemblage are likely to be mainly small- and medium-sized mammalian carnivores. They have left high frequencies of gnawing, crushing and puncture marks on the bones, such as is shown in Figure 7. Additionally, it is likely that raptorial birds also contributed to the bone accumulation, especially that of the rodents (Manthi, 2007). The breakage patterns and skeletal elements of the relatively larger mammals are not characteristic of modern raptorial-bird bone assemblages (Stewart et al., 1999; Sanders et al., 2003; McGraw et al., 2006; Trapani et al., 2006).

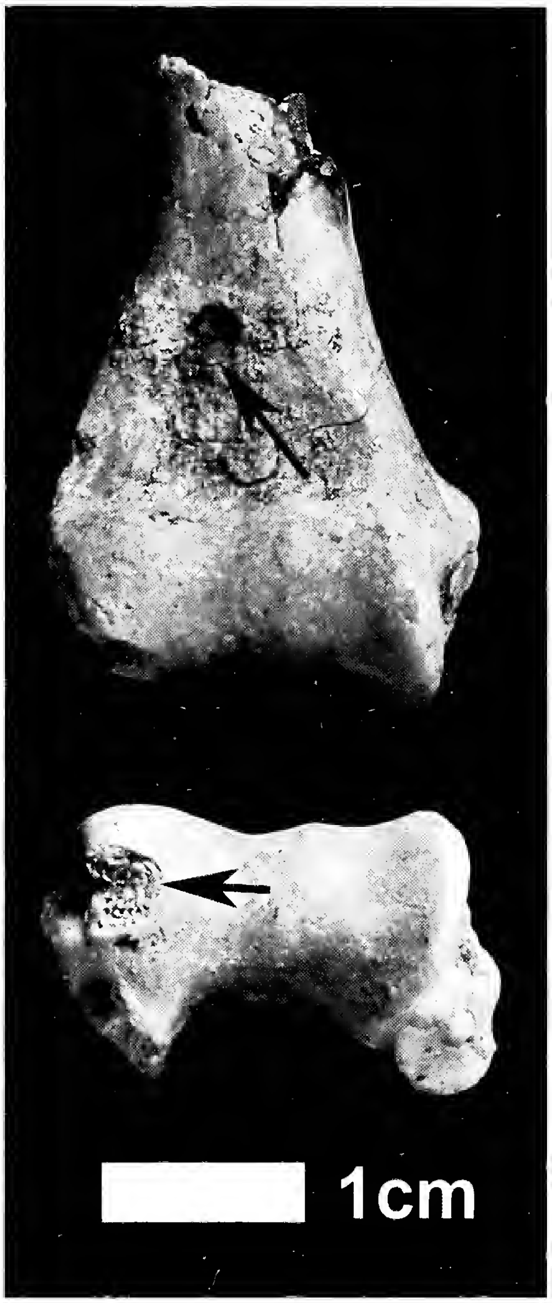

Figure 7. Representative carnivore damage at LEM 1. KNM-NM 41169, cercopithecoid distal humerus with arrows indicating carnivore-tooth puncture marks.

Comparison to Penecontemporaneous Mio-Pliocene Sites

The paleoecology of LEM 1 can be compared with a number of penecontemporaneous late Miocene sites in eastern Africa (Figure 3), including the Nawata Formation of Lothagam (Leakey et al., 1996; Leakey and Harris, 2003), the Lukeino Formation of the Tugen Hills (Pickford and Senut, 2001), the Adu-Asa Formation of the western margin of the Middle Awash Valley (Haile-Selassie et al., 2004b), and Toros-Menalla in Chad (Vignaud et al., 2002), all of which contain the biochronologically diagnostic suid *Nyanzachoerus syrticus* (*tulotos*). However, comparisons to these sites are hindered by the differences in sample sizes between sites, and the taphonomic bias toward small body sizes at LEM 1.

The geomorphological setting of Toros-Menalla 266 is the margin of a fluctuating lake surrounded by a sandy desert. The strata are described as having an aeolian/lacustrine origin, reflecting the deposition and reworking of wind-blown desert sands that were deposited directly into paleolake Chad (Vignaud et al., 2002). The closest modern analog for such a depositional setting may be the Okavango delta in Botswana or modern Lake Chad. Despite the unusual depositional setting, the mammalian faunal assemblage has some overlap with that of LEM 1. Notable differences from LEM 1 include the presence of hominids, giraffids, reduncines, hippotragines, and antilopines, the absence of tragelaphines, and the abundance of crocodylids, fish, turtles, and semi-aquatic large artiodactyls (hippos and anthracotheres are approximately 25% of the fauna). There are very few colobines at TM266, but they may reflect a riparian forest context for the hominid *Sahelanthropus tchadensis* (Vignaud et al., 2002). Although the high-crowned bovids and other species suggest a mosaic of environments including gallery forest, woodland and grassland, and the fish fauna indicates a large and stable fresh-water lake, the overall terrestrial setting is likely to have been more open and drier than at LEM 1.

The Nawata Formation assemblage of Lothagam also contains numerous shellfish, fish, turtle, and crocodile species, reflecting a large, slow-moving river, and the terrestrial-mammal fauna suggests a mosaic of riverine gallery forest, woodlands, and grasslands (Leakey et al., 1996; Leakey and Harris, 2003). The overall paleoenvironmental setting of Lothagam is also apparently somewhat drier than LEM 1 and hominids are absent from the late Miocene Nawata Formation. Compared to Lemudong'o, many large-bodied species and larger and more complete skeletal elements and skeletons were recovered from Lothagam.

Lukeino has perhaps the greatest geomorphological and ecological similarity to LEM 1. The geomorphic setting was a small rift-lake sedimentary basin, but at Lukeino the fossils seem to have accumulated mainly in a shallow lake margin at the base of a lava scarp or cliff (Pickford and Senut, 2001). The fauna associated with the hominid *Ororrin tugenensis* includes a diversity of fish, crocodiles, and turtles, indicating a more stable permanent lake than at LEM 1. The presence of several colobine species, an aepycerotine, tragelaphines, reduncines, hipparions, *Nyanzachoerus*, and giraffids suggest a mosaic of environments that included gallery forest woodland and open grassy woodland (Pickford and Senut, 2001). The most notable difference between Lukeino and LEM 1 appears to be related to taphonomic biases: More skeletal elements of a variety of large species have been recovered at Lukeino.

The Adu-Asa formation of the Middle Awash Valley also samples a faulted rift-margin lake-basin setting as well as riverine fluvial depositional environments, as do LEM 1 and Lukeino (Haile-Selassie et al., 2004b). The Adu-Asa faunal assemblage has many taxa in common with LEM 1, but contains a more diverse artiodactyl community including reduncines, giraffids and several suid species. Additionally, though paleoecologically less revealing, the Adu-Asa Formation localities have also yielded remains of the hominid *Ardipithecus kadabba*, whereas no hominid has yet been recovered from LEM 1.

Implications of the Lemudong'o Paleobasin for Hominid Evolution

One of the primary foci for research in the late Miocene of Africa is to better understand the earliest ancestors of humans, the Hominidae (Hendey, 1976, 1983; Boaz et al., 1987; Hill, 1995; Harrison, 1997; Andrews and Banham, 1999; Pickford and Senut, 2001; Vignaud et al., 2002; Leakey and Harris, 2003; Haile-Selassie et al., 2004b; for taxonomy see White, 2002). As such, no paleoecological reconstruction from this time period is complete without a consideration of its implications for hominid evolution. Although hominid remains have not yet been recovered from LEM 1, our understanding of the paleoecology and paleolandscape of this area provides some insight to early hominid evolution. Understanding the environments that were not habitually occupied by our earliest hominid ancestors may provide insights into the nature of their habitat preferences and adaptations.

Late Miocene and early Pliocene hominids from several localities seem to have occupied wetter, more closed, forest and woodland portions of the mosaic of habitats available (WoldeGabriel et al., 1994; Pickford and Senut, 2001; Haile-Selassie et al., 2004b; Pickford et al., 2004). If further research confirms our interpretation of LEM 1 as close to the shoreline of a lake fed by slow-moving streams, then perhaps the absence of hominid remains indicates that hominids were not regularly spending a considerable amount of time in the wooded habitats at lake margins.

The absence of evidence, of course, is not evidence of absence. Moreover, this assemblage from LEM 1 appears to have resulted primarily from the accumulation of carcasses by carnivorous birds and/or mammals. This site has yielded very few bones of animals that were as large as late Miocene hominids. Therefore, the lack of hominids at LEM 1 may also result from taphonomic biases rather than, or, perhaps, in addition to habitat preferences of our earliest ancestors. If additional research in this paleobasin eventually produces hominid fossils, it will further support the hypothesis of a more forested habitat preference for the earliest bipedal hominids (Boesch-Achermann and Boesch, 1994; WoldeGabriel et al., 1994; Pickford et al., 2004).

Conclusions

The paleoecology of LEM 1 reflects a local environment of permanent gallery-forest near the fluctuating margin of a shallow lake in a small tectonically formed rift-valley basin. More open woodland to wooded grasslands occurred nearby. Its spectrum of terrestrial habitats resembles that of several penecontemporary fossil sites from the late Miocene of the Gregory Rift Valley in eastern Africa, including the Lukeino Formation in the Baringo Basin of northern Kenya, and the western margin of the Middle Awash Valley, Ethiopia. LEM 1 bears less similarity to other equatorial sites adjacent to large lakes and rivers that contain more arid-adapted terrestrial faunas and diverse aquatic faunas, such as Toros-Menalla in the Lake Chad paleobasin, the Nawata Formation of Lothagam in the Turkana basin, and the Manonga Valley paleobasin in Tanzania. Post-depositional taphonomic effects of the high-energy beach depositional environment may account for the bias toward larger species in the lower sandstone. The bias toward smaller species in the upper mudstones may reflect the predominantly small prey sizes brought to this forested location by avian and small mammalian carnivores.

The broader paleoecological context of Lemudong'o can be viewed from the perspective of global paleoclimatic records. The Lemudong'o Formation sedimentary sequence includes early and late phases of predominantly lacustrine and peri-lacustrine deposition, reflecting wetter environments and climates. The middle phase of sedimentation apparently reflects a long period of drier climate. This is consistent with the fluctuating, often arid climates of the terminal Miocene Messinian period, 5–7 Ma, when large quantities of terriginous dust were blown from Africa into the oceans (DeMenocal and Bloemendal, 1995), and water stress-adapted C_4 grasslands expanded globally throughout the tropics (Cerling et al., 1997). Messinian climate changes may have played an important role in the paleobiogeography of Africa, promoting forest and savanna expansions and contractions, speciations, extinctions, and faunal interchanges between northern and southern savannas and between Africa, Arabia and Eurasia (Brain, 1981; Laporte and Zihlman, 1983; Vrba, 1987, 1988; Pickford, 2004). The unexplored paleolake basins in Narok that precede and follow the Lemudong'o Formation paleolake may make important contributions to understanding the local expressions of these global climate changes and for testing hypotheses about the evolution of various terrestrial vertebrates, including hominids.

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GEOLOGY, GEOCHEMISTRY, AND STRATIGRAPHY OF THE LEMUDONG'O FORMATION, KENYA RIFT VALLEY

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ABSTRACT

The Lemudong'o Formation is defined here as part of a late Miocene to Late Pleistocene sequence of stratified lavas, air-fall and waterlain tuffs, lacustrine, alluvial, and fluvial sediments, and paleosols, that crop out over an approximately 25 × 50 km area on the western margin of the southern Kenyan Rift Valley, approximately 100 km west of Nairobi. The study area is deeply incised by three major permanent river systems that expose sediments of three late Neogene lake basins. The Lemudong'o Formation comprises deposits of the second paleolake basin, which formed during the late Miocene. Stratigraphic sections in several localities are described and correlated in this report, the Lemudong'o Formation is defined, and a basin sedimentary history and environmental reconstruction is proposed.

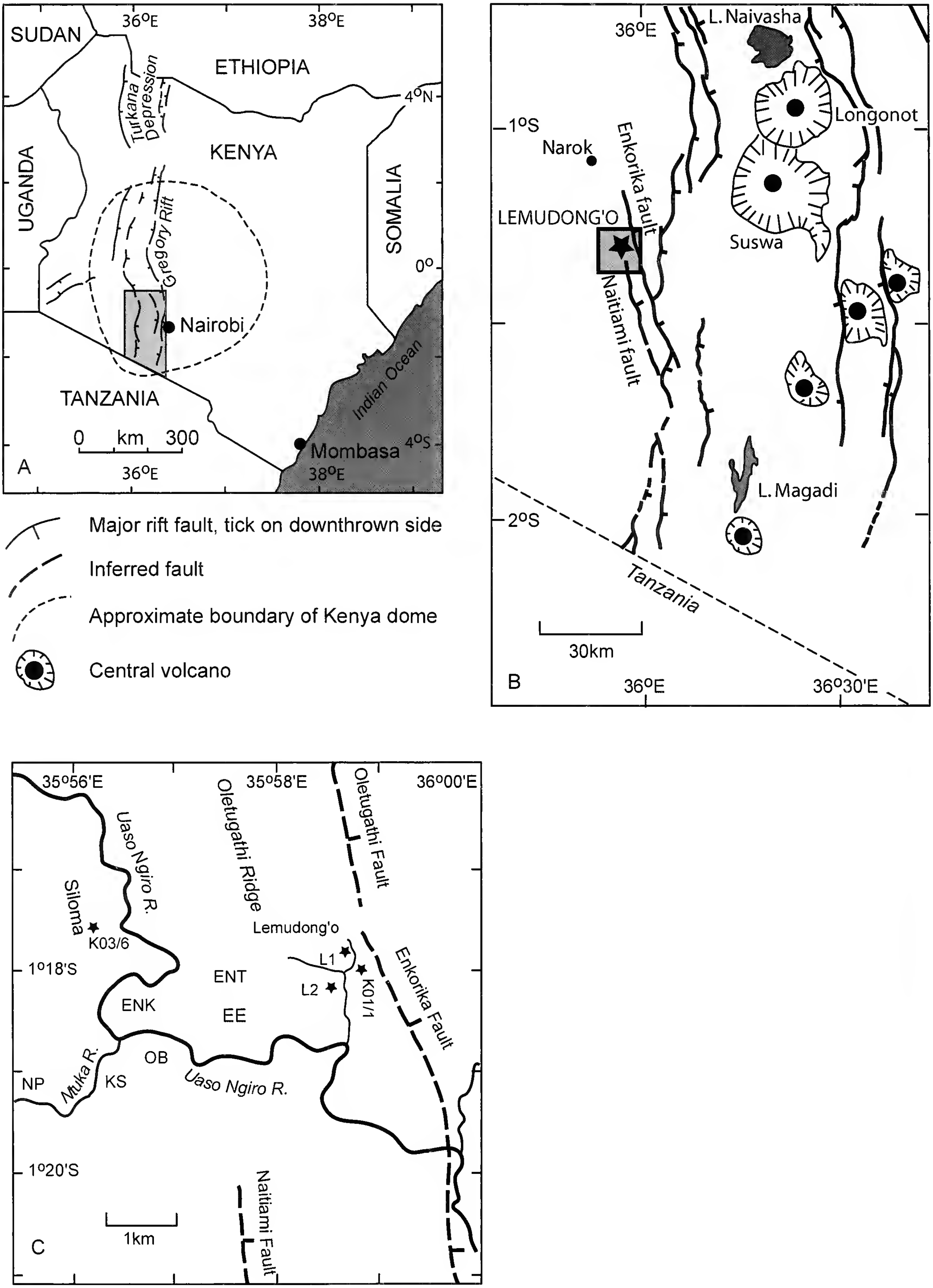
The Lemudong'o Formation has three main phases of sedimentation with a total thickness of 135 m. Phase 1 is represented by predominantly lacustrine and lake-margin siltstones, mudstones, and sandstones. Phase 2 comprises paleosols in the basin center, and fluvial and alluvial sediments on the eastern basin margin. Phase 3 comprises mainly waterlain tuffs and silts, capped by a welded tuff. Phase 2 may reflect a more arid climate, or a lower basin-overflow elevation.

Four tuffs in upper phase-1 mudstones in Lemudong'o Gorge are dated to 6.12–6.08 Ma. The main fossil-bearing horizons at Lemudong'o Gorge Locality 1 lie between, and immediately above, the dated tuffs. Fossils are associated with beach and/or deltaic sands and fine gravels, and silty and sandy claystones representative of an intermittently flooded lake margin.

Introduction

The Lemudong'o Formation is located in the South Narok District of Kenya, approximately 30 km south of Narok town and 100 km west of Nairobi (Figure 1). The regional geological sequence is exposed over an approximately 25 × 50 km area west of the western margin of the southern Kenyan Rift Valley in the confluences and lower reaches of the Uaso Ngiro, Ntuka, and Seyabei river valleys and their seasonal tributaries. The outcrops are characterized by thick sequences of stratified lavas, air-fall and waterlain tuffs, ignimbrites (welded tuffs), and alluvial, fluviolacustrine sediments and paleosols of late Miocene to Late Pleistocene age.

The geology of this region was first described and mapped by J. B.Wright (1967) for the Geological Survey of Kenya. He reconstructed a stratified sequence of three major ancient lake-basins and two smaller isolated lake basins that he thought were formed during the Pliocene and early Pleistocene. The major objective of this report is to describe the stratigraphic sequence of Wright's second paleolake. In this study we refer to deposits of this lake as the Lemudong'o Formation, after Lemudong'o


SUDAN
36°E
38°E
ETHIOPIA
Turkana Depression
4°N
KENYA
UGANDA
SOMALIA
Gregory Rift
0°
Nairobi
TANZANIA
Indian Ocean
0 km 300
Mombasa
4°S
38°E
36°E
A
Major rift fault, tick on downthrown side
Inferred fault
Approximate boundary of Kenya dome
Central volcano
L. Naivasha
36°E
1°S
Narok
Enkorika fault
Longonot
LEMUDONG'O
Suswa
Naitiami fault
L. Magadi
2°S
Tanzania
30km
B
36°E
36°30'E
35°56'E
35°58'E
36°00'E
Oletugathi Ridge
Oletugathi Fault
Uaso Ngiro R.
Siloma
K03/6
Lemudong'o
L1
L2
K01/1
1°18'S
ENT
ENK
EE
Enkorika Fault
OB
NP
Muka R.
KS
Uaso Ngiro R.
1°20'S
1km
C
Naitiami Fault

Gorge, the location of a major fossil site. Masai place names are used for all localities. We will briefly summarize previous geological research and regional and local geology, describe the key stratigraphic sections, define the Lemudong'o Formation, and present a provisional reconstruction of its sedimentary history.

Wright (1967) conducted detailed geological work in the area covered by latitude 1° 00′ S to 1° 30′ S and longitude 35° 30′ E to 36° 00′ E. Crossley (1979) described the stratigraphy, structure and geochronology of the western margin of the rift from 1° 30′ S to 2° 0′ S. Waibel and McDonough (1977) conducted a brief survey of archaeological and paleontological sites in the Ntuka River valley for the University of Massachusetts archaeological research project in 1976. Archeological surveys and excavations in the study area by the University of Illinois team (Kyule et al., 1997; Ambrose et al., 2000, 2003; Hlusko et al., 2002) have identified over 100 new archeological sites and several paleontological occurrences since 1994. University of Illinois team members made numerous brief visits to Lemudong'o from 1994 to 2006. Leslea Hlusko directed intensive paleontological work at Lemudong'o Locality 1 and other sites from 2001 to 2004 (Ambrose, Kyule, and Hlusko, 2007). Deino and Ambrose collected tuffs for dating at Lemudong'o 1 and 2 in 2001. Williams measured and described stratigraphic section at Ol Doinyo Siloma and Lemudong'o in 2001 and 2003, and Ambrose and Williams described two excavated stratigraphic sections of the lower fossil-bearing horizons at Lemudong'o 1. Ambrose, Mathu and Nyamai measured sections at Lemudong'o Gorge, Enamankeon and Kasiolei, and collected samples for petrographic and geochemical analyses during three brief field seasons in 2004–05.

Geological Setting

Regional geology

The Lemudong'o Formation lies on the western shoulder of the Gregory Rift Valley in southern Kenya. The southern section of the rift is superimposed on an uplifted region known as the Kenya Dome (Figure 1A). Prior to the upwarping of the Dome, the region was a peneplaned surface of Precambrian rocks (Mathu and Davies, 1996, p. 522). During the early Miocene, before 15 to 12 Ma, the margins of the future rift began to warp downwards. Faulting of the western margin of the rift, forming a half-graben, commenced during the late Miocene prior to 6.9 Ma (Crossley, 1979). The focus of faulting gradually shifted east towards the rift axis, and recent faulting has been concentrated within an axial zone less than 10-km wide (King, 1978; Shackleton, 1978; Birt et al., 1997).

Volcanism on the west side of the nascent southern Kenya rift began around 15 to 12 Ma with eruption of extensive melanephelinite lavas (Crossley, 1979). By 6.9 Ma more silicic lavas such as trachytes flooded the rift floor and overflowed onto its flanks. During the past 2 Ma volcanism has largely been confined to the rift floor, including a chain of silicic caldera volcanoes including Suswa and Longonot (Figure 1B) (Baker et al., 1972; Williams, 1972; Baker, 1986; Macdonald et al., 1994).

Local geology

The Lemudong'o Formation lies ~40 km east of the western margin of the rift, and 15–20 km west of the N/S-trending late Precambrian Basement System metamorphic rocks of the Loita Hills. Stratigraphic sections described in this report are located in the middle of the eastern margin of the area studied by Wright (1967) from 1° 15′ S to 1° 20′ S, and 35° 55′ E to 36° 0′ E (Figure 1C, Figure 2). The geology here is dominated by Neogene volcanics and sediments of the rift system, with a few exposures of the underlying metamorphic rocks of the Neoproterozoic Mozambique Belt (Figure 3). Photographs of the type-section areas of Enamankeon and Lemudong'o Locality 1 are shown in Figures 4 and 5.

Basal Neoproterozoic Mozambique Belt metamorphic rocks comprising gneisses, schists and quartzites, are exposed at an isolated inselberg named Ol Doinyo Oborosoit (hill of white rock) on the south side of the Ewaso Ngiro River near Kasiolei; a small quartzite outlier extends north of the Ewaso Ngiro River below Emowuo Enkijape. The overlying beds comprise Neogene volcanics and sediments. Earlier Neogene volcanic rocks include melanephelinite and olivine melanephelinite lavas, phonolites, basalts, alkali basalts, and trachytic ignimbrites and trachytes (Wright, 1967). Later Neogene beds include mudstones, siltstones and sandstones, tuffs, and sediments that are in part lacustrine, welded tuffs, trachyte lavas, paleosols (fossil soils), boulder beds, and Uaso Ngiro pebble beds (Figure 3).

The folded metamorphic rocks of Ol Doinyo Oborosoit are resistant to erosion and would have formed an area of high relief during deposition of the Lemudong'o Formation. The Enkorika and Naitiami faults (Figure 1C) are oriented NNW-SSE and are downthrown to the east. The Oletugathi Ridge parallels these faults on the east side of the Ewaso Ngiro River. The Siyabei River valley defines the east side of this ridge. Faulting controls drainage patterns in this region, particularly the trends of some sections of the Uaso Ngiro and Ntuka rivers and their tributaries. Beds of the Lemudong'o Formation are generally horizontal in the center and west side of their distribution area, with occasional tilting near minor faults. However, the elevation of the top of the Lemudong'o Formation decreases by ~70 m between Kasiolei and Lemudong'o, suggesting downwarping, undetected faults and/or subsidence to the east, toward the modern rift valley. The Enkorika fault forms a pronounced, deep, straight gully exposing the main sedimentary sequence at Lemudong'o Gorge. At

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Figure 1. Location of Lemudong'o in relation to major structural features of the Kenya (Gregory) Rift Valley. A, location of the Kenya Dome and the Gregory Rift Valley, adapted from fig. 7 in Mathu and Davies (1996). The shaded trapezoidal area in map A shows the location of map B. B, major faults and volcanic centers in the southern Gregory Rift Valley, adapted from fig. 5 in Baker (1986). The shaded rectangle in map B indicates the area of the map C, which shows the location of sections in relation to major geological and geographic features. Key to map C: L1, Lemudong'o Locality 1; L2, Lemudong'o Locality 2; K01/1, Lemudong'o 1-S step trench 1; K03/6, Ol Doinyo Siloma section; ENK, Enamankeon; KS, Kasiolei; OB, Ol Doinyo Oborosoit; ENT, Entapot; EE, Emowuo Enkijape.

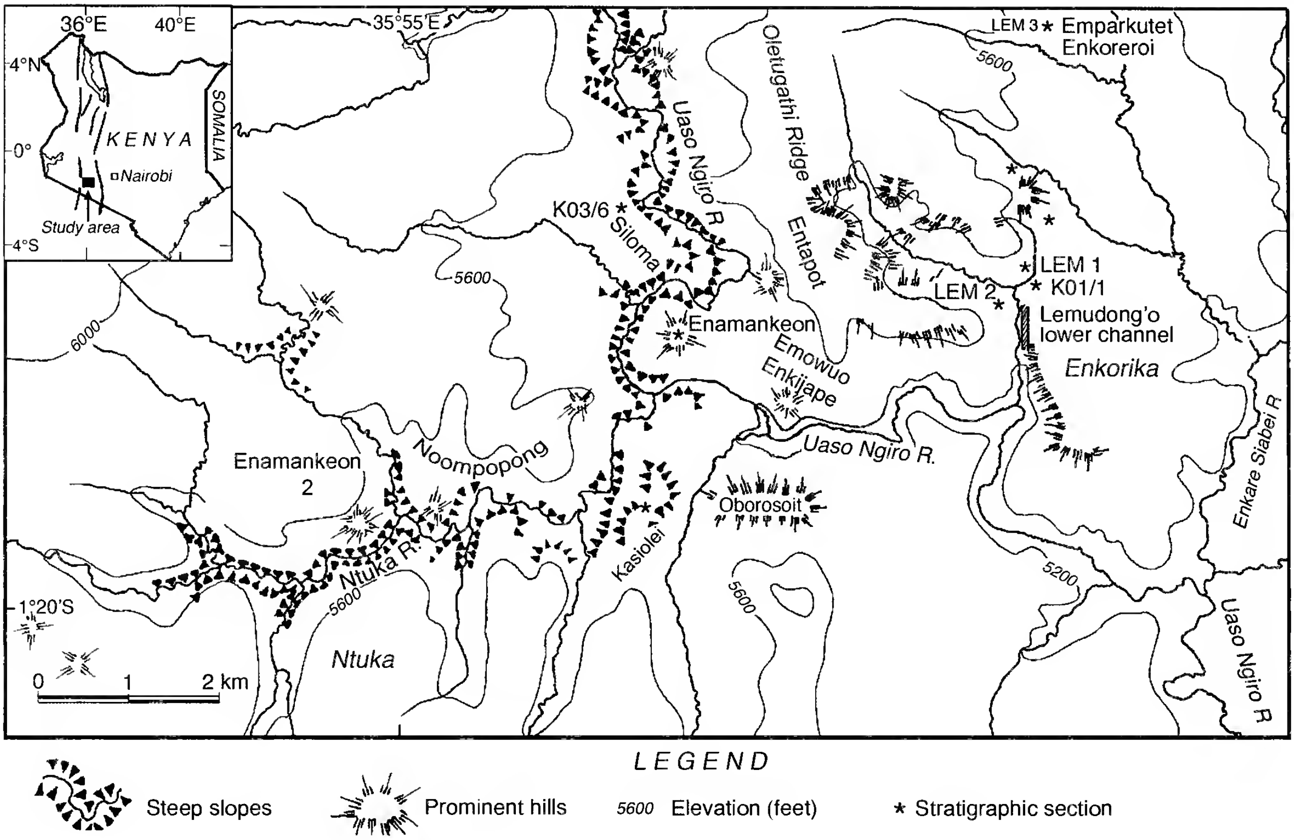

Figure 2. Map of locations of Lemudong'o, Enamankeon, Siloma, Kasiolei and other major localities in relation to the major topographic features of the research area. The inset map of Kenya is adapted from fig. 7 in Mathu and Davies (1996).

Lemudong'o Locality 1, a minor fault oblique to the Enkorika fault separates the north (Lemudong'o 1-N) and south (1-S) sedimentary sections.

Materials and Methods

Figure 2 shows the locations of major sections described in this report. The Uaso Ngiro River separates the Lemudong'o, Enamankeon, Emowuo Enkijape, and Entapot sections to the east from Kasiolei and Ol Doinyo Siloma on the west, respectively; Kasiolei lies on the south side and Siloma on the north side of lower Ntuka River valley near the confluence with the Ewaso Ngiro River (Figure 2). Similar sequences are exposed at several outcrops up to 10 km west and northwest of Lemudong'o at Enamankeon 2, Emowuo Enkijape, Entapot, Kasiolei, and Noompopong.

Sections were measured using a GPS, Jacob's staff, and clinometer. Lithostratigraphic units are formally defined and named using the conventions of the North American Stratigraphic Code (NACSN, 1994) and the *International Stratigraphic Guide* (Salvador, 1994).

A total of 70 samples from three sections were collected for major and trace element analyses by atomic absorption spectrophotometry (AAS) at the Kenya Geological Survey, Nairobi. Petrographic studies of rock sample thin sections with transmitted polarizing microscopy were performed at the University of Nairobi. Correlations of beds between stratigraphic sections are based on stratigraphic relationships, lithology, and field and laboratory petrography and chemical composition. Trace element and petrographic analyses are intended to be reported elsewhere by Nyamai and Mathu.

Stratigraphy

The lowest Neogene lithostratigraphic units that unconformably overlie the Neoproterozoic metamorphic rocks are largely melanephelinite lavas (Table 1). Wright (1967, p. 25–31) considered the overlying pyroclastics to be mainly "ashes and tuffs, in part waterlain" that were subaerially deposited in three Pleistocene lake basins. Radiometric dates of ~6 Ma (Ambrose et al., 2003; Deino and Ambrose, 2007) show that the age of the second lake is late Miocene, so the time range of these three lake basins is likely to be late Miocene to Pliocene. Beds of the oldest lake, mapped by Wright (1967, p. 28) as the "2nd (lower level) Uaso Ngiro lake," lie mainly south of 1°20′ S. Wright's (1967, p. 31) second-oldest lake basin, which he called the "1st Uaso Ngiro lake," lies mainly north of 1°20′ S. We designate the beds of this lake as the Lemudong'o Formation. The youngest lake, mapped by Wright as the "Seyabei lake," lies mainly north of 1°15′ S, but it caps outcrops of the Lemudong'o Formation on the Oletugathi ridge on the east side of the Ewaso Ngiro valley, including sections at Lemudong'o. The highest outcrops of the Seyabei lake reach an elevation of 1794 m at Entapot. Wright (1967) reconstructed the minimum extent of the Lemudong'o Formation lake as 16 km from north to south and 8 km from east to west. The south shore of this lake is partly defined by Ol Doinyo

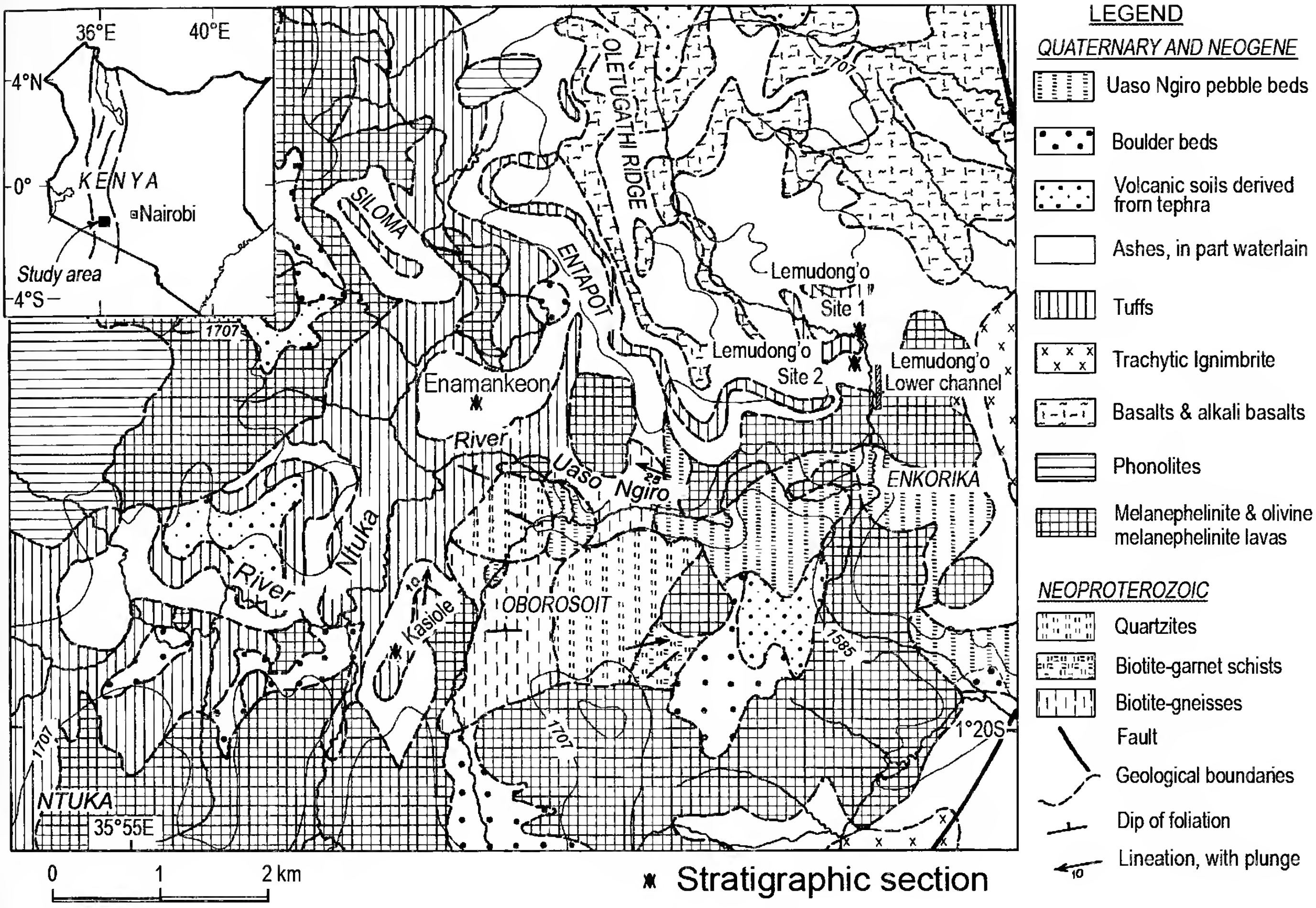

Figure 3. Geological map of Narok area (map modified after Wright, 1967), showing the locations of stratigraphic sections at Lemudong'o, Enamankeon, Kasiolei and Siloma.

Oborosoit and the west shore is bounded by contact with a variety of lavas and sediments. The eastern and northern margins of the basin are poorly exposed and remain poorly defined.

Sections and locations studied in this report will be described from west to east. Bed boundaries are conformable unless noted as unconformable. Elevations are taken from GPS readings. Figure 6 shows the stratigraphic sections of Kasiolei, Enamankeon West, Siloma, Lemudong'o 2, and Lemudong'o 1-S. The view from the top of the section at Kasiolei looking northeast toward Siloma and Enamankeon (Figure 4) shows that upper beds of the Lemudong'o Formation can be visually traced between sections, and are not deformed, tilted or faulted in this part of the paleobasin. The Lemudong'o Gorge sections (Figure 5) are not in direct line of sight of the Enamankeon outcrops, and correlated strata lie at lower elevations, but the major tuffs in the middle and upper part of the Lemudong'o sections are traceable in outcrops throughout the paleobasin (Figures 3 and 6). A fault with substantial displacement occurs between Lemudong'o 1-S and 1-N sections, and distinctive marker beds of the Lemudong'o Formation are absent from Lemudong'o 1-N. Lemudong'o 1-N lies closer to the rift axis and thus may be downfaulted rather than uplifted, and may correlate with the younger beds of Wright's (1967) Seyabei lake.

Representative sections of the central and western side of the paleolake basin at Kasiolei and Enamankeon West are described below (Figure 6). The Siloma sequence closely resembles that in the upper half of the Kasiolei and Enamankeon West sections and does not warrant separate description.

Kasiolei

Kasiolei is located at 1°19′35″ S, 35°55′58″ E; the elevation of the top of the section is 1721 m. The measured section lies south of the Ntuka River west of Ol Doinyo Oborosoit. Metamorphic rocks lie unconformably beneath > 30 m of lavas and tuffs, comprising phonolite, basalt, and gray ignimbrite (welded tuffs) with abundant clasts (< 3 cm) of fiamme (glassy, compacted pumice). Sandy conglomerates unconformably overlie the gray ignimbrite, followed by brown, clayey mudstones with thin bands of interstratified sands, gravels, calcretes, and tuffs (~21 m). Gray, poorly consolidated coarse-grained cindery laminated tuff (~3 m), with red/purple laminations in the middle, lies beneath another series of brown mudstones with calcrete horizons and poorly consolidated gray tuff (~16 m). Yellow-brown laminated and banded silts (~7 m) overlie the mudstones, followed by a pale-yellow tuff with devitrified pumice inclusions to > 1 cm (~8 m). Gray ignimbrite (~11 m) caps the section.

Outcrops at Noompopong, upstream on the Ntuka River, ~2 km west of Kasiolei, have a closely similar sequence, including the basal gray ignimbrite, mudstones, gray cindery laminated tuff with red/purple laminations within the mudstone beds, and the

Figure 4. Photograph of the area around Enamankeon hill, a flat-topped erosional remnant exposing sections of stratified waterlain and terrestrial sediments and tuffs. The view is toward the northeast from Kasiolei, with Ol Doinyo Siloma on the left, Entapot on the right, and Oletugathi Ridge in the background. The cliffs in the foreground, which rise above the deeply incised Ntuka River (left) and Ewaso Ngiro River (right), are exposures of the basal gray ignimbrite that unconformably underlie the Lemudong'o Formation in the western half of the paleobasin. Enamankeon and surrounding outcrops are conformably capped by the upper gray ignimbrite, which defines the upper boundary of the Lemudong'o Formation. Sediments of Wright's (1967) Seyabei lake lie above the upper gray ignimbrite below the horizon on Oletugathi Ridge. The horizontal scarp near the base of Enamankeon is the gray cindery tuff. The light yellow-brown rocks exposed on steep slopes near the top of the section are laminated lacustrine-siltstones and the vertical wall above is the yellow tuff.

pale-yellow tuff and gray ignimbrite at the top of the section at ~1712 m.

Enamankeon

Enamankeon is an isolated, flat-topped, conical hill forming an erosional remnant of horizontally bedded sedimentary rocks and tuffs in the center of the Ewaso Ngiro River valley east of Entapot (Figure 4). Fossil-bearing sediments are exposed on the east, north, and west sides of the base of the hill. The longest stratigraphic sequence in the Lemudong'o Formation is exposed on the west side of Enamankeon, so it is designated as the type section (stratotype).

Enamankeon West

Enamankeon West is at 1°18′33″ S, 35°56′40″ E. The elevation at the top of the section is 1714 m. The Enamankeon West sequence begins at the river bank at an elevation of 1589 m with a dark gray ignimbrite with widely spaced joints (> 7 m), overlain by phonolite (~7.5 m), and massive gray ignimbrite (~40 m) whose upper surface is incised into a deep E-W orientated channel, with up to 35 m of vertical relief. Within this channel, micritic white carbonate (0.7 m) capped by 40 cm of arkosic carbonate-cemented coarse sand (0.4 m) unconformably overlies the ignimbrite, followed by brown-gray clayey mudstones with interstratified lenses of cemented sandstones and poorly-sorted subrounded gravel conglomerates and two calcrete beds that may be tufas (total thickness from 1st to 3rd calcrete ~20 m). Similar clayey and sandy mudstones (~32 m) overlie the upper calcrete. Mammal fossils occur from beneath and within the upper calcrete to near the top of the mudstones. A thin layer of yellow to red-brown massive siltstone (~0.25 m) overlies a weakly developed brown paleosol with carbonate rootcasts and spherical carbonate nodules up to 10 cm in diameter (~0.4 m). Poorly consolidated dark brownish-gray massive cindery tuff (~2.2 m), with black pumice clasts up to 1.5 cm and large black, spherical carbonate nodules at the base, overlies this siltstone and paleosol. A thin layer of coarse tuff grit (5–7 cm) within this tuff marks the transition to ~5 m of dark-gray coarsely laminated waterlain cindery tuff. Brown, massive well-sorted silts overlie this tuff, and grade upward to a series of superimposed reddish-brown to yellowish-brown sandy and silty loam paleosols with sub-rounded blocky- to columnar-blocky structure and occasional mammal fossils (~11 m). Carbonate nodules > 5 cm in diameter occur in some paleosol horizons. Massive, grayish siltstone caps the paleosol bed. The siltstone is overlain by poorly consolidated gray tuff (~1.2 m). Light-gray to light-brown massive sandy tuffaceous to blocky clayey rhythmically banded silts (~3.5 m) follow, overlain by gray clayey columnar-laminated silts (2.5 m). Yellow tuff (~7 m), laminated near the base, becoming massive with devitrified green and yellow pumice, overlies the lacustrine silts. The top of the sequence comprises massive, poorly welded gray ignimbrite (~3 m) that grades into more consolidated gray ignimbrite (~5 m).

Figure 5. Photograph of Lemudong'o Gorge Locality 1, showing the positions of the 2001 and 2004 step trenches (T1, T2), yellow, laminated lacustrine siltstones (1), fossil-bearing coarse gravelly sandstone (2) and finer-grained fossil-bearing clayey mudstones (3), the green tuff (4, behind tree), the speckled tuff (5), silty to sandy mudstones (6), undescribed gray sediments (7), brown-gray mudstones (8) and poorly sorted sandstones (9).

Enamankeon East

Enamankeon East, a gully on the east side of Enamankeon, has a pale blue-gray massive ignimbritic tuff > 1.7 m thick at the base of the section (1°18′31.2″ S, 35°56′53.4″ E, elevation 1621 m). This tuff is overlain by mudstones (~30 m) with terrestrial vertebrate fossils. The mudstones are overlain by cindery tuff (~7 m) and the overlying strata described in the west section. The mudstones in the East section span approximately the same elevations as those above the third carbonate bed in the West section (1624–1656 m). The blue-gray tuff does not appear in the West section, but one or more lithologically dissimilar tuffs crop out in an analogous position in most sections at the base of the Oletugathi Ridge at Emowuo Enkijape and other outcrops between Enamankeon East and Lemudong'o 2.

Lemudong'o Gorge

Lemudong'o Gorge is a fault-controlled, deeply incised gully system bounded on the east by the Enkorika Fault (Wright, 1967). The most productive late Miocene fossil site in the gorge is Locality 1-S, which was initially given an archaeological site designation GvJh15 in the Standard African Site Enumeration System. Locality 2 was originally designated GvJh32. The base of the sedimentary sequence in the lower Lemudong'o channel is defined by an unconformable contact with weathered basalt at an elevation of ~1569 m at 1°18′38″ S, 35°48′53″ E. Mudstones, lacustrine silts, fluvial sands and pale blue-gray laminated tuffs are exposed in several outcrops upstream along the narrow, steep-sided channel of the lower Lemudong'o Gorge, where sections are difficult to measure and GPS readings are inaccurate. Lacustrine silts also occur in the west gully of Lemudong'o 2 and 1-S. Lacustrine beds do not occur in the lower mudstones further west at Kasiolei, Siloma and Enamankeon.

Lemudong'o Locality 2

Lemudong'o Locality 2 is at 1°17′59″ S, 35°59′38″ E. The top of the section is at ~1634 m. The Lemudong'o 2 section is exposed in a small channel on the west side of the gorge. The upper third of this section is partially obscured by trees and shrubs, which reduced the accuracy of GPS elevation readings. The sequence begins at 1577 m with clayey to sandy mudstones and sands (> 1 m) overlain by a pale blue-gray tuff, laminated at the base, becoming massive and cindery upward (~1.6 m), overlain by mudstones (~9 m), and a pale blue-gray coarsely laminated tuff (2.2 m) that dips 6° SSW. Poorly sorted gravelly silt, fining upward to cemented sandstone, siltstone, and claystone (~1.8 m), capped by a thin (1–3 cm) platy carbonate, underlies the mottled

Table 1. Summary of the regional volcanic stratigraphy of Narok (modified from Wright, 1967, p. 14).

Lithostratigraphy	Age
7. pyroclastics (tuffs and ashes) 6. olivine melanephelinite plugs 5. Angata Naado trachytes 4. ignimbrites (Plateau trachytes) 3. alkali basalts	Pleistocene & Pliocene
Unconformity	
2. phonolites 1. Kishalduga melanephelinites	Miocene
Unconformity	
Mozambique-belt metamorphic rocks	Neoproterozoic

and cindery third pale-blue-gray tuff (0.6 m). Brown silty claystone fining upward to green waxy claystone (1.6 m) underlies the fourth blue-gray tuff (1.9 m), which is laminated at the base, becoming massive upward. Brown clayey mudstone (~1.6 m) underlies a bright white fine-grained tuff (0.6 m). Radiogenic-argon dates of 6.10 ± 0.03, 6.087 ± 0.013 and 6.12 ± 0.07 Ma were obtained for the third and fourth gray tuffs and the white tuff, respectively (Ambrose et al., 2003; Deino and Ambrose, 2007). Waxy claystone (0.5 m) laminated siltstones (3.3 m), and clayey to sandy to silty mudstones (~9.5 m) overlie the white tuff. Dark-grey unconsolidated fine-grained laminated tuff (0.5 m) overlies the claystones. Pale-yellow to gray to green fine-grained tuff (~7 m) with large pale-yellow and green devitrified pumice clasts (< 2 cm) lies above the gray ash. Gray ignimbrite (~4 m), overlain by blue-gray trachyte lava (10.5 m) forms the top of the outcrop.

Lemudong'o Locality 1 South

Lemudong'o Locality 1 South is located at 1°18′1″ S, 35°58′44″ E, 1648 m (Figure 4). The Lemudong'o 1-S section is exposed in the upper gorge and in a WNW-trending side gully that forms the southern boundary of the outcrops. Figure 5 shows the view to the west across the main gorge toward the lower end of the west gully, and the locations of step trenches T1 and T2, excavated in 2001 and 2004. Numbers in Figure 5 refer to features described below. Thicknesses of some beds vary widely across the exposures, and beds tilt ~7° NNE in the 2004 step trench (Figure 5, T2). Dense bush and trees obscure the highest parts of the exposures. A fault crosses the north end of the main gorge, defining the boundary with Lemudong'o 1-N. Beds upstream from this fault comprise mainly sands, silts, and clayey sands with three pale brown, pale gray and pale green fine-grained tuffs that do not correlate with those in Lemudong'o 1-S. They may be downfaulted beds from Wright's (1967) youngest paleolake, and will not be described in detail in this report.

Brown clayey mudstones (> 1 m) form the base of the 1-S section. Light yellow to gray and pale brown sandy to clayey laminated siltstone (0.4 to > 4 m) lies above the mudstones, and it thickens substantially toward the west gully (Figure 5, 1). Microscopic study of this silt by Frances Williams revealed no diatoms. Gray-to-brown coarse sandy to well-sorted fine gravelly mudstone (~0.8-2 m) with dark green mammal fossils, sometimes rolled (Figure 5, 2), fines upward to brown-gray sandy to clayey siltstone (~3.6 m) with light-brown to pink well-preserved fossils and abundant round iron pisoliths (~5 mm) (Figure 5: 3). A lens of dark-green tuff (0.2 m) fills an indistinct small shallow channel in the lower sandy/gravelly claystones at the base of the outcrop (Figure 5, 4, behind tree). Pale-gray tuffaceous silt/fine sandstone grades laterally to a pale-yellow speckled tuff (0.2 m), dated to 6.08 ± 0.019 Ma (Figure 5, 5). The speckled tuff contains a micromammal breccia and seeds of *Celtis zenkeri*. Brown-gray-green silty to sandy mudstones continue for ~4 m above the speckled tuff (Figure 5, 6). A light gray bed that has not been sampled and described lies within the upper clayey mudstones (Figure 5, 7). The overlying brown-gray mudstones (Figure 5, 8) coarsen upward to gray clayey to silty poorly sorted sandstones (~12 m) (Figure 5, 9). Brown silicified tuff directly above the main fossil-bearing exposures grades laterally to a light-yellow-brown laminated to massive tuff (~4 m) with devitrified pumice clasts < 2 cm. Gray ignimbrite (~4 m) overlies the yellow-brown tuff. Sandstones overlie the ignimbrite, indicating an unconformity beneath the blue-gray trachyte at the top of the section.

Lemudong'o Formation Definition, Distribution and Sedimentary History

The Lemudong'o Formation is named after exposures at Lemudong'o 1-S and 2, where the most productive fossil beds are located, and where the tuffs of the higher levels of the lower mudstone member have been radiometrically dated to 6 Ma (Ambrose et al., 2003; Deino and Ambrose, 2007). The maximum thickness of the volcanics and sediments in these stratigraphic columns is about 135 m at Enamankeon West. We designate this section as the type locality and stratotype for the Lemudong'o Formation because it is located near the center of the paleolake basin. The pale blue-gray tuff beneath the mudstones in the Enamankeon East section provides an uncertain link to the lower levels of sections on the Oletugathi Ridge and Lemudong'o Gorge.

The Lemudong'o Formation is defined as the conformable sequence of lacustrine, fluvial and alluvial sediments and tuffs that lie beneath the gray ignimbrite and yellow tuff in sections between Noompopong on the west, and Lemudong'o 1-S on the east (Figures 2, 3, and 6). The ignimbrite is the highest point on each outcrop in sections on the west side of this Formation, including Noompopong, Kasiolei, Siloma and Enamankeon. A thick bed of trachyte lava overlies this ignimbrite in sections on the east side of the paleobasin along the Oletugathi Ridge at Entapot, Emowuo Enkijape, Lemudong'o 2, and Lemudong'o 1-S. The trachyte lies unconformably above this ignimbrite at Lemudong'o 1-S. This unconformity defines the top of the Formation. The base of the Lemudong'o Formation at Kasiolei, Enamankeon and Siloma is defined by unconformable contact with the top of a sequence of dark gray tuff, phonolite and a dark gray ignimbrite that often contains fiamme. Weathered basalts lie unconformably beneath the basal Lemudong'o Formation

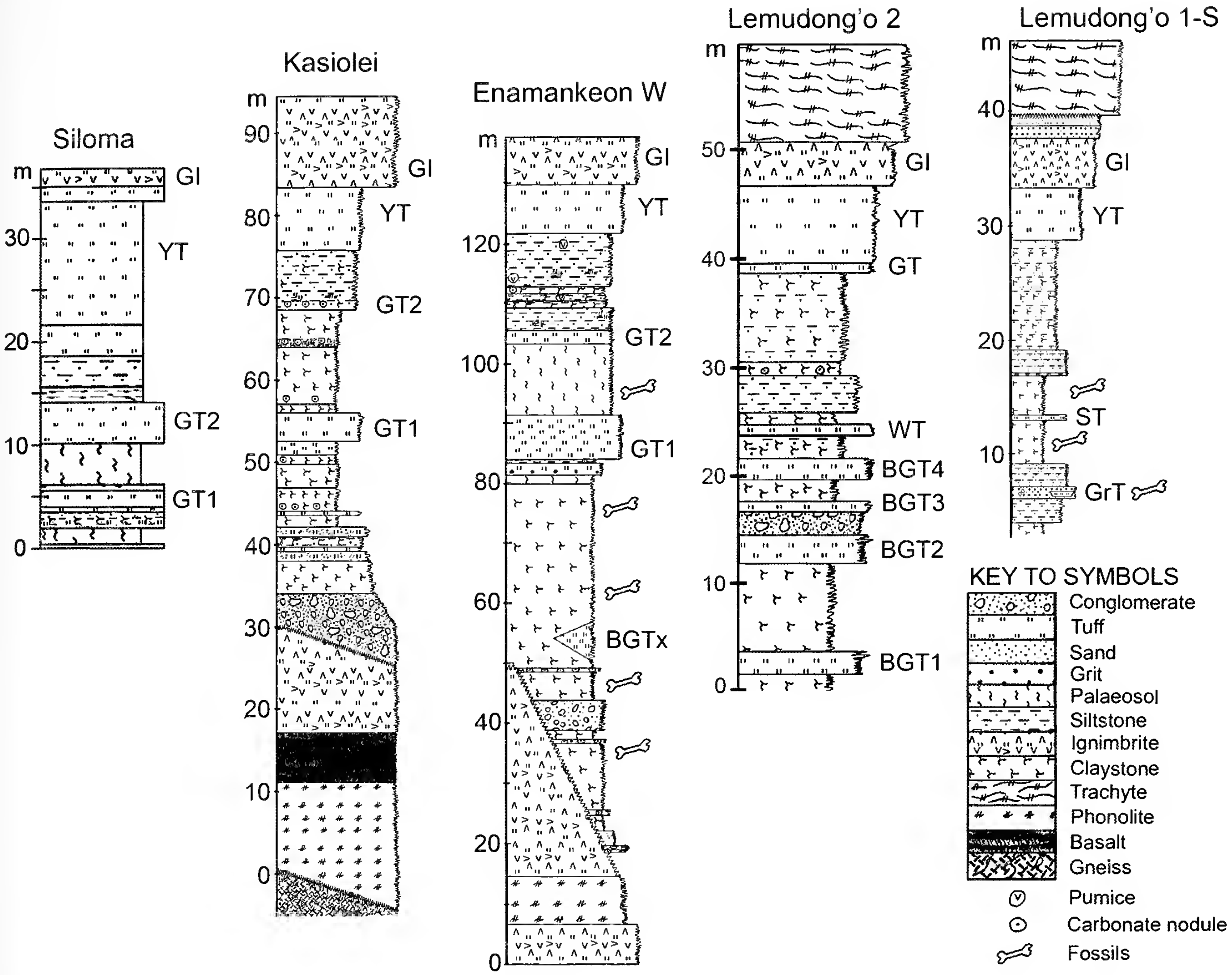

Figure 6. Stratigraphic sections of the sequences exposed at Siloma. Kasiolei, Enamankeon and Lemudong'o 2 and Lemudong'o 1-S, Narok area, southwest Kenya. Stratigraphic correlations between sections are indicated by abbreviations of tuffs: GI, upper gray ignimbrite; YT, yellow tuff; ST, speckled tuff; GrT, green tuff; GT, gray tuff; GT1, gray tuff 1; GT2, gray tuff 2; BGT1–4, pale blue-gray tuffs 1–4; BGTx, pale blue-gray tuff of uncertain correlation.

mudstones in most sections on the east and south side of the Oletugathi ridge, including Entapot and the lower Lemudong'o Gorge.

Three main sedimentary depositional phases are evident within the Lemudong'o Formation. The first phase comprises mudstones, siltstones, sandstones, and fine-grained laminated to massive tuffs, reflecting lake, lake margin, and small stream-channel depositional environments. The second phase of deposition includes predominantly alluvial, fluvial and subaerial sandstones, siltstones and paleosols. The third phase is primarily lacustrine siltstones, mudstones and tuffs, culminating in a thick lacustrine tuff (the yellow tuff) and the subaerial gray ignimbrite. These phases are discussed in more detail below.

The main widespread marker beds and distinctive beds with more restricted distributions within the Lemudong'o Formation are listed in stratigraphic order in Table 2. Within phase-1 deposits at Lemudong'o 1-S, Lemudong'o 2, and the Lower Lemudong'o channel six tuffs are interstratified with lacustrine siltstones and claystones and lake-margin mudstones. The lowest four tuffs are lithologically similar light-blue-gray, fine-grained laminated to massive tuffs. Outcrops on the west side of the Oletugathi Ridge at Entapot and Emowuo Enkijape contain a laminated pale-blue-gray tuff that may correlate with one of the four lithologically similar tuffs at Lemudong'o 2. Correlation with the blue-gray ignimbritic tuff at Enamankeon East remains to be demonstrated. The white tuff occurs only at Lemudong'o 2. Mudstones above the white tuff are overlain by lacustrine siltstones up to 9-m thick in the lower Lemudong'o Gorge and > 4-m thick in the west gully at Lemudong'o 1-S. Lacustrine siltstones do not occur in this stratigraphic position in sections north and west of Lemudong'o Gorge. A dark-green dense tuff lies within a small shallow channel in the coarse sandy to gravelly mudstones of the lowest fossil-bearing deposits above the lacustrine siltstones at Lemudong'o 1-S. The speckled tuff is

Table 2. Presence/absence of major (**bold**) and minor (regular type) marker beds, and their depositional modes in stratigraphic sections of the Lemudong'o Formation at LEM 1, LEM 2, Entapot, Enamankeon East and West, Kasiolei and Ol Doinyo Siloma. These correlations are also shown in Figure 6. Key: A, airfall or subaerial; F, fluvial; L, lava flow; M, lake-margin or shallow-water mudstones; U-, unconformity below; W, waterlain lacustrine; ?, uncertain correlation.

			Enamankeon			
Bed and depositional phase	**LEM 1**	**LEM 2**	**East**	**West**	**Kasiolei**	**Siloma**
trachyte (U-)	x	x				
phase 3						
gray ignimbrite (A) GI	x	x	x	x	x	x
yellow tuff (A/W) YT	x	x	x	x	x	x
yellow siltstone (W)	?	?	x	x	x	x
gray tuff (W/A) GT2	x	x	x	x	x	x
phase 2						
alluvium (A)	x	x				
paleosols (A)			x	x	x	x
gray cindery tuff (A/W) GT1			x	x	x	x
paleosol (A)				x		
phase 1						
mudstones (M)	x	x	x	x	x	x
speckled tuff (A/M) ST	x					
green tuff (F) GrT	x					
fine gravels and sandstones	x					
laminated siltstones (W)	x	x				
white tuff (A/M) WT		x				
blue-gray mottled tuff (A/M) BGT4		x	?			
blue-gray cindery tuff (A/M) BGT3		x	?			
blue-gray laminated tuff (M/W) BGT2	x	?	?			
blue-gray laminated tuff (M/W) BGT1	x	?	?			
mudstones (M, U-)		x		x	x	x
major unconformity						
gray ignimbritic tuff (A)				x	x	x
basalt (L, U-)					x	
phonolite (L)				x		
gray tuff (A)				x		
major unconformity						
Proterozoic metamorphic rocks					x	

discontinuously stratified within the upper fossiliferous mudstones at Lemudong'o 1-S. The green and speckled tuffs are restricted to Lemudong'o Locality 1-S.

The transition to the second phase of sedimentation is marked at Enamankeon West by the paleosol with carbonate nodules underlying the gray cindery tuff. Phase-2 beds comprise siltstones, sandstones, and mudstones, and a series of brown paleosols that reach a maximum thickness of ~11 m at Enamankeon West. At Lemudong'o 1-S, sediments above the fossil-bearing mudstones coarsen upward, reflecting a shift to an alluvial-fan depositional environment. Depositional phase 3 marks a return to deeper water, with thick beds of lacustrine siltstones and tuffs at Enamankeon, Kasiolei. and Siloma. The lacustrine yellow tuff and overlying gray ignimbrite occur at the top of the Lemudong'o Formation in all sections studied.

The topography of the floor of the paleobasin included areas of high and low relief. The metamorphic rocks of Ol Doinyo Oborosoit would have formed the highest point on the paleolandscape, > 100 m above the basal gray ignimbrite. The gray ignimbrite beneath the basal mudstones at Enamankeon West and Kasiolei is deeply eroded, with at least 35 m of vertical relief, possibly reflecting an ancient landscape incised by a river channel. The weathered basalts exposed at the bases of outcrops at Entapot and the Lemudong'o lower channel may have formed a low ridge or line of low hills beneath the modern Oletugathi Ridge.

The earliest stages of deposition of the phase-1 mudstones first filled in the lowest points of the landscape. Upper phase-1 mudstone beds have a wider and more continuous distribution. A relatively deep lake occupied the Lemudong'o Gorge area. The presence of a lake in this part of the basin may reflect syndepositional subsidence of the southeast side of the paleobasin, toward the modern rift axis. Fossil-bearing horizons at Lemudong'o and Enamankeon lie above the lacustrine siltstones in mudstones that represent predominantly lake-margin environments. With the exception of crocodile and hippopotamus, aquatic fauna, including fish and shellfish are absent, suggesting lakes were too small and ephemeral to sustain aquatie (fish and shellfish) faunas. The terrestrial fauna at Lemudong'o 1-S suggests locally forested environments in a wider mosaic of humid grassy woodlands and woodlands (Ambrose et al., 2007). The thick paleosol horizons in phase-2 deposits at Enamankeon indicate a long period of soil formation in dry terrestrial environments. Fossils are present but are rare. Whether these paleosols reflect a period of drier climate, down-cutting of the basin outlet, or tectonic controls on lake levels remains uncertain. Lacustrine siltstones and thick beds of waterlain ash, including the yellow tuff, are found in depositional phase 3. Fossils have not been observed in these beds. Climate change, volcanic eruptions, and/or tectonic activity may have all contributed to high lake levels during the last phase of sedimentation in the Lemudong'o Formation.

Summary and Conclusions

The Lemudong'o Formation represents sediments and volcanic tephra deposited in a terminal Miocene (6 Ma) rift-valley-margin lake basin. The topography of the landscape on which the sedimentary sequence was deposited was heavily eroded. The sedimentary sequence includes claystones, siltstones, sandstones, tuffs, and paleosols. Depositional environments include shallow and deep lakes, lake margins, swamps, and subaerially exposed terrestrial landscapes with paleosols, airfall tuffs, and ignimbrites. Thinner beds of predominantly waterlain ash are common in the middle levels of phase 1 of the sedimentary sequence on the east/southeast side of the paleobasin (Enamankeon East to Lemudong'o 1-S), but are absent from the west side of the basin (Enamankeon West to Kasiolei and Noompopong). This is consistent with prevailing wind directions from the east, which would have carried airfall tephra from Rift Valley volcanoes. Three major sedimentation phases have been recognized, representing a sequence of wetter, drier, and wetter environments. Vertebrate fossils are most abundant in the mudstones of the upper half of phase 1.

The stratigraphic study reported here provides an outline of the geology of the Lemudong'o Formation. More fieldwork is needed to properly define the geometry of this paleobasin. A comprehensive program of mapping of outcrops, tephrastratigraphy, magnetostratigraphy, geochemistry, paleopedology, sedimentology and paleolimnology is needed to complement the lithostratigraphy and paleontology. The beds overlying the trachytes at Lemudong'o 1 & 2 and Entapot belong to Wright's (1967) younger Seyabei paleolake, and an older series of waterlain tuffs and ashes of Wright's 2nd Uaso Ngiro lake extends far south of our present study area. The boundaries and morphologies of these paleobasins remain poorly defined. These lakes may reflect long-lasting structural and tectonic control on drainage and sedimentation between the western margin of the southern rift valley and the east side of the Loita Hills. Long-distance inter-basin correlation of tephra beds in East Africa may be possible.

The Lemudong'o Formation dates to the terminal Miocene, which is one of the most poorly known periods of human evolution. Molecular genetics and paleontology indicate that the human lineage originated and expanded to African savanna environments between eight- and four-million-years ago (Kumar and Hedges, 1998; Leakey and Harris, 2003). Hominins are absent from the diverse faunal assemblage at Lemudong'o and from the late Miocene beds at Lothagam, but are relatively abundant in the late Miocene of the Middle Awash Valley, where more closed habitats predominate (Haile-Selassie et al., 2004). Further research in southern Narok may be able to provide a firm geochronological framework for this period and, if a wider range of paleoenvironmental settings is found, evidence for the environmental context of human origins, and perhaps direct evidence for our earliest hominin ancestors.

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^{40}AR/^{39}AR DATING OF THE LEMUDONG'O LATE MIOCENE FOSSIL ASSEMBLAGES, SOUTHERN KENYA RIFT

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ABSTRACT

The Messinian (uppermost Miocene) Lemudong'o Formation in Lemudong'o Gorge, near the western edge of the southern Kenya Rift, contains fine-grained tuffs stratified below and within fossil-bearing mudstones deposited along an intermittently exposed paleolake margin. This site has yielded a diverse fauna including colobine monkeys, carnivores, and other large land animals, as well as micromammals and seeds. Single-crystal laser-fusion ^{40}Ar/^{39}Ar ages from three tuffs underlying the fossil-bearing horizon are 6.087 ± 0.013, 6.10 ± 0.03, and 6.12 ± 0.07 Ma. One tuff interstratified with the fossiliferous deposits yielded an age of 6.084 ± 0.019 Ma. The narrow analytical spread of these ages suggests rapid deposition of the section and relatively little habitat averaging of the fossil assemblage. Lemudong'o affords a snapshot of Miocene stratigraphy and paleontology in a region of Kenya dominated by Plio-Pleistocene rocks.

Introduction

Lemudong'o is a late Miocene paleontological site in the Ewaso Ngiro River valley above the western edge of the southern Kenya Rift Valley, approximately 30 km south of Narok town (Figure 1) (Kyule et al., 1997; Ambrose et al., 2002; Hlusko et al., 2002; Ambrose et al., 2003; Haile-Selassie et al., 2004; Ambrose, Bell, et al., 2007; Ambrose, Kyule, and Hlusko, 2007; Ambrose, Nyamai, et al., 2007). The site occurs stratigraphically within the Lemudong'o Formation, a widely exposed (25 × 50 km) sequence of deeply incised lavas, tuffs, lacustrine, fluvial and alluvial sediments, and paleosols of middle Miocene to Late Pleistocene age (Wright, 1967; Crossley, 1979). The geology and paleoecology of the site and vicinity are summarized below, followed by details of the ^{40}Ar/^{39}Ar geochronology, and brief discussion of the implications of the age of the Lemudong'o fauna for understanding the origins of Mio-Pliocene hominids.

Geology, Stratigraphy, Paleontology, and Paleoecology

Details of the history of research, and the geology, paleontology and paleoecology of the Lemudong'o Formation are described elsewhere (Ambrose, Bell, et al., 2007; Ambrose, Kyule, and Hlusko, 2007; Ambrose, Nyamai, et al., 2007). Wright (1967) reconstructed three overlapping ancient lake basins in the southern Narok region that he considered to be of Plio-Pleistocene age. Crossley (1979) and Waibel and McDonough (1977) subsequently reported whole-rock K/Ar dates for some of the lavas and tuffs in this region, spanning the middle Miocene to early Pliocene (15–4 Ma). Deposits of Wright's second paleolake basin comprise the Lemudong'o Formation (Ambrose, Nyamai, et al., 2007).

The Lemudong'o Formation comprises a stratified sequence of sediments and tuffs up to 135-m thick (Ambrose, Nyamai, et al., 2007). The base of the formation lies unconformably on a variety of rock types, including Neoproterozoic metamorphic rocks, and Miocene volcanic rocks including basalts, phonolites, and welded ignimbrites. The top of the formation contains a waterlain yellow tuff that is everywhere conformably overlain by a gray ignimbrite. In the eastern part of the paleobasin, encompassing Lemudong'o, a thick blue-gray trachyte lava caps the succession.

Three main phases of sedimentation have been provisionally defined in the Lemudong'o Formation (Ambrose, Nyamai, et al., 2007). Phase 1 comprises predominantly claystones, silty and sandy claystones (mudstones), laminated siltstones and thin, discontinuous beds of sandstones, fine gravels and tufas. Depositional environments are dominantly lacustrine, swamp and lake margin, with occasional small, low-energy streams. The tuffs dated in this study lie within the upper half of this depositional phase. Phase 2 comprises poorly sorted clayey and silty sandstones in the Lemudong'o area, representing distal alluvial-

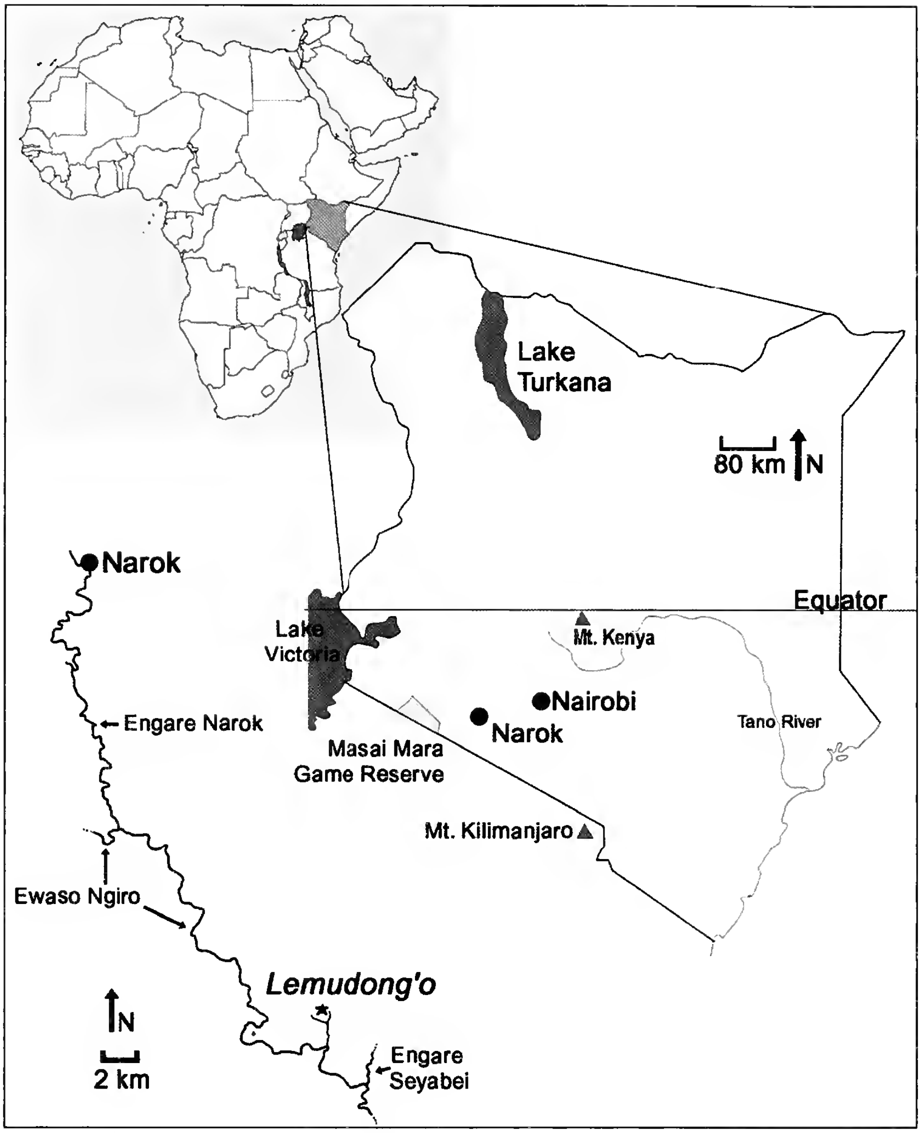

Figure 1. Location of the Lemudong'o paleontological site, southern Kenya Rift Valley.

and colluvial-fan deposition near the paleobasin margin, and paleosols formed on well-sorted silts in the basin center. Phase 3 comprises laminated siltstones, tuffs and ignimbrites, marking a return to lacustrine deposition. This lacustrine phase was terminated by a massive pyroclastic eruption.

The most productive paleontological areas at Lemudong'o (Figure 2) are exposed in the upper reaches of the main gully at Locality 1 (GvJh15 at 1° 18.19 S, 35° 58.74 E). The main outcrops of Locality 2 (GvJh32), exposed ~500 m south in the Lemudong'o Gorge at 1° 17.98 S, 35° 59.04 E), have no diagnostic fossils (Ambrose et al., 2003; Ambrose, Kyule, and Hlusko, 2007; Ambrose, Nyamai, et al., 2007). Locality 1 has two main fossil assemblages. The upper assemblage occurs in a 6-m-thick bed of silty to sandy clayey mudstones (Figure 2), representing near-shore lacustrine, swamp, and intermittently exposed lakeshore depositional environments. Colobine monkeys, hyrax, small carnivores, and bovids dominate the faunal assemblage. The upper mudstones enclose one of the dated tuffs (the "speckled tuff"), which itself contains fossil vertebrates and plants, including micromammals and seeds of the equatorial forest tree *Celtis zenkeri* (Ambrose et al., 2003). The floral and faunal habitat preferences suggest a mesic forest habitat (Ambrose, Bell, et al., 2007).

The lower fossil assemblage at Locality 1 is derived from coarse sandstone, clayey sandstone, and well-sorted fine gravel directly underlying the claystone and above a bed of laminated yellow siltstones. This higher energy depositional environment is provisionally attributed to a moderately high-energy regressive-shoreline beach deposit. It contains rolled fragments of semi-aquatic animals such as hippopotamus and crocodile, and terrestrial mammals including colobine primates, hyrax, bovids, proboscideans (*Anancus*), mustelid carnivores (*Plesiogulo*), suids (*Nyanzachoerus syrticus*), and hyenas. These lower sandstones also contain an undated, thin, lenticular bed of fine-grained dark-green tuff (Figure 2).

Localities 1 and 2 are correlated by the lateral continuity of the key rock units, including the lacustrine silts and the yellow tuff, gray ignimbrite, and blue-gray trachyte at the top of both sections. The base of the sedimentary sequence at Locality 1 exposes the top meter of a thick bed of mudstones below the

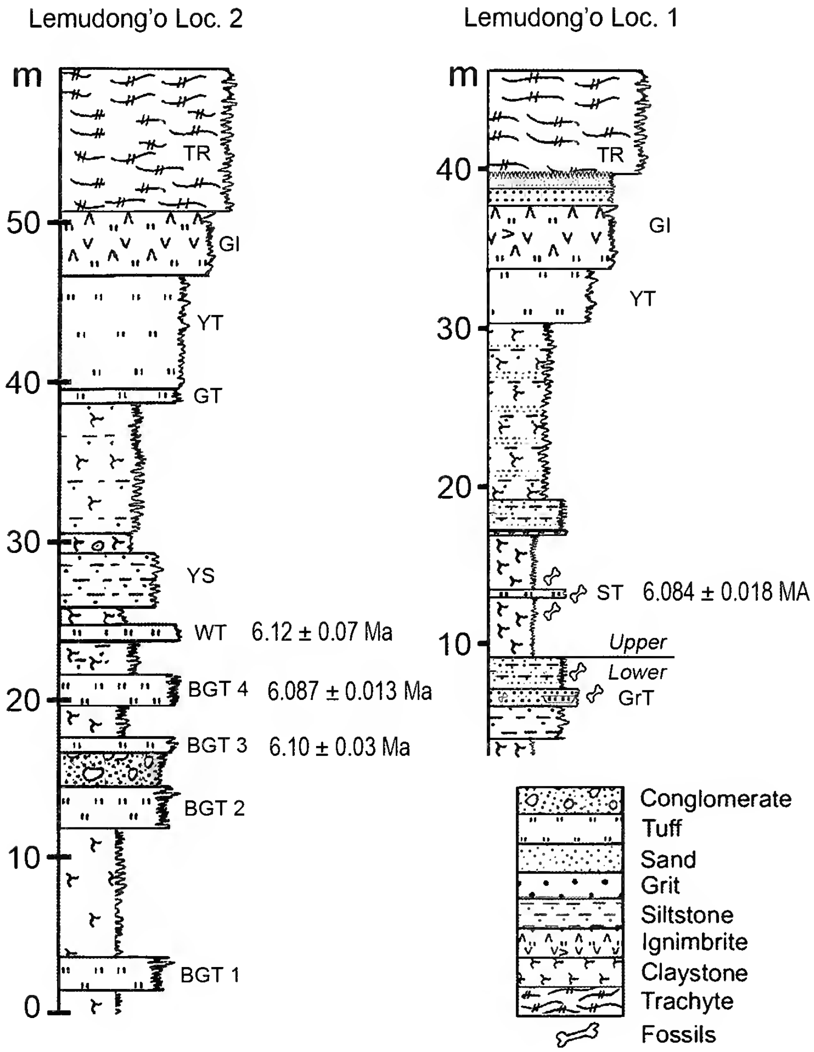

Figure 2. Stratigraphic sections for Lemudong'o Localities 1 and 2, showing ^{40}Ar/^{39}Ar age results from dated tuff samples. The boundary between fossil assemblages from upper mudstone and lower coarse-grained deposits is indicated. Abbreviations for strata: BGT1-4, blue-gray tuffs 1-4; WT, white tuff; YS, yellow laminated lacustrine silts; GrT, green tuff; ST, speckled tuff; GI, gray ignimbrite; YT, tellow tuff; TR, trachyte lava.

lacustrine siltstones. The sequence at Locality 2 extends substantially deeper into older strata, and contains five stratified tuffs below the lacustrine siltstones that afford an opportunity to precisely establish the age of the fossil assemblages through ^{40}Ar/^{39}Ar dating. The four lowest of these tuffs are lithologically similar: light blue-gray in color, massive to weakly laminated, and fine-grained. Similar tuffs occur in outcrops between the lower Lemudong'o channel and the east side of Enemankeon.

^{40}Ar/^{39}Ar Dating

Anorthoclase phenocrysts were extracted for single-crystal, laser-fusion ^{40}Ar/^{39}Ar age determination from four separate tuffs: the "speckled tuff" in mudstones above the main lacustrine siltstone in Locality 1 (sample GvJh15), and three tuffs below the lacustrine siltstone in Locality 2 (from bottom to top, samples GvJh32-8, -6 and -4) (Figure 2). The speckled tuff is stratified within clayey mudstones. Locality 2 dated tuffs are all weakly laminated, quiet-water deposits without obvious detrital contamination in outcrop. The speckled and the upper blue-gray tuffs (BGT4) from Locality 2 contain moderately coarse K-feldspar up to a few mm in size, while feldspars in the other tuffs are finer grained, relatively rare, and proved difficult to date.

Samples were prepared by gentle crushing and sieving to extract the 0.35–1.2 mm size fraction of bulk tuff. K-feldspar (anorthoclase) phenocrysts were concentrated using magnetic and occasionally heavy-liquid separation techniques. The mineral separates were then treated with dilute HCl, HF, and distilled water in an ultrasonic bath to remove adhered matrix, and then hand-selected to obtain pristine, inclusion-free feldspars.

The anorthoclase crystal concentrates were irradiated in two batches in the Cd-lined, in-core CLICIT facility of the Oregon State University TRIGA reactor. Sample GvJh15 received 7 hours of irradiation while the other three samples received 2 hours. Sanidine from the Fish Canyon Tuff of Colorado was used as a mineral standard, with a reference age of 28.02 Ma (Renne et al., 1998).

^{40}Ar/^{39}Ar extractions were performed at the Berkeley Geochronology Center (BGC), using a focused CO_2 laser to fuse and

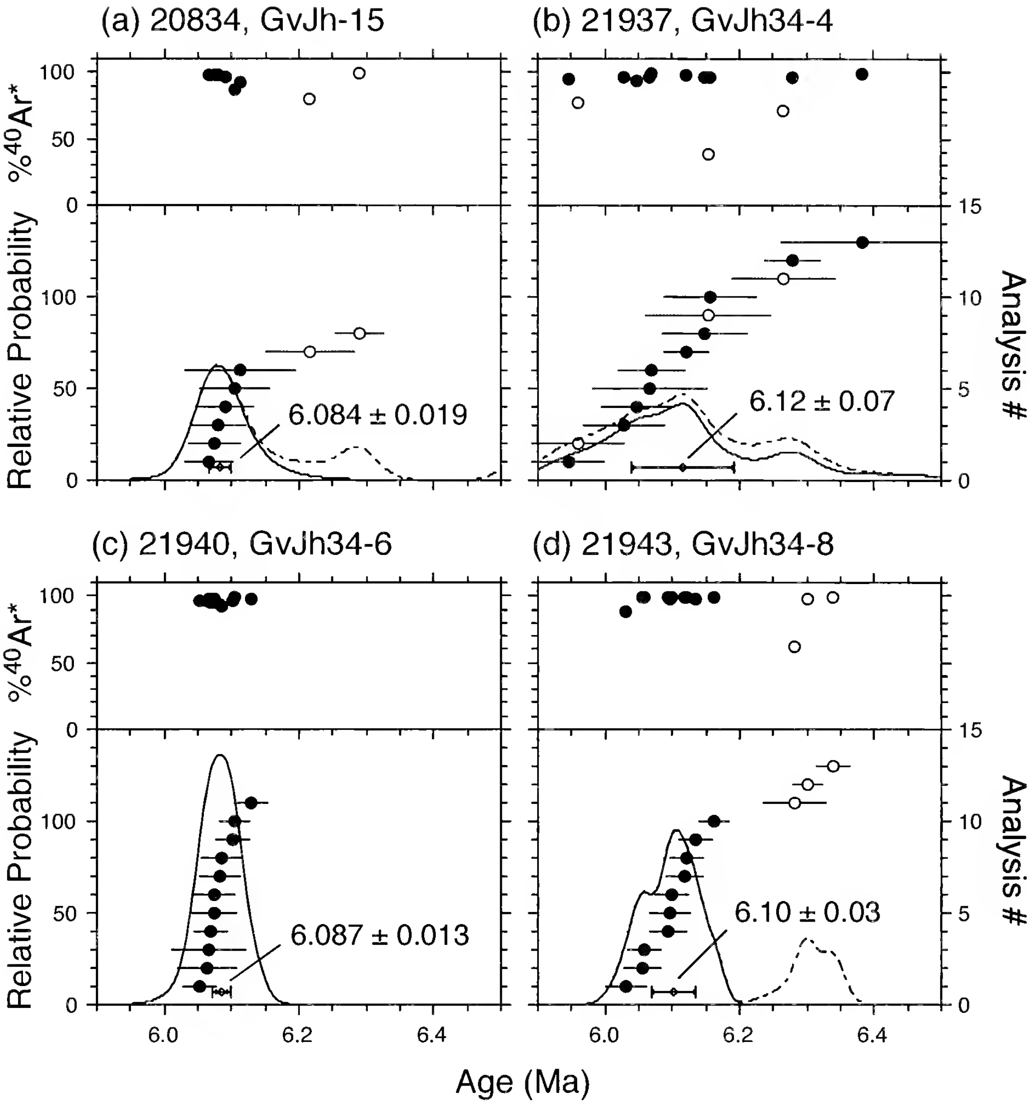

Figure 3. Age-probability density diagrams for the single-crystal, ^{40}Ar/^{39}Ar dating results. Open circles represent analyses omitted from the weighted-mean age (shown toward the bottom of each diagram). Dashed curve is the relative probability calculated with all samples included; the solid line is without the omitted analyses.

rapidly liberate trapped argon from individual feldspar crystals. Gasses were scrubbed with SAES getters for several minutes to remove impurities (CO, CO_2, N_2, O_2, and H_2), followed immediately by measurement of the purified noble gases for five argon isotopes on a MAP 215-50 mass spectrometer for approximately 30 minutes. From 9 to 13 grains were analyzed per sample, totaling 46 single-crystal age determinations. See Deino and Potts, 1990, Best et al., 1995, and Deino et al., 1998 for additional details regarding the ^{40}Ar/^{39}Ar dating method and its implementation at BGC.

Results

Full analytical results for the ^{40}Ar/^{39}Ar determinations are listed in Table 1, and summarized in Table 2. All but a few crystals yielded high proportions of radiogenic (^{40}Ar*) to atmospheric ^{40}Ar, as would be expected for unaltered, inclusion-free K-feldspars of this age. Several exhibited markedly lower percentages of ^{40}Ar*, likely reflecting the presence of small inclusions, trapped pockets of atmosphere, incipient alteration, etc. An arbitrary cutoff of 80% ^{40}Ar* was employed to cull anomalous grains, which were then excluded from further data analysis (5 of 46 analyses). A further four grains were omitted because they were "obviously" too old—i.e., clearly separated in the primary mode on age-probability diagrams (Figure 3).

As illustrated by the age-probability diagrams and demonstrated by population statistics (Table 2), samples GvJh15 and GvJh32-6 yielded unimodal, nearly symmetrical distributions with low MSWD's (0.12 to 1.49, respectively). These distributions are interpreted as representing undisturbed isotopic systematics from a single population of primary volcanic feldspars. They yield weighted-mean ages of 6.084 ± 0.019 (1σ standard error, including error in J, the neutron fluence calibration parameter) and 6.087 ± 0.013. Samples GvJh32-4 and -8, in contrast, yielded broader, multimodal distributions with high MSWD's (> 5) indicating greater scatter in the age distribution than can be explained by the estimated analytical errors alone. Thus, these

Table 1. ^{40}Ar/^{39}Ar analytical results.

	Relative isotopic abundances										Derived results						
Lab ID no.	**^{40}Ar**	**± 1σ**	**^{39}Ar**	**± 1σ**	**^{38}Ar**	**± 1σ**	**^{37}Ar**	**± 1σ**	**^{36}Ar**	**± 1σ**	**^{39}Ar Mol × 10^{-14}**	**Ca/K**	**± 1σ**	**%^{40}Ar***	**Age (Ma)**	**± 1σ**	**w/ ± J ± 1σ**
L1-15																	
20834-05	142.37	0.11	68.80	0.05	0.834	0.003	2.340	0.013	0.0132	0.0014	18.65	0.0667	0.0004	97.4	6.07	0.03	0.03
20834-04	90.00	0.07	43.80	0.04	0.540	0.003	0.155	0.008	0.0052	0.0012	11.86	0.0070	0.0004	98.3	6.08	0.03	0.04
20834-06	109.27	0.09	53.11	0.05	0.646	0.004	0.656	0.009	0.0072	0.0012	14.40	0.0242	0.0003	98.1	6.08	0.03	0.03
20834-07	101.09	0.10	47.93	0.05	0.572	0.003	0.162	0.008	0.0139	0.0012	13.00	0.0066	0.0003	96.0	6.09	0.03	0.03
20834-03	141.1	0.3	60.26	0.06	0.736	0.003	1.196	0.009	0.0643	0.0018	16.32	0.0389	0.0003	86.6	6.10	0.04	0.05
20834-02	34.87	0.06	15.764	0.017	0.195	0.002	0.742	0.010	0.0098	0.0012	4.27	0.0922	0.0012	91.8	6.11	0.07	0.07
												0.03	**0.02**		**6.084**	**0.014**	**0.018**
Omitted, obvious outliers:																	
20834-01	124.22	0.08	58.93	0.05	0.709	0.004	1.602	0.011	0.0042	0.0012	15.96	0.0533	0.0004	99.1	6.29	0.03	0.03
20834-08	103.28	0.08	46.34	0.04	0.562	0.003	0.283	0.008	0.0088	0.0012	12.57	0.0120	0.0003	97.5	6.54	0.03	0.03
Omitted, %40Ar* < 80:																	
20834-09	74.20	0.08	28.52	0.03	0.358	0.002	0.382	0.008	0.0519	0.0014	7.73	0.0262	0.0006	79.4	6.22	0.06	0.06
L2-4																	
21937-18	57.24	0.07	8.606	0.014	0.1042	0.0014	4.473	0.020	0.0116	0.0013	3.03	1.019	0.005	94.6	5.95	0.04	0.04
21937-07	40.93	0.04	6.143	0.010	0.0754	0.0014	0.230	0.006	0.0059	0.0011	2.16	0.0735	0.0018	95.8	6.03	0.05	0.05
21937-14	58.46	0.07	8.490	0.013	0.1066	0.0016	0.062	0.004	0.0139	0.0013	2.99	0.0142	0.0009	93.0	6.05	0.04	0.05
21937-05	31.07	0.04	4.629	0.010	0.0545	0.0012	0.053	0.004	0.0045	0.0012	1.63	0.0224	0.0019	95.7	6.07	0.07	0.08
21937-06	57.04	0.06	8.822	0.013	0.1049	0.0015	0.111	0.005	0.0012	0.0012	3.11	0.0247	0.0010	99.4	6.07	0.04	0.04
21937-11	102.45	0.10	15.458	0.016	0.1887	0.0017	0.208	0.005	0.0077	0.0012	5.44	0.0264	0.0006	97.8	6.12	0.02	0.03
21937-02	44.25	0.06	6.584	0.010	0.0779	0.0013	0.076	0.004	0.0047	0.0012	2.32	0.0227	0.0013	96.9	6.15	0.05	0.06
21937-04	36.09	0.04	5.348	0.011	0.0665	0.0012	0.077	0.004	0.0042	0.0011	1.88	0.0282	0.0015	96.6	6.16	0.06	0.06
21937-10	72.74	0.08	10.584	0.014	0.1308	0.0019	0.102	0.004	0.0081	0.0012	3.73	0.0189	0.0008	96.7	6.28	0.03	0.04
21937-13	20.69	0.04	3.018	0.007	0.0374	0.0010	1.726	0.010	0.0015	0.0012	1.06	1.120	0.007	98.5	6.38	0.11	0.11
												0.03	**0.07**		**6.12**	**0.07**	**0.07**
Omitted, %40Ar* <80:																	
21937-15	65.89	0.08	7.085	0.012	0.0993	0.0014	3.633	0.017	0.0650	0.0016	2.49	1.005	0.005	71.3	6.26	0.07	0.07
21937-16	54.24	0.06	6.572	0.010	0.0874	0.0015	3.150	0.014	0.0441	0.0013	2.31	0.939	0.004	76.4	5.96	0.06	0.06
21937-17	228.5	0.2	13.47	0.02	0.249	0.002	8.12	0.02	0.478	0.003	4.74	1.182	0.004	38.4	6.15	0.08	0.09
L2-6																	
21940-05	264.2	0.3	39.70	0.05	0.485	0.003	0.561	0.007	0.0321	0.0019	14.00	0.0277	0.0003	96.4	6.052	0.018	0.02
21940-01	80.44	0.08	12.098	0.016	0.1516	0.0016	0.140	0.004	0.0090	0.0014	4.27	0.0226	0.0006	96.7	6.06	0.04	0.04
21940-11	53.80	0.06	8.161	0.012	0.1019	0.0015	0.260	0.006	0.0045	0.0013	2.87	0.0624	0.0014	97.6	6.06	0.05	0.05
21940-06	302.6	0.3	44.92	0.05	0.547	0.003	0.626	0.007	0.0461	0.0020	15.84	0.0273	0.0003	95.5	6.068	0.017	0.02
21940-04	146.86	0.10	21.70	0.03	0.2624	0.0020	0.362	0.005	0.0241	0.0015	7.65	0.0327	0.0005	95.2	6.07	0.02	0.03
21940-02	201.07	0.19	29.03	0.04	0.361	0.002	0.695	0.007	0.0470	0.0017	10.24	0.0469	0.0005	93.1	6.08	0.02	0.02
21940-08	167.88	0.16	25.43	0.03	0.306	0.002	3.980	0.014	0.0149	0.0015	8.96	0.3068	0.0012	97.6	6.08	0.02	0.02
21940-03	182.06	0.14	26.16	0.03	0.320	0.002	0.334	0.006	0.0448	0.0016	9.23	0.0250	0.0004	92.7	6.09	0.02	0.02
21940-09	302.2	0.3	45.07	0.06	0.540	0.003	0.808	0.006	0.0364	0.0017	15.88	0.0351	0.0003	96.5	6.101	0.016	0.02
21940-10	341.9	0.3	52.10	0.06	0.636	0.003	0.880	0.008	0.0163	0.0018	18.35	0.0331	0.0003	98.6	6.104	0.015	0.02
21940-07	233.83	0.19	35.19	0.04	0.432	0.003	0.550	0.006	0.0176	0.0017	12.40	0.0306	0.0004	97.8	6.129	0.017	0.02
												0.03	**0.02**		**6.087**	**0.006**	**0.013**
L2-8																	
21944-06	241.9	0.2	33.07	0.04	0.412	0.002	2.521	0.012	0.101	0.002	11.66	0.1494	0.0007	87.7	6.03	0.02	0.02
21943-02	197.90	0.18	30.45	0.04	0.3655	0.0020	1.186	0.009	0.0061	0.0016	10.74	0.0763	0.0006	99.1	6.055	0.018	0.02
21943-03	271.9	0.3	41.53	0.05	0.507	0.002	1.414	0.009	0.0149	0.0018	14.65	0.0668	0.0004	98.4	6.057	0.016	0.02
21944-04	220.83	0.19	33.49	0.05	0.393	0.002	1.343	0.011	0.0126	0.0018	11.82	0.0786	0.0007	98.4	6.094	0.019	0.02
21943-04	308.8	0.3	47.01	0.05	0.560	0.002	2.053	0.011	0.0130	0.0019	16.58	0.0856	0.0005	98.8	6.099	0.015	0.02
21944-07	171.59	0.15	25.67	0.03	0.309	0.002	1.796	0.010	0.0176	0.0016	9.05	0.1371	0.0008	97.1	6.10	0.02	0.02
21944-05	171.66	0.16	26.16	0.04	0.311	0.002	1.246	0.008	0.0048	0.0016	9.23	0.0933	0.0006	99.2	6.12	0.02	0.02
21944-08	271.3	0.3	41.16	0.05	0.494	0.002	1.785	0.011	0.0113	0.0017	14.52	0.0850	0.0005	98.8	6.121	0.017	0.02
21943-01	406.6	0.4	61.17	0.07	0.739	0.003	2.115	0.010	0.0253	0.0020	21.57	0.0678	0.0003	98.2	6.135	0.014	0.02
21944-03	324.5	0.3	49.10	0.05	0.590	0.003	1.036	0.008	0.0089	0.0020	17.32	0.0413	0.0003	99.2	6.162	0.015	0.02
												0.073	**0.020**		**6.10**	**0.03**	**0.03**
Omitted, obvious outliers:																	
21943-05	227.07	0.19	33.47	0.04	0.402	0.002	0.368	0.006	0.0043	0.0015	11.81	0.0215	0.0003	99.5	6.340	0.017	0.02
21944-02	361.7	0.4	52.66	0.06	0.639	0.003	0.248	0.005	0.0292	0.0018	18.58	0.00923	0.00018	97.6	6.300	0.015	0.02
Omitted, % 40Ar* <80:																	
21944-01	518.5	0.5	47.92	0.06	0.698	0.003	4.973	0.019	0.672	0.005	16.90	0.2034	0.0008	61.8	6.28	0.04	0.04

Table 2. Summary $^{40}Ar/^{39}Ar$ dating results.

Sample	Lab ID no.	Ca/K	±1σ	MSWD	Prob.	n/n_{total}	Age (Ma)	±1σ
Locality 1								
speckled tuff: ~0.2 m, khaki-colored, massive, phenocryst-poor (~1%) tuff with subequal amounts of K-feldspar (to 3 mm) and altered mafic minerals, with fossil remains.								
L1-15	20834	0.03	0.02	0.12	0.99	6/9	6.084	0.018
Locality 2								
white tuff: ~0.8 m, very fine-grained phenocryst-poor (< 1% K-feldspar) white massive tuff.								
L2-4	21937	0.03	0.07	6.81	0.00	10/13	6.12	0.07
gray mottled tuff: ~0.4 m, white, well-indurated, pumice (to 2 cm, ~30–40% of rock) tuff with 10–20% euhedral phenocrysts of K-feldspar and minor biotite (< 1%, < 1 mm).								
L2-6	21940	0.034	0.020	1.49	0.13	11/11	6.087	0.013
gray cindery tuff: ~0.5 m, med-fine grained, gray, massive tuff with ~1–2% < 1 mm K-feldspar.								
L2-8	21944, 21943	0.073	0.020	5.73	0.00	10/13	6.10	0.03

experiments are influenced by geologic variability, or underestimated analytical errors, and are poorly diagnostic of the age of the eruptions they represent. Their weighted-mean ages of 6.12 ± 0.07 and 6.10 ± 0.03 Ma are nevertheless concordant with those of the better samples. It should be noted that the final dating results presented here differ slightly from preliminary results presented in Ambrose et al. (2003), due to application of the new data reduction protocols mentioned above.

Discussion

The fossiliferous horizons are bracketed by the stratigraphic interval encompassed by the four tuffs dated in this study. The most precise ages, 6.084 ± 0.019 for the speckled tuff, and 6.087 ± 0.013 for the middle of the three tuffs at Locality 2, are virtually identical, indicating that the 9 m or so of strata that separate these horizons were deposited in a narrow interval of time. Thus the fossiliferous horizons represent time-restricted snapshots of environments occurring in the Late Miocene. Lemudong'o is especially significant as it represents an isolated picture of Miocene stratigraphy and paleontology in a region of Kenya dominated by Plio-Pleistocene rocks.

It is worth noting that the dated sequence at Lemudong'o is almost exactly the same age as the oldest exposures at Kanam, Winam Gulf, northeastern Lake Victoria. Preliminary $^{40}Ar/^{39}Ar$ ages obtained by the author from the Kanam West strata of the Kanam Formation (Pickford, 1987) are virtually the same as those of the dated Lemudong'o tuffs. Lemudong'o lies about 250 km southeast of Kanam. It is possible that these similar, anorthoclase-bearing tuffs are correlative, though no attempt has yet been made to test this hypothesis through geochemical or mineralogical means.

Conclusions

$^{40}Ar/^{39}Ar$ dating of four tuff beds within fossiliferous lacustrine and riparian strata exposed near Lemudong'o, Kenya, yield the narrow age range of 6.08 to 6.12 Ma, or upper Miocene (middle Messinian) for the faunal assemblages. The Lemudong'o strata are precisely time-equivalent to at least part of the Kanam Formation (Pickford, 1987), and are broadly equivalent to the Lukeino Formation (5.88–5.72 Ma; Deino et al., 2002) and Mpesida Beds (7–6 Ma; Kingston et al., 2002) in the Tugen Hills, Kenya, the Nawata Formation at Lothagam (7.4–6.5 Ma; McDougall and Feibel, 1999), and the Adu-Asa Formation in the Middle Awash Valley (5.8–5.5 Ma for the vertebrate fossils; WoldeGabriel et al., 2001).

The environmental context of the Lemudong'o fossil assemblages lies midway along the spectrum of more open (Nawata) to relatively closed and wetter environments (Mpesida and Adu Asa) of six million years ago. Hominids or hominoids are present in wetter, closed habitats at Mpesida and Adu Asa, but have not been recovered from the mesic Lemudong'o and drier Nawata formations. If further research on East African sites belonging to the Messinian stage follows this pattern, then it may suggest that earliest hominid habitat preferences and hominid origins are not closely tied to the origin of savanna environments (WoldeGabriel et al., 1994).

Lemudong'o is one of the most securely dated late Miocene fossil sites in Africa and will provide a biostratigraphic marker for other fossil sites. Correlations with Lemudong'o will be especially important for sites where precise radiometric dating is not possible.

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A NEW LATE MIOCENE SPECIES OF *PARACOLOBUS* AND OTHER CERCOPITHECOIDEA (MAMMALIA: PRIMATES) FOSSILS FROM LEMUDONG'O, KENYA

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ABSTRACT

The Colobinae (Mammalia: Primates) are relatively unknown from the middle to late Miocene of eastern Africa. When they appear in the Pliocene fossil record they are unambiguous and fairly diverse taxonomically, geographically, and ecologically. The primate fauna from the late Miocene of Lemudong'o is dominated by colobines and therefore represents one of the richest fossil assemblages yet published of this subfamily at 6 Ma. At least three species of colobine, including a new species of *Paracolobus*, are represented in this collection. Given the paleoecological reconstruction for Lemudong'o Locality 1, and the postcranial morphology of the cercopithecids, colobines in this area of Africa were occupying a relatively closed or forested habitat, and exhibiting a primarily arboreal habitus, which contrasts with previous hypotheses suggesting that colobines prior to the Pliocene were terrestrial and occupying more open habitats.

Introduction

The cercopithecoids (Old World Monkeys) are commonly thought to have split molecularly from the homininoids (apes) 25–23 Ma, presumably in Africa (Kumar and Hedges, 1998), although a recent analysis suggests that it may have been 34–29 Ma (Steiper et al., 2004). During the early- to mid-Miocene, hominoids dominated the primate fossil record. Cercopithecoids are represented only by isolated teeth and jaw fragments, the oldest being from 19-Ma sediments at Napak, Uganda (Pilbeam and Walker, 1968).

The prevalence of hominoids over cercopithecoids started to shift 15 Ma, as is seen at the site of Maboko, Kenya, where significant numbers of cercopithecoid fossils have been recovered (Benefit, 1993, 1999). The Maboko cercopithecoid specimens are attributed to the genus *Victoriapithecus* and show a combination of traits that are primitive relative to the modern colobines and cercopithecines, and traits that are derived relative to the hominoids. Therefore, Benefit (1993) elevated the *Victoriapithecus* fossils to their own family, the Victoriapithecidae, a sister taxon to the Cercopithecidae that encompasses the Colobinae and Cercopithecinae. The latest known *Victoriapithecus* specimens are from the 12.5-Ma Ngorora Formation in Baringo, Kenya (Hill et al., 2002).

This family-level recognition of the *Victoriapithecus* fossils has been argued to elevate the Colobinae and Cercopithecinae to family level distinction as well (Jablonski, 2002, and references therein). Here, I follow the traditional taxonomic ranking and leave the Colobinae and Cercopithecinae differentiated at the subfamily level within the family Cercopithecidae.

The early evolutionary history of the Cercopithecidae remains relatively unknown. The Colobinae are particularly enigmatic in Africa until the Pliocene when they appear to have undergone a radiation of large-bodied forms. The earliest known African colobine specimens are *Microcolobus tugenensis* from Ngeringerowa in the Tugen Hills, Kenya, and a molar from Nakali, Kenya (Benefit and Pickford, 1986). These specimens indicate that colobines and cercopithecines diverged morphologically sometime before 9 Ma. This compares favorably with molecular data that place the split between colobines and cercopithecines at 17.9–14.4 Ma (Raaum et al., 2005).

Outside of eastern Africa, colobines of late Miocene age are known from Wadi Natron, Egypt (*Libypithecus*, perhaps also at Sahabi, Libya), Menacer, Algeria ("?*Colobus*" *flandrini*), and especially the many specimens of *Mesopithecus* from Eurasia (e.g., see Szalay and Delson, 1979; Delson et al., 2000; Jablonski, 2002).

The lower Nawata beds at Lothagam, Kenya, represent the best known late Miocene African cercopithecid assemblage published to date (Leakey et al., 2003). This collection is dominated by papionins (cercopithecines) that constitute 79% of the cranial collection (Leakey et al., 2003, p. 202). The colobines are relatively rare and are best represented by a partial cranium and mandible attributed to the new species *Cercopithecoides kerioensis* (Leakey et al., 2003, p. 216). This skull, KNM-LT 9277, is of unknown provenience, so its age is also unknown, and it may well derive from sediments much younger than the late Miocene (ibid.).

The secure ~7–6-Ma colobine specimens from Lothagam consist of largely isolated teeth and jaw fragments, a fragment of frontal bone, and a calcaneus (Leakey et al., 2003, p. 218–219). These were all attributed to "Colobinae species B" largely due to their similarity in size, which is slightly larger than the extant *Colobus guereza* (*abyssinicus*) (Leakey et al., 2003, p. 219; revised taxonomy, Grubb et al., 2003, p. 1343). These specimens do not preserve enough morphology to allocate them to genus, and therefore are of limited value to phylogenetic reconstructions. Most of the colobines from Lothagam derive from younger deposits.

The more complete and similarly aged cercopithecid fossils from Lemudong'o (Ambrose, Nyami, et al, 2007) fill an unknown gap in the evolutionary history of the colobines. There are 281 primate specimens recovered from the site of Lemudong'o. Six other specimens are from the associated sites of Kasiolei and Enamankeon. As described by Ambrose, Bell, et al. (2007) these sites are of equivalent age to Lemduong'o Locality 1 and are therefore considered penecontemporaneous at 6 Ma.

All of the specimens are identified to either Colobinae or Cercopithecidae subfamily indeterminate, indicating that the assemblage may be entirely dominated by colobines. This stands in sharp contrast to other late Miocene and early Pliocene sites where colobines are extremely rare (Grine and Hendey, 1981; Harris et al., 2003, p. 47–48; Leakey et al., 2003; Haile-Selassie et al., 2004). The slightly younger (5.65 Ma) Lukeino Formation is also reported to have a dominance and diversity of colobines in the primate fauna (Pickford and Senut, 2001), although these have not yet been fully published. The 4.4-Ma site of Aramis, Ethiopia also has an unusually high colobine representation, however this is more evenly split between colobines and cercopithecines (WoldeGabriel et al., 1994, p. 333; Frost, 2001a).

Although the Narok/Lemudong'o fossils are in some ways more complete than those found at Lothagam, they are still highly fragmentary. Among 174 dentognathic specimens, only 14 are multiple teeth in jaws. Of these 14, four are juvenile. Isolated colobine teeth are not usually taxonomically diagnostic below the subfamily level. Consequently, taxonomic diagnoses rely heavily on jaw and cranial morphology. The alpha taxonomy of this assemblage, which is the focus of this article, is therefore based on a rather small subset of the total assemblage.

Of the 107 postcranial elements recovered, only one was found in association with craniodental material. Although postcranial elements are not highly taxonomically informative, they do provide insights into the locomotor repertoire of the individual. For cercopithecoids, morphological variation in the distal humerus, proximal ulna, and proximal femur have proven to covary with locomotor habitus most closely. Therefore, the more complete humeral, ulnar, and femoral specimens from Lemudong'o will be discussed.

There are at least three colobine species represented at Lemudong'o Locality 1. The first and best-represented is a new species of *Paracolobus* that is intermediate in size between the other two taxa. The second is a much smaller species of indeterminate colobine morphology. The third is represented only by a few isolated teeth, but is a much larger indeterminate colobine.

Abbreviations

KNM	Kenya National Museum.
NK	Narok District, indicates fossils that are from localities within this district, including Lemudong'o Localities 1 and 2, Enamankeon Localities 1, 2, and 3, and Kasiolei Locality 1.

Dental abbreviations follow the convention of upper case letters = maxillary teeth, lower case = mandibular teeth.

Systematic Paleontology

Order Primates Linnaeus, 1758
Suborder Anthropoidea Mivart, 1864
Infraorder Catarrhini E. Geoffroy, 1812
Family Cercopithecidae Gray, 1821
Subfamily Colobinae Blyth, 1863 (1825)
Genus *Paracolobus*

Diagnosis

Following the revised diagnosis of Leakey (1982), the *Paracolobus* face is wide with a moderately long and broad muzzle. The nasal aperture is long with relatively thick lateral margins and a straight lateral profile. The mandibular body is deep and slender with no median mental canal on the symphysis. The premolars are relatively large. The P3 has a small protocone. The maxillary molars are wide relative to length and flare at the cervix. The postcranial elements mainly display features typical of arboreal colobines, but some traits appear to be intermediate between colobine and terrestrial cercopithecine morphology. *Paracolobus* differs from *Cercopithecoides* in having a deep slender mandible and P3 protocone. *Paracolobus* differs from *Rhinocolobus* in the short wide muzzle and may have had relatively larger cheek teeth compared with cranium size.

Type species

Paracolobus chemeroni (Leakey, 1969).

Remarks

Only two named species were previously known for *Paracolobus*, and both date to approximately 2 Ma: *P. chemeroni*, the type species named by R. E. F. Leakey (1969), and *P. mutiwa*, named by M. G. Leakey (1982). *Paracolobus chemeroni* is primarily known from one specimen, KNM-BC 3, a skull lacking the posterior and inferior portions of the cranium but preserving the frontal, face, maxilla, and complete mandible. A partial skeleton is associated with this cranium. Analysis of the postcranial morphology indicates that *P. chemeroni* is somewhat of a locomotory chimera. Although most of its anatomical features match those usually seen in aboreal colobines, a few others are more common to terrestrial colobines (Birchette, 1982). A mandibular corpus from 2.5-Ma deposits in the Afar Region of Ethiopia is also tentatively assigned to *P. chemeroni* (Frost, 2001b, p. 194).

Paracolobus mutiwa is known from the Omo and Lake Turkana drainage system (Leakey, 1982). The type specimen is KNM-ER 3843, a female right maxilla and premaxilla with P4–M3 and some cranial fragments. The hypodigm consists of jaw fragments and isolated teeth from the Omo, Ethiopia, and KNM-ER 125 (a right mandible with m2–3) from Area 130 of Koobi Fora, Kenya. Although there are no postcranial elements included in the original hypodigm of *P. mutiwa*, Leakey (1982, p. 168) maintained a locomotory mix of arboreality and terrestriality for the entire genus.

Paracolobus chemeroni is known only from a male specimen, and *P. mutiwa* from one male and one female specimen. These two species are quite similar in overall size, although *P. mutiwa* is slightly larger (Leakey, 1982, p. 162). The two species differ from each other in that *P. chemeroni* has a higher muzzle, maxillary fossa, and a wider molar region. The gonial region of the mandible in the largest specimen of *P. mutiwa*, L35-59, is expanded, a trait that has been interpreted to possibly be sexually dimorphic in another colobine, *Rhinocolobus* (Frost and Delson, 2002, p. 722).

A small collection of colobine fossils from Laetoli, Tanzania has also been referred to *Paracolobus* sp. indet. (Leakey and Delson, 1987). These specimens are mostly fragmentary jaws and teeth as well as two postcranial elements (femora). The mandibles are referred to *Paracolobus* because they lack the round robusticity and shallow depth of the mandibular corpus of *Cercopithecoides*. They differ from *Rhinocolobus* in that they appear to have bigger teeth relative to cranial size than *Rhinocolobus*, although this is difficult to demonstrate quantitatively because the specimens are so fragmentary (Leakey and Delson, 1987, p. 98). The Laetoli collection does not contain a mandible complete enough to determine the shape of the gonial region, and therefore it is unknown whether or not this structure expands posteriorly in this assemblage. Although they have some characters that most closely align them with *Paracolobus*, these specimens are smaller than both *P. chemeroni* and *P. mutiwa*, and may represent a new taxon (Leakey and Delson, 1987).

The femoral specimens from Laetoli are referred to *Paracolobus* because they are morphologically similar to the partial skeleton of *Paracolobus chemeroni* (KNM-BC 3), and different from *Cercopithecoides* (Leakey and Delson, 1987, p. 99).

The following new species diagnosis relies solely on craniodental features and not postcranial morphology, as the former are less influenced by epigenetic factors than the latter, given what is currently known about the genetic influences on skeletal morphology.

PARACOLOBUS ENKORIKAE sp. nov.

Figures 1–3

Specific diagnosis

Paracolobus enkorikae lacks the significant mandibular gonial expansion seen in *Kuseracolobus*, *Microcolobus*, and *Rhinocolobus*. The mandibular corporeal cross section is less robust and less rounded than is seen in *Cercopithecoides*, but rather deep and somewhat slender as in *Kuseracolobus*, *Paracolobus*, and *Colobus*, but not as slender as is seen in *Rhinocolobus*. The mandibular corpus is of uniform depth, although the inferior margin undulates slightly, reminiscent of both *Colobus* and *Paracolobus*. The anterior surface of the mandibular symphysis lacks both the mental ridges seen in *Procolobus* and the median mental foramen seen in *Procolobus*, *Rhinocolobus*, and *Cercopithecoides*. *Paracolobus enkorikae* has an inferior transverse torus, unlike *Microcolobus*. Unlike *Rhinocolobus* but similar to *Kuseracolobus*, *Paracolobus* and *Procolobus*, *P. enkorikae* has prominentia laterales.

Dentally, the mandibular canines of *P. enkorikae* do not curve labially, unlike *Mesopithecus* and *Colobus*. *Paracolobus enkorikae* has a P3 protocone, similar to *Paracolobus* but different from *Cercopithecoides*. *Paracolobus enkorikae* has a relatively long male p3, as is seen in *Colobus polykomos* and *Paracolobus chemeroni*, compared to *Victoriapithecus* and *Kuseracolobus*. As in *P. chemeroni*, the incisors of *P. enkorikae* are small relative to the first molar, especially in the mandibular dentition, relative to *Victoriapithecus* and *Colobus polykomos*.

The combination of the mandibular corporeal cross-sectional shape, the lack of a posteriorly expanding mandibular gonial region, the lack of mental ridges or median mental foramen, the presence of prominentia laterales, the slightly undulating inferior mandibular margin, and the presence of a P3 protocone aligns this new species most closely with known species of *Paracolobus*.

Paracolobus enkorikae differs from *P. mutiwa* and *P. chemeroni* most markedly in terms of size, as it is considerably smaller. On average, the dental linear measurements for *P. enkorikae* are 15% smaller than the means published for *P. mutiwa* and on average 30% smaller than *P. chemeroni* (KNM-BC 3) (See Table 2). *Paracolobus enkorikae* is approximately the same size as modern *Colobus polykomos* or slightly larger. *Paracolobus enkorikae* also differs from *P. mutiwa* in that it lacks the documented slight posterior expansion of the mandibular body, a character *P. enkorikae* shares with the type species of this genus, *P. chemeroni*.

Etymology

Enkorika is the name of the village near the site of Lemudong'o whose residents have generously hosted and supported our research in the area. This new species is named in their honor.

Holotype

KNM-NK 44770 (Figure 1) is a nearly complete mandible found in 2003 by Gabriel Ekalale in situ in the mudstones just below the speckled tuff in Area 7 at Lemudong'o Locality 1 (Ambrose et al., 2007a). This specimen preserves the right and left sides of the mandible, eight associated isolated maxillary teeth, fragmentary radius with the articular ends, right humeral shaft and separate (non-conjoining) right distal humerus. The mandible is missing the left gonial angle and ramus but preserves the entire mandibular corpus from the left m3 through the symphysis to the right m1. The symphysis is slightly distorted. The right corpus is broken and missing the inferior aspect below the m1–3. Mandibular crowns preserved: left m3–left canine, right i1, right c-p3, right p4 roots, and right m1–3. Maxillary crowns preserved: left I1–2, M1, and RI2–M1.

Hypodigm

KNM-NK 36515, right mandibular corpus with i1, c, and m1–2, left mandibular corpus with i1–p3, m2–3, left maxilla with P3–M3; KNM-NK 36586, left maxilla with broken C root, P3–4 and M2–3; KNM-NK 36587, left and right mandibular fragments with left c–m3, left i1–right i2, right p3, and right m1–2, right maxillary fragment with P3–M3; KNM-NK 40885, left mandibular corpus with m2; KNM-NK 41301, right mandibular corpus with m2–3; KNM-NK 42276, mandibular corpus with left i1, right p3–m3; KNM-NK 42346, associated left I1–right C and M1; KNM-NK 42376, associated maxillary P4–M2; KNM-NK 42388, right and left maxillary canine fragments; KNM-NK 44866, right and left m3 (antimeres); KNM-NK 44870, right p3.

Horizon

All specimens are from Lemudong'o Locality 1. Specimens for which exact provenience is known indicate that they derive from the mudstones and speckled tuff above the sands (Ambrose, Kyule, and Hlusko, 2007).

Description

Mandible

As noted above, KNM-NK 44770 (Figure 1) is a nearly complete mandible. All of the crowns are preserved save for the incisors and right p3–4. The symphysis is distorted and although

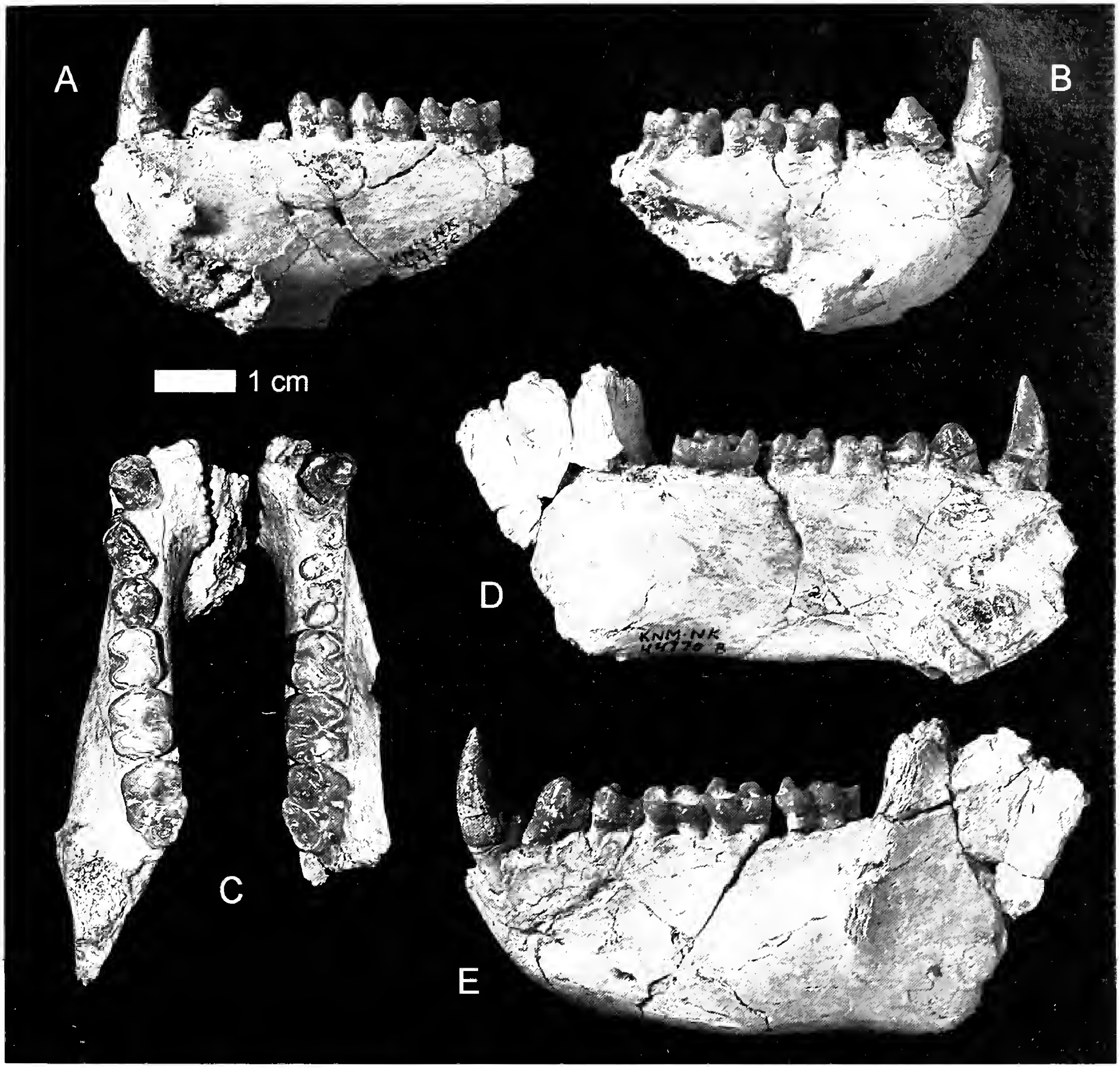

Figure 1. KNM-NK 44770, holotype of *Paracolobus enkorikae*. A, lingual view of the right mandible, mesial is to the left. B, buccal view of the right mandible, mesial is to the right. C, occlusal view, mesial is to the top. D, lingual view of the left mandible, mesial is to the right. E, buccal view of the left mandible, mesial is to the left. Scale bar = 1 cm.

both sides clearly join, the mandibular arch is distorted when they are in articulation.

There is a lateral mental foramen under the mesial root of p4 on both sides of KNM-NK 44770 as it is in KNM-BC 3, and there is no median mental foramen on the anterior aspect of the symphysis. The symphysis is deeper than is seen in *Colobus* with the inferior transverse torus extending to the p4/m1 contact.

The lingual surface of the mandibular symphysis is almost evenly divided from superior to inferior by the genioglossal pit. Modern *Colobus* has a more inferiorly located genioglossal pit compared to *P. enkorikae*. Both tori on KNM-NK 44770 are well developed, unlike *Microcolobus* that lacks an inferior transverse torus. The anterior surface of the KNM-NK 44770 symphysis is smooth and fairly straight, with no breaks in slope as is seen in some other fossil colobines, and no rugosity like KNM-KP 29255, *Cercopithecoides* sp. indet. (Harris et al., 2003, p. 48). The incisor row would have been rather narrow in life, more so than is seen in modern *Colobus*. Additionally, KNM-NK 44770 does not have a significant retromolar space, as is seen in *Colobus* and other fossil taxa, such as *Kuseracolobus*.

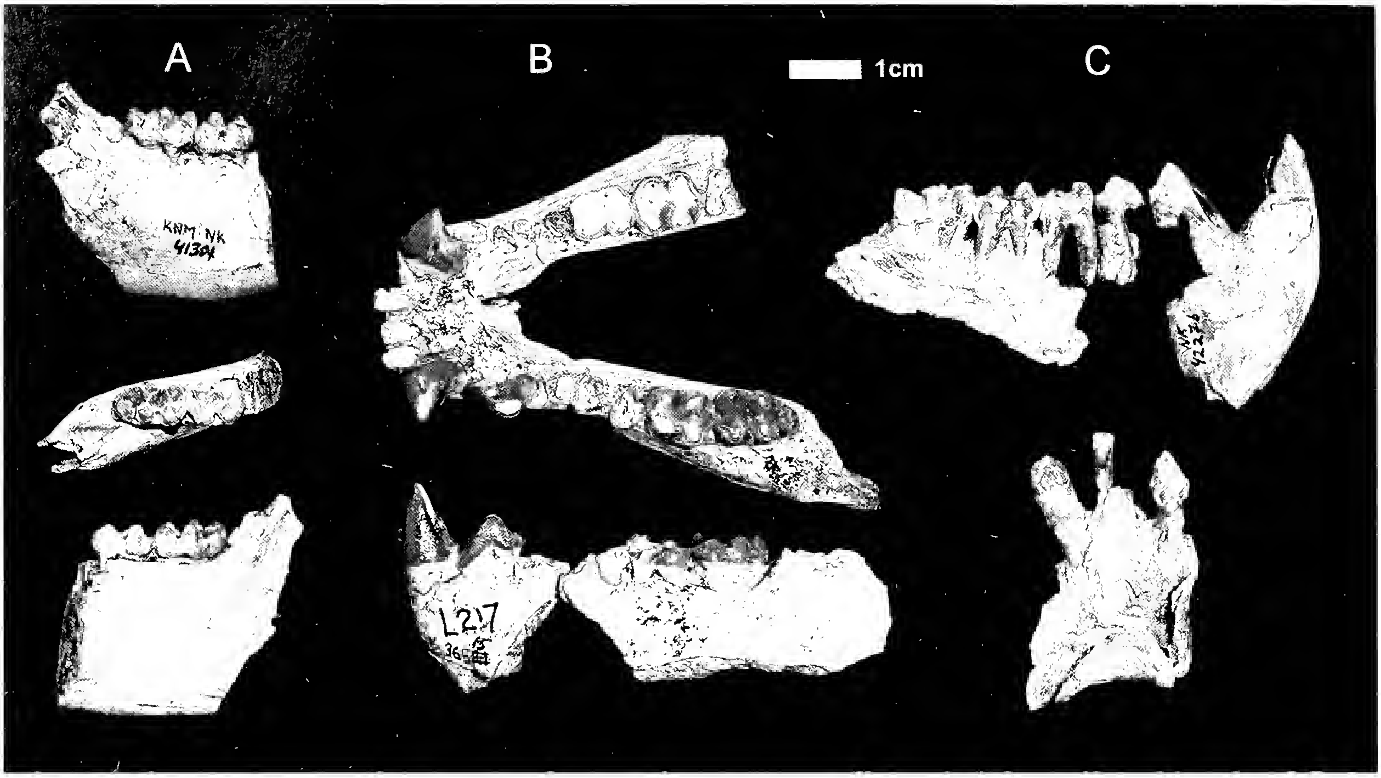

Figure 2. Mandibular material referred to *Paracolobus enkorikae*. A, KNM-NK 41301: (from top to bottom) buccal, occlusal, and lingual views. B, KNM-NK 36515: top, occlusal view; bottom, buccal view, mesial to the left. C, KNM-NK 42276: symphysis and right tooth row; top, buccal view; bottom, lingual view of symphysis. Scale bar = 1 cm.

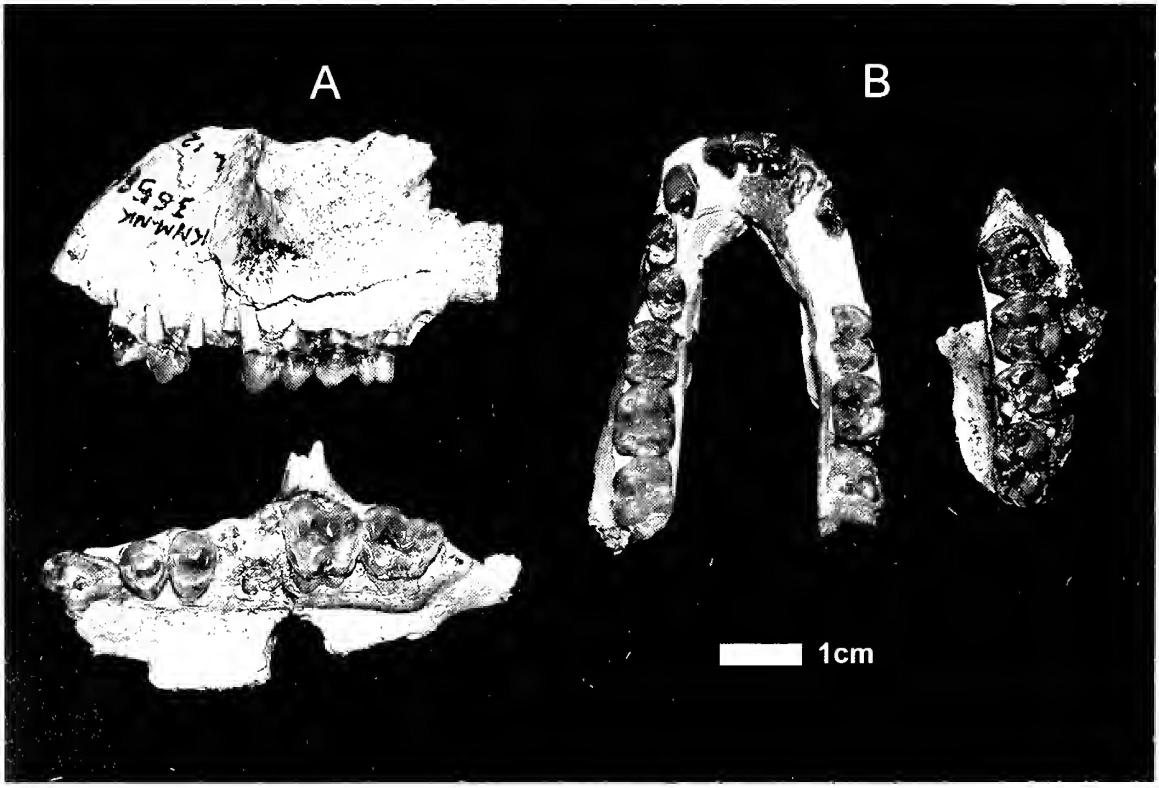

Figure 3. Maxillary and mandibular material referred to *Paracolobus enkorikae*. A, KNM-NK 36586: top, left buccal view; bottom, occlusal view, mesial is to the left. B, KNM-NK 36587: left, occlusal view of the mandible (the white material is molding putty to hold the specimens in approximate anatomical position); right, occlusal view of the maxillary specimen, mesial is towards the bottom. Scale bar = 1 cm.

Table 1A. Measurements of maxillary dental specimens from Lemudong'o Locality 1 by taxon.*

	KNM-NK	M3 md	M3 bl	M2 md	M2 bl	M1 md	M1 bl	P4 md	P4 bl	P3 md	P3 bl	C md	C bl	12 md	12 bl	I1 md	I1 bl
small	36516	6.55	7.21	7.05	8.14	7.10	7.42	5.06	6.81	4.58	5.88	—	—	—	—	—	—
	36550	6.19	6.35	6.05	6.61	5.85	6.06	—	—	3.82	5.23	6.00	4.28	—	—	—	—
	41321	7.06	7.48	7.89	8.14	7.30	7.42	4.77	6.93	—	—	6.72	4.75	—	—	—	—
	Average	6.66	7.01	7.00	7.63	6.75	6.97	4.92	6.87	4.20	5.56	6.36	4.28	—	—	—	—
P. enkorikae	36586	9.40	8.43	9.04	9.00	—	—	5.40	7.73	5.09	6.05	—	—	—	—	—	—
	36587	7.75	7.70	8.28	8.63	—	7.27	5.29	7.09	4.55	5.95	—	—	—	—	—	—
	42388	—	—	—	—	—	—	—	—	—	—	8.72	5.83	—	—	—	—
	44770	—	—	—	—	8.27	7.43	6.19	7.95	6.00	7.28	(7.29)	(5.41)	4.41	4.71	5.66	4.90
	Average	8.58	8.07	8.66	8.82	8.27	7.35	5.63	7.59	5.21	6.43	8.20	6.07	4.41	4.71	5.66	4.90

* Measurements in mm; parentheses = estimate; lower case letters = mandibular; upper case letters = maxillary; md = mesiodistal length; bl = buccolingual width (across the mesial loph(id) for molars, or labiolingual width for incisors); canine md length is the long—axis of the crown in cross—section.

Table 1B. Measurements of mandibular dental specimens from Lemudong'o Locality 1 by taxon.*

	KNM-NK	m1 or m2 md	m1 or m2 bl	m3 md	m3 bl	m2 md	m2 bl	m1 md	m1 bl	p4 md	p4 bl	p3 md	p3 bl	c md	c bl	i2 md	i2 bl	i1 md	i1 bl
Large	36555	—	—	—	—	—	—	10.03	7.77	(8.05)	5.53	11.49	5.62	—	—	—	—	—	—
	36502	10.13	8.04	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	42347	9.68	7.75	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	44860	—	—	—	—	—	—	—	—	—	—	—	—	9.82	7.63	—	—	—	—
	44867	—	—	—	—	—	—	—	—	—	—	11.56	5.66	—	—	—	—	—	—
	44868	—	—	—	—	—	—	—	—	(8.17)	5.66	—	—	—	—	—	—	—	—
	Average	9.91	7.90	—	—	—	—	10.03	7.77	8.11	5.60	11.53	5.64	9.82	7.63	—	—	—	—
Small	36514	—	—	8.50	5.27	6.46	6.06	6.01	5.13	5.03	4.50	5.25	4.63	—	—	—	—	—	—
	41305	—	—	8.72	—	6.86	—	6.14	5.24	—	—	—	—	—	—	—	—	—	—
	Average	—	—	8.61	5.27	6.66	6.06	6.08	5.19	5.03	4.50	5.25	4.63	—	—	—	—	—	—
P. enkorikae	36515	—	—	9.93	6.73	8.30	6.91	7.55	6.04	—	—	9.05	4.17	7.84	5.78	2.61	4.55	2.64	4.81
	36587	—	—	9.47	6.85	8.19	6.83	7.58	—	5.89	4.97	5.87	3.80	5.45	3.85	2.97	4.82	3.49	4.57
	40885	—	—	—	—	8.53	7.20	—	—	—	—	—	—	—	—	—	—	—	—
	41301	—	—	10.12	6.71	8.50	—	—	—	—	—	—	—	—	—	—	—	—	—
	42276	—	—	10.87	—	7.93	—	7.45	—	6.92	—	9.72	4.78	—	—	—	—	2.86	4.82
	44770	—	—	10.21	7.34	8.12	7.15	7.07	5.93	5.92	5.44	9.08	4.46	7.68	5.41	—	—	—	—
	44866	—	—	11.84	7.57	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Average	—	—	10.40	7.04	8.26	7.02	7.41	5.99	6.24	5.21	8.43	4.30	6.99	5.01	2.79	4.69	3.00	4.73

* Measurements in mm; parentheses = estimate; lower case letters = mandibular; upper case letters = maxillary; md = mesiodistal length; bl = buccolingual width, or labiolingual width for incisors; canine md length is the long-axis of the crown in cross-section.

In terms of the dentition, the canine of KNM-NK 44770 is large and the p3 has a long flange and significant wear facet for honing against the upper canine, indicating that this specimen is a male. The premolars and molars have the deep occlusal relief typical of colobines and are fairly worn. The p4 has a well developed talonid and is more square in occlusal outline than are *Colobus* p4s. The p3 is also buccolingually wider than *Colobus*, making both premolars appear more robust than in modern *Colobus*. The canine is similar in height to male *Colobus*, but straighter compared to the labially curved canines seen in *Colobus* males and *Mesopithecus*.

KNM-NK 36587 (Figure 3B) is an associated set of maxillary and mandibular fragments. This specimen is smaller than KNM-NK 44770 but morphologically similar. KNM-NK 36587 is presumed to be female based on its small size. The preserved molar crowns demonstrate the deep occlusal relief typical of colobines.

KNM-NK 42276 (Figure 2C) is a partial mandible preserving the symphysis with the left canine (broken), left i1, and right p3–m3 that join to the jaw fragments. The other three incisors are present but do not conjoin. The incisors are not flared and quite narrow. The right p3 has a heavily worn honing facet. Overall, KNM-NK 42276 is similar in size to KNM-NK 44770. The genioglossal is centered, as in KNM-NK 44770 but deeper, and unlike *Colobus*. The anterior surface of the symphysis is straight with no break in slope and essentially no rugosity, but a slight delineation of a triangle with apex at incisor midline running back to the inferior aspect of the mandibular body below the p3. KNM-NK 44770 has the same flattish surface, but not the slight ridge that delineates it as in KNM-NK 42276. KNM-NK 42276 also has a sharper inferior margin on the symphysis, whereas KNM-NK 44770 is more rounded. Otherwise, these two specimens share the same morphology. The teeth of KNM-NK 42276 are broken and cracked. The incisors are heavily worn. There is no median mental foramen.

KNM-NK 41301 (Figure 2A) is a partial right mandible with a break mesial to m2 and distal to the lateral ramal eminence of the ascending ramus. This specimen is virtually identical to, but slightly smaller than, KNM-NK 44770. The mandibular body is preserved, showing the depth of the corpus and lack of posterior expansion. The m2 is slightly worn and the m3 unworn save for slight wear facets.

Table 2. Measurements of *Paracolobus enkorikae* compared to *P. chemeroni*, *P. mutiwa*, and *Paracolobus* sp. from Laetoli, and *Victoriapithecus macinnesi* and *Colobus polykomos*.*

Maxillary	M3 md	M3 bl	M2 md	M2 bl	M1 md	M1 bl	P4 md	P4 bl	P3 md	P3 bl	C md	C bl	I2 md	I2 bl	I1 md	I1 bl
P. chemeroni	13.16	12.21	11.75	11.93	11.15	10.86	8.10	9.63	8.59	9.37	14.16	11.28	6.4	7.63	6.41	6.93
n =	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
P. mutiwa	14.00	11.4	12.2	13.0	10.4	10.8	7.7	10.2	(7.8)	9.5	—	—	—	—	—	—
n =	1	1	1	1	1	1	1	1	1	1						
Laetoli	10. 5	10.3	9.9	10.0	9.9	8.7	7.1	9.0	7.4	7.7	—	—	—	—	—	—
n =	1	1	2	2	4	2	1	1	1	1						
P. enkorikae	8.58	8.07	8.66	8.82	8.27	7.35	5.63	7.59	5.21	6.43	8.20	6.07	4.41	4.71	5.66	4.90
n =	2	2	2	2	1	2	3	3	3	3	2	2	1	1	1	1
V. macinnesi	6.45	7.14	7.28	8.06	6.17	6.59	4.65	6.5	4.45	5.4	7.6♂ 5.2♀	5.9♂ 4.3♀	3.61	3.95	5.13	4.1
n =	43	43	57	55	38	34	9	9	6	6	40♂ 44♀	40♂ 44♀	15	17	42	46
C. polykomos	7.6	6.9	7.5	7.4	7.0	6.5	5.2	6.7	5.3	5.6	9.8	6.5	4.6	4.4	5.1	4.7
♂ *n* =	43	44	48	48	49	49	47	48	49	48	40	38	42	42	43	44
C. polykomos	7.3	6.5	7.2	6.9	6.8	6.2	5.1	6.2	5.1	5.4	7.0	5.5	4.4	4.3	4.9	4.5
♀ *n* =	27	27	29	28	30	29	28	29	29	29	23	23	26	26	28	29
Mandibular	**M3 md**	**M3 bl**	**M2 md**	**M2 bl**	**M1 md**	**MI bl**	**P4 md**	**P4 bl**	**P3 md**	**P3 bl**	**C md**	**C bl**	**I2 md**	**I2 bl**	**I1 md**	**I1 bl**
P. chemeroni	16.04	10.03	12.44	9.5	11.28	7.77	9.53	7.09	14.28	7.68	11.57	8.13	5.22	6.25	5.09	5.79
n =	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
P. mutiwa	17.2	9.9	12.8	9.0	11.4	7.8	—	—	—	—	—	—	—	—	—	—
n =	7	7	8	8	6	4										
Laetoli	14.4	9.0	11.4	8.8	9.7	6.9	—	—	—	—	—	—	—	—	—	—
n =	2	2	4	3	6	3										
P. enkorikae	10.40	7.04	8.26	7.02	7.41	5.99	6.24	5.21	8.43	4.30	6.99	5.01	2.79	4.69	3.00	4.73
n =	6	5	6	4	4	2	3	2	4	4	3	3	2	2	3	3
V. macinnesi	8.87	6.33	7.38	6.72	6.12	5.26	5.58	4.72	7.2♂ 5.5♀	4.4♂ 4.1♀	6.6♂ 4.5♀	4.9♂ 3.4♀	3.05	3.86	3.37	3.76
n =	75	72	86	85	40	39	41	49	11♂ 9♀	14♂ 9♀	47♂ 28♀	47♂ 28♀	29	30	37	43
C. polykomos	9.6	6.3	7.7	6.3	7.2	5.5	6.1	4.9	9.1	5.2	6.9	6.9	3.8	4.8	3.7	4.4
♂ *n* =	43	44	47	45	47	45	48	46	44	45	37	36	37	38	38	38
C. polykomos	9.4	6.0	7.4	5.9	7.0	5.2	5.9	4.7	7.1	4.9	5.6	5.3	3.7	4.7	3.7	4.2
♀ *n* =	26	24	30	30	30	31	30	30	28	29	26	27	23	24	27	26

* Measurements in mm; parentheses = estimate; lower case letters = mandibular; upper case letters = maxillary; md = mesiodistal length; bl = buccolingual width (across the mesial loph(id) for molars, or labiolingual width for incisors); canine md length is the long-axis of the crown in cross-section. Data for *Paracolobus.* sp. from Laetoli is from Leakey (1982, p. 163–164), which is a more taxonomically conservative representation, and thus smaller sample size, than those data presented in Leakey and Delson (1987, p. 106–107) (Delson, pers. com.). Data for *P. chemeroni*, KNM-BC 3 measurements taken by the author, right and left sides averaged. Data for *P. mutiwa* are from Leakey (1982, p. 163–164). *Victoriapithecus macinnesi* data are from Benefit (1993, p. 94–96), pooled measurements from beds 3 and 5, male and female data presented separately for canine honing complex. *C. polykomos* male and female data from Swindler (2002, Appendix 1, tables 129–132, p. 230–231).

KNM-NK 36515 (Figure 2B) is a partial mandible with left m3, m2, roots of m1 and p4 (not shown), p3–right i1 crowns, right canine, p3–4 roots, and m1–2 crowns, and mesial m3 root. All teeth are very worn. The superior torus and genioglossal pit of the symphysis are preserved and are similar to KNM-NK 44770 but smaller. The left p3 honing facet is only slightly worn and the flange is shorter. This p3 morphology and the gracile canines suggest that it is a female.

Summary

Paracolobus enkorikae mandibles are similar in size or slightly larger than modern *Colobus polykomos*. There is significant sexual dimorphism in the canine/p3 honing complex and males are larger than females in overall size. Estimates of sexual dimorphism are based on a limited number of specimens, but is at most 20%. This range of variation is easily encompassed in the range of variation in modern *Colobus polykomos*, who have an average sexual dimorphism of 5% (Swindler, 2002, calculated from tables 129–132, p. 230–231).

Morphologically, the *P. enkorikae* mandibular body is fairly deep, similar to modern *Colobus*, but not as slender as *Rhinocolobus*. *Paracolobus enkorikae* has an undulating inferior mandibular margin when viewed from lateral, similar to *Colobus* and *Paracolobus chemeroni*, with a slight deepening just below m2, slight shallowing below m3, and then a slight increase in depth posteriorly, but it lacks the significant posterior expansion seen in other colobines such as seen in *Kuseracolobus*, *Rhinocolobus*, *Microcolobus*, and specimens of *P. mutiwa*. The mandibular corpus is not robust like *Cercopithecoides* but does have prominentia laterales where the lateral aspect of the ascending ramus originates below the m3.

The symphysis has a rounded slope on the anterior surface with a slight break just below the midpoint. There are no rugosities or mental ridges on the anterior symphysis. The lingual side of the symphysis has a characteristic cercopithecoid shape with both inferior and superior transverse tori, unlike *Microcolobus*. The genioglossal pit is deep and located at the midpoint, unlike the more inferiorly located genioglossal pit of *Colobus polykomos*. The inferior transverse torus extends to the p4/m1 contact. The superior transverse torus extends to mid p3 and is more inferiorly sloping compared to *P. chemeroni*. The KNM-BC 3 superior transverse torus is well-developed and shelflike extending posteriorly to mid p4.

Maxillae

There are four maxillary specimens attributed to *P. enkorikae*. Only two of these, KNM-NK 36586 and KNM-NK 36587, are relatively complete (Figure 3A and 3B, respectively). The other two specimens are associated isolated teeth and will be discussed in the dentition section below.

KNM-NK 36586 (Figure 3A) was the first fossil found at the site in 1995, discovered by M.D. Kyule. This is a left maxilla with LC root, LP3–4 crowns, LM1 roots, LM2–3 crowns. The palate is preserved from M1 to midline and then anterior, and includes the edge of the incisive foramen at mid P3. The canine root is large, suggesting this specimen is probably a male. The hard palate ends just distal to M3, which is unlike the extended hard palate of *Paracolobus chemeroni* that extends beyond M3. The M3 has a reduced distal buccolingual width but it is mesiodistally elongate with a third pair of cusps. The P3 is bicuspid with a well-developed protocone. The root of the zygomatic arch is at M2, like *Paracolobus* and *Colobus*. This indicates that *P. enkorikae* has a more prognathic face than is seen in *Kuseracolobus* and is more similar to *Paracolobus chemeroni*. The depth of palate is like *Colobus*.

KNM-NK 36587 (Figure 3B) is a maxillary fragment preserving the right P3–M3 and some alveolar bone. The cortical bone is missing on the buccal surface, exposing the roots. The palate is preserved almost to midline from P3–M2, showing that the palate was similar in depth to *Colobus* and narrow. The M3 is not mesiodistally reduced, as it is in the smaller specimens that are attributed to a separate species (see below). The P3 has a protocone. The P4 is bilophid and the molars have the deep cusp relief characteristie of colobines. All three molars have varying degrees of a protocone shelf development and a pit on the buccal surface in the notch between the protocone and hypocone. The M1 crown is broken and missing the mesial half of the paracone. Although it is difficult to say with certitude because of the missing cortical bone, the root of the zygomatic process is superior to the mesial root of M2, as in KNM-NK 36586.

Summary

The maxilla of *P. enkorikae* is smaller but morphologically quite similar to *P. chemeroni*. The root of the zygomatic arch originates superior to the M2 indicating that *P. enkorikae* was probably comparable to *P. chemeroni* in the prognathism of the snout. The root of the zygomatic process in *Kuseracolobus* is above M1, which implies it had a shorter snout. The *P. chemeroni* hard palate extends farther back than in *P. enkorikae*, beyond the M3, but in *P. enkorikae* it ends right at the distal edge of M3.

The postcanine tooth row in *P. enkorika* is more convex than in *P. chemeroni*, with its widest breadth at M2, whereas *P. chemeroni* has relatively straight maxillary postcanine tooth rows.

Dentition

Seven of the 11 specimens attributed to *P. enkorikae* consist of isolated or associated teeth not in jaws. Of these, four are mandibular and three maxillary. The following descriptions are based on these isolated teeth as well as those in the jaws described above. Measurements for all teeth are presented in Table 1.

The mandibular dentition is typically colobine in having deep occlusal relief, bilophid molars, and a paraconid on the p3. KNM-NK 40885 is a left m2 with some mandibular bone surrounding it. This has the deep cusp relief of a colobine and is associated with *P. enkorikae* because of its size (Table 1). KNM-NK 44866 is a pair of antimeric third molars with colobine cusp relief also associated with *P. enkorikae* because of size.

The KNM-NK 36587 mandibular molars that are associated with the maxillary specimens described above have steep cuspal relief and fairly deep grooves on the buccal side between the protoconid and hypoconid with a deep pit, but no interconulid. The molars are relatively unworn, the m3 has only small wear facets on the cusp tips, m2 has small dentine pits, and m1 is only moderately worn.

The p3 specimens of *P. enkorikae* are more narrow than *P. chemeroni* and *C. polykomos*, and more similar proportion-wise to *Victoriapithecus*. The m3 distal lophid is wider than the mesial lophid, a condition common to Asian colobines and sometimes considered primitive for the subfamily, although it is not seen in most African colobines after the late Pliocene (Szalay and Delson, 1979, p. 383).

Variation in the relative sizes of cercopithecid central and lateral incisors is high, but in terms of length, I1 is longer than I2 in both *P. enkorikae* and *Victoriapithecus*, whereas they are subequal in *P. chemeroni* and *C. polykomos*. The breadth decreases from i2 to i1 in *P. chemeroni* and *C. polykomos*, whereas in *Victoriapithecus* and *P. enkorikae* it is about the same. *Paracolobus enkorikae* I1 and I2 have almost the same buccolingual breadth, with I1 being slightly broader, which is the same for *Victoriapithecus* and *C. polykomos*, and different from *P. chemeroni*.

The maxillary specimens also include: KNM-NK 42388, a pair of canines; KNM-NK 42376, associated teeth that are digested and not measured for Table 1; and KNM-NK 42346, associated maxillary teeth.

The distal loph of the M3 of *P. enkorikae* is reduced in buccolingual width but is mesiodistally elongated. The M3 metacone is reduced and about the same size as the paracone, and there is a 3rd cusp pair (accessory cusps) in all known specimens of this new species.

Paracolobus enkorikae has relatively buccolingually narrow maxillary canines compared to other cercopithecids, save for female *Victoriapithecus macinnesi*. The length of the maxillary C is also relatively short compared to the other teeth, more like the proportions seen in female *Victoriapithecus macinnesi*.

Paracolobus enkorikae is quite similar in its dental proportions to *Victoriapithecus*, especially in terms of buccolingual widths (Figures 4 and 5). However, the strong dimorphism of the mesiodistal length of the male p3 is more like that seen in *P. chemeroni* than *Victoriapithecus* (Figure 4). The male maxillary canines of *P. enkorikae* appear to be less mesiodistally long than in male *P. chemeroni*, male *Kuseracolobus aramisi*, male *C. polykomos*, and male *Victoriapithecus macinnesi*.

Discussion

The remains of *P. enkorikae* are quite fragmentary, however they show that 6 Ma in the Narok area there was a colobine with close affinities to *P. chemeroni*, although it was considerably smaller, more like the size of modern *C. polykomos*. *Paracolobus enkorikae* has features that may be more primitive than *P. chemeroni*, such as sharing overall dental proportions with *Victoriapithecus macinnesi* relative to the other taxa compared in Figures 4 and 5. The shape of the mandibular corpus suggests that this genus may have closer evolutionary affinities to the modern *Colobus* monkeys than do many of the better known larger Plio-Pleistocene colobines such as *Rhinocolobus*, *Cerco-*

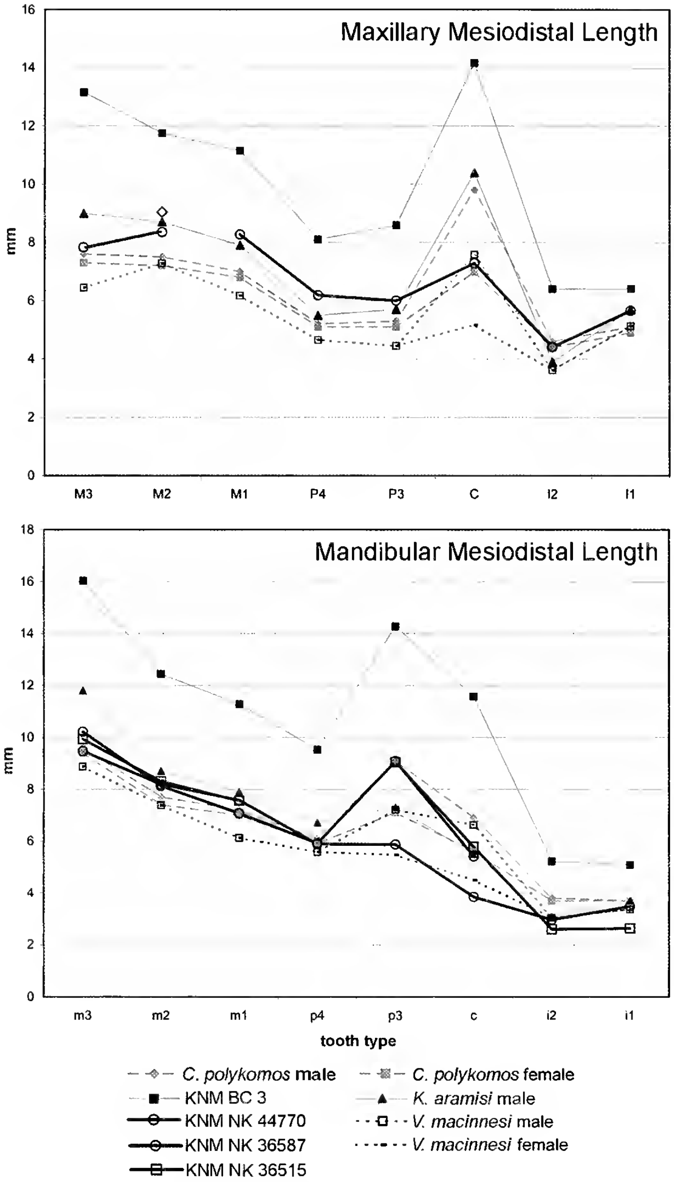

Figure 4. Line graph of maxillary and mandibular mesiodental tooth lengths of *P. enkorikae* and comparative specimens. Measurements are in mm.

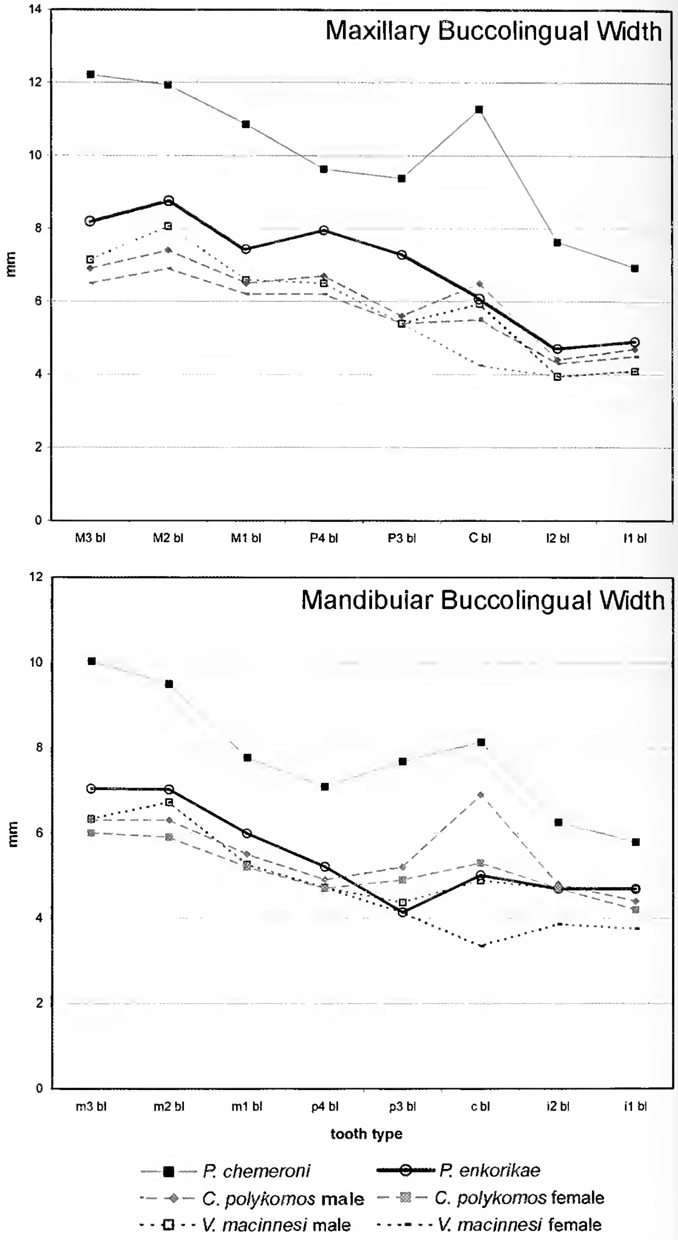

Figure 5. Line graph of maxillary and mandibular buccolingual tooth widths of *P. enkorikae* and comparative specimens. Measurements are in mm.

pithecoides, and *Kuseracolobus*. A better understanding of the genetic and non-genetic influences on mandibular corpus shape needs to be gained before the taxonomic significance of this variation can be adequately assessed.

Family Cercopithecidae Gray, 1821
Subfamily Colobinae Blyth, 1863 (1825)
Genus and species indeterminate
SMALL TAXON
Figure 6

Referred material

KNM-NK 36514 right mandible with p3–m3; KNM-NK 36516 left maxilla with P3–M3; KNM-NK 36550 maxillary fragment with right C–P3 and left M1–3; KNM-NK 41305 mandibular fragments with right m2–3 and left p4–m2; KNM-NK 41321 right maxillary fragment with P4–M3 and associated left M2 and left C.

Description

The premolar cusp relief of KNM-NK 36514 (Figure 6A) is sharp, even when compared to other colobines. There is a mental foramen below p4. The honing wear on the p3 is only on the surface superior to the paraconid, and not on the flange, which is uncommon. The mandibular body is relatively shallow and gracile. The inferior half of the labial surface and the entire lingual surface of the mandibular symphysis is preserved. The inferior transverse torus extends distally/posteriorly to the midpoint of the p4. The inferior transverse torus is diminutive but present, therefore ruling out an affinity to *Microcolobus*. The genioglossal pit is shallow and located inferiorly compared to *P. enkorikae*, and is more similar to modern *Colobus*. The inferior edge of the symphysis is well delineated, and not rounded as in *P.*

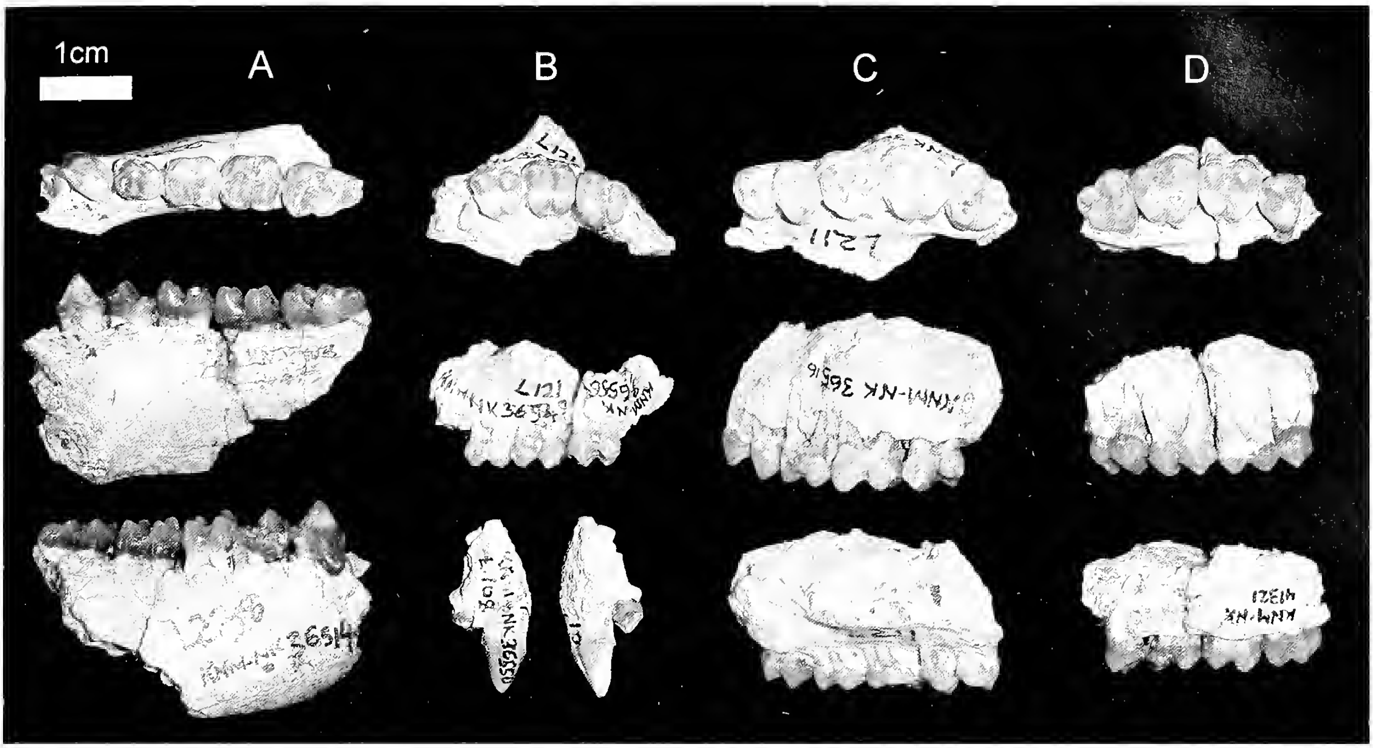

Figure 6. Specimens attributed to the small taxon of Colobinae gen. et sp. indet. A, KNM-NK 36514: from top to bottom: occlusal, lingual, and buccal views. B, KNM-NK 36550: top: occlusal view, mesial to left, middle: buccal view, mesial to the left, bottom left: buccal view, bottom right: lingual view. C, KNM-NK 36516: top to bottom: occlusal, buccal, and lingual views. D, KNM-NK 41321: top to bottom: occlusal, buccal, and lingual views. Scale bar = 1 cm.

enkorikae. Although the symphysis is damaged, it suggests that the shape of the mandible would have been more V-shaped than is common in modern colobines, such as *Colobus*.

KNM-NK 41305 (not shown) is approximately the same size as KNM-NK 36514 but the m3 is slightly longer mesiodistally. The right m1–3 are preserved but the m1 is missing the mesiobuccal side of the protoconid. The entire lingual half of the m2 is missing. The m3 metaconid is broken and missing the mesiolingual aspect, and the buccal enamel of the protoconid is spawled off. Only the superior half of the mandibular corpus is preserved and is identical to KNM-NK 36514. This specimen also has the distal half of the left p4 crown, broken left m1, and left m2 with the surrounding alveolar bone.

Although some of the palate of KNM-NK 36516 (Figure 6C) is preserved, neither the midline nor the anterior part of the greater palatine groove is present. The distal half of the M3 is reduced. The palatal depth is comparable to *Colobus* but the tooth row is more buccally arched. The P3 is more oval in shape than in *Colobus* with a well developed ridge on the mesial aspect and a protocone (bicuspid). The root of the zygomatic process is above the M2 suggesting that this colobine was fairly prognathic.

The fragmentary fossils that comprise KNM-NK 36550 (Figure 6B) were originally accessioned with different KNM-NK numbers that can be seen in the photographs. The zygomatic root is above the M1/M2 contact. The molars have the deep occlusal relief typical of colobines. The M3 is reduced distally. This maxilla is a good size and morphological match for the KNM-NK 36514 and KNM-NK 41305 mandibles, although they are not from the same individuals.

The zygomatic root of KNM-NK 41321 (Figure 6D) is located above M2, and the tooth row is convex as is KNM-NK 36516. KNM-NK 41321 and KNM-NK 36516 are also approximately the same size. The lateral aspect of the greater palatine groove is preserved and again looks like KNM-NK 36516. Maxillary P4 are more asymmetrical than in *Colobus*. An isolated LM2 and LC are associated.

Measurements for all teeth are presented in Table 1.

Discussion

Aside from the size differences between these specimens and those attributed to *P. enkorikae*, there are several morphological differences. The small maxillae have relatively shorter molar rows relative to the premolars, and the maxillary postcanine tooth row is more convex than in *P. enkorikae*. The hard palate of the smaller taxon (e.g., KNM-NK 36516 and KNM-NK 41321) ends at M2 whereas in *P. enkorikae* the hard palate extends to and beyond the M3. The mandible of the smaller taxon lacks the deep genioglossal pit of *P. enkorikae*, as well as the deep mandibular body. These morphological differences coupled with the lack of size overlap indicates that these smaller specimens represent another colobine species.

Due to their fragmentary nature, the taxonomic affinity of these specimens is uncertain. However, they do not share any obviously derived similarities with the known Pliocene genera. When compared to northern African specimens of *Libypithecus*, they are similarly distinct. These Lemudong'o specimens do not show the prognathism or increase in maxillary molar size from

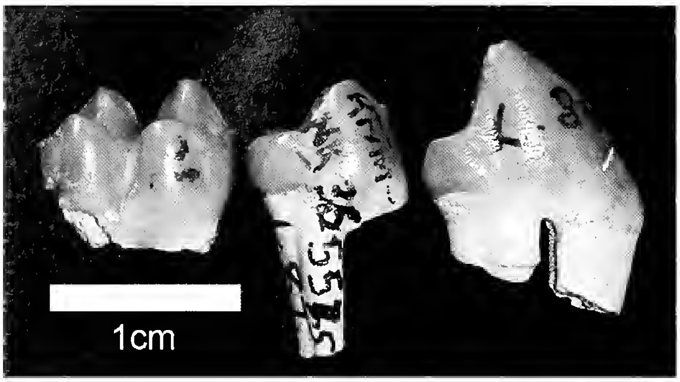

Figure 7. Specimens attributed to the large taxon of Colobinae gen. et sp. indet. KNM-NK 36555, buccal view, mesial is to the right. Scale bar = 1 cm.

anterior to posterior, characteristic of *Libypithecus*. The maxillary tooth row is more buccally curved than in *Colobus* and many other colobines. It is not known whether or not the mandibular corpus expanded posteriorly like *Kuseracolobus* or was uniform in depth like *P. enkorikae*.

Family Cercopithecidae Gray, 1821
Subfamily Colobinae Blyth, 1863 (1825)
Genus and species indeterminate
LARGE TAXON

Figure 7

Referred material

KNM-NK 36502 left m1 or m2; KNM-NK 36555 mandibular dentition with Lp3–4, Rp3–m1, probably associated with KNM-NK 36502; KNM-NK 42347 right m1 or m2; KNM-NK 44860 lower left canine; KNM-NK 44867 right p3; KNM-NK 44868 left p4.

Description

All of these specimens are isolated or associated teeth. There are no jaws. Based on the preservation, it is most likely that these specimens derive from the sands below the more fossiliferous mudstones, from which *P. enkorikae* is predominantly found. Measurements for all teeth are presented in Table 1. These specimens are roughly the size of a female *Papio cynocephalus* (Swindler, 2002, table 124, p. 227).

The morphology of these crowns is typical for colobines, with deep occlusal relief, bilophodont molars, and a paraconid on the p3. Although they are morphologically similar to the other colobines from Lemudong'o, they are attributed to a different taxon because they are considerably larger (Table 1). Figure 7 shows three associated teeth, KNM-NK 36555. The p3 of this set has a short flange, typical of females. When compared to *P. enkorikae*, this female specimen is 25% longer than the length of the male KNM-NK 44770 p3 and the first molar is about 65% longer than the m1 of the small taxon.

The morphology of these teeth does not show any features unusual for a colobine, and no jaw or cranial specimens have been recovered to date. Therefore, the most specific designation that can be made is to Colobinae genus and species indeterminate.

Postcrania

Figure 8

There are 107 non-dentognathic specimens attributed to the Cercopithecoidea from the late Miocene sediments in the Narok District. These include small cranial fragments ($n = 5$), vertebral

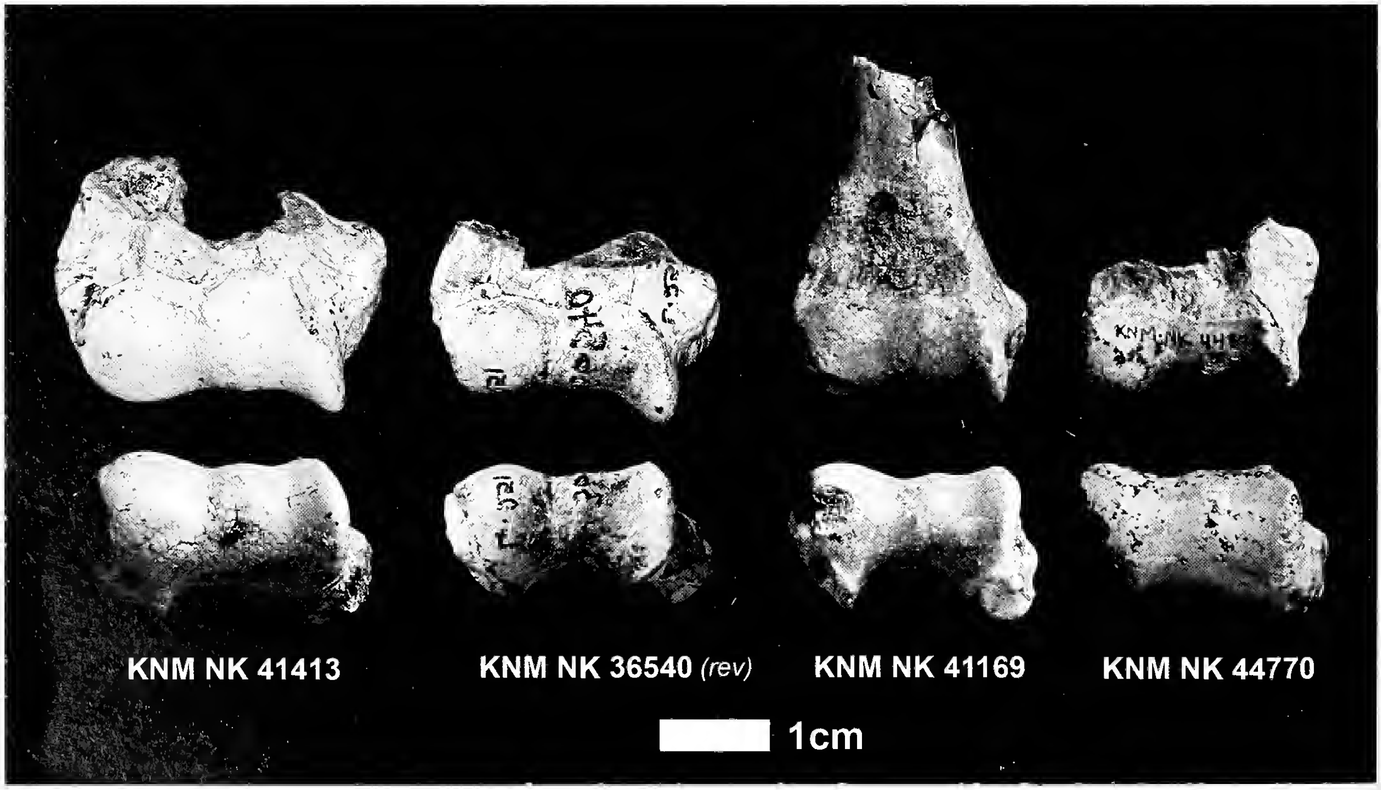

Figure 8. Distal humeral specimens, labeled in figure. Top row: ventral view. Bottom row: inferior view. Scale bar = 1 cm.

Table 3. Ratios and angle measurements for distal humeri from Lemudong'o.*

KNM-NK Specimen No.	Epicondyle ratio	Epidondyle angle	Relative flange length
36540	18	32°	57
41169	7.9	55°	58
41413	13.7	49°	50
44770	—	35°	—

* See text for explanation.

and axial fragments (n = 7), phalanges (n = 20), metapodials (n = 11), carpals/tarsals/patella (n = 14), ulnae (n = 9), radii (n = 14), humeri (n = 17), tibiae (n = 5), and femora (n = 5). All are fragmentary. Only one fragment of distal humerus was found in association with craniodental material, KNM-NK 44770, the type specimen for *P. enkorikae* (see above).

Although isolated and fragmentary cercopithecoid postcranial specimens are not typically useful for alpha taxonomy, some elements demonstrate morphological traits that correlate with various locomotor repertoires in modern cercopithecids (e.g., Birchette, 1982; Rose, 1993; Elton, 2001; Frost and Delson, 2002). Animals are functionally integrated units, and therefore interpretations of locomotor patterns based on partial anatomical information must be done with caution. With this caveat in mind, morphological variation in the primate elbow joint and femur has been demonstrated to correlate with habitual arboreality and terrestriality and can therefore provide information about the locomotor habitus of extinct taxa (Birchette, 1982; Rose, 1993; Elton, 2001).

The Narok collection includes only three complete distal humeri: KNM-NK 41413, KNM-NK 41169, and KNM-NK 36540. These specimens are similar in size (Figure 8) and slightly larger than modern *Colobus guereza* (*abyssinicus*) *kikuyuensis*. Given the similarities between these more complete humeri and KNM-NK 44770, the type specimen of *P. enkorikae*, these humeral specimens may be conspecific (see Figure 8).

Three features of the distal humerus have been suggested to be indicative of the locomotory repertoire in Old World Monkeys: the relative inferior projection of the trochlear keel (flange length), the orientation of the medial epicondyle (epicondyle angle), and epicondyle ratio. The measurements and indices are presented in Table 3.

When compared to Frost and Delson (2002, fig. 12, p. 709), the relative flange-length index categorizes these Lemudong'o specimens with the arboreal *Procolobus*, *Nasalis*, and *Colobus*. This compares with those values reported for *Paracolobus chemeroni* (Birchette, 1982, p. 166).

The epicondyle ratio aligns KNM-NK 41413 and KNM-NK 36540 well within the range of *Procolobus* and *Colobus*. KNM-NK 41169 is located at the lower end of the *Colobus* range, and aligns more with terrestrial genera. However, the more terrestrial-looking epicondyle ratio of KNM-NK 41169 is paired with a relative flange length that looks like more arboreal extant genera (Frost and Delson, 2002, fig. 10, p. 707). This proportion of articular surface compares to that reported for *Paracolobus chemeroni* (Birchette, 1982, p. 163–164).

The epicondyle angles for KNM-NK 41413 and KNM-NK 36540 also fall within the range of variation seen in two modern arboreal colobines, *Colobus guereza* and *Presbytis*. KNM-NK 41169 is within the confidence range for *Colobus guereza*, but better aligns with the variation seen in terrestrial species such as *Chlorocebus aethiops*, *Theropithecus gelada* and *Macaca fascicularis* (Frost and Delson, 2002, fig. 11, p. 708). Again, this compares with the medial epicondyle retroflexion reported for *Paracolobus chemeroni* (Birchette, 1982, p. 161).

These three humeri and the less complete KNM-NK 44770 fall within the range of variation expected for one colobine species that is slightly larger than a modern *Colobus guereza*. Based on dental morphology, KNM-NK 44770 is presumed to be male. The size of the distal humerus aligns with this interpretation, as this specimen is relatively large compared to the three humeri. KNM-NK 41169 is much smaller and may have been a female of the same species.

Ulnae have also proven useful in differentiating terrestrial from arboreal extant colobines. In particular is the retro- or anteflexion of the ulnar olecranon process, as the former is more common in terrestrial taxa and the latter in arboreal taxa (Birchette, 1982, p. 240–242). The ulnae from Lemudong'o Locality 1 have anteflexed olecranon processes, anatomy that is often associated with arboreality in cercopithecoids.

The postcranial specimens thus lend further support to the congeneric interpretation of *P. enkorikae* and *P. chemeroni*, as they both share the same combination of distal humeral and proximal ulnar morphology. The large size difference between these two species suggests that this unusual combination of postcranial features is not an allometric phenomenon.

Femora have also been used to reconstruct locomotor regimes (Frost and Delson, 2002). There is only one relatively complete proximal femur from Lemudong'o, KNM-NK 41175 (not shown). The relative greater trochanter projection for this specimen yields an index of 37.9, which is similar to the arboreal *Colobus guereza* and *Procolobus badius* (Frost and Delson, 2002, fig. 15, p. 712).

Although fragmentary, the postcranial remains from the late Miocene sediments in Narok suggest that the colobines represented in this sample were arboreal. The majority of specimens are within the size range of variation expected for one colobine species similar in sexual dimorphism and slightly larger than modern *Colobus kikyuensis*, and may belong primarily to the new species *P. enkorikae*.

Conclusions

Prior to the recent discovery of, and intense research at, several late Miocene fossil localities in eastern Africa, little was known about the earliest colobines outside of extremely sparse and fragmentary remains (Jablonski, 2002). With its unusually high proportion of colobines, Lemudong'o Locality 1 represents a unique window into the late Miocene evolution of colobines.

Within the Narok material, at least three colobine species are represented: one small, one large, and one intermediate in size belonging to the new species *Paracolobus enkorikae*. These have non-overlapping size ranges, and there are distinct morphological dentognathic differences between *P. enkorikae* and the small taxon.

The two previously recognized species of *Paracolobus* are known from significantly younger deposits: *P. chemeroni* dates from 3.2 Ma (Deino and Hill, 2002, p. 150) and *P. mutiwa* dates from 3.36 to 1.88 Ma (Jablonski, 2002). The new species described here dramatically increases the time range for this genus. The similarities between *P. enkorikae* and *Victoriapithecus* and lack of autapomorphic features does not preclude this genus from being ancestral to any of the Pliocene genera.

These three colobine taxa also inform our understanding of the paleoecology and paleobiology of colobines in the late Miocene. It has been argued that the earliest colobines were predominately terrestrial, in sharp contrast to the largely arboreal habitus of the extant representatives of this clade (Harris et al., 2003; Leakey et al., 2003). There are two lines of disparate evidence used to bolster this interpretation. The first is that two of the Pliocene colobine genera (*Cercopithecoides* and *Paracolobus*) are often described as having some terrestrial adaptations in their postcranial skeletons (Birchette, 1982). The second line of evidence is that the earliest known cercopithecoid, *Victoriapithecus* from the middle Miocene of Kenya, was a terrestrial frugivore (Benefit, 1999, and references therein). If terrestrial substrate use is primitive for the colobine clade, then the current arboreality in Asian and African colobines arose independently through parallel evolution.

However, the presence of an apparently modern type of arboreality in *Rhinocolobus* (Jablonski, 2002) and the arboreal *Kuseracolobus hafu* (Hlusko, 2006) in the early Pliocene indicate that the most parsimonious scenario is that of an arboreal last common ancestor. *Paracolobus chemeroni*'s unique features have been somewhat of an enigma, especially since they are characterized by only one specimen, KNM-BC 3.

The *P. enkorikae* fossils from Lemudong'o therefore provide an important new insight into the precursors to the radiation of large-bodied colobines seen in the Pliocene. The Lemudong'o mudstone-fossil-horizon fauna is best characterized as representative of a fairly closed, if not forested environment (Ambrose, Bell, et al., 2007). This cercopithecoid assemblage is comprised entirely of colobines or specimens that are indeterminate of subfamily. Therefore, there were at least three colobine species living within close proximity of each other, which were possibly sympatric. The combination of these features with postcranial anatomy most similar to modern arborealists suggests that the earliest colobines, or at least some of their descendants in the late Miocene, were occupying an ecological niche quite similar to modern colobines. Or, these fossils indicate that at least a subset of colobines living about 6 Ma inhabited a niche similar to their extant sister taxa.

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EARLIEST EVIDENCE FOR *ATHERURUS* AND *XENOHYSTRIX* (HYSTRICIDAE, RODENTIA) IN AFRICA, FROM THE LATE MIOCENE SITE OF LEMUDONG'O, KENYA

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ABSTRACT

Eleven Hystricidae teeth have been recovered from the mammalian-dominated fossil locality of Lemudong'o, Kenya. This site dates to the late Miocene, making these fragmentary specimens some of the earliest representatives of this family in Africa. As is typical in porcupine systematics, identifications of isolated teeth are based primarily on size. Three taxa are represented: *Xenohystrix* sp. indet., *Hystrix* sp. indet., and *Atherurus* sp. indet. Lemudong'o documents the earliest occurrence of *Xenohystrix* and *Atherurus* in Africa, and is characterized by a relatively wide diversity of porcupines.

Introduction

Porcupines, members of the family Hystricidae, are categorized within the suborder Hystricomorpha of the Rodentia. The hystricomorphs are divided into two geographic and evolutionary groups, the Old World families (e.g., Hystricidae, Thryonomyidae, Petromyidae, and Bathyergidae) and the New World families (often attributed to their own infraorder, the Caviomorpha, including the Erethizontidae, Caviidae, Hydrochaeridae, and others). Based on molecular data, the Old World and New World taxa are estimated to have split between 63 and 46 Ma, and the Hystricidae would have diverged 54–43 Ma from the other Old World hystricomorpha families (Huchon and Douzery, 2001, p. 245).

Extant Old World porcupines typically are categorized into three genera: *Atherurus*, *Trichys*, and *Hystrix* (Kingdon, 1974; Nowak, 1991), although the latter is sometimes divided into *Hystrix* and *Thecurus* (van Weers, 1978). Here, I will follow the taxonomy of Nowak (1991), recognizing only three extant genera.

Old World porcupines have a wide geographic distribution (Kingdon, 1974, p. 679–695; Nowak, 1991, p. 895–900). *Trichys* is found on the Malay Peninsula, Sumatra, and Borneo. *Atherurus* is found in Asia and sub-Saharan Africa. *Hystrix* has the broadest range, and is found in China, Southeast Asia, Indonesia, Indo-Pakistan, the Mediterranean region, and eastern and sub-Saharan Africa.

To date, no fossils of *Trichys* have been found, which may result from their preference for swampy habitats (Lim et al., 1989, p. 23). Fossil specimens attributed to the Asian *Atherurus* have only been published from Pleistocene sites in Asia (van Weers, 2002), and the African *Atherurus* from the late Miocene in Ethiopia (Haile-Selassie et al., 2004). *Hystrix* fossil taxa are much more abundant, and are known from the Miocene through Pleistocene of Asia, Europe, and Africa. The extinct genus *Xenohystrix* is only known from the late Miocene and Pliocene fossil record of eastern and southern Africa (Greenwood, 1955; Howell and Coppens, 1974; Maguire, 1978; Sabatier, 1979; Haile-Selassie, 2001; Haile-Selassie et al., 2004).

The earliest fossils attributable to the Hystricidae date to MN 11/12 and MN 13 (Turolian ≈ 8–6 Ma). These early specimens have recently been reviewed and revised by van Weers and Rook (2003) and, therefore, will not be repeated here. However, to briefly summarize the dental evolution, all of the specimens from this early record have been attributed to the genus *Hystrix*. The earliest species is *Hystrix primigenia*, a very large, low-crowned porcupine from sites in southeastern Europe and Asia ranging from MN 11 to MN 13 (8–6 Ma) (Masini and Rook, 1993; Fistani et al., 1997; van Weers and Rook, 2003). *Hystrix depereti* is slightly larger than *H. primigenia* on average and with relatively somewhat taller cheek-tooth crowns. *Hystrix depereti* ranges geographically from Spain to Turkey during the late Miocene and Pliocene (MN 12–MN 15).

Hystrix aryanensis is only known from the Khurdkabul Basin in Afghanistan, dated roughly to the late Miocene (Thomas and Petter, 1986, p. 361). This species is approximately the same size as the extant *H. cristata*, and, therefore, has smaller, but relatively taller-crowned teeth than *H. primigenia*. The relatively taller crowns seen in *H. aryanensis* and *H. depereti* relative to *H. primigenia* show that the marked increase in hypsodonty seen in later forms probably started to develop in the late Miocene.

These early *Hystrix* species are followed by *H. refossa*, which is known from central and southern Europe and Israel and dates from the early Pliocene through the Pleistocene. This species is also much larger than extant *Hystrix* species, approximating the size of *H. primigenia* although it is distinct from this species and *H. depereti* in having more hypsodont cheek teeth.

During the late Pliocene *Hystrix zhengi* is known from two sites in China, Longgupo in the Sichuan Province and the *Gigantopithecus* Cave in Liucheng, Guangxi (van Weers and Zhang, 1999). This species is larger than all extant *Hystrix* species and its hypsodonty is intermediate between the earlier *Hystrix* species in Europe and later *Hystrix*.

The early and middle Pleistocene fossils from China have been separated as two other species with somewhat overlapping size ranges: *H. kiangsenensis* is smaller than *H. magna* and the two species appear to have been sympatric, or at least to have been recovered from the same sites (van Weers and Zheng, 1998). Both of these Chinese species have much more hypsodont cheek teeth than the earlier *H. zhengi* (van Weers and Shaohua, 1998; van Weers and Zhaoqun, 1999).

Another extinct fossil porcupine, *Hystrix lagrelli* is known from the Pleistocene of both Java and China (van Weers, 1995). This species may represent the sister taxon to the extant *Hystrix* species currently found on Sumatra, Borneo, and the Phillipines that comprise the sub-genus *Thecurus* (van Weers, 1995).

The site of Sangiran on Java in Indonesia has yielded three isolated teeth that van Weers attributed to a large porcupine, *Hystrix gigantean*, whose cheek teeth are larger than *H. indica* and *H. africaeaustralis*, and which are extremely hypsodont (van Weers, 1985, p. 118).

The African-porcupine fossil record has received much less attention than those of Europe and Asia, and therefore is less well understood. The earliest fossil evidence for porcupines in Africa is a dP4 from the Lower Nawata beds at Lothagam, Kenya (estimated to be older than 7.44 Ma), attributed to a small *Hystrix* sp. indet (Winkler, 2003, p. 172–3). Other specimens dated to the late Miocene are also quite limited and fragmentary, and include fossils from the Tugen Hills in Kenya that are conferred only to Hystricidae indet. (Pickford, 1975; Winkler, 2002, p. 241), and partial jaw fragments and isolated teeth representative of three genera (*Xenohystrix*, *Hystrix*, and *Atherurus*) from the 5.7–5.2 Ma West Margin sites in Ethiopia (Haile-Selassie et al., 2004).

The Pliocene documents relatively considerable porcupine diversity in Africa. The site of Makapansgat in South Africa yielded very large porcupine specimens that were described as *Xenohystrix crassidens* (Greenwood, 1955). This genus has also been recovered from Laetoli, Tanzania (Denys, 1987, p. 154). Another fairly large porcupine *Hystrix makapanensis* is also known from Makapansgat (Greenwood, 1955, 1958) and Laetoli (Denys, 1987, p. 154). Specimens similar in size to modern *H. africaeaustralis* have been reported from Makapansgat (Greenwood, 1955; Maguire, 1978) as well as from the Omo and Hadar in Ethiopia (Howell and Coppens, 1974; Sabatier, 1979). A much larger, as yet unnamed, species of *Hystrix* is represented by one isolated lower molar in the Kaiyumung Member (4–3.5 Ma) at Lothagam (Winkler, 2003, p. 173). The smallest species of *Hystrix* to date was recovered from Laetoli, Tanzania, *Hystrix leakeyi* (Denys, 1987, p. 149). Although it is small, *H. leakeyi* is larger than any known species of *Atherurus*.

The relationships between these early porcupines and extant species remain unclear due to the fragmentary nature of the fossil record. The majority of known fossils are isolated teeth or fragmentary jaws. Porcupine teeth are known to be extremely variable morphologically even at the population level, and therefore occlusal morphology is not typically taxonomically informative (van Weers, 1995, p. 17; Sen, 1999, p. 432). Most of the species attributions have relied almost solely on tooth crown size (van Weers, 2002, p. 31), which is also less than ideal given that teeth differ in overall size as they wear (Masini and Rook, 1993, p. 84).

Van Weers (1993) noted that *Hystrix* and the beaver *Anchitheriomys* are morphologically similar, and *Anchitheriomys* has been described as a porcupine by some researchers. The fossils from Lemudong'o show distinct hystricid features: the incisors have smooth and not ribbed enamel as do *Anchitheriomys*; and, the cheek teeth have their largest breadth near the occlusal surface, unlike *Anchitheriomys* teeth that are broadest at the base.

There are 11 Hystricidae specimens recovered from Lemudong'o Locality 1, Kenya, a 6-Ma mammalian-dominated fossil site (Ambrose et al., 2003; Deino and Ambrose, 2006; Ambrose, Kyule, and Hlusko, 2007). Based on size criteria alone, there are four hystricid taxa from these deposits. Although these specimens are fragmentary in nature, they provide the earliest fossil evidence for the appearance of *Atherurus* and *Xenohystrix* in Africa, at least 300,000 years earlier than previously known (Haile-Selassie et al., 2004).

Abbreviations

KNM-NK = Kenya National Museum, fossils from the Narok District, including Lemudong'o Locality 1.

Upper-case letters denote maxillary teeth and lower-case letters denote mandibular teeth, following this convention: M2 = maxillary second molar.

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Rodentia Bowdich, 1821
Family Hystricidae G. Fischer, 1817
Genus *Atherurus* F. Cuvier, 1829
Atherurus species indeterminate
Figure 1D

Referred material

KNM-NK 44892 and KNM-NK 44893, both mandibular incisors.

Remarks

These two specimens were recovered from a sieving operation conducted to recover eroded fossils trapped in a ephemeral small pool of water in the south western edge of the site (Ambrose, Kyle, and Hlusko, 2007; Ambrose, Nyamai, et al., 2007). Therefore, exact stratigraphic provenience is unknown other than that they derive from the 6-Ma deposits at Lemudong'o Locality 1. Given the re-worked nature of this lag, these may represent one individual, although this cannot be confirmed or denied at this time.

These two incisors are smaller than all known species of *Hystrix* (Table 1) and have smooth, rounded enamel unlike lagomorphs and the cane rat *Thryonomys*. KNM-NK 44892 is shown in Figure 1D. These specimens exceed, or almost exceed, the known range of the variation for *Atherurus*. However, they are only

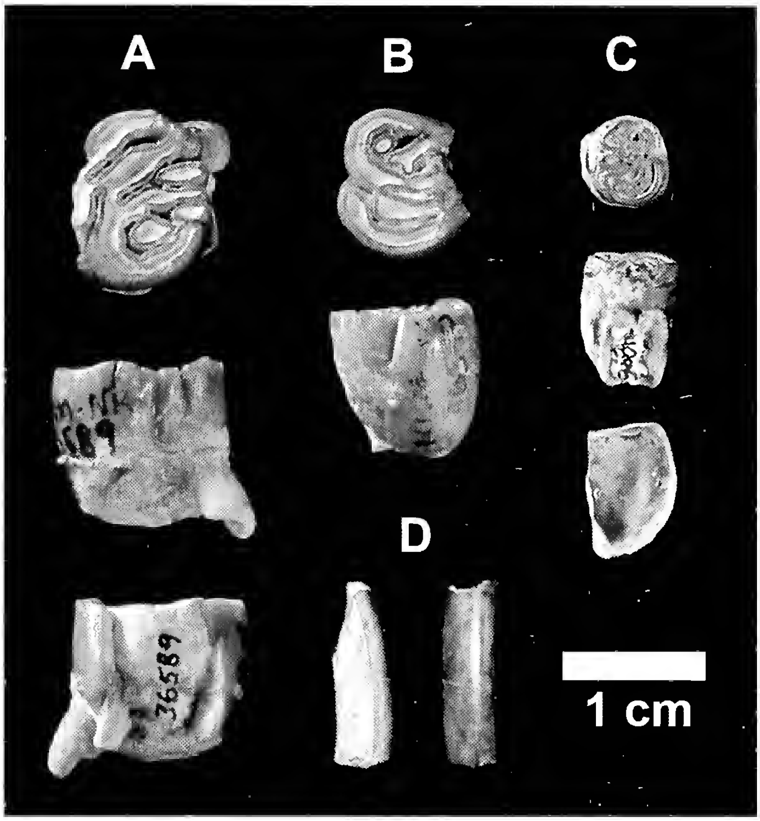

Figure 1. Hystricidae specimens from Lemudong'o Locality 1. A, KNM-NK 36589, left maxillary fourth premolar of *Xenohystrix* sp. indet. in occlusal (mesial is to the top), buccal, and lingual views. B, KNM-NK 36590, right maxillary molar *Xenohystrix* sp. indet. in occlusal and buccal views. C, KNM-NK 44896, right maxillary molar, *Hystrix* sp. indet., in occlusal, buccal and lingual views. D, KNM-NK 44892, mandibular incisor of *Atherurus* sp. indet. in lateral and labial views.

Table 1. Comparison of dental measurements (mm) for various species of Hystricidae and the Lemudong'o specimens.*

Taxon / specimen no.	MD I	LL I	MD i	LL i	MD P4	MD M1/2	MD M3	BL P4	BL M1/2	BL M3
A. macrourus[1]	2.5–3.0	3.1–4.7	2.5–3.3	3.4–4.3	3.8–5.3	3.4–5.2				
A. karnuliensis[1]	3.4	4.5	3.2–3.7	3.9–4.3	4.6–6.0	4.7–5.2				
A. africanus[2]	3.5	4.6			4.9	5.1	4.1	4.6	4.7	4.0
NK 44892			3.8	4.0						
NK 44893			3.7	4.9						
H. leakeyi[3]						7.0–8.8	7.3		5.2–7.2	6.0
H. africaeaustralis[4, 5]	6.3–8.5	6.0–7.4	6.2–8.0	5.0–7.0	8.2–11.0	6.5–9.5	8.0–9.0	7.3–10.5	7.0–9.0	6.5–7.5
H. cristata[4, 5]	7.3–8.0	7.0–7.1	6.5–7.5	9.5–10.5	9.5–10.5	8.0–9.0	8.5	9.0	8.0–9.0	7.0
H. primigenia[6]					10.1–11.5	8.7–10.0	8.0–9.3			
H. depereti[6]					11.0–12.5	9.2–11.2	8.7–10.0			
NK 36893	7.5									
NK 44896						6.7			6.0	
X. crassidens[4]	11.5–12.0	10.5–11.0			12.0	10.5–13.0		12.0	12.0	
NK 36589					11.8			n/a		
NK 36590						10.3			n/a	
NK 44771						10.1			8.8	

*MD = mesiodistal length; LL = labiolingual length; BL = buccolingual length; I/i = upper/lower incisor; P = maxillary premolar; M = maxillary molar.

[1] van Weer (2002, p. 31)

[2] measurements of one specimen from the University of California Museum of Vertebrate Zoology (left side)

[3] Denys (1987, p. 150–151)

[4] means from extant specimens taken from Greenwood (1955, p. 81–82), *H. cristata n* = 2; *H. africaeaustralis n* = 7–10; *X. crassidens n* = 1–2

[5] means from Sabatier (1979, p. 94), *H. cristata n* = 14; *H. africaeaustralis n* = 9

[6] van Weer and Rook (2003, p. 100–101)

Figure 2. *Hystrix* sp. indet. maxillary incisor KNM-NK 36893, in lateral and labial views, from Lemudong'o, Locality 1.

slightly more than half the size of all known *Hystrix* incisors, and, therefore, are referred to the much smaller *Atherurus*.

Genus *Hystrix* Linnaeus, 1758
Hystrix species indeterminate
Figures 1C, 2

Referred material

KNM-NK 36893, a maxillary incisor; KNM-NK 41002, an incisor fragment; KNM-NK 44896, a right maxillary molar.

Remarks

As noted earlier, the occlusal patterns of postcanine porcupine teeth are quite variable even within a population and show little to no consistent morphological change through time. Aside from a family-level identification, isolated cheek teeth cannot be used to differentiate species, and can be difficult to identify to position unless contact wear facets are present (Sabatier, 1979; van Weers, 2002, p. 30–31). However, as these teeth wear, the facets are known to be variably present (change through attrition). Therefore, absence of these facets does not provide positional information. Sabatier (1979, p. 88) and van Weers (2002, p. 30–31) therefore rely only on measurements of dental categories, as is done for the Lemudong'o material in Table 1.

KNM-NK 44896 is a small, relatively unworn brachydont upper molar that does not preserve any interstitial wear facets or root morphology (Figure 1C). The occlusal morphology is typical of the Hystricidae. Measurements are reported in Table 1. The mesiodistal length of this crown falls within the known range of variation for the extant *Hystrix africaeaustralis*; the buccolingual width is smaller and similar in size to *Hystrix leakeyi*. However, the proportions of KNM-NK 44896 do not align it with either species.

KNM-NK 36893 is a fragment of maxillary incisor that falls at the low end of the range of variation for extant *H. cristata* and at the middle for *H. africaeaustralis* (Figure 2, Table 1). Therefore, based on size, it is considered conspecific with KNM-NK 44896. KNM-NK 41002 is an incisor fragment too broken to measure, but almost identical in size and morphology to KNM-NK 36893. These three specimens represent an as yet indeterminate small species of brachydont *Hystrix*.

Genus *Xenohystrix* Greenwood, 1955
Xenohystrix species indeterminate
Figure 1A–B

Referred material

KNM-NK 36589, a left maxillary fourth premolar; KNM-NK 36590, a right maxillary molar; KNM-NK 41052, a fragment of left maxillary molar; KNM-NK 44771, a left maxillary third molar.

Remarks

KNM-NK 36590 is a very large brachydont right maxillary first or second molar (Figure 1B, Table 1). The crown is damaged on the buccal surface and preserves no root morphology. It is slightly smaller (0.2 mm) than the smallest known maxillary first/second molar of *Xenohystrix crassidens* from Makapansgat, South Africa (Greenwood, 1955).

KNM-NK 36589 is a left maxillary fourth premolar with three roots (Figure 1A, Table 1). The lingual side of the crown is damaged so a maximal buccolingual width cannot be measured. This premolar crown falls within the size range of *Xenohystrix crassidens* as well.

These two crowns were collected in 1995, during the first year of collection at Lemudong'o Locality 1. During that field season, exact stratigraphic provenience and proximity between specimens were not being recorded. However, these two specimens have close field numbers (98 and 102), suggesting that they were collected at the same time and close to each other spatially. Therefore, it is likely that KNM-NK 36590 may represent the same individual as KNM-NK 36589.

KNM-NK 44771 is more complete and represents a left maxillary third molar similar in size to KNM-NK 36590 (Table 1). Like KNM-NK 36589 and KNM-NK 36590, this tooth is also brachydont.

These specimens from Lemudong'o also fall within the size range of *H. depereti* from Europe, ranging from Spain to Turkey, see Table 1 (van Weers and Rook, 2003). At this time, I refer the Lemudong'o specimens to *Xenohystrix* until the phylogenetic relationship between *H. depereti* and *Xenohystrix* is resolved. It is quite possible that they are congeneric or conspecific.

KNM-NK 41052 is broken and cannot be measured accurately. However, it is extremely similar in size and morphology to these other three crowns and is, therefore, included in the same taxon.

Family Hystricidae
Genus and species indeterminate

Referred Material

KNM-NK 44894 and KNM-NK 44895, both cheek-tooth fragments.

Remarks

These two fragmentary teeth are fairly large and brachydont. However, they are too broken to confidently assign to either *Hystrix* sp. indet. or *Xenohystrix* sp. indet.

Discussion

The hystricid assemblage from Lemudong'o Locality 1 consists of only isolated and fragmentary dental specimens. However, these preserve enough anatomy to indicate that they represent three species from three genera, *Atherurus*, *Hystrix*, and *Xenohystrix*. These fragments represent the earliest occurrence of both *Atherurus* and *Xenohystrix* in Africa. This predates the previously reported earliest occurrence by more than 300,000 years (Haile-Selassie et al., 2004).

Xenohystrix is an extinct genus found only in southern and eastern Africa to date. There is one recognized species of this genus, *X. crassidens*, which has been recovered from deposits at Makapansgat in South Africa (Greenwood, 1955; Maguire, 1978), Laetoli in Tanzania, and Hadar in Ethiopia (Sabatier, 1979; Denys, 1987). This species lived between 3.7 and 2.5 Ma (Denys, 1987, p. 154) and is found at fossil sites also yielding specimens of two species of early hominids, *Australopithecus afarensis* and *A. africanus* (Maguire, 1978; Sabatier, 1979; Denys, 1987). Although this species has a fairly wide geographic range, Maguire (1978, p. 144) suggests that *X. crassidens* was a soft-diet, forest-dwelling form, based on its brachydont dentition and restriction within South Africa to only Members 3 and 4 at Makapansgat (and is not seen at other fossiliferous localities).

Extant species of East African *Hystrix* tend to be most common in hilly, rocky country but are highly adaptable and are found in all types of habitats (Kingdon, 1974, p. 692; Nowak, 1991, p. 897–900). *Hystrix* adults often live in burrows dug by aardvarks, caves, or crevices exposed along river edges. These porcupines are nocturnal and terrestrial, and can swim well. Their diet includes bark, roots, tubers, rhizomes, bulbs and fallen fruits, and sometimes they will eat insects and small vertebrates. Although they are known to frequently gnaw on bones (e.g., Plug and Keyser, 1994), they only rarely eat carrion.

The extant African brush-tailed porcupine (*Atherurus africanus*) is found in Gambia, western Kenya, southern Zaire, and many places in between. Currently, *Atherurus africanus* is only found in forests (Kingdon and Howell, 1993, p. 232). These small porcupines have long bodies with short limbs; like *Hystrix*, *Atherurus* is nocturnal and can swim; their diet consists of green vegetation, bark, roots, tubers, and fruit (Kingdon, 1974; Emmons, 1983; Nowak, 1991).

The limited hystricid assemblage from Lemudong'o Locality 1 indicates that 6 million years ago this area was inhabited by a taxonomically diverse range of porcupines, ranging from the very small *Atherurus* to the large *Xenohystrix*. The primary habitat indicated by the presence of these organisms in extant ecologies is a forested or relatively closed environment, with the possibility of more open habitats nearby. By extrapolation, the fossil assemblage from Lemudong'o Locality 1 may well sample a similar habitat.

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

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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.

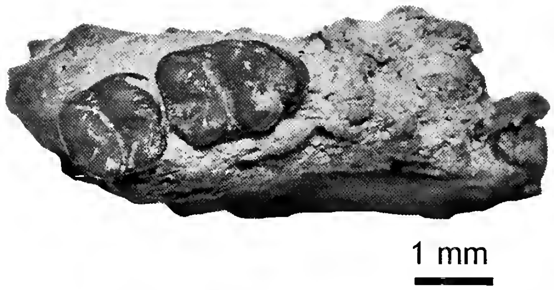

Figure 2. *Acomys* sp. indet., KNM-NK 42315, left mandibular fragment w/ M_{1-2}.

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 ± 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

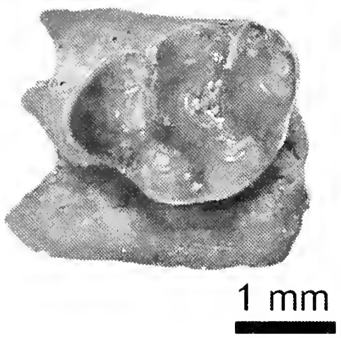

Figure 3. *Aethomys* sp. indet., KNM-NK 44921, left M^1 in maxillary fragment.

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).

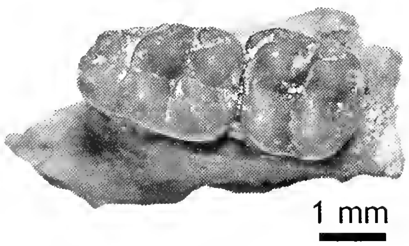

Figure 4. *Arvicanthis* sp. indet., KNM-NK 41089, right mandibular fragment w/ M_{1-2}.

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.

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.

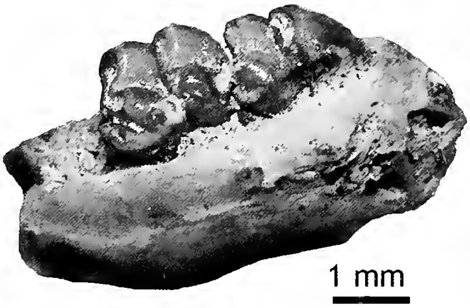

Figure 7. *Lemniscomys* sp. indet., KNM-NK 41088, left mandibular fragment w/ M_{2-3}.

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 dispersion 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).

Subfamily MURINAE
Genus and species indeterminate

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}.

Subfamily GERBILLINAE Gray, 1825
Genus TATERA Lataste, 1882
TATERA species indeterminate
Figure 9

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).

Subfamily GERBILLINAE
Genus and species indeterminate

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.

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).

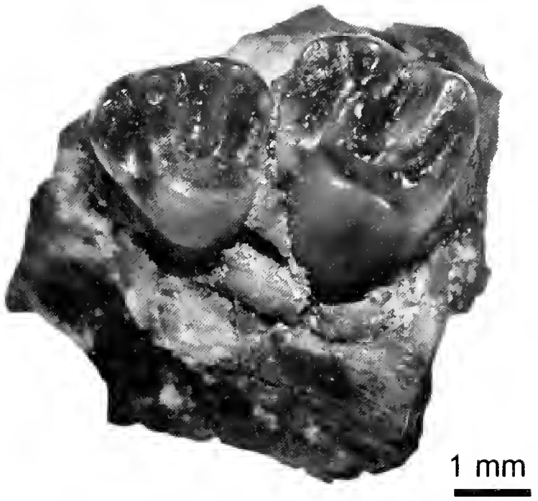

Figure 11. *Xerus* sp. indet., KNM-NK 41046, left maxillary fragment w/ P^4–M^1.

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.

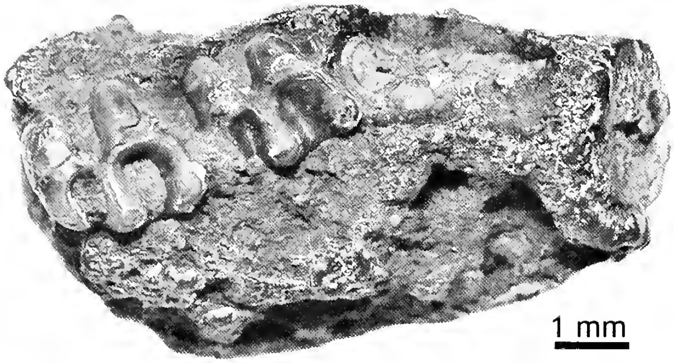

Figure 12. *Thryonomys* sp. indet., KNM-NK 45945, left mandible w/ I and M$_{1-2}$.

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$_{1-2}$.

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 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 abundanee 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 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

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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LATE MIOCENE PROCAVIID HYRACOIDS (HYRACOIDEA: *DENDROHYRAX*) FROM LEMUDONG'O, KENYA

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ABSTRACT

A small sample of hyracoid fossils from the late Miocene (~6.1 Ma) deposits at Lemudong'o, Narok, Kenya, belong to *Dendrohyrax*. This genus was unknown in the fossil record until recently, when almost simultaneously it was discovered at Lukeino (6 Ma) and Lemudong'o, both in Kenya. The fossils from Lemudong'o belong to a small species of the genus, not very different from *Dendrohyrax validus*. The Lukeino specimens are larger, and have been attributed to a new species *Dendrohyrax samueli*. The presence of tree hyraxes at these sites is indicative of forest at the time of deposition of the strata.

Introduction

Lemudong'o Locality 1 is a late Miocene (~6.1 Ma) mammalian-dominated fossil locality within the Narok District of Kenya (Ambrose et al., 2003; Ambrose, Bell, et al., 2007; Ambrose, Kyule, and Hlusko, 2007; Ambrose, Nyamai, et al., 2007; Deino and Ambrose, 2007). The primary fossil assemblage derives from the mudstone horizon and is dominated by specimens attributed to Bovidae and Cercopithecidae. However, the Hyracoidea are the third most commonly found taxon, comprising approximately 9% of the collection (112 specimens) (Ambrose, Bell, et al., 2007). This large proportion of the total mammalian assemblage is rare among Miocene and Plio-Pleistocene fossil localities in eastern and southern Kenya, and provides an uncommon insight into the paleoecology of this region.

All extant members of the Hyracoidea are classified within the family Procaviidae. The living Procaviidae are classified into two or three genera, depending on which authority one reads. All researchers are agreed that *Procavia* is distinct from the *Heterohyrax/Dendrohyrax* pair, but it is the relationship between the latter two that is subject to debate, with some researchers, such as Ellerman and Morrison-Scott (1951), Roche (1972) , and Hoeck (1978), classifying *Heterohyrax* as a subgenus of *Dendrohyrax*, and others (Hahn, 1934; Bothma, 1967, 1971; Skinner and Smithers, 1990, p. 553–563; Rasmussen et al., 1996) accepting that they represent distinct genera. Even though their dentitions are similar to each other in many ways, the cranial morphology, reproductive biology, life history variables, territoriality and vocalization reveal that they represent two separate genera, the view accepted here.

Fossil Procaviidae are known from many Plio-Pleistocene localities in East and South Africa (Churcher, 1956; Kitching, 1965; Jaeger and Wesselman, 1976; McMahon and Thackeray, 1994; Schwartz, 1997), but Miocene occurrences are rare, the only ones known prior to publication of this paper being from Namibia (Rasmussen et al., 1996) and Kenya (Fischer, 1986). In both the latter occurrences, the procaviids were identified as *Heterohyrax*. Procaviids have recently been collected at two late Miocene sites in Kenya, Lukeino in the Tugen Hills (Pickford, 2005), and Lemudong'o, near Narok.

At Lukeino, the Aragai palate is complete enough to reveal that it belongs to a new species of *Dendrohyrax*, *D. samueli* (Pickford, 2005). The Lemudong'o fossils in contrast are fragmentary and many of the features that are diagnostic for identifying *Heterohyrax* and *Dendrohyrax* are lacking. However, the base of a symphysis preserves morphology that is usually only found in *Dendrohyrax* (presence of roughened ridges separated from the body of the symphysis by grooves), and the ectoloph morphology of the upper molars suggests the same identification.

The dental remains from Lemudong'o plot within the ranges of metric variation of both *Dendrohyrax* and *Heterohyrax*. If they are *Heterohyrax* then they represent a large species of the genus, but if they are attributed to *Dendrohyrax*, then they would denote a small species of the genus. The assumption is that only one

Table 1. Measurements of the upper teeth (in mm) of *Dendrohyrax* sp., from Lemudong'o, Kenya.

Specimen	Tooth	Length	Breadth
KNM-NK 40909	left I1/ male	3.9	4.1
KNM-NK 42257	left I1/ female	3.5	4.2
KNM-NK 41460	left I1/ female	3.6	4.1
KNM-NK 44804	right P1/	3.8	2.9
	right P2/	5.0	4.5
	right M2/?	6.2	6.4
	left M1/?	5.7	6.3
	left M3/	6.2	7.0
KNM-NK 42300	left M3/	6.7	7.0

Table 2. Measurements of the lower teeth (in mm) of *Dendrohyrax* sp., from Lemudong'o, Kenya.

Specimen	Tooth	Length	Breadth
KNM-NK 41304b	left m/3	6.9	4.3
KNM-NK 40993	right m/3	7.0	4.0
KNM-NK 36575	right p/2	4.9	2.8
	right p/3	4.9	3.3
	right p/4	5.4	3.7
	right m/1	5.3	3.6
	right m/2	5.8	3.9
KNM-NK 42395	left m/1	5.8	3.5
KNM-NK 36534	left p/4	6.0	3.9
	left m/1	6.0	3.9
	left m/2	6.2	4.3
KNM-NK 41289	right p/2	4.8	2.9
	right p/3	5.0	3.5

genus is present at the site, and, if so, then it is a *Dendrohyrax* close in size to *D. validus*.

Sample and Methods

The entire collection of procaviids from Lemudong'o consists of 112 fossils. As recommended by White (2000), we agree that the best approach for describing fossils is to work with original material. However, due to circumstances at the National Museums of Kenya that were beyond the control of the authors, the first author was able to examine only a minor part of the collection, and this only in the form of casts and photographs. Therefore, this study focuses on the 18 most complete specimens of the Procaviidae assemblage, and size measurements of the other dental specimens (taken by the second author). Therefore, the results and conclusions presented herein are qualified with this unavoidable hindrance. Measurements of the cheek teeth were taken twice by L. H. and averaged. These are presented in Tables 1 and 2. Measurements of the upper incisors and the humeri were taken on casts by M. P.

Abbreviations

KNM stands for the National Museums of Kenya, and NK for the Narok District, in which the site of Lemudong'o occurs. Maxillary teeth are indicated with capital letters and the numerical tooth position followed by a back-slash (e.g., M2/ for maxillary second molar). Mandibular teeth are indicated with lower case letters and the numerical tooth position preceded by a back-slash (e.g., m/2 for mandibular second molar). Dental terminology is based on Rasmussen and Simons (1988).

Systematic Paleontology

Order Hyracoidea Huxley, 1869
Family Procaviidae Thomas, 1892
Genus *Dendrohyrax* Gray, 1868
Dendrohyrax cf. *D. validus* True, 1890
Figure 1

Referred material

KNM-NK 36534, left mandible with p/4–m/2; KNM-NK 36575, right mandible with p/2–m/2; KNM-NK 36934, fragment of mandible with molar; KNM-NK 40909, left I1/ male; KNM-NK 40993, right mandible with m/3; KNM-NK 41006, base of mandibular symphysis; KNM-NK 41289, right mandible with p/2–p/3; KNM-NK 41304a, edentulous mandible fragment; KNM-NK 41304b, left mandible with m/3; KNM-NK 41304c, fragment of right mandible; KNM-NK 41304d, edentulous mandible fragment; KNM-NK 41460, left I1/ fragment female; KNM-NK 42257, right I1/ female; KNM-NK 42272, distal end right humerus; KNM-NK 42300, left M3/; KNM-NK 42395, left mandible with m/1 and roots m/2; KNM-NK 44776, distal end of left humerus; KNM-NK 44804, various pieces of maxilla and mandible, one with right P1/–P2/, one with two worn molars, and three isolated unworn upper teeth.

Description

Mandible

The base of a mandible, KNM-NK 41006 (Figure 1E) lacks teeth, but has the floors of the alveoli of the left and right i/2 preserved. The external surface of the symphysis is marked by two distinct swollen ridges which extend parallel to the sagittal plane from a point 8 mm from the rear of the symphysis upwards for a distance of 8.5 mm.

Upper dentition

Three upper incisors in the examined sample are tusklike, permanently growing teeth (Table 1). One specimen has a sharp anterior ridge with concave sides, indicating that it is from a male individual, while the other two have a blunter ridge with less concave or even convex sides, indicating female status.

The P1/ in maxilla fragment KNM-NK 44804 has a prominent steep ectoloph with two buccal ridges descending from apex towards cervix either side of a central groove (Table 1). Lingually, in line with the two buccal ridges, there are two transverse crests which extend to the lingual side of the crown, but which are separated throughout their length by a deep valley. These internal ridges correspond to the protocone and hypocone, but the cusps are not as clearly differentiated as those in the posterior premolars and the molars. The postprotocrista curves distally as it extends towards the lingual side of the tooth. There is a low parastyle at the anterior limit of the ectoloph, from the base of which a low cingulum extends lingually and distally, but there is no metastyle. The tooth has three roots, one lingual, the other two buccal.

The P2/ in the same maxilla is more molariform. It is a bigger tooth, trapezoidal in outline, with four roots. The ectoloph is steep with two prominent buccal ridges fading out towards the cervix. The protocone and hypocone are oriented obliquely with their anterior crests positioned centrally, and their distal crests ending near the lingual side. There is a deep central fovea and there is no sign of transverse spurs.

KNM-NK 42300, a left M3/, has an ectoloph with a prominent parastyle and mesostyle but a weaker metastyle (Table 1). These

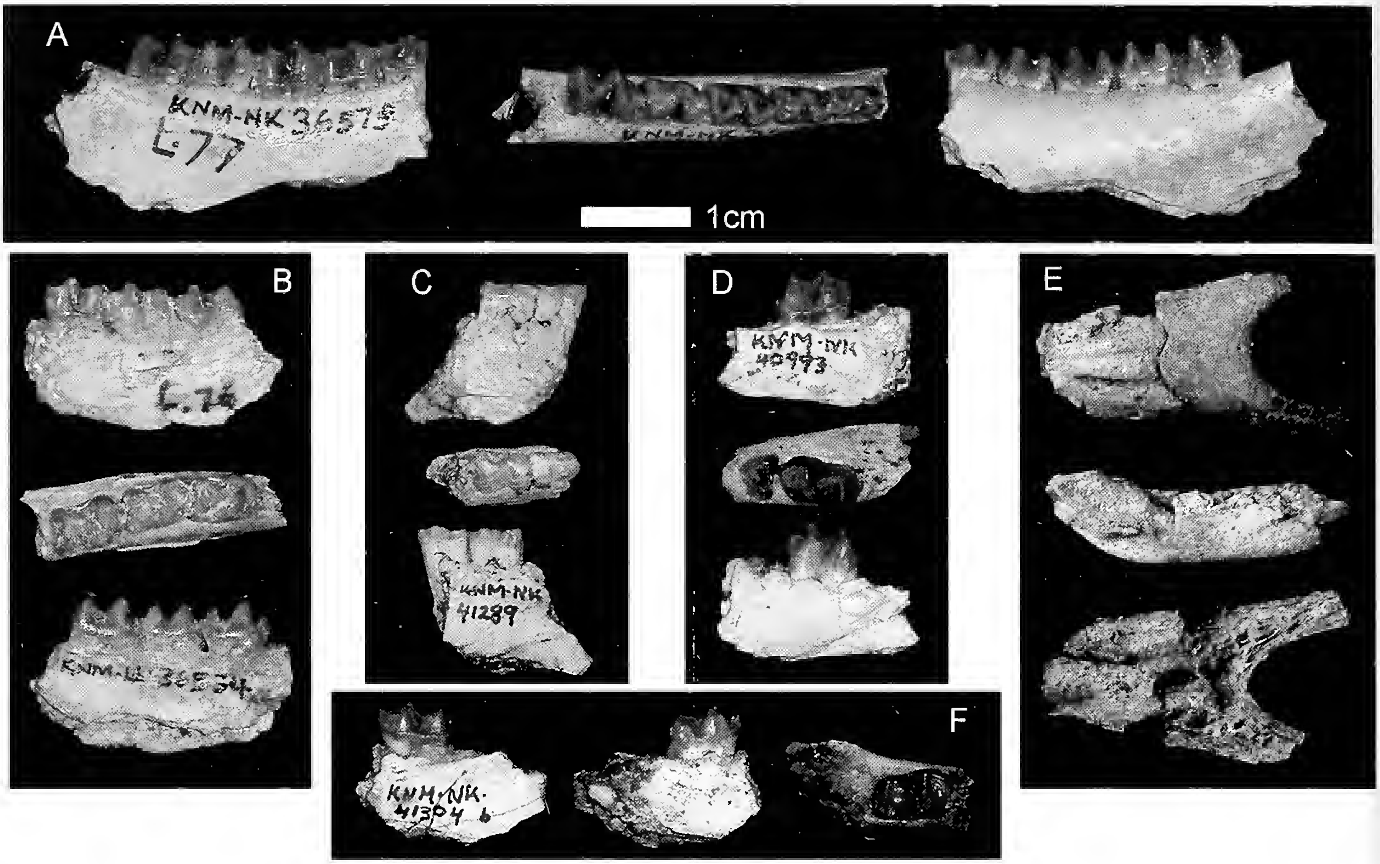

Figure 1. *Dendrohyrax* sp., Lemudong'o, late Miocene (~6.1 Ma), Kenya. A. KNM-NK 36575, right mandible with p/2–m/2 (m/3 in crypt). From left to right: buccal (mesial is to the right), occlusal (mesial is to the right), and lingual (mesial is to the left) views. B. KNM-NK 36534, left mandible with p/4–m/2. Top to bottom: buccal (mesial is to the left), occlusal (mesial is to the right), and lingual views (mesial is to the right). C. KNM-NK 41289, right mandible with p/2–p/3. Top to bottom: buccal (mesial is to the right), occlusal (mesial is to the right), and lingual (mesial is to the left). D. KNM-NK 40993, right mandible fragment with m/3. Top to bottom: buccal (mesial is to the right), occlusal (mesial is to the left), and lingual (mesial is to the left). E. KNM-NK 41006, mandibular symphysis. From top to bottom: inferior, left lateral, and superior views (anterior is to the left). F. KNM-NK 41304b, left mandible fragment with m/3. Left to right: buccal (mesial is to the left), lingual (mesial is to the right), and occlusal (mesial is to the right). Scale = 1 cm

styles are almost vertical with respect to the cervical plane. The paracone and metacone, in contrast, are inclined lingually, which imparts a strongly zigzag cutting edge to the ectoloph. The protocone and hypocone are oriented obliquely. There is no sign of spurs. The tooth has a fifth root which leans distally and is located distinctly behind the two main distal roots, rather than between, or immediately behind, them. The disposition of the roots indicate that this tooth is an M3/.

In the lot of specimens labelled KNM-NK 44804, there is an unworn isolated right upper molar with a fifth root vertically oriented and lying between the two main distal roots. This tooth is probably an M2/. Its crown morphology is similar to that of the M3/ described above. There is another specimen with the fifth root leaning distally, and this is likely an M3/ (Table 1). A further specimen is a rootless crown, which is smaller than the other molars. It is possibly an M1/. With the same catalog number there is a maxilla fragment with deeply worn and damaged molars or posterior premolars. This specimen indicates that there is more than one individual represented by this catalog number.

Lower dentition

KNM-NK 36575 is the most complete of the mandibular specimens, and its teeth are barely worn (Figure 1A). It has five cheek teeth in occlusion, and a sixth one in its crypt distally. KNM-NK 41304b (Figure 1F) and KNM-NK 40993 (Figure 1D) are small mandible fragments each bearing m/3. By a process of elimination it is possible to determine that the teeth in occlusion in KNM-NK 36575 are the p/2 to m/2, and the tooth in the crypt is the m/3. This inference is supported by the evidence of the root of the ascending ramus, which terminates anteriorly opposite the rear of m/2, and the eruption pattern (in lateral view the cervix of m/1 is located distinctly higher than that of p/4).

In occlusal view the cheek teeth of KNM-NK 36575 are formed of two V-shaped crescents arranged one behind the other to form an overall W-shaped occlusal surface. The rear limb of each V is almost at right angles to the long axis of the tooth row, whereas the anterior part of the V is obliquely oriented. The paraconid is lower than the rest of the cusps and it is centrally positioned. The protoconid, metaconid, hypoconid, and entoconid are high. The

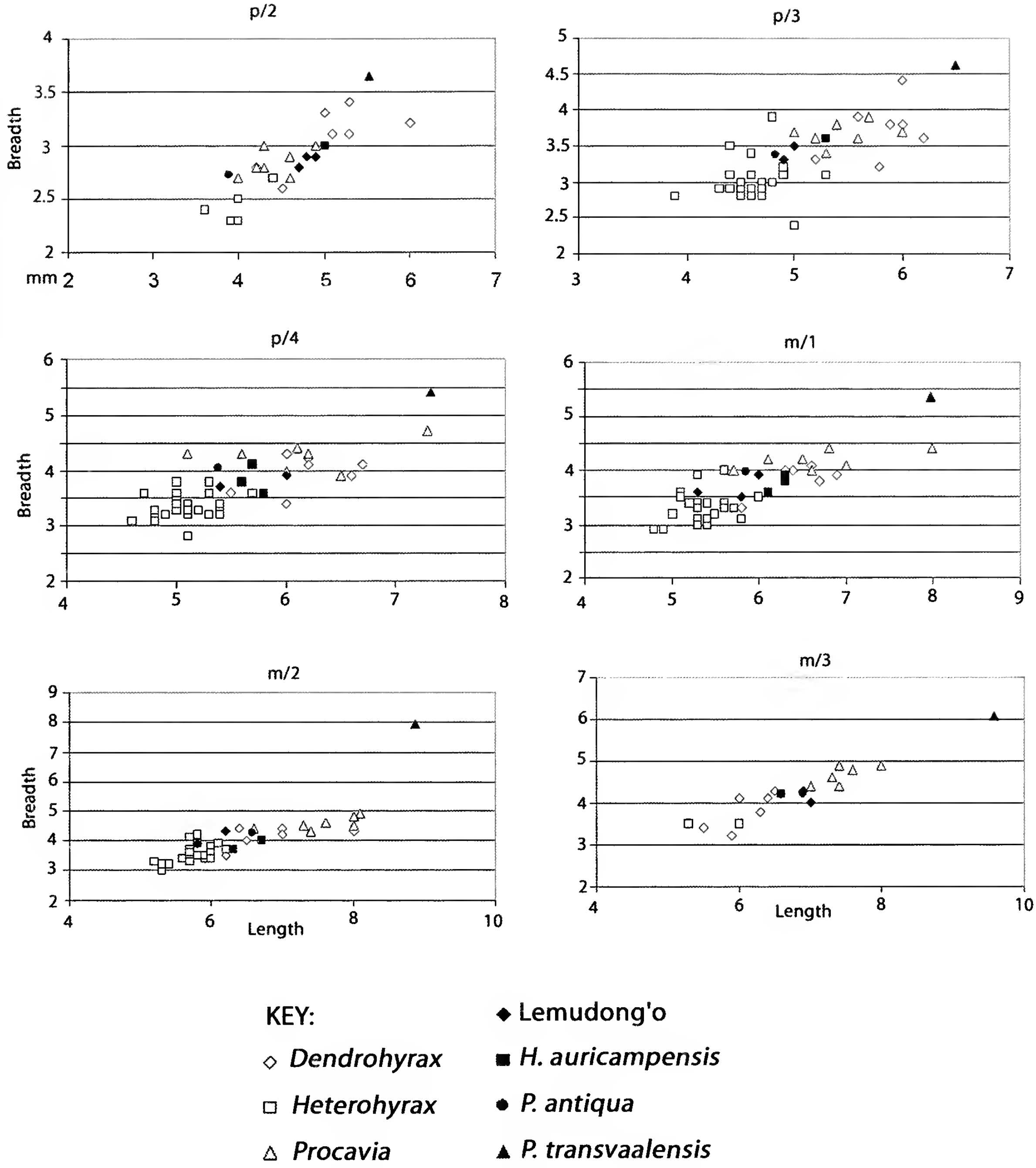

Figure 2. Scatter diagrams of length vs. breadth (in mm) of p/2–m/3 of extant and fossil Procaviidae (open symbols = extant species, solid symbols = fossils).

cristid obliqua descends gently from the hypoeonulid and terminates beneath the summit of the flattened metaconid. There is a well formed buccal cingulum which extends onto the distal surface of the tooth. The trigonid and talonid basins are deep and open lingually slightly above cervix level.

KNM-NK 36534 (Figure 1B) contains left p/4 to m/2, similar in all details to those in KNM-NK 36575, and the teeth are in a similar stage of wear.

The m/3s in KNM-NK 40993 and KNM-NK 41304b are W-shaped in occlusal view, and they do not have a third lobe. Nevertheless, in both specimens the distal cingulum rises in the center to form a low, vertical, distal ridge that fades out at about half the height of the crown. This ridge is probably the remnant of a third lobe.

The premolars in KNM-NK 41289 (Figure 1C) are deeply worn, but the W-shaped occlusal outline is preserved. The buccal cingula are low but rounded.

Humerus

Two distal ends of humeri from Lemudong'o, KNM-NK 42272 and KNM-NK 44776 (not shown), are typically procaviid in articular morphology. The specimens are compatible in size with the available dental elements. The epiphyses are 13.5 and 13.3 mm in mediolateral dimensions respectively.

Discussion

The most diagnostic specimen for the purposes of determining the generic status of the Lemudong'o hyracoid is the base of a mandible, KNM-NK 41006. Among extant procaviids, the mandibular symphyses of *Procavia* and *Heterohyrax* do not possess such ridges, being evenly curved from side to side. Mandibles of *Dendrohyrax* can be devoid of ridges, but many specimens possess them. In *Dendrohyrax* the ridges increase in size ontogenetically, and are often more strongly developed in males than in females. KNM-NK 41006 provides strong evidence that the genus *Dendrohyrax* is represented in the collection. The Lemudong'o hyrax fossils are close in size to the extant species *D. validus* True, 1890, but are smaller than *D. dorsalis* Frazer, 1852.

Both *Heterohyrax* and *Dendrohyrax* possess sexually dimorphic upper central incisors similar to the two specimens from Lemudong'o.

In the Lemudong'o hyrax upper molars the surfaces of the ectoloph on either side of the mesostyle are in line with each other as in *Dendrohyrax*, not offset from each other as in *Heterohyrax* (Allaerts et al., 1982, p. 221).

It is clear from the upper and lower molar morphology that the Narok hyrax does not represent *Procavia*. The available dental fossils resemble both *Dendrohyrax* and *Heterohyrax*. In favor of attribution to *Dendrohyrax* is the morphology of the ectoloph of the upper molars. As Allaerts et al. (1982, p. 221) pointed out, the parts of the ectoloph on either side of the mesostyle lie in the same plane in *Dendrohyrax* but are offset from one another in *Heterohyrax*. Whilst ectoloph morphology is somewhat variable in procaviids, and visual assessment of its morphology is affected by wear, the Lemudong'o specimens accord closely with *Dendrohyrax*.

None of the Lemudong'o mandibular material is complete enough to employ any of the usual criteria (ratio of lengths of premolar row to molar row, length of diastemata relative to premolar and molar rows, depth of mandible beneath the rear of m/1 relative to molar row) used to separate *Dendrohyrax* from *Heterohyrax*. The lower dentitions of these two genera are extremely similar to each other, and it is virtually impossible to determine to which genus isolated teeth or even partial tooth rows belong.

The m/3s appear to be relatively large when compared to the molars of other procaviids, falling above the scatter for extant *Dendrohyrax* species. All the other cheek teeth (Figure 2) plot at the small end of the range of variation of extant *Dendrohyrax*. Given the small sample available, and the uncertainties involved in measuring procaviid teeth that are incorporated in tooth rows, it is not possible to decide whether the Lemudong'o tree hyrax possessed relatively large third molars, or not. Considering the fragmentary condition of the examined sample of Lemudong'o procaviids, it is not realistic to attribute them to a species, although it is noted that they are close in size to extant *Dendrohyrax validus*.

Paleoecological Considerations

Extant *Dendrohyrax* is an arboreal, forest-dwelling mammal, although it sometimes lives in rocky areas especially in high altitude situations. It is generally nocturnal, highly territorial and is a browser. There are several species recognized, and many subspecies have been named, although there is almost no agreement in the literature about the quantity and geographic distribution of these subspecies. Three species are generally accepted (Skinner and Smithers, 1990, p. 553–563): *D. dorsalis* in the West African rainforest, *D. arboreus* in seasonal forests of East and South Africa, and *D. validus* in drier forests of East Africa. Some authorities recognise that the limits between the three species are gradational, and on this basis have argued that there is only one species of tree hyrax (*D. arboreus*) with 15 subspecies (Haltenorth and Diller, 1980). In general, *Dendrohyrax* from humid forests are larger than those from drier environments. The Lemudong'o fossils belong to quite a small species (Figure 2), from which it is surmised that even though the Lemudong'o area was forested in the late Miocene, it would probably have been a relatively dry forest rather than a humid tropical forest.

Conclusions

The Lemudong'o material is too incomplete for employment of many of the usual criteria used to determine to which of the genera (*Dendrohyrax* and *Heterohyrax*) it belongs. It is clearly not a *Procavia*. However, the morphology of the ectoloph of the upper molars suggests that it belongs to *Dendrohyrax*. The most convincing evidence that the fossils represent *Dendrohyrax*, rather than *Heterohyrax*, is the morphology of the base of the mandibular symphysis. The presence of two ridges on the ventral surface of the symphysis only occurs in *Dendrohyrax*. Young individuals of this genus sometimes show no sign of this structure, in which case they are difficult to distinguish from *Heterohyrax*, but when the ridges are present there is little doubt that the specimen belongs to *Dendrohyrax*.

Dendrohyrax, as its name implies, is indicative of forest, as this genus is arboreal, and usually lives in holes in trees. It is mostly nocturnal, but does have some diurnal activity when conditions are suitable. It is a browser, the cheek teeth being brachyodont. The presence of this genus in the late Miocene deposits at Lemudong'o, Kenya, can be taken to mean that the region was forested during the late Miocene, and on the basis of the small size of the species, probably dry forest rather than rain forest.

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LAGOMORPHS (MAMMALIA) FROM LATE MIOCENE DEPOSITS AT LEMUDONG'O, SOUTHERN KENYA

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ABSTRACT

Remains of 51 fossil Lagomorpha specimens were recovered from late Miocene deposits (ca. 6 Ma) at Lemudong'o, Narok, Kenya. The majority of the fossil remains are postcranial elements and are identified as Leporidae (n = 40) based on their morphological characteristics; they represent a minimum of four individuals. Quantitative analysis of the postcranial remains suggests that this assemblage comprises a single population. A maxillary fragment that includes P2 through P4 is tentatively assigned to genus *Alilepus* (Dice, 1931). Taphonomic analysis of this assemblage indicates element preservation is density mediated, but fragmentation is limited and this suggests carnivorous-bird accumulation. The Lemudong'o sample represents the first record of cf. *Alilepus* sp. at this locality and only the second record of *Alilepus*, or a closely allied, genus in Africa (Winkler 2003). These remains confirm an expansion of leporids into the Narok region by ca. 6 Ma.

Introduction

This paper presents an initial descriptive analysis of 51 lagomorph-fossil skeletal specimens collected from late Miocene (ca. 6 Ma) deposits at the Lemudong'o paleontological site, near Narok, southern Kenya (Ambrose et al., 2003; Ambrose, Kyule, and Hlusko, 2007). In this paper, a specimen is a "bone or tooth, or fragment thereof, from an archaeological or paleontological site, while an element is a single complete bone or tooth in the skeleton of an animal" (Grayson, 1984, p. 16, following Shotwell 1955; Shotwell, 1958). Like other groups of mammals, Lagomorpha "took advantage of the opening of terrestrial connections" to enter Africa during the late Miocene (Lavogat, 1978, p. 84); however, less is known about the early evolutionary history of Lagomorpha (Kingdon, 1974; Lavogat, 1978) than of many other mammalian groups. Thus the results presented here are important to the overall documentation and appreciation of lagomorph evolution in general, and in particular, they contribute to understanding the geographic range of some of the earliest African leporids.

The order Lagomorpha, with only two extant families and 12 extant genera, are herbivorous and have a moderately broad adaptive range. Extant lagomorphs inhabit forested areas, grasslands, deserts, and tundra, a range which most likely characterizes their fossil allies as well. Ochotonidae, or pikas, are more limited in their modern geographic distribution—Holarctic and often high altitude—than are Leporidae, or rabbits and hares, which have become ubiquitous (albeit introduced by humans in the case of Australasia and South America) to all but the West Indies, Madagascar, and Antarctica (see Kingdon, 1974; Nowak, 1991).

First recognized from late Paleocene deposits in northern China and Mongolia, lagomorphs have been relatively stable morphologically, with general evolutionary trends that include simplification of the cheek-tooth pattern, increased hypsodonty, and some gradual, adaptational changes related to locomotion (Dawson, 1967). Although the origin of this order is still under question, recent phylogenetic analysis of character traits on fossil specimens from Mongolia suggest that lagomorphs, along with rodents (collectively known as the superorder Glires), diverged from other placentals within a few million years of the Cretaceous-Tertiary boundary (Ascher et al., 2005). Lagomorpha radiation begins with fossil Leporidae in the late-middle to late Eocene with at least nine different genera represented in the Asian fossil record (see Van Valen, 1964; Meng et al., 2005). The diversity of ochotonids and leporids, expressed by the number of known genera, varies over time, with Ochotonidae appearing in the middle Oligocene, and radiating in the late Oligocene through the Miocene to achieve their greatest variety and geographic distribution—North America and Eurasia. Leporidae, however, increased gradually and eventually overtook ochotonids in variety and range beginning in the late Pliocene (Dawson, 1967; Dawson, 1981).

The earliest Ochotonidae in Africa come from Miocene deposits at Nambib, Namibia (*Australagomys* Stromer, 1926) and from Rusinga Island, Kenya (*Kenyalagomys* MacInnes, 1953), with these latter materials dating to the early Miocene, around 18 Ma (Van Couvering and Miller, 1969). Although the ochotonid *Prolagus* is reported from late Miocene-late Pliocene deposits of North Africa (Benammi et al., 1996), by the end of the

Miocene Ochotonidae are entirely replaced by Leporidae in subsaharan Africa.

Fossil evidence indicates that Leporinae likely originated from Archaeolaginae (which likely descended from Oligocene Palaeolagine) in North America sometime in the middle to late Miocene (White, 1991). Leporids in the form of *Alilepus* (Schlosser, 1924) and *Hypolagus* (Dice, 1917) first appear in northeastern Asia around 8 Ma. Recent research, based on morphological and mtDNA evidence, suggests at least three intercontinental exchanges occurred between North American and Asian leporids during the Miocene, and most likely an additional three dispersals of leporids occurred from Eurasia into Africa (Matthee et al., 2004). By the Mio-Pliocene boundary genera such as *Pliopentalagus*, *Trischizolagus*, and *Serengetilagus* derive from an *Alilepus*-like population with *Pliopentalagus* and *Trischizolagus* spreading across Eurasia and giving rise to various extant Old World genera, and *Serengetilagus* spreading into Africa (Patnaik, 2002, p. 449). *Serengetilagus* disappears after the early Pleistocene, with *Lepus* (ubiquitous) and *Pronolagus* (southern Kenya to the Cape of Good Hope) emerging in the middle to late Pleistocene (Dawson, 1957; Kingdon, 1974). *Oryctolagus* is a recent Holocene arrival to northwestern Africa from southern Europe (Kingdon, 1974).

Modern Leporidae comprise rabbits and hares that presently inhabit forests, shrub areas, grasslands, tundra, and alpine slopes, and feed on a variety of plants. Taxonomic controversies over the extant genus *Lepus*, and in particular the Old World *Lepus*, are largely due to the fact that interspecific variation in qualitative and quantitative morphological characteristics is small compared to intraspecific geographic and individual differences (Angermann, 1983). This detail makes the identification of skeletal leporid remains below the family level somewhat problematic.

Materials and Methods

At Lemudong'o Locality 1, 40 lagomorph specimens were amassed over five separate field seasons by intensive surface collection of this locality in 1995, and between 2000 and 2004 (Ambrose, Kyule, and Hlusko, 2007). In addition, 11 specimens (KNM-NK 41457) were recovered from geological deposits at Enamankeon in 2001 using similar recovery techniques. Both localities are demonstrated to be of a similar depositional environment and are contemporaneous (Ambrose, Nyamai, et al., 2007). Field sorting and specimen photography was undertaken by L. Hlusko; casts of the specimens were prepared in Nairobi by L. Hlusko at the National Museums of Kenya, Division of Casting. The original specimens are curated with the Division of Palaeontology, National Museums of Kenya, under the prefix KNM-NK. Specimen casts are housed in the Department of Integrative Biology at the University of California, Berkeley. For the purpose of this analysis all Lagomorpha specimens are considered to be a single sample. KNM-NK 42368, a maxillary cheektooth recovered in 2002 from modern silts, is excluded from the total specimen count and analysis.

The majority of the specimens described here are postcranial (84%), and with the exception of one maxillary fragment, the cranial specimens are limited to isolated teeth. The emphasis for this analysis, therefore, is on the postcrania. Casts and photographs of the Lemudong'o postcranial specimens were compared with African leporid postcrania in the Department of Mammalogy at the Smithsonian Institution's National Museum of Natural History. This is probably the largest collection of African leporids in North America with 646 individuals, but only six of these have postcranial elements. (By comparison, the Museum of Vertebrate Zoology at the University of California, Berkeley, houses 33 specimens of African leporids, but none have postcranial skeletal elements.) The fossil specimens were also compared with western North American leporid postcrania from the Zooarchaeology Laboratory, University of California, Davis. Fossil and extant specimens were measured with digital metric calipers to the nearest tenth of a millimeter following standards set by von den Driesch (1976). Dental abbreviations follow Smith and Dodson (2003).

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Lagomorpha Brandt, 1855
Family indeterminate

Material

KNM-NK 40901, phalanx, fragment; KNM-NK 40997, tooth, fragment; KNM-NK 41254, incisor, fragment; KNM-NK 42249, proximal/middle phalanx, distal end; KNM-NK 42317, proximal/middle phalanx, distal end; KNM-NK 44812, incisor, fragment.

Remarks

A total of six specimens were recovered, which comprise broken phalanges, and incisor or cheektooth fragments. With the exception of the two fragmentary incisors, the specimens were field identified but not photographed or cast. Given their fragmentary state these elements could not be confidently identified to a lower taxonomic level than order Lagomorpha.

Family Leporidae (Fischer de Waldheim, 1817) Gray, 1821

Remarks

The family Leporidae was first defined in a French publication by German paleontologist Fischer de Waldheim in 1817, who was professor of Natural History at Moscow University, but Leporidae was also later defined in an English publication by Gray in 1821 (McKenna and Bell, 1997); both are typically cited for this family. The vast majority of the lagomorph-fossil specimens recovered from Lemudong'o were identified to family Leporidae; these remains are composed of postcranial elements ($n = 40$) and isolated teeth ($n = 4$).

In the Tugen Hills sequence of the Kenyan Rift Valley, the first leporids appear in the Mpesida Beds after a substantial gap in this sequence between about 8.5 and 6.5 Ma, and they continue to be represented in the subsequent Lukeino Formation (ca. 6.2 to 5.6 Ma) (Hill, 1999, p. 90). These leporids are represented by only three isolated tooth specimens—an incisor from the Mpesida Beds, and a cheektooth and premolar from the Lukeino Formation (Winkler, 2002, p. 240), the latter of which (LP3) may be attributable to *Alilepus* (Winkler, 2003, p. 171). Winkler (2002, p. 250) further suggests that the Lukeino leporid is congeneric with comparable-aged leporids from the Siwaliks, Pakistan, which implies interchange between these two areas.

From the lower Nawata Formation, at the site of Lothagam, in the Turkana desert region of northern Kenya, another early record of Leporidae is represented by cranial and postcranial remains of at least two individuals, which have been assigned to *Alilepus* and dated to 6.57–6.54 Ma (Winkler, 2003, p. 170). Only the p3 specimens are illustrated and described. Later Pliocene specimens of the leporid *Serengetilagus* have been identified from Lake Eyasi in Tanzania (MacInnes, 1953), from Kossom Bougoudi in northern Chad (Brunet et al., 2000), and most

Figure 1. KNM-NK 41457, Leporidae specimens recovered from Enamankeon; tibia, calcaneus, astragalus, cuboid, metatarsals, proximal phalanges (hindlimb).

recently from the Apak Member (ca. 4.2 Ma) of Lothagam (Winkler, 2003).

Family Leporidae (Fischer de Waldheim, 1817) Gray, 1821
Genera and species indeterminate
Figure 1

Material

KNM-NK 36961, L. tibia, distal end; KNM-NK 36962, R. calcaneus, tuber calcus; KNM-NK 40876, R. and L. humerus (distal end), R. and L. radius (proximal end); KNM-NK 40895, L. calcaneus; KNM-NK 40917, L. ilium, caudal 1/2 and acetabulum; KNM-NK 40991, R. tibia, distal end and 1/4 shaft; KNM-NK 41001, R. tibia (distal end and 1/4 shaft), navicular; KNM-NK 41003, L. femur, proximal end and 1/4 shaft; KNM-NK 41025, R. tibia, distal end; KNM-NK 41065, proximal hindlimb phalanx; KNM-NK 41078, maxillary cheek tooth; KNM-NK 41323, R. astragalus, L. astragalus; KNM-NK 41457, R. tibia, R. astragalus and calcaneus, L. cuboid, R. metatarsal I, R. metatarsal III, L. metatarsal IV (proximal end and 1/4 shaft), metatarsal (distal end and 1/3 shaft), metapodial (midshaft fragment), two proximal hindlimb phalanges; KNM-NK 41478, L. calcaneus, tuber calcus; KNM-NK 41486, L. femur, caput femoris; KNM-NK 41493, metapodial, distal end and 1/4 shaft; KNM-NK 42253, L. cuboid; KNM-NK 42265, R. astragalus; KNM-NK 42290, calcaneus, tuber calcus; KNM-NK 42292, maxillary cheek tooth; KNM-NK 42299, L. LP3; KNM-NK 42307, R. humerus, distal end; KNM-NK 42356, R. astragalus, condyle fragment; KNM-NK 44763, L. humerus, distal end; KNM-NK 44772, L. femur, distal end; KNM-NK 44773, L. femur, distal end; KNM-NK 44813, middle phalanx, distal and 1/2 shaft; KNM-NK 44824, proximal phalanx, distal and 1/2 shaft; KNM-NK 45801, mandibular cheek tooth.

Descriptions and remarks

A total of four isolated teeth from Lemudong'o were identified as leporid. KNM-NK 42299 is an isolated left mandibular third premolar, which has a mesio-distal dimension of 3.3 mm and a buccal-lingual dimension of 2.9 mm. Although the tooth compares favorably to the general characteristics of a leporid p3, the occlusal surface has postmortem wear and edge chipping which makes further identification difficult. Among Leporidae the occlusal or enamel patterns of maxillary (post P2) and mandibular (post p3) cheek teeth exhibit little variation. The maxillary (KNM-NK 41078 and 42292) and mandibular (KNM-NK 45801) cheek tooth specimens from Lemudong'o are no exception and follow the general leporid pattern.

An additional 40 postcranial elements were assigned to family Leporidae, and measurements of these remains are presented in Table 1. Four humeri were recovered and all of the fragments are the distal end with no remains of the shaft. A left distal end fragment from two different individuals (KNM-NK 40876 and 44763) and a right distal end fragment (KNM-NK 42307) are quite eroded on the margins and the fragments do not extend to the olecranon foramen (supratrochlear fenestra) but they resemble *Lepus*. The other right distal end fragment (KNM-NK 40876) extends to just past the olecranon foramen, which is a characteristic trait of leporids. However, this fenestra is quite wide and more prominent than found in modern leporids and is more similar to descriptions for *Palaeolagus* (Scott et al., 1940), which suggests that the elbow joint of this fossil leporid might have had more flexibility than its modern counterpart. Only the proximal end of a right and left radius were preserved (KNM-NK 40876), both compare favorably with general leporid radial head and neck morphology.

The ilium, KNM-NK 40917, which includes the acetabulum, the anterior inferior spine and the caudal portion of the iliac blade, is basically similar to the general leporid innominate, albeit the acetabular rim has a less prominent margin than *Lepus* and is more similar in this characteristic to *Sylvilagus*.

The largest femoral fragment is KNM-NK 41003, a left anterior surface of the proximal end with an unfused head (caput femoris). The first trochanter of the greater trochanter is missing, and the edges of the anteriolateral margin of the third trochanter are worn. Although in overall appearance it compares favorably

Table 1. Postcranial element measurements (in mm) of Lemudong'o Leporidae (KNM-NK) specimens. GL = greatest length, GB = greatest breadth, Bp = breadth proximal, Bd = breadth distal, Dd = depth distal, SD = smallest breadth diaphysis, DC = depth caput, LAR = length of acetabulum at rim (von den Driesch, 1976).

KNM-NK no.	Skeletal Element	GL	GB	Bp	Bd	Dd	SD	DC	LAR
41323	Astragalus (R.)	12.5	–	–	–	–	–	–	–
41323	Astragalus (L.)	12.4	–	–	–	–	–	–	–
41457	Astragalus (R.)	13.1	–	–	–	–	–	–	–
40895	Calcaneus (L.)	24.1	7.4	–	–	–	–	–	–
41457	Calcaneus (R.)	27.4	8.4	–	–	–	–	–	–
41457	Cuboid (L.)	9.7	–	–	–	–	–	–	–
42253	Cuboid (L.)	9.2	–	–	–	–	–	–	–
41486	Femur (L.)	–	–	–	–	–	–	7.8	–
44772	Femur (L.)	–	–	–	13.5	–	–	–	–
44773	Femur (L.)	–	–	–	13.8	–	–	–	–
40876	Humerus (R.)	–	–	–	13.4	–	–	–	–
40876	Humerus (L.)	–	–	–	13.5	–	–	–	–
41457	Metatarsal I (R.)	43.7	–	–	5.8	–	–	–	–
41457	Metatarsal III (R.)	47.1	–	–	4.7	–	–	–	–
41001	Navicular	–	8.1	–	–	–	–	–	–
40917	Ilium (L.)	–	–	–	–	–	–	–	9.7
41457	Proximal phalanx, hindlimb	17.6	–	5.1	4.8	–	3.2	–	–
41457	Proximal phalanx, hindlimb	17.5	–	5.2	4.7	–	3.3	–	–
40876	Radius (R.)	–	–	9.1	–	–	–	–	–
40876	Radius (L.)	–	–	8.5	–	–	–	–	–
36961	Tibia (L.)	–	–	–	12.1	8.0	–	–	–
40991	Tibia (R.)	–	–	–	12.4	7.2	–	–	–
41001	Tibia (R.)	–	–	–	12.3	7.0	–	–	–
41025	Tibia (R.)	–	–	–	12.8	7.2	–	–	–
41457	Tibia (R.)	123.8	–	–	–	8.1	7.1	–	–

with leporids in general, the third trochanter is more similar to *Trischizolagus* (Averianov, 1995, p. 381–382) and *Sylvalagus*, than to *Lepus*, as the crest is less developed. Since this is a juvenile femur, the lack of crest development could be due to age and reduced muscle development; however, the trochanters are more developed than on *Palaeolagus* (Dice, 1932; Scott et al., 1940). KNM-NK 41486 consists only of a left femoral head; KNM-NK 44772 comprises the distal condyles of a left femur with a faint fusion line, and 44773 is also a left distal end but it is completely fused. All are well within the norm for leporids.

A complete tibia was recovered in three fragments that were refit (KNM-NK 41457), and it is remarkably similar both to modern and fossil leporids (e.g., *Trischizolagus* [Averianov, 1995, p. 381–382]) in morphological characteristics. This specimen has a greatest length (GL) of 123.8 mm (Figure 1), which is well within the range of modern jack-rabbits and cape hares (*Lepus* spp.). Complete tibiae are rare in the fossil record, but by comparison, an Oligocene-aged *Palaeolagus* is reported to be 56.3 mm (Dice, 1932, p. 303), which is considerably smaller. The other tibiae recovered from Lemudong'o are right and left distal ends, and right distal ends with one quarter of the distal shaft, and they derive from the same population as the above described complete tibia.

A total of five astragali, five calcanei, two cuboids, one navicular, metatarsal I, III, and IV, two metatarsal fragments, one metapodial fragment, three hindlimb proximal phalanges, and a proximal and middle phalange were recovered from Lemudong'o. These hindfoot (pes) elements represent a minimum of four individuals. KNM-NK 41323 are complete right and left astragali, 41457 (Figure 1) and 42265 are complete right astragalii with slight erosion on the boney margins, and 42356 is an articular condyle fragment. The astragalonavicular articular facet is narrower and extends more posteriorly than in *Palaeolagus* (Szalay, 1985, p. 118) and *Lepus* and is more similar in width to *Trischizolagus* (Averianov, 1995, p. 381) and *Sylvilagus*. However, this facet forms a somewhat elongated point in the Lemudong'o specimens. The shape of the sustentacular and the overall proportions are the same as other leporids.

The lagomorph calcaneus of *Palaeolagus* has been well described by Szalay (1985) and the presence of an enlarged calcaneal canal in fossil lagomorphs (Leporidae: *Palaeolagus* and *Hypolagus*) has been noted by Bleefeld and Bock (2002). Like *Palaeolagus* and *Hypolagus* (Bleefeld and Bock, 2002) the calcaneal canal is quite prominent in the Lemudong'o specimens (KNM-NK 40895 and 41457, Figure 1), whereas this canal is small and sometimes absent in modern *Pronolagus*, *Oryctolagys*, *Lepus*, and *Sylvilagus*. The proximal calcaneoastragalar facet has a distinctive transverse ridge dividing it into two parts, which is considerably different from the smoother, sloped appearance of *Palaeolagus* (Szalay, 1985, p. 117). This ridge is found in modern leporids and is reported for *Trischizolagus* (Averianov, 1995, p. 382).

Both the cuboid and navicular are the same as modern Leporidae. The metatarsal shafts are slightly stockier than the long, slender appearance of *Lepus*, but not as short, proportionally, as *Palaeolagus* (Scott et al., 1940) and are more similar to *Trischizolagus* (Averianov, 1995), but in every other respect (i.e., articular facets) the specimens do not differ from *Palaeolagus* *Hypolagus*, *Trischizolagus*, or modern leporids. The phalanges are identical to those of other fossil and extant leporids.

Since the distal tibia is the most commonly occurring element portion in the Lemudong'o fossil-leporid assemblage, further comparison with extant African and North American leporid tibiae was undertaken (Table 2, Figure 2). The smallest distal tibiae in this sample are the western North American desert (*Sylvilagus audubonii*) and Nuttall's cottontails (*Sylvilagus nuttal-*

Table 2. Distal tibiae measurements (in mm) of Lemudong'o Leporidae (KNM-NK) compared to modern African (SI) and North American (UCD) Leporidae. Bd = Breadth distal; Dd = Depth distal (von den Driesch, 1976).

Taxa	Tibia Specimen No.	Bd	Dd
Sylvilagus audubonii (Audubon/desert cottontail)	UCD 1011	10.2	4.8
Sylvilagus nuttallii (Nuttall's cottontail)	UCD 1169	10.5	5.1
Lepus capensis (cape hare)	SI 326766	11.1	5.4
Leporidae	KNM-NK 36961	12.1	8.0
Leporidae	KNM-NK 41001	12.3	7.0
Lepus capensis (cape hare)	SI 341059	12.3	8.2
Leporidae	KNM-NK 40991	12.4	7.2
Lepus californicus (black-tailed jack rabbit)	UCD 1168	12.4	7.6
Leporidae	KNM-NK 41025	12.8	7.2
Lepus californicus (black-tailed jack rabbit)	UCD 1161	12.9	7.2
Lepus capensis (cape hare)	SI 18818	13.0	7.9
Lepus californicus (black-tailed jack rabbit)	UCD 1368	13.3	7.3
Lepus californicus (black-tailed jack rabbit)	UCD 1016	13.8	8.5
Lepus saxatilis (scrub hare)	SI 221372	14.1	8.3
Pronolagus crassicaudatus (Natal's red rock hare)	SI 22972	14.4	7.2
	Average	**12.5**	**7.1**
	Minimum	**10.2**	**4.8**
	Maximum	**14.4**	**8.5**
	Standard Deviation	**1.2**	**1.7**

lii), which are more than a millimeter narrower in distal breadth, and nearly three millimeters narrower in distal depth, than any of the Lemudong'o specimens. At the other extreme, the distal tibia specimens of the African scrub hare (*Lepus saxatilis*) and African red rock hare (*Pronolagus crassicaudatus*) are minimally two-millimeters wider in distal breadth but equivalent in distal depth to the Lemudong'o specimens. The distal tibiae from Lemudong'o overlap, albeit on the smaller end, with those of both the African cape hare (*Lepus capensis*) and the North American black-tailed jackrabbit (*Lepus californicus*).

Family Leporidae Gray, 1821
Genus *Alilepus* Dice, 1931

Remarks

The genus *Alilepus* was first defined by Dice (1929, p. 342; 1931, p. 159) and assigned to the family Leporidae (McKenna and Bell, 1997). The type specimen, which was found in Mongolia, was originally described as *Lepus* [*Alilepus*] *annectens* (Schlosser 1924, p. 44). Further, description of this genus was emended by White (1991, p. 69) based on his analysis of late

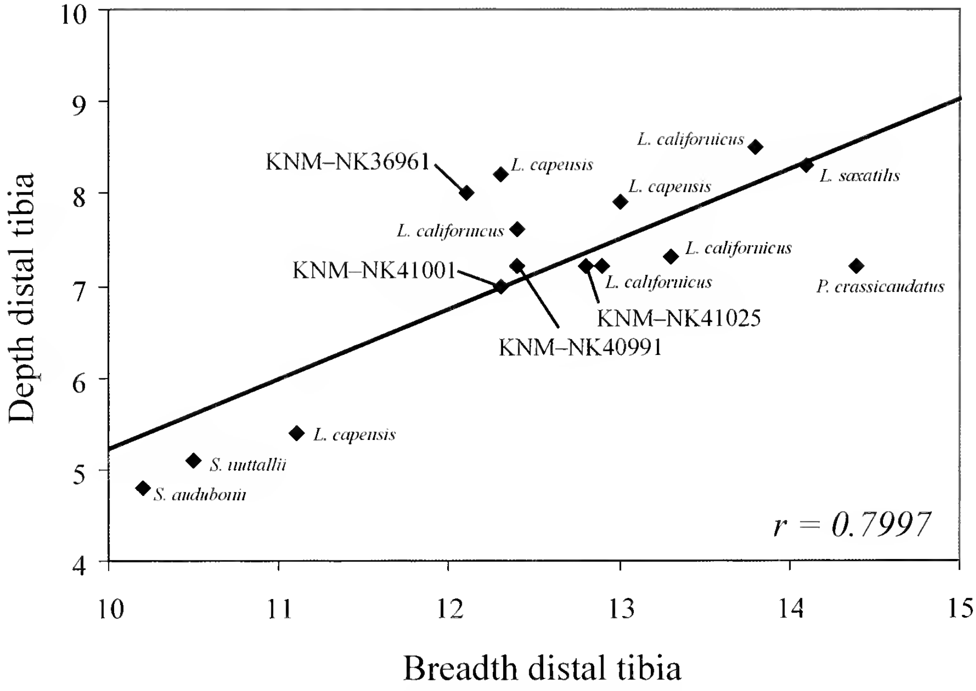

Figure 2. Scatterplot comparing distal breadth of tibia to distal depth of tibia (in mm) for the Lemudong'o specimens and other leporid species. Specimens and their corresponding measurements from Table 1.

Miocene to Pliocene North American Leporinae specimens. The morphology of the LP3 in particular and to a lesser degree the UP2 was determined to be the most useful for identifying leporines (White, 1991, p. 67; see also Hibbard, 1963; Voorhies and Timperley, 1997).

The earliest *Alilepus* fossils were recovered from late Miocene deposits in northern China (Qui et al., 1985; see also Schlosser, 1924), and have a distribution in Eurasia from the late Miocene to early Pliocene. In North America various species of the genus *Alilepus* have been identified from Miocene deposits across the Great Plains and the Southwest (see White, 1991 for a summary; also Voorhies and Timperley, 1997), and this genus has been identified from late Miocene deposits, Lower Nawata Formation, Lothagam, Kenya (Winkler, 2003).

Genus cf. *Alilepus* Dice, 1931
Figure 3, 4A

Material

KNM-NK 36939, R. maxillary fragment with UP2–P4.

Description and remarks

KNM-NK 36939 is fragmentary specimen of the right maxilla comprising P2–4 and only the palate and alveolar bone surrounding the teeth (Figure 3). The P2 has a buccal-lingual length of 3.2 mm and a mesial-distal width of 2.0 mm. It has a deeply incised main anterior reentrant (MAR) that extends nearly halfway across the tooth, a very shallow external anterior reentrant (EAR), and no internal anterior reentrant (IAR) (Figure 4). The other two premolars are typical of leporids; they are both bilobate and oval-shaped in occlusal view with a slight ridge separating the higher mesial lobe from the lower distal lobe. The P3 has a buccal-lingual length of 4.7 mm and a mesial-distal width of 2.1 mm, and the P4 has a buccal-lingual length of 4.7 mm and a mesial-distal width of 2.2 mm. Although association with a p3 is preferred for identification to genus (Dawson, 1967), KNM-NK 36939 is tentatively assigned to *Alilepus* based on visual assessment of the P2 cast and photographs following criteria established by White (1991).

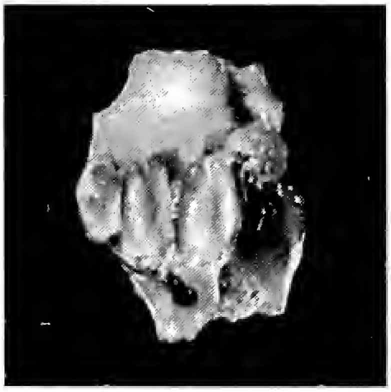

Figure 3. Occlusal view of KNM-NK 36939, cf. *Alilepus*, a right maxillary fragment with P2–4. Buccal is to the top of the photograph. The P2 has a buccal-lingual width of 3.2 mm and a mesio-distal length of 2.0 mm.

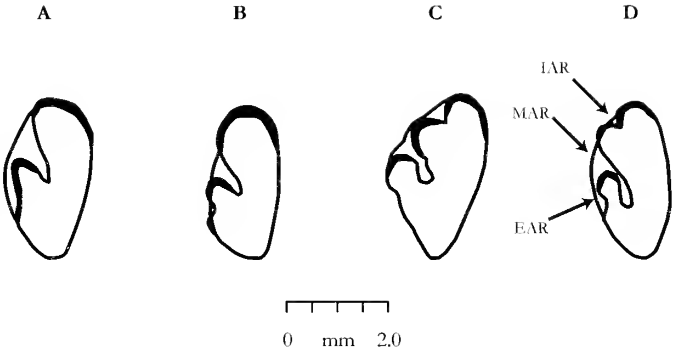

Figure 4. Occlusal view of Leporidae P2's: A = cf. *Alilepus* (KNM-NK 36939) from Lemudong'o; B = *Alilepus hibbardi* (White 1991, p. 73, fig. 6); C = *Serengetilagus praecapensis* (MacInnes 1953, p. 28, fig. 16); D = *Lepus capensis* (MacInnes 1953, p. 28, fig. 17). Location of main anterior reentrant (MAR), external anterior reentrant (EAR), and internal anterior reentrant (IAR) are noted on D.

Taphonomic Analysis

Of the 51 fossil specimens identified to the order Lagomorpha, 45 are assigned to the family Leporidae, representing a minimum of four individuals. Minimum number estimates are based on the recovery of four distal right tibiae and four right astragali (Table 3). The Enamankeon specimens comprise only 28.2% of the total leporid assemblage with an NISP of 11 and an MNI of one, and they derive only from the lower hind-limb portion: one tibia, three tarsals, five metatarsals, and two phalanges. Conversely, the leporid remains from Lemudong'o Locality 1 are represented by portions of front and hind limbs, the pelvis, and the maxilla.

To assess the extent of post-depositional bone attrition at this locality, the ratio of NISP:MNE and the average relative frequency of complete skeletal elements was used to gauge the extent of fragmentation (following Lyman, 1994). The results reveal that fragmentation of this assemblage is limited; this outcome likely is driven both by the high percentage of compact tarsal bones (33.3%) relative to other skeletal elements and by small sample size.

The postcranial remains were compared with published volume density values for leporid skeletal elements in order to assess the extent to which the Lemudong'o assemblage is density mediated (Table 4). Pavao and Stahl (1999) computed volume density values for Leporidae in two ways to account for the small size of their skeletal elements: 1) $VD_{LD/BT}$, or standard volume density, and 2) VD_{SA}, or shape-adjusted volume density. Standard volume density is bone mineral density divided by bone volume (normed to a square or rectangular shape); whereas, shape-adjusted volume density calculates bone volume using a more precise estimate of the cross-sectional geometry of the skeletal element. Using a Spearman's rank-order correlation coefficient, the normed relative frequency of leporid minimal animal units is compared with volume density values. The results of this analysis indicate a positive and significant correlation with standard volume density ($r_s = 0.66$, $P = 0.05$), and a positive but insignificant correlation with shape-adjusted volume density ($r_s = 0.52$, $P = 0.15$). Thus, overall the Lemudong'o assemblage is skewed toward denser skeletal elements, which accounts for the high frequency of tarsal bones and the low frequency of crania

Table 3. Frequency of Leporidae postcranial skeletal elements from Lemudong'o (Locality 1) and Enamankeon (Locality 1). Terms follow Lyman (1994): NISP = number of identified specimens; MNE = minimum number of complete skeletal elements necessary to account for all observed specimens; N whole = absolute frequency of whole or complete skeletal elements; percent whole = 100 (Σ N whole/Σ NISP).

Element	NISP	N Whole	MNE	NISP:MNE	%Whole
Astragalus	5	4	5	1.00	80.0
Calcaneus	5	2	5	1.00	40.0
Cuboid	2	2	2	0.00	100.0
Femur	4	0	2	2.00	0.0
Humerus	4	0	4	1.00	0.0
Ilium	1	0	1	1.00	0.0
Metapodial	2	0	2	1.00	0.0
Metatarsal	1	0	1	1.00	0.0
Metatarsal I	1	1	1	0.00	100.0
Metatarsal III	1	1	1	0.00	100.0
Metatarsal IV	1	0	1	0.00	0.0
Navicular	1	1	1	0.00	100.0
Phalanx, proximal, hindlimb	2	2	2	0.00	100.0
Phalanx, proximal	1	0	1	1.00	0.0
Phalanx, middle	1	0	1	0.00	0.0
Radius	2	0	2	1.00	0.0
Tibia	5	1	5	1.00	20.0
Total	**39**	**14**	**37**		
Average				**1.05**	**35.8**

and mandibles (except for isolated teeth). This pattern is similar to reported raptor-pellet accumulations (e.g., Terry, 2004).

Discussion

The fossil remains from Lemudong'o represent a relatively large sample of Lagomorpha—6% of entire vertebrate assemblage (Ambrose, Bell, et al., 2007)—and specifically leporid specimens from the late Miocene of Africa. Even though the leporid assemblage appears to be driven by density-mediated attrition, generally the fossil remains are well preserved and the elements are relatively complete. Of the 43 postcranial specimens in the Lemudong'o assemblage, 40 are identified to Leporidae with a minimum of four individuals represented. An additional eight cranial fragments were recovered, four of which are identified as leporid and one tentatively as *Alilepus* (P2–4). By comparison, the leporid (*Alilepus*) remains recovered from slightly older late Miocene (Lower Nawata) deposits at Lothagam comprise 14 postcranial and seven cranial specimens, and represent a minimum of two individuals (Winkler, 2003, p. 170).

A single maxillary fragment (P2–4) recovered from Lemudong'o compared most favorably with descriptions of the genus *Alilepus*. As illustrated in Figure 4, KNM-NK 36939 compares most favorably with published descriptions and diagrams of late Miocene *Alilepus* (Schlosser, 1924; White, 1991, p. 73) rather than the early Pliocene-Pleistocene African leporid *Serengetilagus* (Detrich, 1942; MacInnes, 1953, p. 28; Winkler, 2003, p. 172); however, it does resemble some illustrations of *Trischizolagus* (Averianov and Tesakov, 1997, p. 148), which has been identified from late Miocene-Pleistocene Eurasian deposits and may be one and the same with *Serengetilagus* (see Winkler, 2003, p. 171). Both of these genera likely derive from the "Alilepus" pattern, which supports the identification of the Lemudong'o specimen as *Alilepus* species indeterminate.

One problem with the use of a P2 is its high degree of variability both morphologically and in terms of size. Averianov and Tesakov (1997, p. 147) have suggested that smaller P2's with only 1–2 grooves may come from younger animals, whereas larger P2's with three grooves are most likely from older individuals. *Trischizolagus dumitrescuae* from Ruscinian (early Pliocene)

Table 4. The minimal animal unit (MAU) is scaled for the number of specific skeletal elements in a rabbit and %MAU are these values normed against the most commonly occurring skeletal element. Volume density values for rabbit skeletal elements are based on analysis by Pavao and Stahl (1999). LD/BT = linear density or bone mineral density/scan site volume (i.e., standard volume density); SA = shape-adjusted volume density. Nonparametric or rank-ordinal statistic, Spearman's rho (r_s) used to compare %MAU to density values.

Element	MNE	MAU	%MAU	Density (LD/BT)	Density (SA)
Astragalus	5	2.5	100.0	0.07	0.24
Calcaneus	5	2.5	100.0	0.11	0.26
Femur	2	1.0	40.0	0.08	0.28
Humerus	4	2.0	80.0	0.10	0.37
Ilium	1	0.5	20.0	0.07	0.39
Metatarsal	3	0.3	12.0	0.04	0.13
Phalanx	4	0.1	3.2	0.03	0.03
Radius	2	1.0	40.0	0.07	0.16
Tibia	5	2.5	100.0	0.07	0.43
				$r_s = 0.66$	**$r_s = 0.52$**
				$P = 0.05$	**$P = 0.15$**

deposits in Moldova and the Ukraine show a gradual shift from the "*Hypolagus*" pattern toward the dominant "*Alilepus*" pattern (Averianov and Tesakov, 1997, p. 148, Fig. 3a–u). Occlusal-surface illustrations of younger P2 from these Eurasian deposits show a high degree of similarity with KNM-NK 36939, which reinforces the cf. *Alilepus* moniker. Recovery of KNM-NK 36939 from ca. 6 Ma sediments at Lemudong'o (Ambrose et al., 2003) makes this the first occurrence of cf. *Alilepus* in southern Kenya and is one of only two reported occurrences of this genus in Africa, the other being the late Miocene Lower Nawata Formation, at Lothagam in northern Kenya (Winkler, 2002, 2003).

Association of postcranial elements with the cf. *Alilepus* sp. maxillary fragment, and given the lack of morphological variation within the Lemudong'o postcranial leporid assemblage suggests that the postcrania could also be *Alilepus*. The overall morphology of the postcrania is well within the range of fossil and modern Leporidae. Both primitive (e.g., calcaneal canal, wide olecranon foramen) and derived (e.g., proximal calcaneoastragalar ridge) characteristies are identified on the postcranial elements, which suggests a transition between archaeolagine and leporine morphology.

The leporids from Lemudong'o are larger than modern cottontail rabbits, smaller than scrub hares and rock hares, and roughly the size of small black-tailed jackrabbits (hares) or mid-sized cape hares. Evaluation of the size of the Lemudong'o fossils to a sample of modern leporids (Figure 2) is not meant to discern any phylogenetic or taxonomic relationships; it does, however, illustrate their relative size. In addition, the Lemudong'o leporids are considerably larger than paleolagines (e.g., Dice, 1932). Since leporids currently occupy both open and forested environments, and because these small mammals could have been transported to the site by carnivorous mammals or birds of prey, it is difficult to determine the late Miocene environment of Lemudong'o based solely on their remains. However, what these fossils do demonstrate is that leporids had expanded in the late Miocene into the Narok region of southern Kenya by at least ca. 6 Ma.

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CARNIVORA (MAMMALIA) FROM LEMUDONG'O (LATE MIOCENE: NAROK DISTRICT, KENYA)

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ABSTRACT

Lemudong'o, a fossiliferous locality in Narok district (Kenya), adjacent to the southern reaches of the Kenya Rift Valley, yields vertebrates in the still poorly-known span of the African late Miocene. The associated isotopic age is ~6.1 Ma, correlative with well-known local faunas of western Eurasia assigned to the final Turolian or MN-13 (Mammal Neogene-Zone). This local fauna comprises Canidae (1 species), Felidae (2 species), Viverridae (2 species), Herpestidae (at least 4 species), Hyaenidae (1 species), Mustelidae (1 species), and Procyonidae (1 species). The assemblage both confirms and amplifies the overall composition of such mammal fauna from other African localities of comparable, or rather younger or older age(s), and enhances the basis for comparison with well-known counterparts of western Eurasia.

Introduction

The Lemudong'o locality is of particular interest and importance due to the demonstrable uppermost Miocene age of the attendant sedimentary sequence (Ambrose et al., 2003; Deino and Ambrose, 2007). The lowermost exposed sediments are of ≥ 6.1 Ma (^{39}Ar/^{39}Ar [SCLF]) age, and the several fossil-bearing horizons, exposed at Locality 1, are of comparable or just slightly younger (6.04 Ma) age. This age is within the span of MN-13 (Mammal Neogene-Zone), the last of the tripartite Turolian-ELMMZ (European Land Mammal Megazone) of the circum-Mediterranean/western Eurasian realm (Mein, 1999; Steininger, 1999). Hence, it is broadly correlative in age with many classic fossil localities from western Asia to the Iberian Peninsula. Thus, we have one of those still uncommon African occurrences of the late Cenozoic, affording some most welcome insight into the natural world of the end-Miocene in a near equatorial setting.

Among the fossil assemblages from Lemudong'o is a sample of the often poorly represented order Carnivora. The available sample of Carnivora species is generally both fragmentary and of limited diversity in light of expectations for a local fauna of this uppermost Miocene age. Nonetheless, it is both interesting and important as it affords some representation of Canidae, Mustelidae, Procyonidae, Viverridae, Herpestidae, Hyaenidae, and among Felidae, both Machairodontinae and Felinae.

Abbreviations

KNM	Kenya National Museum.
NK	Narok District indicates fossils that are from localities within this district, including Lemudong'o Localities 1 and 2, Enamankeon Localities 1, 2, and 3, and Kasiolei Locality 1.

Dental abbreviations follow the convention of upper case letters = maxillary teeth, lower case letters = mandibular teeth.

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Infraorder Cynoidea Flower, 1869
Family Canidae Gray, 1821
Subfamily Caninae Fischer von Waldheim, 1817

Figure 1. *Eucyon* aff. *intrepidus* (KNM-NK 41284), right M1 in occlusal view. Scale bar = 1 cm.

Genus *Eucyon* Tedford and Qiu, 1996
Eucyon aff. *intrepidus* Morales, Pickford and Soria, 2005
Figure 1

Description and remarks

A small canid, here considered to be of the tribe Canini, is represented by elements of upper and lower dentition. KNM-NK 41053 consists of a left P1 with root. This element is readily identified as a P1 of a small canid. Its dimensions (Table 1) and simple morphology are compatible with homologs attributed to genus *Eucyon*.

KNM-NK 41284 is a right M1, lacking a root. A well-preserved upper molar crown, scarcely worn, is demonstrably canine (Figure 1). A distinction among some canids, even *Eucyon* and *Vulpes*, with relatively complete material is not always readily effected. To an extent, this is similarly the case in respect to the raccoon-dog *Nyctereutes*, several species of which are now well documented in the Pliocene of Eurasia.

Specimen KNM-NK 41284 replicates most particularly the morphology and size of its homolog in samples now attributed to the genus *Eucyon* (Tedford and Qiu, 1996). A comparison of M1 crown dimensions in such samples and KNM-NK 41284 is set out in Table 2; characters are set out in Table 3. Comparison is effected diversely with the holotype of *E.* (ex-*Canis*) *davisi* (UCMP-545), associated M1–M2 from Rattlesnake Creek (Oregon) (Merriam, 1911a, b) and associated cranio-dental material from Little Valley and from Juniper Creek Canyon (Oregon), described and figured by Shotwell (1970), from Hemphillian age faunas of the John Day region, Oregon. A newly recognized species, *E. intrepidus*, from the Lukeino Formation, Baringo, Kenya (Morales et al., 2005, p. 48) is the first nominate species of *Eucyon* from Africa.

KNM-NK 41285 consists of a left m1, preserving a posterior root, and lacking the mesio-lingual (paraconid or pad) portion of the trigonid. This small carnassial is comparable in size to some homologs attributed to *Eucyon davisi*, e.g., the UO-26742 individual, comprising associated upper and lower jaws with dentition (and postcranials) (Shotwell, 1970). Although incomplete, it is well preserved and shows scant wear. The protoconid (pr^{d}) is salient with the usual steep, sub-vertical distal slope to the talonid. There is a distinct but low buccal cingulum at the base of the protoconid. The metaconid (med) is distinct, enlarged and disto-lingually offset from the back of the protoconid with which it is joined by a low, salient crest. The talonid is elongate and bears marginally both hypoconid (hy^{d}), the larger and more posterior, and entoconid (en^{d}) subequal cusps, the latter a bit more distally set. There is no linkage between these cusps similar to *E. davisi.* Sometimes it may bear accessory cusplets adjacent anteriorly to hy^{d} and/or en^{d} (Shotwell, 1970). On KNM-NK 41825 there is only a small marginal beadlike elevation anterior to the entoconid. The posterior-most part of the talonid basin is simple and constricted by the aforesaid cusps. The lingual outline of the talonid is slightly convex and the buccal outline is incurved between the pr^{d} and hy^{d}. This dental element is still unknown in *E. intrepidus.*

Table 1. Anterior (P1) premolar dimensions (mm) in some *Eucyon davisi* and other *Eucyon* samples. North American and Odessa samples after Rook (1993); *E. minor* after Tedford and Qiu (1996).

	P1	
	length	breadth
Lemudong'o (Narok, Kenya) KNM-NK 41053	4.7	3.15
Little Valley (Ore) UO-26742	5.8	3.4
BirdBone Q (Az) F: AM-63019	5.1	3.3
F: AM-63034	4.8	2.8
Edson LF (KS) F: AM-49464	5.0	3.1
Renfro Pit (TX) F: AM-61981	4.8	2.9
Old Cabin Q (AZ) F: AM-72661	4.8	2.8
Odessa (UKR) (*E. odessanus*) $n = 4$	6.1 (5.9–6.3)	3.45 (3.3–3.9)
China (*E. minor*) $n = 8$	5.675 (4.9–6.4)	2.86 (3.0–4.0)

Tedford and Qiu (1996) assigned abundant material from elsewhere in western and central North America, represented in various museum collections, as well as from the Mio-Pliocene of Asia, to the new genus *Eucyon.* It was considered by them, as well as by Berta (1988), as a stem-taxon for *Canis*-group species as well as for a set of South American canid genera. The earliest documented appearance of the genus is in the (late) middle Miocene (Clarendonian) of North America; but, it is most commonly represented there in subsequent Hemphillian local faunas. *Eucyon davisi* appears in (earlier) Pliocene Age local faunas in China, along with a larger, derived species, *E. zhoui.* The arrival of *Eucyon* into western Eurasia is documented in the latest Miocene (late Turolian, MN-13) of Brisighella (Italy) by a derived *Canis* species, among the oldest such known in Europe (Rook et al., 1991, p. 19). It was initially attributed to "*C.*" *monticinensis* (Rook, 1992, p. 152), and only subsequently transferred to *Eucyon* (Rook, 1993, p. 25). The same, or related, species is recorded from Alatini (Macedonia, Greece), represented by a mandible, once (and originally) referred to *Nyctereutes donnezani* (Sickenberg, 1972, p. 501–503) and known now to derive from a Ruscinian (lower Pliocene) context (Koufos, 1997, p. 43). A canid sample from the Ruscinian-age karstic infillings ('catacombs') of Odessa (Ukraine), assigned to *Vulpes odessana* (Odintzov, 1967, p. 130), is also now attributed to *Eucyon* (Tedford and Qiu, 1996). However, a still older canine (MN-12 attribution) in Western Europe is, perhaps, *Canis cipio* (Crusafont, 1950, p. 45–47; Pons and Crusafont, 1978), first documented at Concud (or Cerro de la Garita) (maxilla with P4-M2) and subsequently at Los Mansuetos (an m1), Teruel basin, Spain (Alcala, 1994).

The African record of the Mio-Pliocene Canidae is still scant. Langebaanweg has yielded cranio-dental remains perhaps representative of *Eucyon* (Hendey, 1974; Rook, 1993). Younger, about mid-Pliocene age, occurrences of several canid taxa, including *Canis* sp., are reported from Laetoli (Tanzania) (Barry, 1987) and from south Turkwell (Turkana, northern Kenya) (Werdelin and Lewis, 2000).

In the latter instance, gnathic and several postcranial parts definitely attest to the genus *Canis* (*Canis* sp. nov. A of the authors, p. 1176) at 3.5 Ma. In the former instance incomplete cranio-dental and various postcranial remains, attributed to aff.

Table 2. Upper molar (M1) dimensions (mm) in some samples of *Eucyon* species and in KNM-NK 41284. *E. intrepidus* after Morales et al. (2005), *E. davisi* after Rook (1993), *E. monticinensis* after Rook (1992), *E. odessanus* after Rook (1993), *E. minor* after Tedford and Qiu (1996), cf. *Eucyon* Langebaanweg (after Hendey, 1976; Rook, 1993) and *C. cipio* after Crusafont (1950).

	M1	
	length	**breadth**
Lemudong'o (Narok, Kenya) KNM-NK 41284	8.06	11.6
Lukeino Fm. (Baringo, Kenya) BAR 2127 '01 (*E. intrepidus*)	9.3	11.0
BAR 719 '02 (*E. intrepidus*)	9.6	12.7
Eucyon davisi		
Rattlesnake Creek (Ore) UCMP-545	10.0	11.6
Thousand Creek (Ore) UO-12505	10.1	12.7
Little Valley (Ore) UO-26742	11.2	13.7
Bird Bone Q (AZ) *n* = 13	11.08 (10.0–12.5)	13.2 (11.3–15.7)
Clay Banc Q (AZ) *n* = 4	11.05 (10.9–11.05)	12.85 (12.4–13.4)
Edson LF (KS) *n* = 1	8.9	12.0
Optima LF (OK) *n* = 2	11.0–11.2	12.7–13.1
Miami Q (TX) *n* = 3	10.9 (10.3–11.4)	11.1 (8.0–13.2)
Old Cabin Q (AZ) *n* = 6	10.53 (9.7–11.3)	12.8 (12.0–14.0)
Monticino (Brisighela, It) *n* = 1 (*E. monticinensis*)	12.0	13.7
Venta del Moro (Sp.) *n* = 1 (*E. monticinensis*)	11.2	12.7
Concud (Sp.) *n* = 1 (*C. cipio*)	13.1	15.8
Odessa (Ukr.) *n* = 7 (*E. odessanus*)	11.0 (10.1–11.8)	13.0 (11.5–14.4)
China *n* = 9 (*E. minor*)	9.94 (10.0–11.8)	13.17 (12.2–13.9)
Langebaanweg *n* = 2 (cf. *Eucyon* sp.)	10.1	11.5–13.0

Canis brevirostris (Euer) by Barry (1987, p. 237–240), with a size comparable to extant *Nyctereutes*, actually exhibits features found within the morphometric range of *Eucyon* (Rook, 1993) and at substantially younger, mid-Pliocene, age than previously discussed Kenyan localities.

Infraorder Arctoidea Flower, 1869
Parvorder Mustelida Tedford, 1976
Family Mustelidae Swainson, 1835
Subfamily Guloninae Gray, 1825
Genus *Plesiogulo* Zdansky, 1924

Plesiogulo botori Haile-Selassie, Hlusko, and Howell, 2004
Figure 2

Description and remarks

The holotype, KNM-NK 41420, is a cranial fragment corresponding to a partial right temporal with glenoid cavity and teeth from both sides: right P3 (two crown fragments), P4-M1, and left P3-M1 and left M2 (belonging to the same individual) (Figure 2). KNM-NK 36518a consists of a left upper canine. KNM-NK 36518b consists of a right lower canine.

Table 3. Upper (M1) molar morphology (characters after Wang et al., 1999) in some samples of *Eucyon* species and KNM-NK 41284.

		Eucyon intrepidus		*Eucyon davisi* (North America)		
		KNM-NK 41284[1] Lemudong'o, Kenya	BAR 2127'01-719'02[3] Lukeino Fm., Kenya	UCMP–545 (type)[1] Rattlesnake Creek, Ore.	UCMP-12505[1] Thousand Creek, Nev.	UOE-26742[2] Little Valley, Ore.
Crown form	51	1a - subtriangular	1a - subtriangular	1a - subtriangular	1a - subtriangular	1 - subquadrate
Distal border of crown	57	00 - scarcely incurved	00 - scarcely incurved	0 - slightly incurved	00 - scant incurvature	0 - slightly incurved
Buccal cingulum…						
re paracone	50	0 - present, weak	0 - present, weak	0 - present	0 - present, broken, inc	0 - present
re metacone	49	0 - present, stronger	0 - present, stronger	0 - present	? broken	0 - present
Lingual cingulum	52	1 - extended anteriorly around pr	1 - extended anteriorly around pr		2 - thickened anteriorly	0 - largely set and extended linguo-distally
Parastyle	48	2 – lost	2 - lost	2 - lost	2 - apparently lost	2 - lost
Buccal cusps pa re me	55	1 - pa larger, higher	1 - pa larger, higher	1 - pa larger, higher	1 - pa larger, higher	1- pa larger, higher
Hypocone	54	3 - thickened lingual cingulum	3 - thickened lingual cingulum	0 - absent	3 - thickened lingual cingulum	2 - as broad lingual cingulum and displaced disto-lingually
Paraconule	56	1 - distinct cusplet, on anterior loph	0/1 - semi-distinct anterior loph cusplet	1 - thickened part of anterior loph	1 - distinct cusplet, on anterior loph	0 - absent
Metaconule	53	1 - distinct cusplet at junction anterior loph & distal cingulum	1 - distinct, enlarged cusplet	1 - thickened part of lingual-distal cingulum	1 - distinct cusplet at junction anterior loph & distal cingulum	0 - weak swelling on loph
Protocone		distinct, enlarged m-l cingulum cusp	subangular, m-l cingular cusp	indistinct, ? thickened m-l cingulum	weak enlargement m-l cingulum	distinct, small on mesial crista

[1] Personal observations

[2] After J.A. Shotwell (1970)

[3] After Morales et al. (2005)

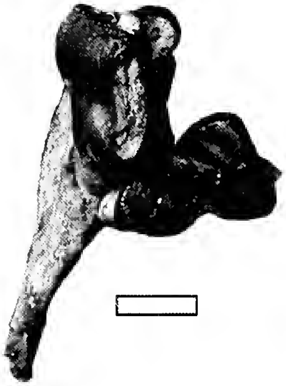

Figure 2. *Plesiogulo botori* (KNM-NK 41420), right temporal with P4 and M1 in occlusal view. Scale bar = 1 cm.

The two canines could well correspond to a different, smaller individual as they appear small compared to the large dimensions of the P3-P4-M1 of the holotype (KNM-NK 41420).

The new species of *Plesiogulo*, described elsewhere by Haile-Selassie et al. (2004a), is represented both at Lemudong'o and at the Adu Dora locality, Middle Awash (Afar depression, Ethiopia). The latter, a paratype, comprises an isolated left M1 (ADD-VP-1/10, NME). Up until the introduction of the new species, a total of about seven seemingly valid species, including synonymies, have been proposed (Kurtén, 1970). Two, *P. monspessulanus* (Asia, Europe, S. Africa) and *P. lindsayi* (N. America), are large, and five, *P. minor* (Asia), *P. crassa* (Asia, Europe), *P. brachygnathus*, and *P. praecocidens* (Asia, E. Africa), and *P. marshalli* (N. America), are smaller, even considerably so (Harrison, 1981). The first known occurrence in Africa was the recovery at Langebaanweg (South Africa) of cranial, jaw, teeth, and postcranial bones referred by Hendey (1978a) to *P. monspessulanus*. *Plesiogulo botori* is distinguished (Table 4) on dental characteristics only (thus far) as the largest yet known species, with P3 and P4 both longer and wider, and M1 longer (than for *P. monspessulanus*), lacking an anterior cingulum on P4, a notably expanded internal lobe of M1, high protocone and discontinuous lingual cingulum of M1. Postcranial remains are not yet definitively known for *P. botori*. *Plesiogulo praecocidens*, an Asian species, has recently been recognized (by Morales et al., 2005, p. 52) from upper teeth, at localities of the Lukeino Formation (Baringo basin), Kenya.

Parvorder Mustelida Tedford, 1976
Family Procyonidae Gray, 1825
Subfamily Simocyoninae Dawkins, 1868
Genus *Simocyon* Wagner, 1858
Simocyon species indeterminate
Figure 3

Description and remarks

KNM-NK 45780 consists of a left M1/crown, complete and unworn (Figure 3). The specimen is distinguished by a subtriangular crown, trigon basin dominated by the two buccal cusps, subconical with pointed tips and each with an anterior and posterior low descendant crest. These cusps, paracone (pa) and metacone (me), are closely appressed in their bases, though separated above by a strong fissure; the paracone (pa) is overall larger and notably higher than the metacone (me). The salient mesial and posterior trigon crests (pre- and post-protocrista) are simple, unadorned, and are confluent curvingly at the position of the protocone (pr) that is, however, undifferentiated as a distinct cusp. The inner margin of the crown is markedly prolonged lingualward of the trigon, distinguished by its massive basal cingulum, which girds the whole lingual extent of the crown and hence affords a somewhat linguate or trapezoidal form to the crown. There is a distinct, rather weak buccal cingulum along that outer margin of the paired buccal cusps.

The single element of the upper molar dentition matches in every respect its homolog in (at least) three specimens (from Pikermi and Halmyropotamus in Europe, and from Fugu in China) representing the genus (and species) *Simocyon primigenius* (Wagner, 1858). It is at the smallest end of the known range of variation of a total of ten such molars representing this species (Table 5). It is here referred to *Simocyon* sp. indet., and constitutes, to our knowledge, the first known record of the taxon in Africa.

Simocyon is not a very common element, although it is persistent within upper Miocene faunas to which it is largely confined. It is known now from over a dozen localities, including Concud (MN-12) in Spain, Eppelsheim (MN-9, type of the species *S. diaphorus*) and Dorn-Dürkheim (MN-11) in Germany, Montredon (MN-10) in France, Csákvár (MN-11, source of the purported species, *S. hungaricus*) in Hungary, Kalimanci (MN-12) in Bulgaria, two localities in Ukraine, and three in central China, as well as those set out in Table 5 in which dimensions of M1 are given. Attributed to *S. batalleri* are specimens from Sabadell environs (type) and Bovila Sagués (or San Miguel del Taudell), both Catalonia, and the recently investigated Cerro de Batallones-1 (MN-10) locality near Madrid. It had been thought to have a strictly Eurasian distribution. However, there is definite evidence for its dispersal into western North America (Qiu, 2003), as it is documented in the late Miocene (Hemphillian) of Oregon (Rattlesnake Formation), once recognized as *Pliocyon* (Thorpe, 1921), then *Araeocyon* (Thorpe, 1922), now *S. marshi*. Subsequently, it has been recorded as well from such local faunas in southern Idaho and in Nevada (Tedrow et al., 1999). In western Eurasia it is temporally limited in occurrence in Vallesian and Turolian faunas (Ginsburg, 1999); in China it has been documented in Baodean and, later, Yushean faunas (Qiu and Qiu, 1999). Its postcranial skeleton was once apparently wholly unknown; among the recently recovered, rich carnivore assemblage of Cerro de Batallones (Madrid province, Spain), partial skeletons of *Simocyon* are represented (Peigné, Salesa, et al., 2005) and are still under study.

Even cranial remains have been uncommon, and were first known only in Europe (initially Pikermi, subsequently, Veles and Halmyropotamus). Other localities in China (Shaanxi and Shanxi) afforded further material; recently the situation has been improved by the local faunas of Fugu (Shaanxi) (Wang, 1997) and, especially, Batallones-1 (Spain) (Peigné, Salesa, et al., 2005) which afforded much welcome insight into details of both cranial and dental morphology. Since its recovery and recognition a century and half ago the systematics, affinities, and phylogenetics of *Simocyon* became a matter of considerable controversy. Altogether as many as four species (in Eurasia) and, perhaps, another in North America, have been proposed. Possibly an older, less derived species (*S. diaphorus*), with unreduced premolar dentition, is to be distinguished from another subsequent and more derived species (*S. primigenius*) with much reduced/lost

Table 4. Comparison of upper dental dimensions[1] in *Plesiogulo*.

	***P. botori* sp. nov.**	***P. monspessulanus* (= major)**	***P. brachygnathus* (ex-*Lutra brachygnatha*)**	***P. crassa* (= minor)**	***P. praecocidens***	***P. marshalli***	***P. lindsayi***	***G. gulo***
P3								
Length	14.6	13.9	no data	11	no data	11.6	13.0	10.4
Breadth	10.2	9	no data	6.9	no data	8	9.3	6.3
Length/breadth	1.43	1.54	no data	1.59	no data	1.45	1.39	1.65
P4								
Length	24.5	23.2	17.1–20.5	18.3–20.8	17.2	20.1	23.5	19.75
Breadth	16.7	15.6	11.1–14.0	12.9	10.9	13.9	17.3	11.9
Length/width	1.47	1.49		1.51		1.45	1.36	1.66
M1								
Breadth	21.2	18.6	13.8–19.4	15.8–17.8	13.8	18.2	20.0–21.5	13.9
Lingual-lobe length	15.9	15.4	12.0–16.3	13.2	12.4	15.1	13.3–15.5	8.3
Minimum length	10.1		8.4–11.7	8.4	7.8	9.1	9.7	
Max/min length	1.57	(1.54e)		1.57	1.59	1.67	1.51	(1.34e)
Width-/lingual-lobe Length	1.33	1.21		1.28	1.11	1.21	1.41	1.68
P3/P4 length	0.59	0.59	no data	0.57	no data	0.58	0.55	0.53
P3/P4 breadth	0.61	0.58	no data	0.54	no data	0.57	0.53	0.53

[1] Data for *P. monspessulanus*, *P. brachygnathus*, and *P. crassa* are from Hendey (1978b) and Alcalá et al. (1994), Zdansky (1924), and Kurtén (1970), respectively. Dimensions of *P. marshalli* and *P. lindsayi* are from Harrison (1981). Measurements of *Gulo gulo* are from Kurtén and Rausch (1959); e = estimated from published images, all reported measurements are in mm

anterior premolar dentition and altered lower carnassial (m1) crown proportions. There is now good reason to accept the validity of a third species taxon, *S. batallerii*, from Spain, previously and first recorded in Catalonia and now very well represented at Batallones (province of Madrid). An antecedent source of *Simocyon* has ultimately come to be recognized as *Alpecocyon* (ex-*Alopecodon* Viret, 1933) *leptorhynchus* (Camp and Vanderhoof, 1940), known from middle Miocene localities of MN-6 (as at Göriach, Neudorf) or MN-7/8 (La Grive-St-Alban, Oppeln) ages (Thenius, 1949; Beaumont, 1964).

The phylogenetic affinities of *Simocyon*—whether among caniniformes (Cynoidea), amphicyonids/ursids (Arctoidea), or mustelids (Mustelida)—were long debated and disputed. Major contributions toward resolution of the issue have been those of Pilgrim (1931), Thenius (1949), Schmidt-Kittler (1981), Wolsan (1993) and, recently and notably, Wang (1997); and, in respect to molecular phylogeny among procyonids, Slattery and O'Brien (1995) in their definitive work toward resolution of ailurine, red panda (*Ailurus fulgens*) phylogentic affinities. Among the family Procyonidae are four subfamilies, Basarisinae (Gray, 1869, p. 246), Procyoninae (Gray, 1825, p. 339), Ailurinae (Gray, 1843, xxi), and Simocyoninae (Dawkins, 1868, p. 1). The detailed morphological evidence afforded by structure of basicranium (Wang, 1997) has finally brought to resolution the procyonid character of *Simocyon* and, as well, enabled full-blown explication of craniodental anatomy and its similarities and differences with the only still extant ailurine.

Figure 3. *Simocyon* sp. (KNM-NK 45780), left M1 crown in occlusal view. Scale bar = 2 cm.

Table 5. Dimensions (mm) of first upper molars (M1) among known *Simocyon* samples.

	M1 (length × breadth)
Pikermi (M.9032)[1]	15.5 × 19.0
Halmyropotamus (1967.8)[2]	16.0 × 19.0
Eppelsheim (*S. diaphorus*)[3]	15.0 × 20.0
Tchobroutchi (Molodova)[4]	15.0 × 17.0
Titoe Veles (Bulg)[5]	16.7 × 19.0
Iberia ('*Metarctos*' *batalleri* Viret)	
Sabadell[6]	16.0 × 17.5
Tarrasa[7]	15.0 × 17.0
Batallones-1[10] ($n = 2$)	16.4 × 19.25
Baode (Loc.31) Shanxi, PRC[8]	14.9 × 19.4
Fugu, Shaanxi, PRC[9]	15.5 × 17.0
Lemudong'o (Kenya) (KNM-NK 45780)	13.4 × 16.9

[1] G. E. Pilgrim (1931), p. 16

[2] J. Melentis (1968), p. 312

[3] M. Schlosser (1887–90), p. 329

[4] M. Pavlow (1914), p. 43

[5] R. Garevski (1974), p. 190

[6] J. Viret (1929), p. 565

[7] J.F. Villalta Comella & M. Crusafont Pairó (1948), p. 86

[8] O. Zdansky (1924), p. 6

[9] X. Wang (1997), p. 193

[10] S. Peigné et al. (2005), p. 230

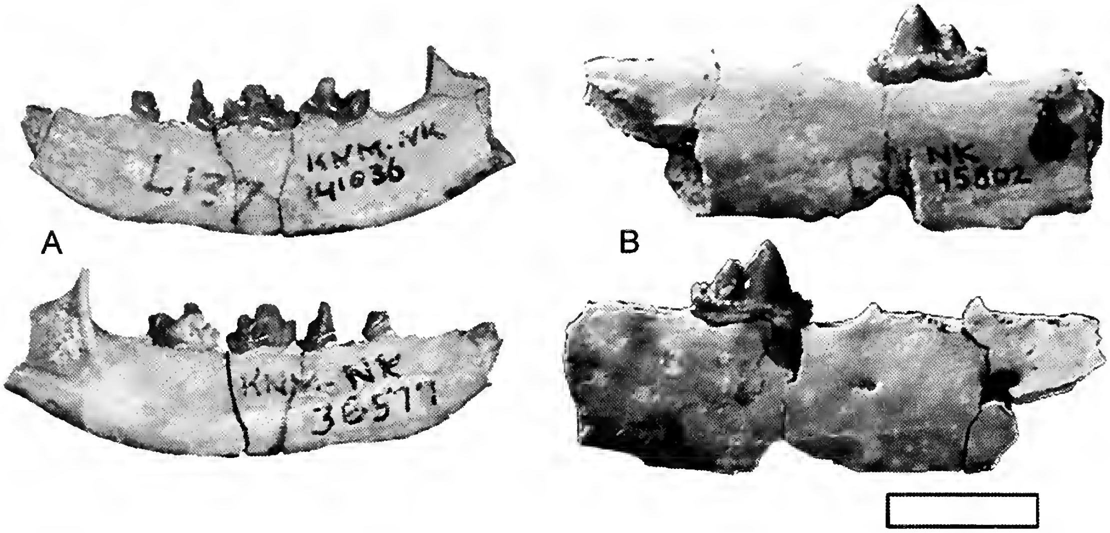

Figure 4. A, *Herpestes* sp. (KNM-NK 36577 and KNM-NK 41036), right mandible in labial (lower) and lingual (upper) view. B, *Ichneumia* aff. *albicauda* (KNM-NK 45802), right mandible with p4 in labial (lower) and lingual (upper) view. Scale bar = 1 cm.

Suborder FELIFORMIA Kretzoi, 1945
Family HERPESTIDAE Bonaparte, 1845
Subfamily HERPESTINAE Bonaparte, 1845

Remarks

The late Cenozoic fossil record of African herpestines is overall scant, except for representation at the Laetoli and Olduvai localities. Whether this is due to the lack of screen-washed situations or whether it is a natural circumstance is difficult to establish. At Lemudong'o there are several herpestines now distinguished only by their differences in size. Some are included within the size range of the small mongooses, genus *Helogale*.

Genus *HELOGALE* Gray, 1861
HELOGALE sp.

Description and remarks

KNM-NK 36892 consists of a left horizontal mandibular fragment with partial crown of a p3, and KNM-NK 41114, a right horizontal edentulous mandibular fragment. These two specimens constitute the smallest of the carnivores in the Lemudong'o assemblage. Their fragmentary state and general lack of dentition obviates further identification and attribution. The dwarf mongoose, *Helogale*, is now represented by two species in sub-Saharan Africa, one widely distributed, the other (*H. hirtula*) found only within the northeastern horn of eastern Africa. An apparently extinct, but ill-known species of *Helogale* is known from the upper Miocene of western Afar.

Genus *HERPESTES* Illiger, 1811
HERPESTES species indeterminate
Figure 4A

Description and remarks

Other remains are within the size range of the genus *Herpestes* and are considered *Herpestes* sp. indet., a form that is somewhat larger than the smallest form attributed above to *Helogale*. There are now four species of *Herpestes* recognized in Africa, two of which are documented as distributed within Ethiopia. The material consists of: KNM-NK 42319, a right edentulous mandibular fragment with alveolus of m2-m1-p4 and posterior p3; KNM-NK 36577, a right mandibular ramus with partial crown of c, alveolus of p1, broken crowns of p2 and p3 and complete p4; and KNM-NK 41036, a right lower mandibular ramus with talonid and metaconid of m1 and alveoli for m2. These latter mandibular fragments (36577 and 41036) conjoin and thus comprise one nearly complete right mandible body, lacking only the ascending ramus (Figure 4A). They now bear the former number, KNM-NK 36577. This herpestine resembles, and might be the same as, an undescribed, probably new species of *Herpestes* known from the upper Miocene of the western Afar (Ethiopia) (Haile-Selassie, 2001). A small herpestine, referred by Peigné, Salesa, et al. (2005) to the extant *H.* (*galerells*) *saguineus*, and considered by them a distinct genus, is now known from the Toros-Mellala (Chad) locality TM 266, among this older fauna. With the scant material at hand it is difficult to ascertain probable affinities among these finds. Dimensions of some genera and species of herpestines are set out in Table 6.

Genus *ICHNEUMIA* Geoffrey Saint-Hilaire, 1837
ICHNEUMIA aff. *ALBICAUDA* Geoffrey Saint-Hilaire, 1837
Figure 4B

Description and remarks

KNM-NK 45802, consists of a right p4. This is the largest herpestid of the Lemudung'o association. It matches in size and in morphology the extant white-tailed mongoose, *Ichneumia albicauda*.

Family VIVERRIDAE Gray, 1821
Subfamily VIVERRINAE Gray, 1821
Genus *GENETTA* G. Cuvier, 1816
Figure 5

Remarks

There are remains of two forms of genet, having robust mandibular body and distinguishable by their differences in size (Table 7a).

Table 6. Some lower dentition dimensions (crown length; mm) of Mio-Pliocene herpestines and of extant herpestines.

Taxon	p4	m1	Notes
Ichneumia albicauda KNM-NK 45802	7.5		
Herpestes sp. KNM-NK 36577	4.45		
Herpestidae indet, BAR-1085'99; 2638'03[4]	4.5	6.0	4
Herpestes sp. A, Lbwg[1] L-11847	5.75	6.7, 6.8	1
Herpestes sp. B, Lbwg[2] L-16177a	3.75	4.2, 4.3	2
Herpestes sp., Klein Zee[1] 1930. x1, 5.	5.5, 5.2	6.8, 6.3	1
Herpestes sp., MALM[3] ALA 2/314	4.55	6.3	3
Herpestes sp., MALM[3] ASK 3/64	5.9	—	3
H. (*Galerella*) *sanguinea*, TM-266[5]	5.0	6.0	5
Herpestes sp., Dhok Pathan, Siwalks[6], GSP-217	7.3	—	6
Atilax paludinosus	8.5	10.0	J. A. Allen 1924
Bdeogale nigripes	7.8	8.5	J. A. Allen 1924
Crossarchus alexandri	6.0	7.1	J. A. Allen 1924
Helogale hirtula	5.7	5.7	J. A. Allen 1924
Helogale hirtula (3)	3.6	4.0 (3.8–4.3)	G. Petter 1987
Herpestes (*G.*) *sanguineus*	6.5	8.3	J. A. Allen 1924
Herpestes (*G.*) *sanguineus* (21)	4.67 (4.1–5.4)	5.36 (5.0–6.2)	G. Petter 1987
Herpestes (*H.*) *ichneumon*	7.6	9.0	J. A. Allen 1924
Herpestes (*H.*) *ichneumon* (21)	8.78 (8.1–9.5)	4.7 (4.0–5.0)	G. Petter 1987
Herpestes naso	8.0	9.0	J. A. Allen 1924
Herpestes (*G.*) *pulverulenta* (19)	5.45 (5.0–6.0)	6.10 (5.6–6.8)	G. Petter 1987
Mungos mungo	6.9	7.5	J. A. Allen 1924
Mungos mungo (22)	4.89 (4.3–5.3)	(4.2–5.8)	G. Petter 1987
Ichneumia albicauda	7.6	8.1	J. A. Allen 1924

[1] Hendey (1974) considers Lbwg sp. A as 'virtually indistinguishable' from Klein Zee 1930. x1, 5. (in Stromer, 1931)

[2] Hendey (1974) considered sp. B comparable to *Herpestes sanguineus*

[3] Haile-Selassie (2001) considers these and other MALM specimens of similar morphology and to constitute same, probably new *Herpestes* species; it is smaller than *H. ichneumon and H. (G.) palaeoserengetensis*; but is much larger than Lbwg. *Herpestes* sp. B. It is similar in size and some morphology to *H. pulverulenta*

[4] Herpestidae indet, Tabarin, Baringo (after Morales et al., 2005)

[5] *H.* (*Galerella*) *sanguinea*, Toros-Menalla (Chad) (after S. Peigué et al., 2005)

[6] Barry (1983) reported on various herpestine dental/gnathic elements from the Pakistan Siwaliks, and considered that several taxa, based on size, were likely represented. The GSP-217 mandible fragment with p4 is of a size and morphology comparable to extant *H. ichneumon*

Genetta sp. indet. "X"
Figure 5A

Description and remarks

KNM-NK 36581 consists of a fragment of a right mandible body with p4-m1 and root/alveolus of m2. KNM-NK 36578 is a fragment of right mandible body with p3 and the anterior cusp (only) of p4. These two mandible fragments represent parts of different individuals.

Both mandible fragments (36581 and 36578) constitute a large form of genet, and perhaps different from others described heretofore. The body of the mandible is thick and deep and has a very straight inferior border. This contrasts with the curved body figured as *Genetta* sp. A and *Genetta* sp. B at Lothagam (Werdelin, 2003a, p. 279). The masseteric fossa extends to the posterior end of the m2. The p4 has a distinct though small anterior accessory cusp set lingually. In this area a cingulum originates that extends over the labial side of the crown to reach the posterior edge, where it becomes more robust and individuated slightly lingual to the mid-line. The main (protocone) cusp is high and pointed. The posterior accessory cusp is very distinet and is set slightly labially.

The lower carnassial (m1) exhibits high trigonid cusps and a broad talonid. This is unlike the narrow talonid of the Kanapoi specimen (*Genetta* sp. nov.) figured by Werdelin (2003b, p. 130). Paraconid and protoconid are similar in size and together compose a blade set 45° to the main axis of the crown, as described in the Kanapoi specimen. This orientation of the blade is observed in a number of modern genets. The metaconid is set directly posterior to the paraconid and diverges from the midline toward the lingual side.

The Lemudong'o *Genetta* sp. "X" differs also from the Kanapoi specimen in having a slightly larger alveolus of m2.

Genetta sp. indet. "Y"
Figure 5B

Description and remarks

Four specimens comprise largely edentulous mandible fragments of a small genet species. These are: KNM-NK 38310, a right mandible fragment with alveoli and p3 crown; KNM-NK 36595, a right mandible fragment with p and m alveoli; KNM-NK 36927, a left anterior mandible fragment with p alveoli; and KNM-NK 42320, a right posterior mandible fragment with m alveoli.

This form ("Y") is overall smaller than specimens referred to *Genetta* sp. "X." The material is clearly insufficient to seek to ascertain specific affinities except by exclusion from known extinct (and extant) larger species. Genet remains of comparable or still younger age are known from some other African localities, among them: Langebaanweg (South Africa), Klein Zee (Nami-

Figure 5. A, *Genetta* sp. indet "X" (KMN-NK 36581), right mandible with p4-m1 in lingual (top), occlusal (middle), and labial (bottom) view. B, *Genetta* sp. indet "Y" (KMN-NK 36578), right mandible with p3 in labial and lingual view. Scale bar = 1 cm.

bia), Lukeino (Kenya), Lothagam (Kenya), Kanapoi (Kenya), some late Miocene localities (MALM) of the Middle Awash, Afar (Ethiopia), and Beni Mellal (Morocco).

Genetta is often considered to comprise some nine species, essentially in sub-Saharan Africa, except for a single species reaching into southwest Europe and Arabia. These are: *G. genetta*, *G. tigrina*, *G. angolensis*, *G. servalina*, *G. victoriae*, *G. abyssinica*, *G. thierryi*, *G. johnstoni*, and *G. maculata* (Wilson and Reeder, 1993). *G. genetta* is a (late) Holocene introduction into countries of Western Europe. Those documented for Ethiopia and the adjacent Horn are *G. genetta*, *G. abyssinica*, and *G. rubiginosa* (that may or may not be a part of *G. tigrina*). The relevant comparative dimensions of six of the lesser taxa, and two other samples comprising their subspecies, are set out in Table 7b.

Following new molecular (cytochrome b) sequence analysis, combined with morphological character (some 50) studies, a total of sixteen species were differentiated (Gaubert et al., 2004). Some have previously been considered as subspecies of the aforementioned taxa. In their newest overview (Gaubert,Taylor, Fernandes, et al., 2005; Gaubert, Taylor, and Veron, 2005), 17 species are recognized in all (number after each indicate number of existent sympoteic species): *G. ayssinia* (2), *G. angolensis* (4), *G. bourloni* (3), *G. cristata*, (2), *G. felina* (4), *G. genetta* (3), *G. johnstoni* (3), *G. letabae* (3), *G. maculata* (9), *G. pardina* (5), *G. piscivora* (4), *G. poensis* (6), *G. schoutendeni* (8), *G. servalina* (5), *G. thierry* (3), *G. tigrina* (2), and *G. victoriae* (4). (Comparative dimensions of cheek teeth of some extant African *Genetta* are given in Table 7B). This is

Table 7A. Comparative mandibular cheek-tooth dimensions (mm) in African *Genetta* spp. of late Mioeene Age.

	Lothagam[1]			Kanapoi[2]	Klein Zee[3]	MALM[4]			Lemudong'o		Kapsomin (Lukeino Fm)[5]
	Genetta sp. A		*Genetta* sp. B	*Genetta* sp. nov.	*Genetta* sp.	*Genetta* spp.			*Genetta* sp. 'X'		*Genetta* sp. indet.
	KNM-LT 25409	KNM-LT 23031	KNM-LT 23945	KNM-KP32815	1930. XI-6a	ADD-1/7	AME-1/43	ALA 2/169	KNM-NK 36581	KNM-NK 36578	BAR 155'01
Lp3	5.3				5.0					5.8	
Wp3	2.8				2.5					2.3	
Lp4	5.9		(5.1)		5.6				8.1		
Wp4	3.1		2.6		3				3.6		
Lpp4	3		2.3						4.3		
Lm1		6.5		≈7.5	6.5	7.0	8.9	6.96	9.3		8.5
Ltm1	5.3	4.3							6.8		
Wm1	3.9	3.9		≈4.3	3.2	3.6	3.6	—	5.2		4.0
Hm1	8.9				8.0				11		

[1] Werdelin (2003a)
[2] Werdelin (2003b)
[3] Stromer (1931)
[4] Haile-Selassie (2001)
[5] Morales et al. (2005)

Table 7B. Comparative cheek tooth dimensions (mm) in some extant African species of *Genetta*. The L (length), W (width), and H (Height) diameters are self evident. Lpp (length of protocone cusp of p) and Ltm1 (length of lower molar trigonid) are evidently less so.

	G. genetta *n* = 4	*G. tigrina* *n* = 6	*G. angolensis* *n* = 5	*G. servalina* *n* = 7	*G. victoriae* *n* = 6	*G. macalata* *n* = 6	*G. schoutedeni* *n* = 6	*G. johnstoni* *n* = 2
	QBH 1974	QBH 1974	RJ 2005	RJ 2005	RJ 2005	RJ 2005	RJ 2005	RJ 2005
Lp3	6.4 (6.2–6.5)	6.0 (5.6–6.2)						
Wp3	2.3 (2.2–2.3)	2.4 (2.2–2.5)						
Lp4	6.6 (6.5–6.7)	6.7 (6.1–6.9)	6.13 (5.73–6.58)	6.12 (5.78–6.65)	7.94 (7.43–8.38)	6.14 (5.65–6.87)	8.26 (5.26–6.73)	5.3
Wp4	2.8 (2.7–2.8)	2.9 (2.7–3.1)	2.72 (2.53–3.1)	2.41 (2.17–2.54)	3.69 (3.39–4.1)	2.68 (2.31–3.09)	2.72 (2.35–3.11)	1.8
Lpp4								
Lm1	7.6 (7.4–7.7)	7.5 (7.2–7.6)	7.4 (7.05–7.93)	6.5 (6.12–7.13)	8.96 (8.11–9.48)	6.91 (6.39–7.1)	7.03 (6.28–7.83)	5.5–6.1
Ltm1								
Wm1	3.8 (3.7–3.9)	3.8 (3.5–4.1)	3.74 (3.44–3.97)	3.38 (2.93–3.75)	4.87 (4.14–5.54)	3.72 (3.26–4.15)	3.82 (3.51–4.08)	2.6–2.7

Measurements from Hendey (1974) and from collections of Musée Royale de l'Afrique Centrale, Tervuren, Belgium, kindly provided by Ms. Rebecca Jabbour (2005)

an important and sweeping revision based on over a dozen museum collections and a sample of over 5,000 specimens. Five such species found within the southern African sub-region—*G. angolensis*, *G. tigrina*, *G. maculata*, *G. genetta*, and *G. felina*—the third and fourth having broadly African distributions, have been examined in depth, their species validity confirmed, and the presence and degree of ocyptic hybridization sometimes confirmed (Gaubert et al., 2005). Molecular assessments (cytochrome b), assuming clocklike behavior, affords estimates of minimum divergence date(s) (mdd) initially within the late Miocene, subsequently within the Pliocene, and ultimately Plio-Pleistocene, even to mid-Pleistocene (Gaubert et al., 2004). Such cladistic hypotheses can and will be testable from the expanding fossil record. At this stage, and given the nature and limitations of the genet samples, it is probably premature to seek to resolve questions of phylogenetic affinities and, hence, their primary systematics.

However, it has been possible to distinguish the principal size morphs (Table 7C).

As often said elsewhere by various investigators, the genus *Genetta* merits further investigation and systematic revision, now particularly that the fossil record is enhanced, although admittedly largely fragmentary. Most importantly it is essential to provide a phylogenetic perspective to the seemingly speciose genus *Genetta* as now known.

Family Hyaenidae Gray, 1821 (1869)
Hyaenictis A. Gaudry, 1861
Hyaenictis aff. *hendeyi*
Figure 6

Description and remarks

KNM-NK 36598 is a partial right mandible body with p4 and partial roots of p3 and m1 (Table 8). The complete fourth lower right premolar (p4) is almost fully erupted in a partial ramus fragment. It presents a small but distinct anterior accessory cusp and a large trenchant posterior cusp and a high main cusp (pr^d). A posterior cingulum forms a crest that runs from the groove of the principal cusp and posterior accessory cusp (through the lingual face) towards the posterior end of the crown.

The morphology of p4 with its posterior cingulum crest is especially characteristic of the genus *Hyaenictis* and of the lineage (*Hyaenictitherium-Hyaenictis*) (Werdelin et al., 1994). It also fits

Table 7C. Principal size morphs of African species of *Genetta*.

Northern Africa:	**Beni Mellal** (Morocco)
	A diverse vertebrate assemblage, of attributed pre-Vallesian affinity (and age), including amphicyonid, mustelids (2), hyaenids (2), a small feline and a viverrine (Ginsburg, 1977). The latter is clearly a *Genetta* sp., about the size of *G. tigrina*. It comprises only an M2 and mandible with dp4 (5.2 × 2.25), not sufficient for a systematic attribution.
Eastern Africa:	**Lothagam** (Kenya)
	Genetta sp. A (LT-25409), from the lower Nawata formation, about the size of *G. servalina* (Werdelin, 2003a). It may also be represented at MALM/Ethiopia by ALA-2/199 (Haile-Selassie, 2001).
	G. sp. B. (LT-23945), from the upper Nawata formation, is a smaller form (by about 20%), and perhaps about the (dental) size of *G. johnstoni*.
	Kapsomin, Lukeino Formation (Kenya)
	A single left m1 (BAR 155 '01) that is referred to, and clearly represents *Genetta* sp. (Morales et al., 2005). Its species affiliation remains unresolved, although it is close morphologically to *G. genetta* though rather larger and having an enlarged talonid. In size it is not distant from a MALM (Ethiopia) specimen, AME-1/43.
	Kanapoi (Kenya)
	G. sp. C (KP-32565, 32815) a larger form about comparable (dentally) in size to *G. genetta*.
	MALM (Ethiopia)
	ADD-1/17, a form with morphological distinctiveness suggestive of a *Genetta* sp. nov. D.
	Lemudong'o (Kenya)
	A larger form, *G.* sp. "X," dentally comparable in size to extant *G. victoriae*, and seemingly distinct morphologically from *G.* sp. A and B (Lothagam) and from *G.* sp. C. (Kanapoi).
Southern Africa:	**Klein Zee** (Namibia)
	A larger form (1930.XI. 6a specimen) comparable in size to *G. genetta*.
	Langebaanweg (South Africa)
	A rather smaller form (L-11191 specimen) comparable in size to *G. tigrina*.

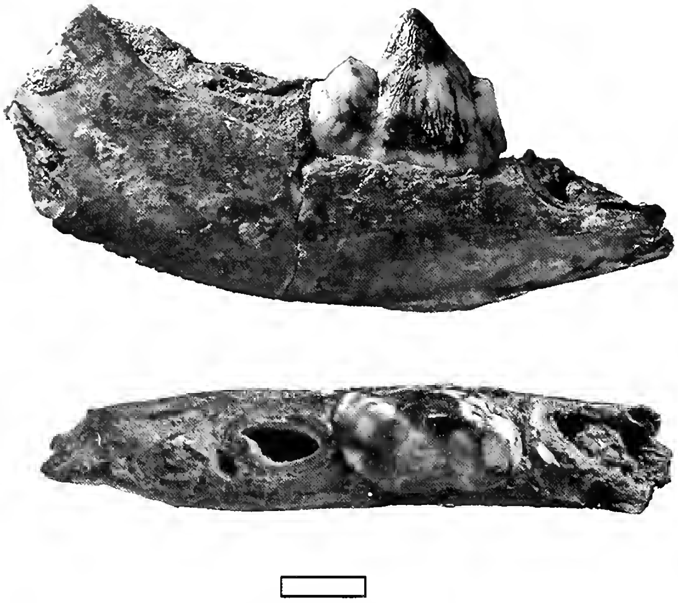

Figure 6. *Hyaenictis* aff. *hendeyi* (KNM-NK 36598), right mandible with p4 in labial and occlusal view. Scale bar = 1 cm.

well with the description of *Hyaenictitherium* cf. *H. parvum* from Lothagam (Werdelin 2003a). However, the Lemudong'o specimen is larger than the latter, and is of a size comparable to *Hyaenictis hendeyi*. We suggest attribution to this genus, and possible affinities to *H. hendeyi*.

The genus type, *Hyaenictis graeca* Gaudry, remains still ill-known, both in terms of specimens and morphologically (Gaudry, 1861; Werdelin and Solounias, 1991). The genus was first documented in Africa at Langebaanweg (Hendey, 1978a). Important distinctions and relationships between several hyaenid taxa were made by Werdelin et al. (1994), wherein *Hyaenictis hendeyi* sp. nov. was proposed. Cf. *Hyaenictis* sp. has been recognized by Werdelin (2003) at Lothagam (lower Nawata formation), Kenya. In the Tugen Hills, Baringo district (Kenya) remains referred to *H. hendeyi* have been recovered in other Mio-Pliocene formations, notably several localities of Lukeino Formation (6.1–5.7 Ma) and the succeedent Mabaget formation (at Tabarin) (5.1–4.5 Ma) (Morales et al., 2005). The remains are exclusively isolated upper or lower teeth, and species identification is insecure. Other attributed remains of *Hyaenictis* sp., probably *H.* sp. nov., derive from localities (AME, AMW and STD) of the MALM/Ethiopia, and are of comparable antiquity (Haile-Selassie, 2001; Haile-Selassie et al., 2004b). It is probable that a form of *Hyaenictis*, termed *H. almerai* Villalta and Crusafont (1943), is represented as well in the Catalan locality of San Miguel de Taudell (Spain), of upper Vallesian (MN-10) age.

Family Felidae Gray, 1821
Subfamily Machairodontinae Gill, 1872
Genus *Lokotunjailurus* Werdelin, 2003a
Lokotunjailurus emageritus Werdelin, 2003
Figures 7–8

Description and remarks

KNM-NK 36928 comprises most of the crown, minus the distal tip, of a left upper canine. The only material that can be reasonably certainly referred to this sabre-tooth cat is this partial and distal upper canine of large size. The tooth is markedly mediolaterally compressed and both anterior and posterior edges exhibit very fine serrations throughout their length (Figure 7). Thus, this fossil is excluded from consideration as any species of either *Megantereon*, *Dinofelis*, or *Metailurus*. The generic attribution proposed here is based on its very close approximation in overall size and in shape to the upper canine (KNM-LT 25405) of the newly named machairodont from Lothagam (Kenya), *Lokotunjailurus emageritus*, described recently by Werdelin (2003a), and with which it is comparable overall.

KNM-NK 45896 consists of a right proximal femur, from the upper shaft and including neck and head, of a felid similar in size and morphology to *L. emageritus*. The femur was damaged by carnivore ravaging, which largely destroyed the greater trochanter, much of lesser trochanter, and the margins of the articular head (Figure 8). The projected original proximal breadth (66/67 cf. 63/73) and head (32.5 cf. 34.6) diameters are quite suitable to an *L. emageritus* individual.

A damaged proximal portion of left mt-3 (KNM-NK 45789) represents a felid of at least medium size (Figure 8). It is questionably included here with *L. emageritus*, but without a formal attribution.

A substantial larger element (KNM-NK 44755), perhaps mc-3/4, comprising a good part of the diaphysis, up to but not including the proximal articulation, is also felid, but of still unknown affinity.

This is only the second record of the machairodont *Lokotunjailurus emageritus* Werdelin, first recorded from the Nawata Formation, Lothagam, both lower and upper levels, and including a partial skeleton and other skeletal parts of several individuals. There are reasons put forward in respect to specific aspects of dental (and other) morphology to consider this form as recognizably derived relative to the more commonly known and late *Machairodus*, *M. giganteus*. The latter genus, at least, is

Table 8. Comparative dimensions (mm) of p4 of *Hyaenictis* and of *Hyaenictitherium* spp.

	Lothagam[1] (Kenya)			Lemudong'o (Kenya)	Langebaanweg[2] (S.Africa)		MALM deposits[3] (Ethiopia)
	Hyaenictitherium cf. *H. parvum* KNM-LT 10032	*Hyaenictis* sp. KNM-LT 25057	KNM-LT 23033	*Hyaenictis* aff. *hendeyi* KNM-NK 36598	*Hyaenictitherium namaquensis* (*n* = 5)	*Hyaenictis hendeyi* (*n* = 4)	*Hyaenictis* sp. nov.
Lp4	18.9	20.7	20.9	23.1	20.7–21.52	22.8–26.0	19.5–19.8; 21.2
Wp4	9.4	9.8	10.9	12.5	10.8–11.3	11.7–13.2	10.9–11.1; 11.3
Lpp4	9.9		9.5	10.7	10.2–10.9	10.6–12.0	

[1] Werdelin (2003a)

[2] Werdelin et al. (1994)

[3] Haile-Selassie (2001)

Figure 7. *Lokotunjailurus emageritus* (KNM-NK 36928). left upper canine in labial and lingual view. Scale bar 2 = cm.

elsewhere represented (in Africa) at Wadi Natrun (Egypt), at Sahabi (Libya), and at Langebaanweg (South Africa).

Subfamily FELINAE Trouessart, 1885
Genus *LEPTAILURUS* Severtzon, 1858

Description and remarks

KNM-NK 42269 consists of a fragment of a right m1. This fragmentary first lower molar represents a small-sized felid. It is incomplete, and hence affords no measurements. Its small size and observable morphology is comparable to that of *Leptailurus*, the serval.

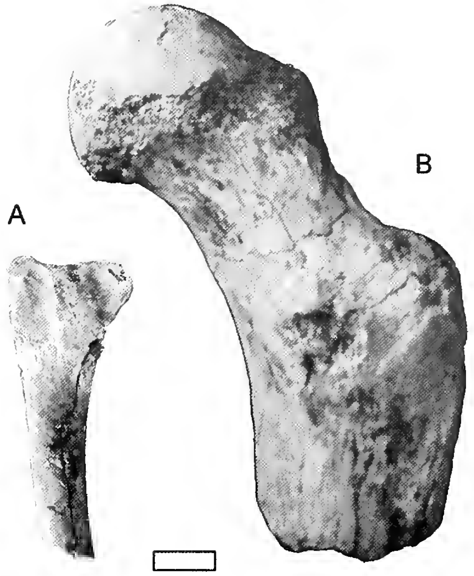

Figure 8. *Lokotunjailurus emageritus*: (KNM-NK 45789) left metatarsal (A) and (KNM-NK 45896) right proximal femur (B). Scale bar = 2 cm.

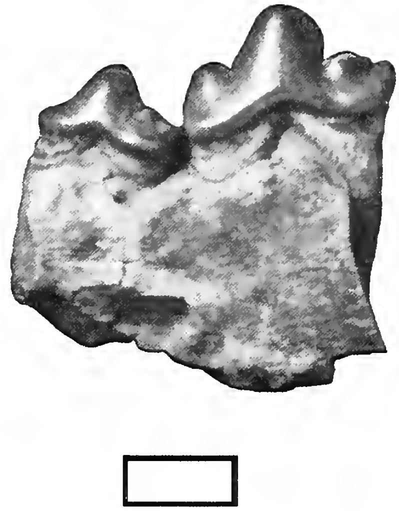

Figure 9. *Metailurus major* (KNM-NK 45832), left mandible with p3 and p4. Scale bar = 1 cm.

Subfamily FELINAE Trouessart, 1885
METAILURUS Zdansky, 1924
METAILURUS MAJOR Zdansky, 1924
Figure 9

Description and remarks

KNM-NK 45832 consists of a portion of the alveolar part of a left mandible body with well preserved p3 and p4. The size and morphology of the dentition replicates that of the widely distributed, but still incompletely (postcranially) known feline, *Metailurus major* Zdansky. The p3 has a low, broad cusplet below a salient anterior crest; the pac (posterior accessory cusp) is a distinct cusplet, at the base of a posterior crest with which it is aligned; another small accessory cusplet is set disto-lingually near that margin of the talonid. The p4 is a much larger tooth, with notably enlarged and salient aac (anterior accessory cusp) mesial to a salient anterior crest; the talonid is markedly broadened, particularly medially, with an uplifted shelflike, encircling, thickened cingulum; the pac (posterior accessory cusp), somewhat worn, is substantial and was apparently once rather larger than its mesial counterpart. Another exterior p3 fragment (KNM-NK 45863), bearing a small pac, is most parsimoniously also referred to *M. major* on the basis of comparable size and morphology. Dimensions of this and other specimens of the *M. major* are set out in Table 9.

This genus, and its initially recognized species, was first (Zdansky, 1924) and perhaps is still best known in eastern Asia (China), from which it has been reported at multiple upper Miocene fossiliferous localities (eg., Yushe, Baote). It has been found in central Europe (Polgardí, Hungary), in mainland (Pikermi, Halmyropotamus) and insular (Samos) Greece, in the western Appennine peninsula (Baccinello V3, Italy), and at localities in the Iberian Peninsula of Spain (Alfacar, Ademuz, and Concud). It is essentially a component of latest Miocene age (Turolian) faunal assemblages (Ginsburg, 1999). It has been certainly documented previously in Africa only at the Lothagam locality (Kenya), from its Nawata Formation, and largely by a few postcrania and a distinctive upper canine (Werdelin, 2003a). And, the Lukeino Formation (Kapsomin) has yielded a partial maxilla with P3 referred recently by Morales et al. (2005) to

Table 9. Some dental dimensions (mm) of *Metailurus major* specimens. Sources of metrics: 1 = Zdansky (1924, p. 125, 127); 2 = Chang and Houyi (1964, p. 183, 184); 3 = Teilhard de Chardin and LeRoy (1945, p. 21); 4 = Roussiakis (2001, p. 124); 5 = Melentis (1968), metrics in S. Roussiakis (2001, p. 124); 6 = Rook, Ficcarelli, and Torre (1991, p. 12); 7 = Morales and Soria (1979, p. 498); 8 = Pons-Moya (1987, p. 67) (this distinctive Metailurine was designated as the type of *Fortunictis acerensis*).

	Paóte[1] Loc. 30 (Shansí) Type	Xialou[2] (Shansí)	Yushé[3] (Shansí)	Pikermi[4] (Gr)	Halmyropotamus[5] (Gr)	Baccinello V3[6] (It.)	Concud, Teruel[7] (Sp.)	Casa de Acero, Teruel[8] (Sp.)	Lemudong'o (Kenya)
		v. 2896/1+2	un-numbered	P.A. 1257/91 P.G. 95/1532	1967/1				KNM-NK 45832
P3	20.2 × 8.9	16.3 × 8.5	20.0 × 10.0	19.0 × 9.7 18.8 × 9.6	19.0 × (10.2) 18.8 × (9.7)			19.7 × 9.0	
P4	31.2 × 14.0	29.0 × 12.5	32.0 × 16.0	29.7 × 14.1 28.9 × 14.9	(28.8) × (13.8) — × 14.5			30.8 × 14.3	
M1	5.5 × 11.9	5.0 × 8.5		5.5 × 12.0 5.9 × 12.5 (4.9) × (12.2)					
			no. 10.368						
p3	15.5 × 8.4	12.5 × 6.0	14.0 × 8.0				15.0 × —		13.0 × 7.6
p4	21.0 × 9.3	18.5 × 8.0	21.0 × 9.0			19.9 × 7.8		20.2 × 8.4	18.6 × 9.3/8.7
m1	23.2 × 10.1	21.5 × 10. —	24.0 × 10			21.1 × 8.6	23.5 × 10.0	23.8 × 9.5	

this genus, and apparently a smaller species. A related metailurin—*Fortunictis*—is recorded at Casa del Acero (Fortuna basin), Spain (Pons Moya, 1987).

Discussion

Lemudong'o is but one of an increasing number of African fossiliferous localities of late Miocene age. Those that have yielded representatives of the order Carnivora are set out in Table 10. This effort affords some insight, as reliable information permits, on taxonomic representation and diversity. The columns are expressed strictly geographically, reading from north to south by scanning from left to right. Some such localities are not listed although having afforded one or more taxa of particular interest or significance; attention may be drawn to several such in the following comments.

The maximum span of concern, the upper Miocene, is arbitrarily delimited as between just over eleven million (11.1) and just under five (4.9) million years ago (Ma) (Steininger, 1999). In western Eurasia, including the peri-Mediterranean region, this encompasses the two last European Land Mammal Megazones (ELMMZ) of the Miocene, the Turolian and antecedent Vallesian zones. Their respective subdivisions are tripartite (MN-11, 12, and 13) and bipartite (MN-9, 10) and, in aggregate, are now estimated to encompass the time between 8.7 and 4.9 Ma, and between 11.1 and 8.7 Ma, respectively. All of the fossiliferous localities enumerated in Table 10 are either of known radiometric (isotopic)-determined age or of biostratigraphically-based estimated age as correlative with the younger, Turolian, ELMMZ. There are a few African localities of Vallesian-equivalent age, in both northwest (the Maghreb) Africa and in eastern Africa; however, still fewer yield remains of Carnivora (see below), and even then some remain unstudied (or insufficiently reported). Some localities, in particular those of Lothagam and of Sahabi, are known to, or must have sampled, a considerable range of time. At Lothagam the bulk of the vertebrates derived from the lower (7.4–6.5 Ma) of two members of the Nawata Formation, with at least nine taxa persisting into the overlying upper member (6.5–5.0 Ma, extrapolated age); a few taxa (two or so) recur in the succeedent (lower) Apak Member (of the Nachukui Formation) of lowermost Pliocene age. At Sahabi an uppermost Turolian (MN-13 Zone) age has been considered most probable for much of the (carnivore) assemblage; but, some evidence has been claimed by some workers to indicate both younger (MN-14) (Bernor and Pavlakis, 1987) and, perhaps, still older (MN-12) ages encompassed within the depositional succession of the Sahabi Formation (Géraads, 1989). These obscurities can, and doubtless will be, clarified through renewed geological and paleomagnetic investigations.

At this stage it is probably the wiser course to consider the available documentation rather subjectively. It would be misleading to employ one or more measures (indexes) of faunal diversity, as commonly applied, in view of the preliminary and incomplete state of alpha taxonomy and, particularly, the absence of requisite comparative analyses of lineage components purportedly represented at multiple localities. Hence, it is best to err on the more conservative side.

The entries of Table 10 reveal that an increasingly better, that is more inclusive, representation of the order Carnivora is now emerging for roughly the last three million years of the African Miocene. It should be noted that such fossil localities span the length of the African continent, and there are a number in the Mediterranean area, one in the southernmost subcontinent, and an increasing number in sub-equatorial reaches of eastern Africa. Others, still under investigation and awaiting study and publication, sample sub-Mediterranean reaches of northern Chad.

Eleven mammalian families are represented: five Feliformia (Felidae, Viverridae, Herpestidae, Hyaenidae, Nandiniidae); one Cynoidea (Canidae); three Arctoidea (Ursidea, Amphicyonidae, Phocidae); and two Mustelida (Mustelidae, Procyonidae). The number of genera approaches 40. The recognizable species of large- to mid-sized taxa are in number, at least, as follows: Felidae (5); Hyaenidae (7); Canidae (2); Ursidae (2); Amphicyonidae (3); Phocidae (2); Mustelidae (10); and Procyonidae (1). The number of lesser-size species might well equal half of this number, if the available fossil evidence ultimately proves satisfactorily amenable to taxonomic resolution, in respect to small felines, and to viverrids and herpestids.

Among the Felinae the genera *Metailurus* and *Dinofelis* have Eurasian affinities, if not actual roots, and are characteristic of this interval in Africa. The lesser cats are less well-represented and certainly very imperfectly known overall. One or more caracal/lynxlike forms and a serval are demonstrably represented, again with both extra-African and, perhaps, autochthonous affinities.

Several machairodonine felids occur in this and the antecedent time span in Africa. *Machairodus* has been commonly recognized,

Table 10. Current status of distribution of Carnivora in African upper Miocene local faunas (sources within text).

Taxon	Sahabi (Libya)	Wadi Natrun (Egypt)	MALM (Ethiopia)	Lothagam (Kenya)	Lukeino (Kenya)	Mabaget (Kenya)	Lemudong'o (Kenya)	Langebaanweg (So. Africa)	Klein Zee (Namibia)	Kanapoi (Kenya)
FELIFORMIA										
Felidae										
Felinae										
Metailurus major				cf.	sp.		+			
Dinofelis diastemata			+	sp.	+			+		
D. petteri										+
F. (Leptailurus) serval							cf.	+		
F. (Lynx) issiodorensis								+		
Felis sp.										+
Felinae indet.	+				+			+		
Machairodontinae										
Machairodus sp.	+	cf.	sp.					+		
Lokotunjailurus emargeritus				+			sp.			
Homotherium sp.								+		+
?Megantereon obscura					+			+		
Viverridae										
Viverra (Megaviverra) leakeyi	+		+	+	+			+		
Viverra howelli	+			cf.						
Viverrinae indet.	+									
Genetta sp.			+	sp. A, sp. B	sp.		sp. X, sp. Y	+	+	sp. nov
Civettictis howelli						+				
Herpestidae										
Helogale sp.			+				sp.			+
Herpestes sp.			sp. nov.		indet.		spp. indet.	spp. A,B,C,D,E	sp.	
Ichneumia albicauda					cf. sp.		+			
Nandinidae										
Nandinia sp.					+					
Hyaenidae										
Ikelohyaena abronia				cf.		+		+		
Hyaenictis hendeyi	cf.		sp.nov	cf. *H.* sp.	sp.	+	sp.	+		
Chasmaporthetes australis	sp.							+		
Hyaenictitherium namaquensis	sp.	+	+	cf. *H. parvum*		+		+	+	
Adcrocuta eximia	+									
Ictitherium sp.				ebu						
A. (Dinocrocuta) senyureki	cf.									
Parahyaena howelli										+
CYNOIDEA										
Canidae										
Vulpes sp.								+		
Eucyon intrepidus					+		aff.			
ARCTOIDEA										
URSIDA										
Ursidae										
Indarctos sp.	+									
Agriotherium africanum	sp.		sp.					+		
Agriotherium aecuatorialis						+				
Amphicyonidae				spp. A,B						
Phocidae										
Homiphoca capensis								+		
Monachina indet.	+									
Pliophoca etrusca		+								
MUSTELIDA										
Mustelidae										
Lutrinae										
Vishnuonyx angololensis				+						
Sivaonyx africana					+					
Enhydriodon hendeyi			+			sp.		+	+	ekecaman
Torolutra ougandensis					+					sp.
Lutrinae gen./sp. indet.		+	+							
Mellivorinae										
Mellivora benfieldi			+					+		
Ekorus ekakeran				+						
Erokomellivora lothagamensis				+						
Mellivorinae indet.				+						
Guloninae										
Plesiogulo botori			+				+			
Plesiogulo monspessulanus								+		
Plesiogulo praecocidens					+					
Procyonidae										
Simocyoninae										
Simocyon sp.							+			

sometimes without certain specific designation, but apparently comparable to *M. giganteus* in size. *M. robinsoni* was proposed on the basis of incomplete mandible body and upper canine from (upper) Beglia Formation, Tunisia; it is *M. aphanistus*-like, but rather smaller (Kurtén, 1976).

An uncommonly large form, attributed to *M. kabir* sp. nov. (Peigné, de Bonis, et al., 2005), has recently been recognized from a locality (TM-266) in the Toros-Menalla area (northern Chad) in a (lower) Turolian-equivalent faunal context. The recognition of *Lokotunjailurus* (at Lothagam), through the Nawata Formation, raises the possibility that this taxon may be represented elsewhere (perhaps among the MALM localities), as suggested here also for Lemudong'o. Moreover the roots of this form remain unknown and, for the moment, unresolved. A once enigmatic "machairodontine," termed *Vampyrictis vipera* (Kurtén, 1976), occurs in the (lower), pre-Vallesian age Beglia Formation (Tunisia); it is distinct in upper canine and lower carnassial morphology and now considered a member of Barbours felinae (see McKenna and Bell, 1997), along with *Sansanosmilus* (Eurasia) and *Syrtosmilus* (Africa).

This void is in spite of the often acknowledged presence of upwards of a purported dozen species, in western Eurasia alone, of *Machairodus—M. pseudailuroides*, *M. romeri* (both Turkey), *M. kurteni*, *M. laskareri*, *M. aphanistus*, *M. giganteus*, *M. copei*, *M. alberdiae*, *M. irtyschensis*, and *M. taracliensis*. There is a single instance, probably valid, of the presence of *Homotherium*, whose roots are otherwise ill-appreciated.

Those lesser carnivores, viverrids and herpestids, are actually not so rare, given appropriate recovery procedures in the proper sedimentary paleoenvironments. However, as there are only generally fragmentary gnathic/dental remains, and modern systematic and phylogenetic evaluation is still needed, there remains substantial uncertainty at the specific level. None the less, the former family is not infrequently represented, notably by the large viverrine *V.* (*Megaviverra*) *leakeyi*, rarely by another smaller taxon, recently named *V. howelli* Rook and Martinez-Navarro, 2004, and the almost ubiquitous African genus *Genetta*. There may be more than six species in the now known African late Cenozoic record. Three antecedent genera—the common, polyspecific *Semigenetta*, and *Viverrictis* and *Plioviverrops*—are not uncommon in the west Eurasian Miocene.

Herpestids, better represented in the Plio-Pleistocene, are now coming to be better known in the African Mio-Pliocene. Certainly there are manifold mongoose species of *Herpestes* represented in the known record, differentiated both in terms of size and, to an extent, morphology; however, this family certainly requires revision. Fuller knowledge of each of these families is in fact requisite toward more comprehensive insight of biogeographic relations with southern Asia.

Hyaenidae are now probably the best represented and hence best known of upper Miocene African Carnivora. However, the documentation of taxa is still very uneven, and the overall skeletal biology per taxon is most unevenly, if at all known. Led by the familial revision by Werdelin and Solounias (1991), building on earlier work by Howell and Petter (1980, 1985), the former constitutes a most impressive, comprehensive, and effective undertaking; it has enabled major progress in the clarification of the systematics, synonomy, and phylogenetics of this important pan-continental mammalian group.

The African group comprises endemic taxa (*Ikelohyaena*, *Parahyaena*), those of Afro-Asian affinity (*Chasmaporthetes*, *Hyaenictitherium*), those of Afro-Palearctic affinity (*Adcrocuta*, *Ictitherinae*, and *Percrocuta*), and those of Afro-European affinity (*Hyaenictis*). Such differentiation is probably both oversimplified and, to an extent, inadequate. It is, however, suggestive. Although the presence of some distinctive clades has begun to emerge, as Werdelin and Solounias (1991) and some others have discerned, there remains much in the way of uncertainty, not to mention mystery in regards to affinities, origins, distributions, and extinctions among them. Other ranges (Vallesian-equivalent) of the African upper-Miocene yield different, and mostly quite unrelated "hyaenoid" taxa. These include percrocutids (Percrocutidae) and, if as accepted by some, allohyaenids (genus *Allohyaena*), and the gigantic *Dinocrocuta*. We confess that the higher taxonomy in this matter is clearly muddled and in need of study and revision. The African occurrence of *Percrocuta tobieni* (Ngorora; Bled Douarah) parallels that (earlier) of *P. miocenica* (Croatia), and of *P. abassalomi* (Georgia), in MN-6. A very large (allohyaenid) is *A.* (*Dinocrocuta*) *algeriensis* (Bou Hanifia, Menacer, Algeria) and, perhaps, *A.* (ex-*Hyperhyaena*) (*D.*) *leakeyi* (Nakali, Kenya). The type is *Allohyaena kadici* (Csákvár, Hungary). The genus is also known in Ukraine, where it is represented by *A. sarmatica*. And, other taxa are *A.* (*D.*) *salonicae* (Thessaloniki, Greece, probably MN-9), *A.* (*D.*) *senyureki* (Yassioren, Turkey, MN-9) and several other localities, as at Sahabi (Libya). The Asian counterpart is (*Dinocrocuta*) *gigantea* (Gansu). It is worth noting that the Beni Mellal (Morocco) locality purportedly yields a form (*graeca*) of *Hyaenictis*, said to be the same as the holotype species from Pikermi (this, however, might equally well be a *Hyaenictitherium*) as well as an ictithere (*I.* cf. *arambourgi* Ozansoy), purportedly like the type species from the Sinap, Anatolia. Two hyaenids occur in another pre-Vallesian age mammal assemblage at Bled Douarah (Beglia formation), an ictithere (*Protictitherium punicum*) and an indeterminate *Lycyaena* species. In the still older, and mid-Miocene age locality of Arrisdrift (Namibia) no hyaenids are represented at all, although six other carnivore families (nine species) are quite adequately documented (Morales et al., 1998).

The palm civet (*Nandinia binotata*), now considered part of a separate family (and that is otherwise Asian in distribution), is almost unknown in the African fossil record. There is now a single occurrence of the genus reported from Lukeino. It is largely tied to pan-African, peri-equatorial tropical forests, and including those eastern montane areas extending meridionally from Kenya toward Zimbabwe.

The presence within Cynoidea of the subfamily Caninae (within Canidae) within the upper Cenozoic of (western) North America came to light almost a century ago. It was repeatedly confirmed, particularly in Hemphillian local faunas, without any counterpart in the western Palearctic until some 50 years ago. *Canis cipio* is still the oldest occurrence in western Eurasia (in MN-12, mid-Turolian) at Concud, and maybe, at Los Mansuetos (Spain). (Both *Vulpes* and *Nyctereutes* have long been known to occur later, in MN-15 (mid-Pliocene) in Mediterranean Europe.) In recent decades the presence of North American *Eucyon* in eastern Asia has been securely documented. And, there are now multiple occurrences—at South Turkwell, at Lukeino, and at Lemudong'o, and probably elsewhere as well—in equatorial Africa of this same taxon, but of slightly younger age, somewhat over 6 Ma. Unfortunately, the documentation remains fragmentary, but the general pattern of the dispersal westwards through the Palearctic into the Ethiopian realm is at least established. The definition of species of *Eucyon* in Asia, as well as of *Nyctereutes* and, to an extent *Vulpes* within Eurasia, has similarly been enabled by significant fossil documentation across these continents.

Ursids have long been Palearctic in distribution. The Miocene witnessed the ultimate demise of older subfamilies and the appearance of ursines. Two major taxa, *Indarctos* and *Agriotherium*, of older origins are significant members of Holaretic faunas of later Tertiary age. The former is more speciose than the latter in the Palearetic, and constitute trans-Beringian Asian emigrants into the Americas. The trans-continental dispersal of both taxa, some 8–7 million years ago, along with other important elements (*Machairodus*, and Mustelida-like *Simocyon*, *Plesiogulo*, and *Eomellivora*) is now well documented (Qiu, 2003). They are representative of Vallesian and/or Turolian age local faunas. *Indarctos* has only been documented in Mediterranean Africa, at the Sahabi and Menacer (Algeria) localities. *Agriotherium africanum* occurs in quantity, and in excellent preservation at Langebannweg. The genus is recorded at Sahabi and in the western rift (Uganda), and a new species, *A. aecuratorialis*, recently was documented at Mapaget (Tugen Hills, Baringo basin, Kenya) (Morales et al., 2005).

The arctoid family Amphicyonidae (bear dogs) was among the most successful, persistent, and speciose family among the larger Cenozoic carnivores. The roots of amphicyonoids are in the Paleogene. Diverse genera dispersed from (east) Eurasia through Beringia into North America in the course of the earlier Miocene. One of, if not, the last African occurrences known is that at Lothagam in which larger (A) and smaller (B) species have been found to persist there in successive levels of the Nawata formation (Werdelin, 2003a). Their phylogenetic affiliations are still unknown, although the smaller might constitute a unique and new genus. This is later than the youngest known (upper) Miocene occurrence (that is, MN-9) in Europe and, perhaps, even within Eurasia. Other occurrences of slightly older, but still upper Miocene age, are known at Beni Mellal, Morocco (*Agnotherium* cf. *antiquum*) and similarly as well as also rather older at Bled Douarah (Beglia Formation, Tunisia), at Qued Mya-I, Tademait, Algeria (and, termed *Myacyon dojambir* Sudre and Hertenberger [1992, p. 107–109]), and at Kabasero, Ngorora (Kenya, also an *Agnotherium*). Middle Miocene occurrences are at Fort Ternan, Kenya (*Agnotherium* sp.), at Djebel Zelten, Libya (*Afrocyon burolleti* Arambourg n. g., n. sp.), and at Arrisdrift, Orange River, Namibia (*Amphicyon giganteus* and *Ysengrinia ginsburgi*) (Morales, Pickford, Soria, and Fraile, 1998, p. 30). Other amphicyonid species, *Cynelos euryodon* and *C. macrodon*, are represented in earlier Miocene local faunas in western Kenya and in eastern Uganda (Schmidt-Kittler, 1987). A couple taxa persist into the Pliocene in the south Asian Siwaliks. Overall, over 30 amphyicyonid lesser taxa (in eight genera) are recorded in the European Miocene (Ginsburg, 1999).

There are several occurrences of pinniped Carnivora in the African upper Miocene. There are fossil representatives of Miocene Phocidae from both southernmost Africa and from the African east Mediterranean. The southern Atlantic province Langebaanweg has yielded abundant remains of monachine seal, *Homiphoca* (Muizon and Hendey, 1980), specifically the species *H. capensis* (Hendey and Repenning, 1972). It is an Antarctic lobodontine seal with counterparts in the Mio-Pliocene of the American (east) coastal plain. In the south Mediterranean, monachine seals occur at Sahabi (gen. and sp. indet.) and at Wadi Natrun (*Pliophoca etrusca* Tavani), the last having a counterpart in the Italian Mediterranean.

These last occurrences are best viewed in the perspective of pinniped diversity within the Mio-Pliocene of the Paratethyan realm of west Eurasia. Overall there are eleven recognized species of Miocene age and five species of (mostly earlier) Pliocene age in the central/eastern Paratethys (Koretsky, 2001). The taxonomic status and phylogenetic affinities among phocids remain a matter of some debate. The different perspectives are, in part, set out in Berta and Wyss (1994), Koretsky (2001), and McKenna and Bell (1997).

The taxonomic composition and attendant (species) diversity of mustelids differs very substantially between those African localities (Table 10) and those of western Eurasia. The overall (known) diversity is similar, if not identical, with about ten and thirteen or more, lesser taxa respectively. The main differences are in the dominance of Palearctic mustelines (a *Martes* is found only at Beni Mellal), melines, and mephitines in the latter region. There are partial generic overlaps (about half) between the areas in respect to several lutrines, but none at the species level; the non-overlaps of the former are instead shared with southern Asia. The mellivorines, including very large forms, are distinctively African, and presumably authocthonous. A large gulonine—*Plesiogulo*—is both African and Holarctic in distribution, in the latter instance an Asian emigrant dispersed into northern America. Almost certainly the African mustelid diversity was still greater, and regionally differentiated than presently indicated. The masked, often nocturnal behavior, and, probably, habitat specificity have constrained their appearance in local fossil faunas.

Finally, there is the issue of the Simocyoninae, accorded (by most) subfamilial status, comprising a single eponymous genus with perhaps several species. It, or the genus (or even genera) have historically been inferred to have various higher relationships or, even as Werdelin (1996) probably correctly at the time, left in limbo as "family indet." It has come to be encompassed within Procyonidae (McKenna and Bell, 1997) or within a separate Ailuridae family (Ginsburg, 1999) according to different authors and their approach to taxonomy. However, the abundance of its relatives is within the earlier and middle Miocene, in substantial diversity and seemingly strictly Eurasiatic in distribution. Its roots are often acknowledged to lie within *Alopecocyon*, of middle Miocene age, a genus which is still insufficiently known but presumptively (only?) European in distribution. Hence *Simocyon* is acceptable as a terminal taxon of its lineage, and have extra-Eurasian dispersal into both Africa and North America.

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assignments by J. Viret initially to *Cephalogale* and, subsequently, to *Metarctos*. An earlier amphicyonid attribution of *batalleri* had led us to the inference that, as at Lothagam (and elsewhere in northern Africa) an amphicyonid was apparently also present, if not readily identifiable at Lemudong'o. Hence, on the basis of the aforesaid description and analysis, the attribution of the single Lemudong'o specimen here has been to *Simocyon* sp. indet. And, as Morales cautioned, it is not readily and certainly feasible to differentiate between upper cheek teeth of these higher taxa.

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NEW LATE MIOCENE ELEPHANTOID (MAMMALIA: PROBOSCIDEA) FOSSILS FROM LEMUDONG'O, KENYA

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ABSTRACT

The late Miocene marked a time of significant geographic dispersal and radiation for many mammalian taxa within Africa, including the proboscidean lineages. The ~6.1 Ma site of Lemudong'o, Kenya, yielded two elephantoid specimens. The first is a mandibular fragment with the third molar. This specimen represents a primitive member of the *Anancus kenyensis* lineage, with similarities to a specimen from Lukeino, another late Miocene site in Kenya. The second specimen is a shattered isolated mandibular molar with associated fragments of a second tooth. Although this second specimen is fragmentary, it may represent a new elephantid taxon as it has a combination of unique crown and root characters that do not align it with any currently known taxa.

Introduction

During the late Miocene, the proboscidean lineages experienced great morphological and adaptive changes that preceded their vast radiation during the glacial and inter-glacial climatic cycles of the Pleistocene. Africa is considered the continent where elephants originated and where the basic features of the three major genera of elephants, *Loxodonta, Elephas*, and *Mammuthus*, evolved. Two lines of evidence support this. First, the most primitive form of elephants, *Stegotetrabelodon* (Maglio, 1973; Tassy, 1986; Kalb and Mebrate, 1993) is found in Africa (Maglio, 1973; Beden, 1985; Tassy, 1986; Kalb et al., 1996), the adjacent Arabian Peninsula (Tassy, 1999), and southern Italy (Ferretti, 2003). Second, the most primitive species of the three major genera of elephants, *Loxodonta*, *Elephas*, and *Mammuthus*, are only known in Africa (Aguirre, 1969; Maglio, 1973; Beden, 1983, 1985, and 1987). Fossils of late Miocene proboscideans, especially those from Africa, are therefore critical to the understanding of all subsequent proboscidean evolutionary events, including the origins of the extant elephants.

Our current understanding of late Miocene Proboscidean evolution is limited due to a paucity of fossil sites and scarce and fragmentary remains. The sites of Lemudong'o Localities 1 and 2 have yielded important elephantoid specimens that date by ^{40}Ar/^{39}Ar single crystal laser fusion to ~6.1 Ma (Ambrose et al., 2003; Ambrose, Hlusko, and Kyule, 2007; Ambrose, Nyamai, et al., 2007; Deino and Ambrose, 2007). Like most other penecontemporaneous sites, proboscidean fossils are also poorly represented in the Lemudong'o fauna, comprising only the two specimens described below. However, these two specimens, especially that of the elephantid, provide us with precious information about the relatively unknown late Miocene proboscideans of eastern Africa.

The previously known late Miocene proboscidean African fossils have been described from: Sahabi, Libya (Petrocchi, 1954; Gaziry, 1987); Ukondo, Uganda (Tassy, 1995); Mpesida, Kenya (Maglio, 1973; Tassy, 1986; Sanders, 1999); Lukeino, Kenya (Maglio, 1973; Tassy, 1986); Lothagam, Kenya (Maglio, 1973; Tassy, 2003); the Middle Awash, Ethiopia (Kalb and Mebrate, 1993); Manonga Valley, Tanzania (Sanders, 1997); and Toros-Menalla, Chad (Vignaud, et al., 2002). Except for recently collected samples from the Middle Awash, Ethiopia and Toros-Menalla, Chad, most of the assemblages from these localities are composed of only a handful of specimens. Because of this paucity of specimens, basic dental features such as the presence of lower tusk (*Primelephas*: Maglio, 1973; Tassy, 2003) or fourth premolar (*Anancus kenyensis*: Tassy, 1986) are still a matter of debate. The new species of primitive elephants from Ukonodo, Uganda (Tassy, 1995) and Lothagam, Kenya (Tassy, 2003) suggest that the early radiation of elephants was a rather complicated process that is currently known only from very small samples.

Terminology

In the description of the gomphothere from Lemudong'o we employ the dental terminology used by Tassy (1986, 1996) and Metz-Muller (1995). However, these authors' definitions differ for one feature. In the lower molars of *Anancus*, the anterior pretrite central conule is much reduced and fused with the mesoconelet of the same half-lophid (Tassy, 1986, p. 87 and 94, fig. 3 of pl. XIII). This fusion results in the formation of a cusp being located mesio-adaxially to the main cusp and more or less rudimentary. This cusp contacts both the posterior pretrite central conule of the preceding lophid and the posttrite mesoconelet of the same lophid. Tassy (1986) calls this feature neither a mesoconelet nor an anterior pretrite central conule, but rather just the "anterior tubercle," because of the amalgamate nature of the cusp. On the other hand, Metz-Muller (1995) called the same tubercle of *Anancus arvernesis* a mesoconelet, although it can also be an amalgam of the mesoconelet and the central conule. We find that this amalgam is always single and not subdivided. Therefore, we follow the terminology of Metz-Muller (1995) and call this amalgam a "mesoconelet," irrespective of its relative position to the main cusp.

We find that the current anatomical terminology does not suffice to describe molar morphological variation adequately, and we introduce several new terms here. A full account of this new nomenclatural system will appear elsewhere, but the terms relevant for the mandibular molars are briefly introduced here. The root system of the proboscidean molars has been only briefly described and discussed previously (e.g., Anthony and Friant, 1941), except for Sher and Garutt (1987). Their description of the general feature of the root of the elephants molar is obviously based on what can be seen in highly derived elephants, *Mammuthus*, and thus what is described in their paper cannot be directly applicable to the molars of early elephants, stegodons and gomphotheres. The following is a generalization of the molar root of Elephantoidea.

For the mandibular molars of Elephantoidea, the root has three components: the mesial, intermediate, and distal roots. The mesial root (= main anterior root of Sher and Garutt, 1987) supports the anterior cingulum and first lophid, but as shown below, the second lophid is also supported by it in elephants and stegodons. The rest of the crown is supported by the distal root (= middle and posterior segment of Sher and Garutt, 1987), although frequently its mesio-lingual margin is separated from the rest of the root and forms a smaller intermediate root. The apical half of the distal root is frequently subdivided into numerous apices. These apices may be erroneously perceived as separate roots rather than as parts of a single distal root.

Abbreviations and Metrics

KNM	National Museum of Kenya, Nairobi.
NK	Fossils from the Narok District, Kenya.
L	Greatest distance between the mesial and distal ends of the crown.
h	Height of the lophids.
H	Greatest height of the molar.
w	Distance between the buccal and lingual ends of the lophid.
W	Greatest width of the molar.
e	Thickness of the enamel measured at the wear surface or broken surface of the crown.
LF (lamellar frequency)	The lamellar frequency is calculated following the method described in Maglio (1973).
m	Mandibular molar.
ccprp	Posterior pretrite central conule.

All measurements were made by L. H. from the original specimens and casts.

Systematic Paleontology

Proboscidea Illiger, 1811
Elephantoidea Gray, 1821
Gomphotheriidae Hay, 1922
Anancus Aymard in Dorlhac, 1855
Anancus kenyensis (MacInnes, 1942)
Figures 1–2

Referred material

KNM-NK 41502, fragment of left hemi-mandible with lower m3 and distal root of m2.

Description

All dental measurements of KNM-NK 41502 are given in Table 1.

KNM-NK 41502 is a left hemi-mandible with m3 crown and distal root of m2. The hemi-mandible lacks the mandibular condyle, much of the coronoid process, distal margin of the mandibular angule, anterior one-third of the horizontal ramus, and the mandibular symphysis. The mandibular corpus is robust and its ventral border curves distinctly ventrally, as is usual in *Anancus*. The mandibular angle is damaged but the remaining morphology suggests that it was flat medio-laterally and located slightly high at the distal end of the corpus mandibulae. Although KNM-NK 41502 lacks its symphysis, features of the ventral border of the corpus and mandibular angle perhaps suggest a brevirostrine condition for the mandible. The mandibular foramen is relatively small and located about the halfway between the condyle and the distal end of the third lower molar. The mylohyoid groove is clearly visible and runs from the mandibular foramen (foramen mandibulae) anteroinferiorly.

The third molar is preserved intact and erupting from the jaw such that the distal third of the crown is partially hidden in the crypt. It has a mesial cingulum, five lophids, and a postcingulum. Thus the lophid formula of the molar can be expressed as X5X. The molars are at an early wear stage with dentine exposed only at the mesial cingulum and pretrite half of the first lophid. The lophs are not closely packed together and the crown tapers distally.

The main cusps and mesoconelets of the first and second lophids are set in a line running slightly oblique to the mesiodistal axis of the molar, except for the mesoconelet of the second pretrite half-lophid, which is slightly displaced mesially. On the third and fourth lophids, however, the posterior central conule of the pretrites are slightly displaced distally, and they shallowly mesh with the mesoconeles of the posttrite half-lophids making a weak zigzag pattern along the median axis of the molar. Thus, only the distal half of the molar shows faint anancoidy.

The first to fourth posttrite half-lophs are each composed of a main cusp and a lower and smaller mesoconelet. The mesoconelet of the first posttrite half-lophid is only slightly smaller than the corresponding main cusp in occlusal view. However, the mesoconelets are smaller on the more posterior lophid, and at the fourth lophid, the mesoconelet is about one fifth of the accompanying main cusp in occlusal view. Nevertheless, the mesoconelets of the posttrite half-lophids are always larger than those of the pretrite of the same lophid. On the first and the second pretrite half-lophids, the mesoconelets are about

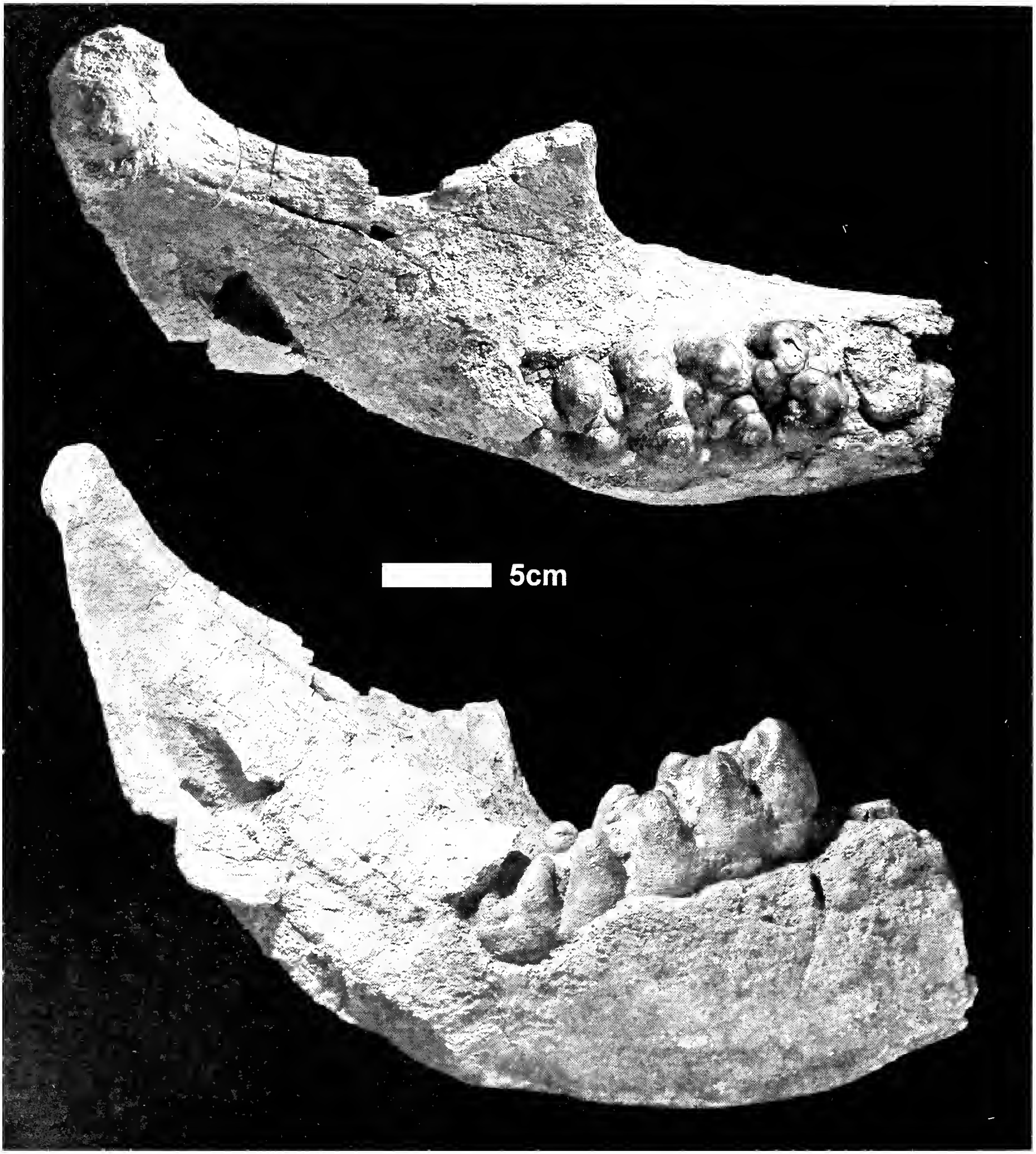

Figure 1. *Anancus kenyensis*, KNM-NK 41502, left hemi-mandible with m3. Top: occlusal view, anterior is to the right, and lingual is to the bottom of page. Bottom: lingual view, anterior is to the right of the page.

the one third of the main cusps in occlusal view and are separated from the latter by a distinct groove, while those of the third and fourth pretrite half-lophid are very small, flat transversally, and separated from the much larger main cusp by a faint groove. The fifth lophid is composed of a pair of pre- and posttrite main cusps only. It is followed by the postcingulum consisting only of a single large tubercle.

On the distal face of the first to fourth pretrite half-lophids, there are large and distinct central conules (ccprp1–4). They are reduced slightly on the more distal lophids. The ccprp are clearly

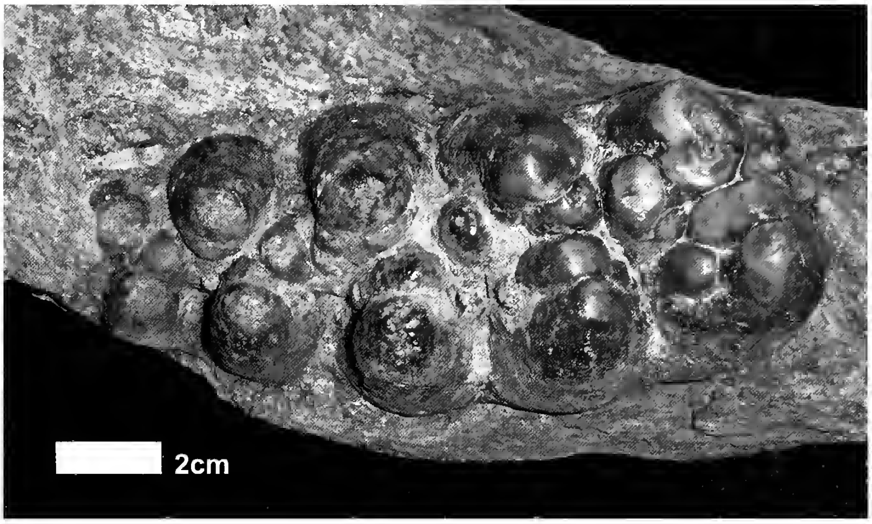

Figure 2. *Anancus kenyensis,* KNM-NK 41502, left m3. Closeup occlusal view, anterior is to the right, and lingual is to the bottom of the page.

detached from the main cusps and mesoconelets, but they are connected with the mesoconelet on first lophid and the main cusp on the second to fourth lophids by strong protuberances or blunt ridges on the distal side.

Posterior posttrite central conules are present on the distal flank of the first to third posttrite half-lophids. The conule on the first lophid is fairly distinct with its apex superficially subdivided. Those conules on the second and third lophids are subtle swellings on the middle height of the distal face of the half-lophids. There is no anterior central conule on either side of the lophids.

Thin cement remains in the bottom of the inter-lophid valleys. Judging from the rugged condition, the present surface of the cement does not represent the original wear surface. However, the enamel surface of the valley is polished for about two thirds of its depth, suggesting that the cement cover was removed by wear at least to that degree during the life of the animal.

Only the distal root of the second molar is preserved in the alveolus.

Discussion

KNM-NK 41502 represents a member of the genus *Anancus* because the anterior pretrite central conule is degenerated and merged with the mesoconelet, and the distal displacement of the pretrite main cusp is more or less accentuated, as diagnosed by Tassy (1986, p. 87).

According to Tassy (1986), there are two morphotypes within *Anancus*: primitive *kenyensis* and derived *petrocchii* morphs. The former and the latter are represented respectively by the type specimen of *A. kenyensis* from Kanam, Uganda originally described by MacInnes (1942) and the *Anancus* sample from Sahabi, Libya described by Petrocchi (1954). The *petrocchii* morph is distinguished from *kenyensis* morph by the derived traits of molars and is thought to represent an evolutionary level of *Anancus kenyensis*. Although both morphs were treated as two evolutionary levels of *A. kenyensis* by Tassy (1986), he did not define them as distinct taxonomic units or evolutionary levels of a species because of the presence of an intermediate morphotype. KNM-NK 41502 is also somewhat intermediate between these two morphs because it has incipient posterior posttrite central conules on the second and third lophids, which is a derived feature shared by the *petrocchii* morph.

Despite this one derived feature, we attribute KNM-NK 41502 to the *kenyensis* morphotype within *Anancus* because it has a smaller dimension of the cheek teeth relative to that of *Anancus arvernesis*, has weak or no anancoidy, and has development of cement in the interlophids (following Tassy, 1986).

Table 1. Dental Measurements (in mm) of elephantoid specimens from Lemudong'o.

KNM-NK 41502 (m2)						
L	W	H	LF	e		
168	69.4	45.7	3.2	7.25		
lophids	1st	2nd	3rd	4th	5th	6th
w	60	66.7	69.4	–	–	–
h	45.7	45.4	44.7	–	–	–
KNM-NK 42396 (m3)						
L	W	H	LF	e		
163	95.7	57.1	3.5	–		
lophids	1st	2nd	3rd	4th		
w	89.7+	90.3	92.5	95.7		
h	–	–	57.1	–		

Kalb and Mebrate (1993) divided sub-Saharan *Anancus* into four successive taxonomic units, *Anancus kenyensis, Anancus* sp. (Lagebaanweg type), *Anancus petrocchii*, and *Anancus* sp. (Sagantole type), mostly based on the specimens from the Middle Awash, Ethiopia. They then used them in a cladistic analysis of elephantoids, but did not give these units formal scientific names or definite morphological diagnoses (Kalb and Mebrate, 1993).

Kalb and Froehlich (1995) and Kalb et al. (1996) compared their *Anancus* "*kenyensis*" from the Middle Awash with Tassy's "*kenyensis* morph," but they did not address the relationship between "*petrocchii* morph" of Tassy (1986) and their *Anancus* sp. (Lagebaanweg type), *Anancus petrocchii*, and *Anancus* sp. (Sagantole type). Recently, Tassy (2003) added the new samples from Lothagam to his morph *kenyensis* and *petrocchii,* but he did not review the four taxonomic units of *Anancus* proposed by Kalb and Mebrate (1993), Kalb and Froehlich (1995), and Kalb et al. (1996).

Although these analyses are incomplete because they do not consider the entirety of the available fossil evidence, they do suggest that there is an evolutionary trend within the African *Anancus* towards greater complexity of the crown pattern over time. At this time though, there is not enough evidence with which to define new species or subspecies within this evolving lineage. Unfortunately, this new specimen from Lemudong'o does not resolve the current situation, but rather bolsters the need for a new analysis investigating the relative frequency of morphological variation within this growing late Miocene fossil assemblage.

As noted by Tassy (2003), some derived traits, for instance pentalophodonty, are not always associated with other derived features, such as supplementary accessory cusps. Anancoidy, number of loph(id)s, supplementary cusps, and cementodonty, are the morphological traits that have been used in the characterization of morpholgical types or informal taxonomic units in previous studies. However, new fossil finds are showing that they do not appear to evolve in a coordinated manner. Derived and primitive features can be combined almost at random in any given collection, as is seen in the new sample from the Late Miocene of the Middle Awash (personal observations of H. S. and Y. Haile-Selassie). No morphological feature can be found universally in all populations.

KNM-NK 41502 is characterized by the lowest level of the development of anacoidy among the East African *Anancus*, which differentiates it from the late Miocene specimens from the Middle Awash. Of the previously described anancine m3's from eastern Africa, the Lemudong'o specimen is most similar to that from Lukeino (KNM-LU 57). The pretrite main cusp of the second lophid of the Lemudong'o specimen appears to be located more mesially than that of KNM-LU 57. However, this difference in appearance could be explained by the difference in the degree of the wear rather than an actual difference of the position of the cusps; because the distal wall of the main cusp slopes more gently than the mesial one does, the worn figure of the cusp extends more distally than mesially, and this gives the impression that the center of the worn cusp is located more distally than that of the un-worn cusp. The extent of the dislocation of the 3rd and 4th pretrite half-lophids of KNM-NK 41502 is comparable to that of KNM-LU 57 figured in Tassy, Plate XIII, fig. 4, and is not as marked as those of the "*petrocchii* morph." The size and arrangement of the cusps and conules of these lophids are fairly similar to that of KNM-LU 57, except for the rudimentary size of the pretrite mesoconelets. Strong degeneration of the pretrite mesoconelet may be a derived feature of *Anancus*, as it is frequently observed on lower molar of species in this genus. On the other hand, in *Tetralophodon longirostris* from *Dinotherium* sands, the pretrite mesoconelet and ccprp are basically the same size; the pretrite mesoconelet is never degenerated and only in few cases it is smaller than the ccprp (Saegusa, unpublished observation). KNM-NK 41502 is slightly more derived in having incipient posterior posttrite central conules on the second and third lophids, but such a subtle difference could result from mere individual variation seen in the same taxon.

Because of these similarities, we place the *Anancus* from Lemudong'o in the most primitive evolutionary level of *A. kenyensis*, together with that from Lukeino. The current evidence suggests that KNM-NK 41502 is older and more primitive than the *Anancus* from the Middle Awash (personal observations of H. S. and Haile-Selassie), which is dated ca. 5.6 Ma, although this relationship is clearly tentative since it is based on only a single specimen from Narok.

ELEPHANTIDAE Gray, 1821
Genus and species indeterminate
Figure 3

Referred Material

KNM-NK 42396, right lower second molar and fragments of an associated tooth.

Description and remarks

At the first glance, KNM-NK 42396 looks like an upper intermediate molar because of its mesiodistally shortened crown proportions. However, the following four features of KNM-NK 42396 indicate that the molar is a lower one:

1) *The structure of the root.* On the convex side of KNM-NK 42396, the mesial two lophids are supported by a mesial root (= anterior root of Sher and Garutt, 1985), while the rest of the lophids are supported by a distal root (= the middle and posterior segment of Sher and Garutt, 1985). The relationship between the roots and the lophids observed at the convex side of KNM-NK 42396 is precisely like that of early elephants and stegodons, in which the mesial root supports the mesial two lophids at the lingual side (= convex side) (Saegusa et al., 2005; the holotype of *E. nawatensis* described by Tassy, 2003). In contrast, the mesial root supports the first lophid only at the buccal side (= convex side) of the upper molars of stegodons and early elephants.
2) *The angle of the eruption of the molar.* In KNM-NK 42396, the wear surface develops on the first lophid only, and the molar is still at its early stage of wear. At the same time, the angle of the eruption is fairly low, judging from the angle between the wearing surface of the first lophid and the cervical line. The low angle of eruption at such an early stage of molar wear is consistent with identification as a lower molar rather than that of an upper molar.
3) *No divergence of lophids in lateral view.* Lophs of upper intermediate molars of early elephants and stegodons diverge markedly in lingual and buccal view (e.g., KNM-LT 358, figured in Maglio and Ricca, 1978, pl. 2). In KNM-NK 42396, the lophids run parallel to each other in lingual and buccal view rather than diverge.
4) *Strong buccal curvature and twist of the molar crown.* The extent of the curvature and S-twist of the crown of KMN-NK 42396 is comparable to that of lower intermediate

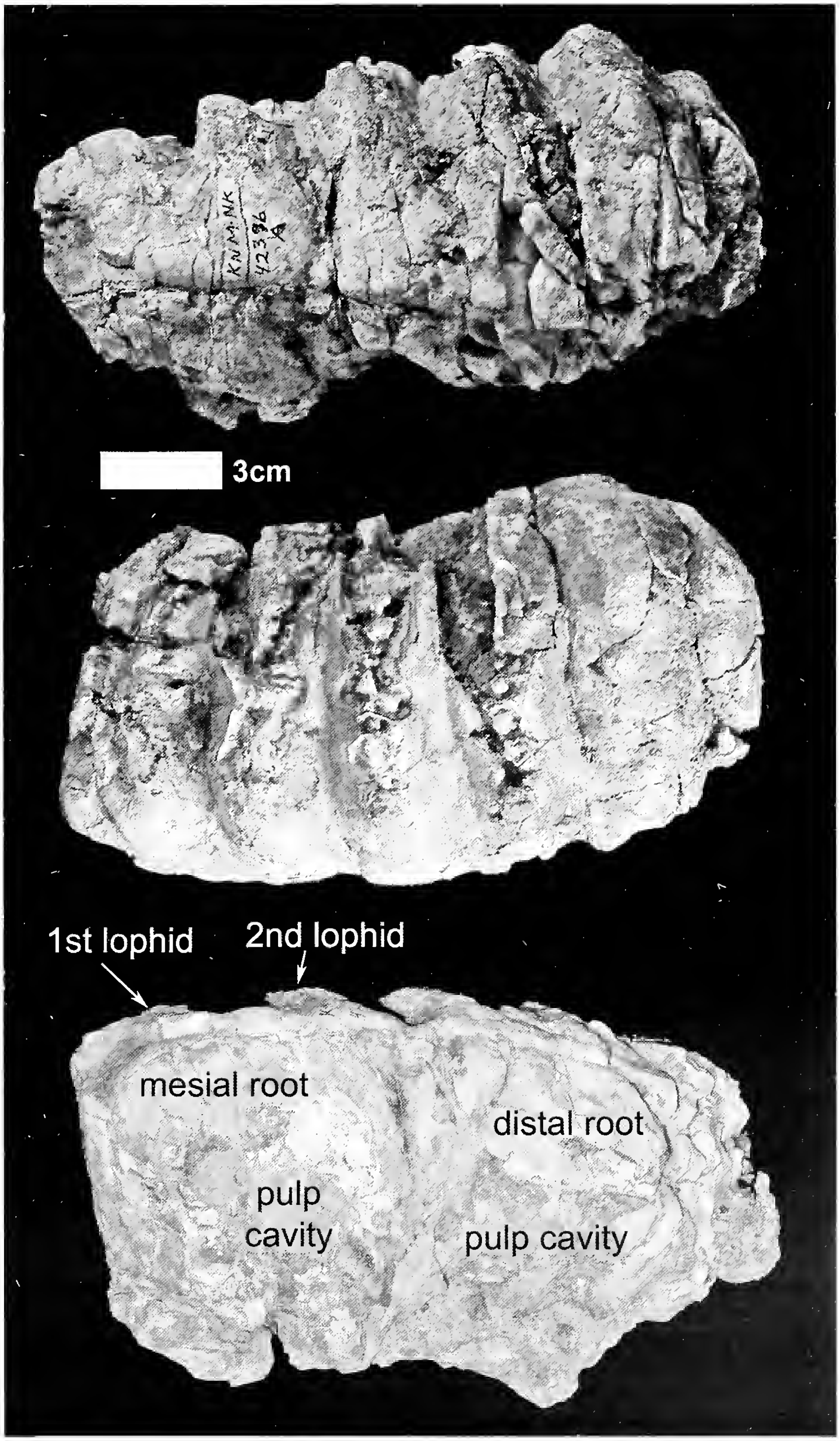

Figure 3. Elephantidae gen. and sp. indet., KNM-NK 42396, right m2. Top: lingual view, mesial is to the left of the page. Middle: occlusal view, mesial is to the left, and the buccal is to the top of the page. Bottom: apical view, mesial is to the left, and the lingual is to the top of the page.

molars of early elephants and stegodons rather than that of the upper intermediate molars of these taxa.

Besides the ratio of length to width of the molar, the only marked feature that contradicts the above identification of KNM-NK 42396 as a lower molar is the development of the mesial cingulum at the meiso-lingual corner of the molar. As has been suggested by Tassy (1994, p. 86), antero-lingual cingulum is reduced in Elephantoidea and this feature can be considered as a synapomorphy of this group. Although most primitive elephants and stegodons follow this rule, in some lower molars of these taxa the antero-lingual cingulum is only slightly thinner than the buccal one (e.g., Coll. Dub. No. 2231 figured in Hooijer, 1955, pl. 3). In such cases, the thickness of the mesial cingulum cannot be used for the distinction of the upper and lower molars unless the both sides of the cingulum are fully preserved. In KNM-NK 42396, the thickness of the buccal half of the anterior cingulum cannot be reliably estimated because of the postmortem distortion.

This molar has five fully developed lophids and a postcingulum. Although it is quite damaged, there is a lingual part to the mesial cingulum as well. Thus, the lophid formula of the molar can be expressed as X5X. The lophids and cingula are packed tightly. The crown is twisted to the extent that the last lophid is rotated lingually about 15 degrees relative to the first lophid. The mesial three lophids are straight transversally, while the distal two lophids are slightly convex-convex shaped. The last lophid and postcingulum are nearly covered up with the cement. On the mesial four lophids, the enamel surface can be seen on the lateral faces and their apices.

The basal part of the mesial root is also preserved. This mesial root supports the first and second lophids, while the distal root is totally damaged such that the pulp cavity of the third to postcingulum is widely exposed. The root of the molar shows the derived condition shared by elephants and stegodons.

Most of the apex and the buccal wall of the first to third lophids are damaged. The lingual wall along the cervix of the last two lophids is also damaged. Because of the damage, it is not clear how many mammillae were present on each lophid but it appears that there were no less than five mammillae on each lophid. Where the lophids are exposed above the worn cement surface, it is evident that the apical ends of at least the second and third lophids are mesio-distally compressed. The groove separating the mammillae appears to be very shallow and restricted to the upper part of the lophids, judging from the smoothness of the exposed surface of the upper part of the second lophid. The enamel folding also appears to be very weak or absent. At the distolingual face of the first and the second lophids there are small median columns which are compressed to the main body of the lophids. Presence or absence of the central conule on the more distal lophids cannot be determined because of the thick cement cover. Overall, the tooth is low crowned and pentalophodont with mesial and distal cinugula.

The mesial root supports the first and second lophids, while the distal root supports the rest of the molar. The first and second lophids are worn. The fifth lophid is almost completely covered with cement, while only the lower one-third of the depth of the first valley is filled. Behind the first and second lophids, there are centrally located columns (posterior central conule), half embedded in the wall of the distal faces of the lophids.

The width of the crown does not increase markedly toward the rear part of the crown (Table 1).

Discussion

KNM-NK 42396 is a m2 of a primitive elephant, but it does not resemble any of the known m2's of *Stegotetrabelodon*, *Primelephas* or the Elephantidae gen. et sp. indeterminate from Lothagam. The molar is comparable to that of *Stegotetrabelodon orbus* in having only five lophids, but it differs in showing no posterior enlargement of the crown. KNM-NK 42396 is also different from the m2 of *Primelephas gomphotheroides* (KNM-LT 358) because it has only five lophids and a much transversally wider crown. It differs from the m2 of Elephantidae gen. et sp. indeterminate from Lothagum (KNM-LT 350) described by Tassy (2003) in that it has only five lophids, and lacks the marked distal widening of the crown. In KNM-NK 42396, the median pillar (distal central conule) is more compressed to the main body of the lophid than is seen in the m2 of *P. gomphotheroides*, *S. orbus* and Elephantidae gen. et sp. indet from Lothagam. In this respect, KNM-NK 42396 is definitely derived relative to these other taxa.

The KNM-NK 42396 mesial root supports the first and second lophids. This is the same condition as is seen in the lower second molar of *Stegodon zdanskyi* from North China (unpublished data of H. S.) and *Primelephas gomphotheroides* (Maglio and Ricca, 1978), and is derived compared to that of the gomphotheres.

This unique combination of the derived root and primitive crown characters in KNM-NK 42396 suggests that it represents a previously unrecognized diversification of the early elephants, and precludes the allocation of this specimen to any known taxon of Elephantidae. However, it would be premature to establish a new taxon based on such a fragmentary lower molar. Pending further findings of primitive elephants from East Africa, the specimen is identified as Elephantidae gen. and sp. indeterminate.

Conclusions

KNM-NK 41502 can be allocated to the most primitive evolutionary level of the *A. kenyensis* lineage, together with specimens from Lukeino, Kenya. Although KNM-NK 42396 is identified as Elephantidae gen. and sp. indeterminate, it may represent a new primitive elephantid.

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THE LATEST MIOCENE HIPPARIONINE (EQUIDAE) FROM LEMUDONG'O, KENYA

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ABSTRACT

Four cheek teeth recovered from the latest Miocene Kenyan locality of Lemudong'o, Kenya, are described herein. All specimens are those of a medium-sized hipparion species, which is small for East African hipparions. The two lower cheek teeth demonstrate that these specimens are referable to the endemic African lineage, *Eurygnathohippus*. Comparison with other materials that have been studied by the author from Ethiopia, Kenya, and Tanzania suggest a referral to *Eurygnathohippus* cf. *feibeli* Bernor and Harris, 2003. Wear on a single upper cheek-tooth fragment suggests that the local *E.* cf. *feibeli* may not have been a dedicated grazer, but incorporated some browse into its diet. The fact that the entire hipparion sample from Lemudong'o is composed of cheek teeth, three out of four of which are fragmentary and appear to have been transported by fluviatile agencies, suggests that they are sampled from a distal taphonomic community. Given that *E. feibeli* is known to have had elongate, slender, distal limbs and was a cursorial form, one can hypothesize that the Lemudong'o hipparion inhabited open country habitats.

Introduction

Lemudong'o is a late Miocene mammalian-dominated fossil locality in the Narok District of Kenya, on the western margin of the Gregory Rift Valley. Vertebrate fossils derive from primarily two horizons within a continual sequence consisting of sands that fine upwards to a claystone and a re-worked tuff (Ambrose, Nyamai, et al., 2007). These sediments have excellent chronometric control based on a single-crystal argon age of just over 6 million years ago (Deino and Ambrose, 2007). More than 1,300 vertebrate fossils identifiable to family level have been recovered from this site since its discovery by scientists in 1994 (Ambrose, Hlusko, and Kyule, 2007). However, the equid fauna within this collection from Lemudong'o is sparse, and represents what would appear to be a single species of a smaller African hipparion. I report here on four cheek-tooth specimens attributable to the genus *Eurygnathohippus* Van Hoepen, 1930.

Materials and Methods

The nomen *Hipparion* has been applied in a variety of ways by different authors. A history of Old World hipparion systematics has been provided by Bernor et al. (1996), while the African record has been addressed by Bernor and Armour-Chelu (1999), Bernor and Harris (2003), and Bernor et al. (2005). The evolutionary relationships of African hipparions and Eurasian members of the "*Sivalhippus*" Complex (sensu Bernor and Hussain, 1985) was first noted by Bernor and Lipscomb (1995).

The Lemudong'o material available for study is limited to cheek teeth, as no other skeletal elements have been recovered to date. This allows basic morphological description following the methodology of Bernor et al. (1997) and Bernor and Harris (2003). In that these cheek teeth are rolled, very limited statistical analysis can be effectively undertaken. I provide a single bivariate plot of a p4 specimen's occlusal length (M1-occlusal maximum length) versus maximum width (M8, across metaconid-protoconid band). Here, as in the previous studies cited above, I produce a 95% confidence ellipse using the Eppelsheim (Germany, ca. 10 Ma) population sample, and plot late Miocene–early Pliocene specimens from the Middle Awash (Ethiopia) and Lothagam (Kenya) against these. This provides some very basic information about the Lemudong'o hipparion's relative size. There is no reason to believe that this small sample represents more than a single hipparion species.

All measurements are in millimeters (mm). Measurement numbers (i.e., M1, M2, M3, etc.) of cheek teeth used here, as well as anatomical nomenclature follows Bernor et al. (1997).

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Suborder Hippomorpha Wood, 1937
Superfamily Equoidea Hay, 1902
Family Equidae Gray, 1821

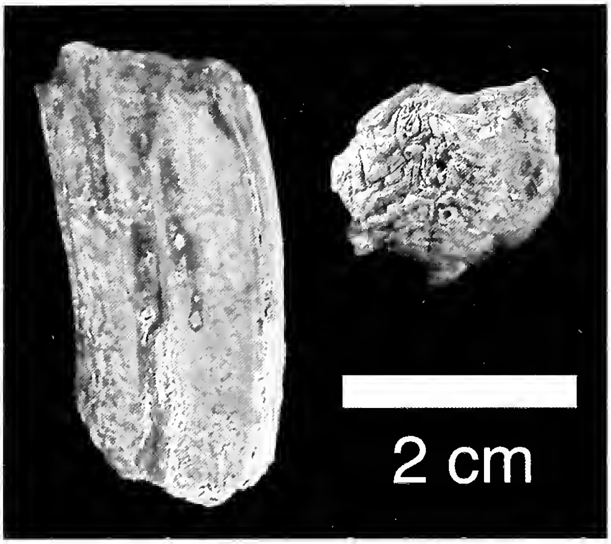

Figure 1. KNM-NK38312, right maxillary M3. Left, labial view; right, occlusal view.

Subfamily Equinae Steinmann and Doderlein, 1890
Genus *Eurygnathohippus* Van Hoepen, 1930

Remarks

All African hipparions of the genus *Eurygnathohippus* are united by the synapomorphy of the presence of ectostylids on the permanent cheek teeth. Eurasian and North American hipparions do not have this character except very rarely in extremely worn hipparion teeth from the Dinotheriensandes, Germany (MN9, ca. 10.5–10 Ma). *Stylohipparion* is the junior synonym of *Eurygnathohippus* by year priority.

Eurygnathohippus cf. *feibeli* Bernor and Harris, 2003
Figures 1–2

Type locality of *E. feibeli*

Upper Nawata Formation, Lothagam Hill, Kenya.

Geographic range

Ethiopia, Kenya, and possibly Tanzania.

Material

KNM-NK36935, left maxillary cheek-tooth fragment; KNM-NK38312, right maxillary M3; KNM-NK41375, right mandibular p4 fragment; KNM-NK40994, left mandibular p4.

Description

KNM-NK36935 is a central fragment of a left maxillary cheek tooth of a smaller East African hipparion. Here, most of the prefossette and all of the postfossette are preserved. The posterior border of the prefossette is complexly ornamented, as is the opposing border of the prefossette. There is a moderately deep groove across the middle of the tooth that would have extended from the lingual surface of the protocone to the labial border of the mesostyle (both missing in this specimen). This feature, characteristically deeper in most populations of *Hippotherium primigenium*, functionally correlates with rounded-to-sharp and high facets on the ectoloph, and is correlated with a mixed grass/browse to a browse diet (Kaiser et al., 2000). Given that this functional trough is shallow, we can only safely estimate that this individual did not likely have a purely grass diet: It likely browsed somewhat.

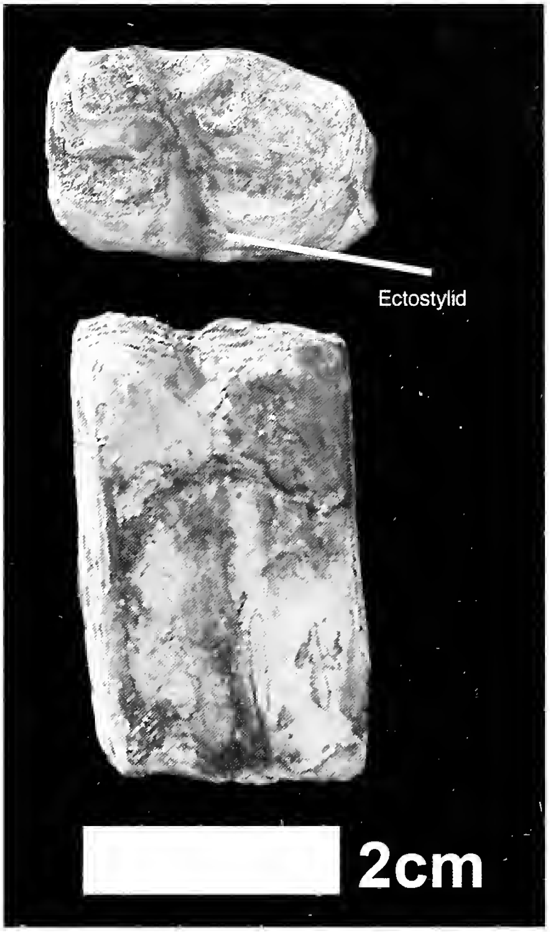

Figure 2. KNM-NK40994, left mandibular p4. Bottom, labial view; top, occlusal view.

KNM-NK38312 (Figure 1) is a more complete, and small maxillary M3. The occlusal surface is eroded and appears to have been in relatively early wear. The pre- and postfossettes can be distinguished but are not yet sufficiently worn to have any developed plications. There is a single pli caballin and the protocone is rounded labially, and strongly flattened lingually. No other morphological features are clearly displayed on this apparently rolled specimen.

KNM-NK41375 is a fragmentary right mandibular p4 of a similarly sized hipparion. The mesial portion of the tooth is broken away. The following morphological features are preserved: a rounded metastylid with a straight sloping mesiolingual border; an elongate, unplicated postflexid; a shallow ectoflexid, not separating metaconid-metastylid; a distinct pli caballinid, and what appears to be a tiny ectostylid immediately labial to the pli caballinid.

KNM-NK40994, a complete mandibular p4, is the best preserved specimen in this sample (Figure 2). Its salient features include: rounded metaconid and square-shaped metastylid; linguaflexid a deep, broad U-shape*; preflexid and postflexid elongated, labiolingually compressed and lacking any plications*;

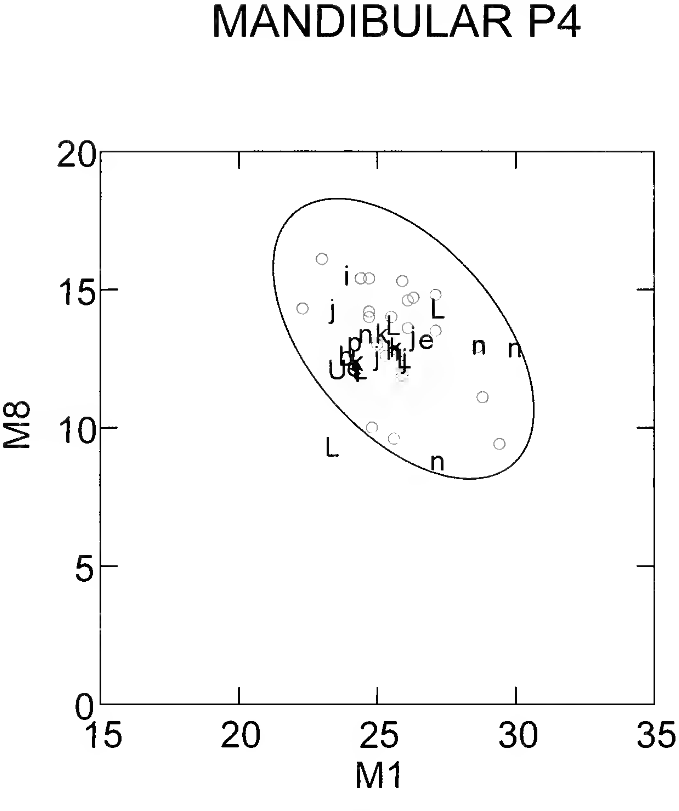

Figure 3. Bivariate plot of KNM-NK40994, left mandibular p4: M8 versus M1, 95% confidence ellipse representing variability in the Eppelsheim sample, 10 Ma., Germany.

protoconid enamel band showing some flattening*; ectoflexid not separating metaconid-metastylid; pli caballinid small; ectostylid a distinct, albeit small, elongate, enamel circle on the mid-labial margin of the tooth* (* indicates features typical of *Eurygnathohippus*). This was the only specimen for which measurements (Table 1) could be effectively made.

Haile-Selassie (2001) has recognized that it is difficult to distinguish the two lineages of late Miocene–medial Pliocene East African hipparions from cheek teeth alone: they are well characterized by distal postcranial elements (Bernor et al., 2005). This is exacerbated by the fact that cheek teeth reduce their mesiodistal dimension through wear, so that old individuals have much shorter dimensions than young individuals. Nevertheless, these studies have recognized a smaller hipparion during this time interval, and it is interesting that its cheek teeth are consistently the size of Central European late Miocene *Hippotherium primigenium*.

Figure 3 is a bivariate plot of KNM-NK40994 in comparison to the Eppelsheim sample (95% confidence ellipse and plotted points indicated by circles). The Lemudong'o specimen is indicated by a U and placed near the left border of the Eppelsheim ellipse. Lothagam (L) has specimens both inside the ellipse and further to the right (and hence are longer), as well as outside, lower and to the left of the ellipse (and hence being narrower). The remaining lower case indications (i, j, k, n, etc.) are latest Miocene-earliest Pliocene Middle Awash localities. In that these localities are not yet published, I will only note here that they are between 5.7 and 4.9 Ma, and are of the same species-lineage. The Lemudong'o specimen was in approximate middle wear, and its size is clearly that of Eppelsheim *Hippotherium primigenium*. Although fragmentary, all other specimens in the Lemudong'o hipparion are the size of this hipparion.

Remarks

Hipparionine horses originated in North America circa 16 Ma and first entered the Old World between 11.1 and 10.7 Ma. The Eurasian late Miocene record is extensive and includes several multispecies superspecific groups. Members of the major clades including *Hippotherium*, *Hipparion s.s.*, and *Cremohipparion* became extinct at the end of the late Miocene (Bernor et al., 1996). The "*Sivalhippus*" Complex is first recorded in the late Miocene of IndoPakistan and East Africa, and later had ranges that extended across Eurasia and Africa (Bernor and Lipscomb, 1995). The Chinese taxa *Plesiohipparion* and *Proboscidipparion* appear to have extended their ranges into Europe and southwest Asia in the early Pliocene (Bernor et al., 1996), while *Eurygnathohippus* was a vicariant lineage restricted to East and South Africa in the late Miocene (Bernor and Lipscomb, 1995; Bernor and Harris, 2003; Bernor et al. 2004), and is known throughout Africa during the Plio-Pleistocene (Bernor and Armour-Chelu, 1999).

Bernor et al. (2005) have analyzed Ethiopian hipparion metapodials and 1st phalanges between 6.0 and 2.9 Ma in age. They have found evidence of two hipparion lineages during this interval. A rare robust form, related to Lothagam *Eurygnathohippus turkanense*, and a predominant gracile lineage that they refer to the *Eurygnathohippus feibeli-hasumense* lineage. This lineage would appear to have progressively evolved greater size (= body mass) and to have lengthened the metapodials and increased the size of the phalanges from 6 to 2.9 Ma. The earliest members of this lineage are referable to *Eurygnathohippus feibeli s.s.*, and are the smallest members of this lineage. The Lemudong'o sample is similar to *E. feibeli*, and has all the morphological hallmarks of *E. feibeli*, but the absence of metapodial and 1st phalangeal material necessitates a referral to *E.* cf. *feibeli*.

Conclusions

The Lemudong'o hipparion sample is small for East African hipparions, and referable to *Eurygnathohippus* cf. *feibeli*. Referral to *Eurygnathohippus* is clearly supported by the occurrence of an ectostylid on at least one, and probably two permanent mandibular cheek teeth. The small size and morphology of this sample support the specific referral to *E.* cf. *feibeli*. Wear on the upper cheek tooth suggests that there may have been some component of browse in this sample. The Lemudong'o hipparion would appear to correlate well with Upper Nawata Formation (Bernor and Harris, 2003), Middle Awash latest Miocene hipparions (observations of myself and Y. Haile-Selassie) and the oldest Manonga Valley hipparion-bearing levels (Bernor and Armour-Chelu, 1997): all have this size hipparion, most likely referable to *E. feibeli*.

The fact that hipparions are so poorly represented at Lemudong'o, coupled with the fact that the specimens are largely fragmentary and appear to be transported by fluviatile agencies, suggests that they are sampled from a distal taphonomic community. *Eurygnathohippus feibeli* is known to have had elongate distal limb elements, and is believed to have lived in open country habitats. These lines of evidence support the observations elsewhere in this volume that Lemudong'o principally sampled a more closed ecological setting (i.e., the proximal taphonomic community), and that the hipparions sample a somewhat distant open country community (Ambrose, Bell, et al., 2007).

Table 1. Measurements on KNM-NK40994, left mandibular p4.

Measurement*	Description	KNM-NK 40994
M1	occlusal length	23.6
M3	metaconid-metastylid length	13.6
M4	preflexid length	8.1
M5	postflexid length	10.2
M8	width across plane of metaconid-protoconid enamel band	12.1
M9	width across plane of metastylid-hypoconid	11.1
M11	length of ectostylid	2.3
M12	width of ectostylid	1.2

*All measurements in mm.

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NYANZACHOERUS SYRTICUS (ARTIODACTYLA, SUIDAE) FROM THE LATE MIOCENE OF LEMUDONG'O, KENYA

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ABSTRACT

Lemudong'o Locality 1 is a late Miocene mammalian-dominated fossil site in the Narok District of southern Kenya. Suidae specimens from this site are scarce and fragmentary, however the recovered specimens can be confidently assigned to *Nyanzachoerus syrticus* based on the size and morphology of the third molars and the relative size of the third and fourth premolars. This species designation indicates a late Miocene/early Pliocene biochronological age, which accords with ^{40}Ar/^{39}Ar determinations of ~6.11 Ma (Deino and Ambrose, 2007). These Lemudong'o specimens indicate that *N. syrticus* inhabited the southern part of what is now Kenya by 6 Ma, the earliest known appearance of the species south of Lothagam, Kenya.

Introduction

Lemudong'o is a 6-million-year-old fossil site in the Narok District of southern Kenya (Ambrose et al., 2003, 2007; Deino and Ambrose, 2007). Primarily, mammalian fossils have been recovered from the Lemudong'o Locality 1 (LEM 1) and nearby contemporaneous localities, consisting of a large number of colobine primates and hyracoids. Along with other taxa, there is a relatively sparse and fragmentary assemblage of suids. Collecting between 1997 and 2004 yielded 44 suid specimens, representing less than 1% of the total collection (Ambrose et al., 2007). Eight of these are postcranial specimens, twenty-eight specimens are isolated teeth, and six are associated teeth or partial jaws. The more complete specimens for which exact stratigraphic proveniences are known come from the sands at or near the base of the fossiliferous sequence at LEM 1.

The fossil record documents relatively rapid morphological evolution in several well-represented Plio-Pleistocene suid lineages (e.g., Harris and White, 1979; Brunet and White, 2001). Given that suids are commonly found at terrestrial fossil sites, and much of their evolution is relatively well-understood, various taxa in the family are often used as biochronological markers (e.g., White and Harris, 1977; Cooke, 1985). As such, the African Suidae have played a significant role in our understanding of the evolution of many other African mammals, including that of humans. Suid taxa can also provide insight into paleoecology (Bishop, 1999).

The last decade has witnessed a dramatic increase in the recovery of late Miocene and early Pliocene mammalian fossils from sites in eastern and central Africa such as Lothagam (Harris and Leakey, 2003) and Lukeino (Pickford and Senut, 2001) in Kenya, Aramis and the West Margin of the Middle Awash (WoldeGabriel et al., 1994; Haile-Selassie et al., 2004) in Ethiopia, the Warwire and Nkondo Formations in the Albertine Rift of Uganda and Zaire (Pickford et al., 1994), and Toros-Menalla in Chad (Brunet and M.P.F.T., 2000; Vignaud et al., 2002). Many new suid specimens have been recovered from these sites, including at least two new species: *Kolpochoerus deheinzelini* and *Kolpochoerus cookei* (Brunet and White, 2001). Because of this significant increase in the fossil data, our current understanding of African suid evolution has been subjected to major revisions (van der Made, 1999; for previous reviews of African suids and Old World suids see Pickford [1986, 1993, respectively]).

The LEM 1 suid assemblage, although fragmentary and sparse, contributes new specimens of tetraconodontines to the growing late Miocene database. Given the fragmentary nature of the Lemudong'o suid assemblage and lack of taxonomic diversity, we do not undertake a full revision here. Rather, we describe the relevant Narok specimens in order to facilitate the revisions undertaken by researchers with larger collections. We follow the taxonomy used in Haile-Selassie (2001), based on Cooke (1987).

The LEM 1 suid material represents a single species in the Tetraconodontini. This tribe is thought to have migrated into

Africa from Asia during the late Miocene (van der Made, 1999). Almost all of the LEM 1 suid teeth fall into the size and morphological range of *N. syrticus* from the Lower Nawata of Lothagam, and therefore represent some of the earliest members of this taxon in eastern Africa. Two dental features that are of particular importance to deciphering the various genera and species within the Tetraconodontinae are the relative size of the premolars and the size and complexity of the third molars (van der Made, 1999). Here, we focus our discussion on these characters.

Abbreviations

KNM	Kenya National Museum.
KNM-NK	Narok District, Kenya, indicates fossils are from localities within this district, including Lemudong'o Localities 1 and 2, Enamankeon Localities 1, 2, and 3, and Kasiolei Locality 1. Locality, when different from Lemudong'o Locality 1, is noted in the text. See also Appendix 1 in Ambrose et al. (2007).
KNM-LT	Lothagam, Kenya, indicates fossils from this site.
KL	Kalb Locality; here this refers to fossils now known to be from the Adu-Asa Formation in the Afar Region of Ethiopia.
Ma	million years ago.

Dental abbreviations follow these conventions:

R. M1	right maxillary first molar.
L. p4	left mandibular fourth premolar.
md	maximum mesiodistal measurement of the crown not accounting for wear.
bl	maximum buccolingual width of the crown through the mesial pair of cusps.

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Suidae Gray, 1821
Tribe Tetraconodontinae Simpson, 1945
Genus *Nyanzachoerus* Leakey, 1958
Nyanzachoerus syrticus (Leonardi, 1952)
Figure 1

Remarks

Nyanzachoerus was first described by Leakey (1958, p. 4) as a suid with enlarged 3rd and 4th lower premolars that are laterally more compressed than seen in *Tetraconodon*. The genus was rediagnosed by Cooke and Ewer (1972, p. 154) and Harris and White (1979) as having, in part, cheek teeth similar to modern *Potamochoerus* but with much more columnar and hypsodont molar cusps, and with relatively larger third and fourth premolars compared to the second premolar and molars. This genus was an Asian migrant that entered Africa during the late Miocene (van der Made, 1999, p. 220). Therefore, the fossils recovered from the Narok District in southern Kenya represent some of the earliest specimens of this genus in eastern Africa.

Specimens from Sahabi, Libya, were first referred to *N.* (= *Sivachoerus* Pilgrim, 1926) *syrticus* by Leonardi (1952). Morphologically similar specimens from eastern Africa were named *N. tulotos* (Cooke and Ewer, 1972), given that the original *N. syrticus* material was temporarily lost and unavailable for comparison (Cooke, 1987, p. 256). Subsequent to the recovery and revised description of the Sahabi specimens (Kotsakis and Ingino, 1980), *N. tulotos* has since been recognized as a junior synonym of *N. syrticus* (White and Harris, 1977; Cooke, 1987). This species has been documented from numerous late Miocene African sites such as Beglia in Tunisia (Pickford, 1990), Toros-Menalla in Chad (Vignaud et al., 2002), Middle Awash, Ethiopia (Haile-Selassie et al., 2004), and Lothagam, Kenya (Harris and Leakey, 2003). It has also been documented from late Miocene deposits of the Baynunah Formation in Abu Dhabi, United Arab Emirates (Bishop and Hill, 1999).

Nyanzachoerus syrticus is characterized as being the least advanced *Nyanzachoerus* species due to its retention of both the maxillary and mandibular first premolars (Arambourg, 1968; White and Harris, 1977; Cooke, 1978). This species also has large third and fourth maxillary and mandibular premolars (such that the length of the P3 and P4 is more than half that of the molar row), and relatively low-crowned third molars composed of only two pairs of lateral cusps and a small talon or talonid (Harris and White, 1979, p. 11, for *N. tulotos*).

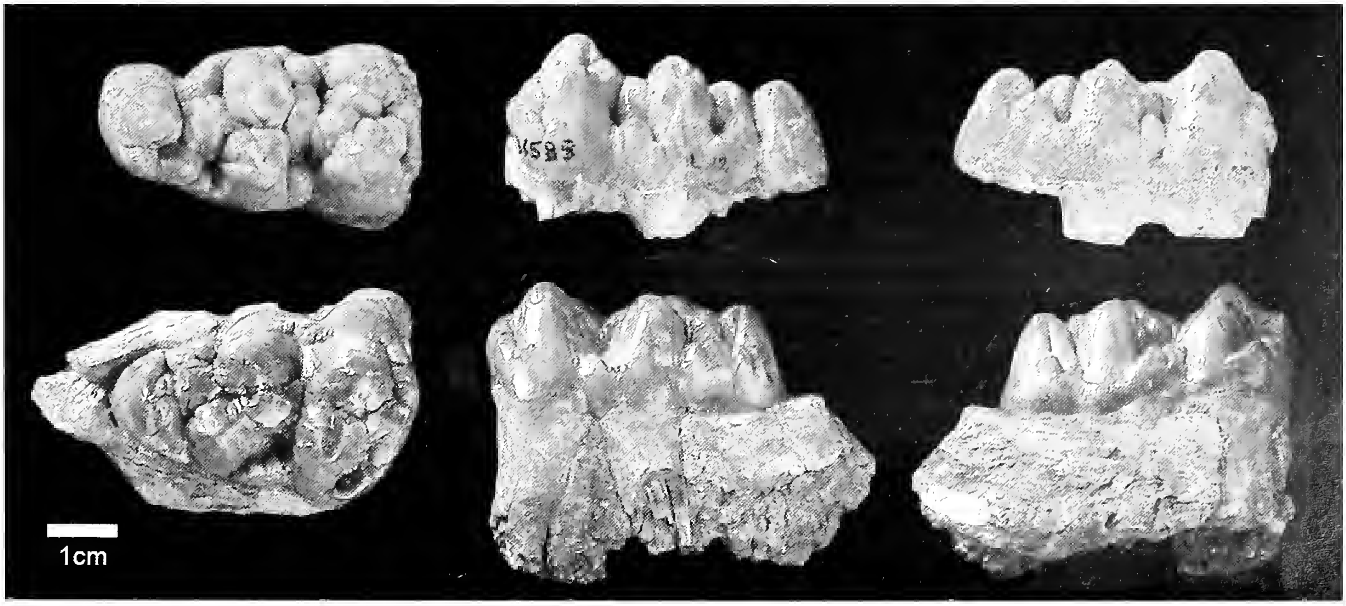

Figure 1. *Nyanzachoerus syrticus.* Top row: KNM-NK 36585, a left m3; bottom row: KNM-NK 45783, a right M3. From left to right: occlusal, buccal, and lingual views.

Table 1. Narok suid mandibular third-molar metrics compared to other *Nyanzachoerus* samples.

Specimen number	md*	mbl	dbl
KNM-NK 36585	45.3	25.9	24.4
KNM-NK 44803	–	23.8	–
KNM-NK 36568a (left)	–	–	20.83
KNM-NK 36568b (right)	–	–	20.7
mean	45.3	24.9	22.0
N. syrticus (Lothagam)[1]			
n	20	21	20
mean (stdv.)	43.5 (3.0)	24.2 (1.2)	21.7 (1.4)
N. devauxi (Lothagam)[1]			
n	8	7	8
mean (stdv.)	37.0 (1.6)	21.3 (1.8)	19.1 (1.3)
N. pattersoni (= *kanamensis*) (Kanapoi)[2]			
n	20	21	n/a
mean (stdv.)	53.0 (3.1)	25.1 (1.8)	n/a
N. kanamensis (Manonga Valley)[3]			
n	2	2	n/a
mean (stdv.)	59.4 (2.0)	28.2 (0.1)	n/a
N. kanamensis australis (Langebaanweg)[4]			
n	18	18	n/a
mean (stdv.)	61.1 (3.4)	29.6 (2.3)	n/a

[1] Data from Harris and Leakey (2003, tables 10.14 and 10.20).

[2] Data from Harris et al. (2003, p. 80–83, table 26).

[3] Data from Bishop (1997, p. 209, table X).

[4] Data from Cooke and Hendy (1992, p. 8, table 3).

* Mesiodistal length = md; mbl = buccolingual width across the mesial cusp pair; dbl = buccolingual width across the second, or distal, cusp pair.

Material

KNM-NK 36568, R. & L. m3 distal fragments (one originally labeled as KNM-NK 41417); KNM-NK 36585, L. m3; KNM-NK 44803, L. mandible with p4-m3 (fragment); KNM-NK 45783, R. M3.

Description

KNM-NK 44803 is a left mandibular specimen with complete p4–m2, and the mesial portion of the m3 (measurements presented in Table 1). The molars are quite worn, and the m1 is preserved merely as a ring of enamel around dentine. The mandibular body is broken, only preserving about half of the corpus inferior to the tooth row. This specimen is morphologically quite similar to KNM-LT 23752 from the Lower Nawata Formation at Lothagam (Harris and Leakey, 2003, p. 488–491), although the KNM-NK 44803 molar row would have been a bit longer if the m3 were complete. The p4s of KNM-LT 23572 and KNM-NK 44803 are similarly sized and the mesial aspect of KNM-NK 44803 is more worn so that the cingulum on the anterior/mesial surface is not as pronounced as on KNM-LT 23752. The large premolars, relative to the molars, align this specimen with *N. syrticus* rather than other members of this genus who are characterized by relatively reduced premolars.

KNM-NK 36585 is a virtually unworn left m3 preserved to just below the cervix (Figure 1 top row, Table 1). There is very slight wear on the protoconid, but no dentine is exposed. This molar has features characteristic of *N. syrticus* (Harris and White, 1979, p. 10–19), such as: two cusp pairs and a terminal cusp; buccal cingulum; small endostyle between metaconid and entoconid; single median pillar behind distal pillar pair; talonid has only one primary cusp and two small distolingual cusplets. KNM-NK 36585 is very similar to KNM-LT 388 from Lothagam, which is assigned to *N. syrticus tulotos*. The Lemudong'o specimen KNM-NK 36585 is larger than the Lothagam *N. devauxi*, broader than the Upper Nawata *N. syrticus*, and greater in both dimensions from the Lower Nawata *N. syrticus* (Harris and Leakey, 2003, fig. 10.44, p. 491).

KNM-NK 36585 is also similar to specimens from the Adu-Asa Formation of Ethiopia assigned to *N. syrticus*. When KNM-NK 36585 is compared to KL 164-1, a specimen from the Adu-Asa Formation, they have the same crown height although the cusp tips are slightly more worn on KNM-NK 36585. KNM-NK 36585 also has a small endostyle between the metaconid and entoconid whereas KL 164-1 does not. The development of the buccal cingulum is equivalent in both specimens and the talonid morphology and complexity are almost identical (KL 164-1 md = 43.5 mm and bl = 22.8 mm). Another specimen from the Adu-Asa Formation, KL 174-1, has approximately the same crown height as KNM-NK 36585, although the cusps on the former are a little more worn. The morphological differences between KNM-NK 36585 and KL 174-1 are the same as between KNM-NK 36585 and KL 164-1 noted above (KL 174-1 md = 43 mm and bl = 21.9 mm).

KNM-NK 36568 consists of right and left m3 distal fragments (not figured). These specimens preserve only the worn talonid region of the mandibular third molars. Although found separately in 1997 and 1999, these two m3's appear to be perfect mirror images with the same morphology and amount of wear. Therefore, they are interpreted to be antimeres from the same individual. The crowns are low and with a simple talonid region, identical to that of KNM-NK 36585 although more worn.

All of the Lemudong'o m3 specimens described above show characteristic *N. syrticus* morphology and size. They are generally smaller than all ~4.1-Ma specimens identified as *N. pattersoni* (= *N. kanamensis*) from Kanapoi (see Table 1; Feibel, 2003; Harris et al., 2003), *N. kanamensis* from Manonga Valley (Bishop, 1997), *N. kanamensis australis* from Langebaanweg in South Africa (Cooke and Hendey, 1992), and even more so when compared to the younger *N. jaegeri* from the Apak Member of Lothagam (data not shown, Harris and Leakey, 2003). In contrast, the Lemudong'o m3's are much larger than *N. devauxi* from Lothagam (see Table 1; Harris and Leakey, 2003). Morphologically, the Lemudong'o m3's have only two cusp pairs and a small talonid, differentiating them from the expanded talonids and added cusp pairs of all other known *Nyanzachoerus* species with the exception of *N. devauxi*.

KNM-NK 45783 (Figure 1, bottom row; Table 1) is a right M3 with some of the alveolar bone preserved. As for the m3's, this crown is less hypsodont and with less complex distal occlusal morphology than is seen in *N. kanamensis*, and shows strong similarities to the M3's from Lothagam, especially KNM-LT 26110, a right M3 from the Upper Nawata. Both crowns have a reduced talon region; KNM-LT 26110 is overall slightly larger. Measurements for KNM-NK 45783 are as follows: mesiodistal length = 44.0 mm; buccolingual width across the mesial pair of pillars = 31.4 mm; buccolingual width across the second pair of pillars = 26.9 mm.

Nyanzachoerus cf. *syrticus* (Leonardi, 1952)

Material

KNM-NK 36573, L. m1; KNM-NK 36574, P3 germ; KNM-NK 36584, L. dp4; KNM-NK 40990, R. p1; KNM-NK 41362, R. p3; KNM-NK 41435, L. m2; KNM-NK 41462, L. i1, L.; p1, R.

dp4, R. m1, L. m1; KNM-NK 42370, R. I1; KNM-NK 42385, broken i1 and R. p2; KNM-NK 44760, R. di2; KNM-NK 44887, L. m2; KNM-NK 44888, R. m1; KNM-NK 44889, R. di1; KNM-NK 44890, L. p4.

Description

Almost all of these teeth fall into the size range of *N. syrticus* from Lothagam, except for KNM-NK 41462 that is slightly more narrow relative to its length (Table 1; Harris et al., 2003). Morphologically, there are no characteristics that would preclude the inclusion of any of these teeth within that species. However, they also lack any derived characteristics that would confirm a *N. syrticus* designation. Therefore, these teeth are tentatively assigned to *N.* cf. *syrticus* since no other suid taxon has been found from the site.

Discussion

The age of LEM 1 was initially determined biochronologically using the limited number of suid specimens. Later ^{40}Ar/^{39}Ar dating has refined this initial late Miocene biochronological date to ~6.11 Ma (Deino and Ambrose, 2007). Since then, the suid collection has not increased substantially, particularly in the number of relatively complete specimens. Despite the fragmentary and sparse nature of the LEM 1 collection, these fossils of *N. syrticus* indicate that members of this genus had a wider distribution in eastern Africa extending from the Middle Awash in the north to as far south as southern Kenya before 6 Ma.

Although widely known from late Miocene fossil localities across northern and eastern Africa and the Arabian Penninsula, *N. syrticus* appears not to be present in the late Miocene sediments of the Manonga Valley (Ibole Member, 5.5–5 Ma), Tanzania (Harrison and Mbago, 1997, p. 16). The difference in the faunal composition of these two sites (Lemudong'o and Manonga Valley) is interesting given their temporal and geographic proximity. The Manonga Valley is located in the northern part of Tanzania, relatively close to the southern Kenyan site of Lemudong'o.

The Manonga Valley specimens have been attributed to *N. kanameusis* (Bishop, 1997), a more derived species of *Nyanzachoerus* known from Pliocene deposits (Harris and White, 1979), such as the 5–4 Ma deposits in the Albertine Rift Valley of Uganda and Zaire (Pickford, 1994, p. 352). The Manonga Valley third-molar specimens are larger than the third molars of *N. kanamensis* described from other eastern African localities (Table 1; Bishop, 1997). The Manonga Valley third-molar metrics are comparable to those reported for the subspecies of *N. kanamensis australis* (= *N. australis*) from the ca. 5.5–4.8 Ma deposits of Langebaanweg in South Africa (Table 1; Cooke and Hendey, 1992). Bishop (1997, p. 215) argues that the Manonga Valley suid dental metrics are not statistically significantly different from the Langebaanweg specimens attributed to *N. k. australis*, but, she argues, given the lack of comparable cranial specimens, Mangonga Valley suids cannot be attributed to this new subspecies/species.

However, the Manonga Valley speeimen counts are quite small (e.g., $n = 2$ for m3's), and therefore statistical tests would be expectedly non-robust. Therefore, the Langebaanweg and Manonga Valley specimens may ultimately prove to sample the same taxon. But whether or not the Manonga Valley specimens remain categorized as *N. kanamensis* or are moved to a new species or subspecies of *Nyanzachoerus*, it is unlikely that they are *N. syrticus*. Therefore, it appears as though *N. syrticus* either evolved quite rapidly in the region of northern Tanzania into *N. kanamensis* or another larger species, or there were two congeneric species existing in close temporal and geographic space.

A number of *N. syrticus* specimens have been recovered from the Adu-Asa Formation of the Middle Awash, Ethiopia (Haile-Selassie, 2001). The sediments that yielded these specimens are radiometrically dated to between 5.77 and 5.54 Ma (WoldeGabriel et al., 2001), an age slightly younger than Lemudong'o (Deino and Ambrose, 2007). However, despite the minor age difference, the upper and lower third molars assigned from both sites to *N. syrticus* are metrically and morphologically similar. The Middle Awash *N. syrticus* upper molars range in their length from 40.2 mm to 43.5 mm ($n = 6$). The length of the Lemudong'o *N. syrticus* M3 (44 mm) lies slightly above the highest range of the Middle Awash sample, even though it lies within the range of the larger sample of *N. syrticus* from the Nawata Formation of Lothagam (Harris and Leakey, 2003). Morphologically, they are united by the small and simple talon, which is characteristic of *N. syrticus*. The lower third molars are also metrically and morphologically similar, other than the minor differences described above. However, it should be noted that there are a number of variations in the number and size of cusplets on third-molar talonids in a larger sample of the species such as the Lothagam sample.

The scarcity of suids in the Lemudong'o collection stands in contrast to many other mammalian-dominated fossil sites from this time period (e.g., Lothagam, Harris and Leakey, 2003; Middle Awash, Haile-Selassie et al., 2004). Given that the main fossil horizon at LEM 1 samples a fairly restricted ecology, it is reasonable to surmise that *N. syrticus* was either not abundant in this habitat, or was not preyed upon by the carnivorous birds which have been thought to have accumulated much of this assemblage (Ambrose et al., 2007). *Nyanzachoerus* has been associated with more forested, or closed habitats (Harris, 1983; Pickford, 1994; see Harris and Cerling, 2002 for a contrary view), and therefore its recovery may suggest that such habitats were not far from the sands in which these specimens were fossilized.

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LATE MIOCENE HIPPOPOTAMIDAE FROM LEMUDONG'O, KENYA

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ABSTRACT

The late Miocene deposits from Lemudong'o have yielded few and fragmentary remains of hippopotamids. These remains document the presence of a large hippopotamid and extend southward the late Miocene distribution of the family. Although the general morphology of the dentition is similar to that of other late Miocene Hippopotaminae, some peculiarities were noted in molar endocrista development and the relative size of the premolars. This could indicate a distinct form at Lemudong'o, but further evidence is required for confirmation.

Introduction

Up to 8 million-years-ago (Ma), the family Hippopotamidae is mostly represented by material attributed to the genus *Kenyapotamus*. *Kenyapotamus coryndoni* Pickford, 1983, is recorded between 11 Ma and 9 Ma, from Ngorora, Nakali, and Ngeringerowa in Kenya (Pickford, 1983), from the Beglia Formation in Tunisia (Pickford, 1990), and from Chorora in Ethiopia (Geraads et al., 2002). Only known in Kenya, *K. ternani* Pickford, 1983, has more uncertain affinities with the family Hippopotamidae and is dated from 15.7 Ma at Kipsaramon (Behrensmeyer et al., 2002) to ca. 14 Ma at Fort Ternan (Pickford, 1983). The fragmentary and rare material assigned to these forms indicates that hippopotamids were rather infrequent in middle and early late Miocene African ecosystems.

After 8 Ma, however, their frequency seems to have dramatically increased. At Lothagam in Kenya, hippopotamids were mostly found in the late Miocene Nawata Formation and are the most frequently collected mammals, accounting for 27% of the mammal specimens collected (Weston, 2003). They are also among the most common mammals in the upper Miocene of Toros-Ménalla in Chad (Vignaud et al., 2002; Boisserie et al., 2005), representing more than 20% of the total assemblage.

Several species coexisted at Lothagam (Weston, 2000, 2003) and may also be the case at Toros-Ménalla (Boisserie et al., 2005). The dominant species (*Archaeopotamus harvardi* (Coryndon, 1977) at Lothagam and *Hexaprotodon garyam* at Toros-Ménalla) were large-sized, almost as large as the modern *Hippopotamus amphibius* Linné, 1758, and were interpreted as dwellers of riparian environments (Boisserie, 2002; Weston, 2003).

Other late Miocene hippopotamids have been recorded from the late Miocene Baynunah Formation at Abu Dhabi, United Arab Emirates (Gentry, 1999), and from Sahabi, Libya (Gaziry, 1987). By 7 Ma, Hippopotaminae, excluding the dentally more archaic Kenyapotaminae (Pickford, 1983), were geographically disperse, very abundant in some localities, and taxonomically diverse with at least five different forms. After this date, which is also the last appearance date of the Anthracotheriidae in Africa (Vignaud et al., 2002), the Hippopotamidae solely occupied the niche of large semi-aquatic herbivores in African ecosystems.

In this regard, hippopotamids constitute an important element of African wetland dynamics and ecology. This is well illustrated by the significant impact of extant *Hip. amphibius* on those environments, in terms of hydrographic-network geomorphology (McCarthy et al., 1998; Deocampo, 2002), trophic input and quality of waters (Wolanski and Gereta, 1999; Grey and Harper, 2002), and surrounding vegetation growth and diversity (Field, 1970; Lock, 1972; Olivier and Laurie, 1974; Eltringham, 1999).

The end of the late Miocene is also a critical period for the evolutionary history of the Hippopotamidae in terms of their biogeography. The late Miocene records the oldest known hippopotamids outside of Africa, in southern Europe (Made, 1999) and in the Indian sub-continent, with a first-appearance date at 5.9 Ma in the Pakistani Siwalik hills (Barry et al., 2002).

As a consequence, the discovery of any new hippopotamid remains from this time period is important, including those recovered from the late Miocene of Lemudong'o, near Narok in southern Kenya (Ambrose, Kyule, and Hlusko, 2007). These fossils represent the most southern known late Miocene Hippopotamidae, and date to 6.087 ± 0.013 to 6.12 ± 0.07 Ma (Deino and Ambrose, 2007). Although they are few and fragmentary, I here provide a brief description of the more significant specimens and compare them to other known late Miocene hippopotamids.

Abbreviations

KNM = Kenya National Museum; KNM-NK = indicates fossils from localities within the Narok district (Ambrose, Kyule, and Hlusko, 2007); KNM-LT = indicates fossils from Lothagam.

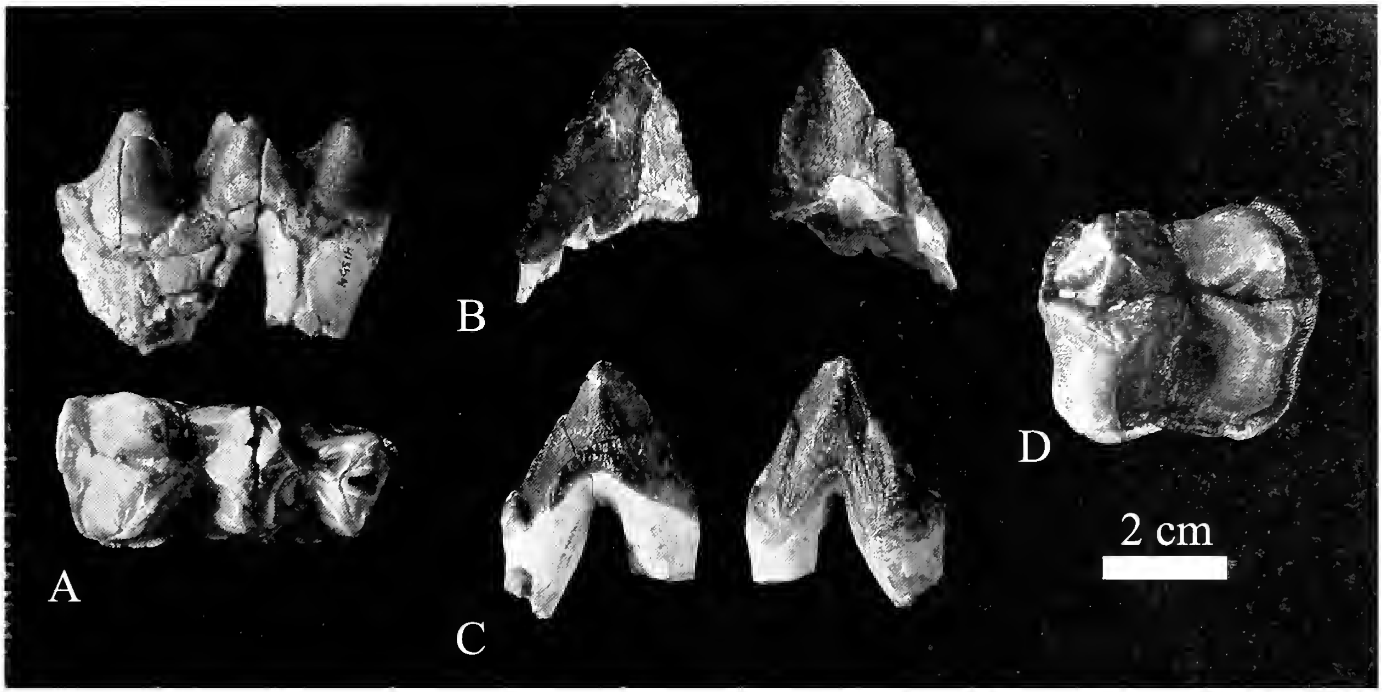

Figure 1. Dentition of Hippopotamidae indet. from Lemudong'o, Kenya. A, right d4 KNM-NK 41354 in buccal view (top) and occlusal view (bottom); B, right P1 KNM-NK 41353 in buccal view (left) and lingual view (right) (these two pictures were inversed in order to facilitate comparison with the tooth below); C, left D2 KNM-NK 41353 in buccal view (left) and lingual view (right); D, right M1 KNM-NK 41353 in occlusal view.

Dental abbreviations follow this convention: M1 = maxillary first molar; p4 = mandibular fourth premolar.

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Hippopotamidae Gray, 1821
Subfamily Hippopotaminae Gray, 1821
Hippopotaminae indeterminate
Figure 1

Studied material

KNM-NK 36501, upper incisor; KNM-NK 36503, fragmentary p4; KNM-NK 36504, fragmentary M; KNM-NK 36506, fragmentary m; KNM-NK 36537, apical fragment of lower incisor; KNM-NK 36875, premolar fragments; KNM-NK 36876, fragmentary molar; KNM-NK 36964, apical fragment of lower canine; KNM-NK 36965, p1 fragment?; KNM-NK 38315, fragmentary molar; KNM-NK 38317, molar fragments; KNM-NK 40857, molar and premolar fragments; KNM-NK 40915, fragmentary lower molar; KNM-NK 41147, fragmentary m1 or m2; KNM-NK 41352, lower molar fragments; KNM-NK 41353, right P1, D2, and M1; KNM-NK 41354, right d4.

A dozen fragmentary postcranial remains were also collected at Lemudong'o, but given their weak significance to taxonomic considerations, they are not included in this publication.

Description

KNM-NK 41354 is a right d4 (Figure 1A). The crown of this tooth is almost complete and well preserved. It exhibits a moderate stage of wear that could roughly correspond to an individual of *Hip. amphibius* from Laws' age group III to IV, i.e., between 1 and 3 years old (Laws, 1968). The tooth retains three pairs of cuspids and its width increases from the mesial pair to the distal pair. A finely crenulated cingulum is present mesially. It remains low and thin. Buccally, the cingulum is attenuated, being essentially expressed between cuspids and on the hypoconid. No cingulum appears lingually. In contrast, the distal side exhibits a higher and thicker cingulum that protrudes distally. The enamel is finely wrinkled.

The first pair of cuspids exhibits a strong and simple primoconid (nomenclature following Made, 1996), triangular to crescentiform in shape. The paraconid is the most selenodont cuspid of the tooth, and bears a strong endocristid. Although the protoconid and the metaconid are in an early stage of wear, their dentine islands are already totally fused medially. In occlusal view, they display the trilobate shape characteristic of hippopotamid molars, although it is not strongly expressed here. The wear pattern of the largest cuspid, the hypoconid, is clearly trilobate. On the contrary, the smaller entoconid appears bucco-lingually compressed and simple in shape, lacking mesial and distal lobes.

KNM-NK 41353 is a set of three teeth that most probably belonged to the same individual given their proximity on the outcrop and similar degrees of wear. The first tooth (Figure 1B) is an unworn right P1 lacking its roots. Its general shape is triangular in lateral views. In occlusal view (not shown), it is mesio-distally elongated with a transverse constriction. A low and thin cingulum appears on each side of the tooth, being slightly thicker mesially. The main cusp is asymmetrical in lateral view, the apex being mesially positioned. On the mesial side of the main cusp, a finely crenulated mesial crest links the apex to the cingulum and flares lingually. Its distal counterpart runs straight between the apex and a small accessory cuspule positioned at mid-height of the crown, then divides into two roughly crenulated crests that delimit a distal triangular area of heavily pustulate enamel. Other parts of the crown enamel are only wrinkled.

The second tooth is a slightly worn left D2 (Figure 1C) that retains most of its distal and mesial roots. Its general shape is similar to that of the P1. However, while it is still proportionally elongated, the crown is proportionally wider and shorter. In occlusal view (not shown), this tooth is also divided in two lobes (the distal one being wider) separated by a transverse constriction. A cingulum is present on each side, but it is reduced to a simple thin strip of enamel lingually. The distal cingulum is the most developed, while the others (mesial and buccal) are intermediate in thickness. The main cusp is less asymmetrical and more robust than on the P1. Its mesial crest is marked apically, but divides just above mid-height of the crown into a smooth and robust lingual crest almost similar to an accessory cuspule, and in a buccal crenulated crest that runs disto-lingually along the buccal side of the crown and joins the top of the buccal cingulum at the level of maximal tooth constriction. The lower part of the mesial crown exhibits ridged to pustulate enamel, in opposition to the wrinkled to smooth enamel of the rest of the crown. The distal crest gives rise to short crests just above the cingulum. On its buccal flange, the crown is slightly concave and limited at its base by an inflated portion of the distal cingulum. A conical accessory cuspule is positioned distolingually at mid-height of the crown.

KNM-NK 36503 is the distal portion of a p4 in an advanced stage of wear. The distal cingulum is stronger than in the aforementioned premolars. However, the lateral cingula are very attenuated. Two conical accessory cuspids of unequal sizes are inserted between the distal cingulum and the main cuspid. The enamel of the tooth is smoother than is that of KNM-NK 41353.

KNM-NK 41147 is a fragmentary m1. Both mesial and distal sides are missing. The tooth is heavily worn and cuspid morphology cannot be recognized. However, it shows the presence of lateral cingula, more developed on one side. On the opposite side, the transverse valley bears a strong transverse crest. The enamel appears rather smooth and the cingula are not crenulated.

The third tooth of specimen KNM-NK 41353 is the unworn crown of a right M1 that lacks most of its buccal cervix area. The tooth appears low-crowned and subquadrangular in occlusal view (Figure 1D). Cingula are present and form a continuous low circle around the crown. However, the mesial cingulum and the buccal part of the distal cingulum are much more developed, especially in height. The protocone and metaconule are similar in shape, exhibiting an occlusal trilobate pattern with a bulging lingual lobe. The paracone is more triangular with poorly individualized mesial and distal lobes. It exhibits a small apico-basal crest on its lingual aspect similar to an endocrista. The metacone is more complex in shape, with a general trilobate pattern altered by a well-developed endocrista. No accessory cusps are visible, and the enamel is finely wrinkled, including that of the cingula.

Discussion and Conclusion

All of these specimens were collected in the early years of work at this site (1995 and 1999; Ambrose, Kyule, and Hlusko, 2007), and therefore exact stratigraphic data are unknown. However, the nature of the preservation on many of these specimens suggests that they derive from the lowest fossiliferous horizon at Lemudong'o (L. Hlusko, personal communication), which is a coarse gritty sand (Ambrose, Kyule, and Hlusko, 2007; Ambrose, Nyamai, et al., 2007). The minimum number of hippopotamid individuals collected in this sand is at least two. In the material described above, given its wear stage, the d4 KNM-NK 41354 could belong to the same individual as the dental series KNM-NK 41353. The m1 KNM-NK 41147 shows a more advanced juvenile stage. On the contrary, the distal part of p4 KNM-NK 36503 is already well worn, some dentine appearing even on the distal cingulum. This tooth corresponds to a fully adult specimen clearly distinct from the one represented by the d4. The anatomical attributions of the other remains do not bring more information in this regard.

Cranio-mandibular features traditionally played a major role in the study and identification of fossil Hippopotamidae, and in the reconstruction of their phylogenetic relationships (Coryndon, 1977; Gèze, 1980). More recent accounts on taxonomy and phylogeny of the family (Weston, 2003; Boisserie, 2005) also emphasized the importance of those characters, notably of key regions like the mandibular symphysis. In contrast, dentition, and particularly cheek teeth, are considered less informative: "It is unfortunate that, as far as hippopotamids are concerned, molar teeth are very conservative in development and are possibly the least useful element for diagnosis, slight variation in enamel pattern often reflecting slight differences in feeding habits rather than morphogenetic characters" (Coryndon, 1977, p. 63). Whether or not hippopotamid cheek teeth vary accordingly to diet is still to be determined, but variation is found in most mammalian species known by a sufficiently large tooth sample.

In this regard, it is not surprising that the above description of material from Lemudong'o generally matches that of teeth from other African Mio-Pliocene hippopotamids. Most of the morphology can be found in the variation ranges of the two best known late Miocene hippopotamids: 1) *Archaeopotamus harvardi* from Lothagam, Kenya, described in detail by Weston (2003) and previously named *Hexaprotodon harvardi* (new classification following Boisserie, 2005); and, 2) *Hexaprotodon garyam* from Toros-Ménalla, Chad (Vignaud et al., 2002; Boisserie et al., 2005). The d4 KNM-NK 41354 differs from that of KNM-LT 1 (*A. harvardi*, Lothagam) only by the somewhat more developed cuspid distal lobes, whereas the same general cuspid pattern is observed in the worst preserved remains from Toros-Ménalla.

As for Lemudong'o lower premolars, multiple distal crests, cingula surrounding the crown but stronger distally in p3, locally pustulate enamel, and the possible presence of a lingual accessory cusp are features seen in *A. harvardi* and *Hex. garyam*. For the p4, the distal morphology observed in KNM-NK 36503 is similar to what is seen for *A. harvardi* KNM-LT23908 (Weston, 2003, fig. 10.18, p. 392) and *Hex. garyam* TM069-98-001. For m1, invagination of the cingulum between mesial and distal cusps forming a strong transverse crest and cingula on the lateral faces of the lower molars may occur in both species, although lateral cingula tend to be attenuated in *Hex. garyam*. Finally, the M1 morphology also agrees with that of both species, including the often simpler shape of metaconules and paracones (Weston, 2003), the latter case being found in KNM-NK 41353. This specimen exhibits a marked difference from the equivalent teeth of *A. harvardi* and *Hex. garyam* in that its metacone bears a well-developed endocrista. According to personal observations, the most similar structure in *A. harvardi* and *Hex. garyam* is a poorly developed lingual ridge that may occur on the M1 metacone. Measurements show that the Lemudong'o P1 and M1 fall in the

Table 1. Cheek-tooth measurement ranges of late Miocene hippopotamid remains from Lemudong'o, Kenya, compared to various hippopotamids. Abbreviations used: NK = Hippopotamidae indeterminate (Lemudong'o); KEN = *Kenyapotamus coryndoni* (Ngeringerowa and Nakali, Kenya) (data from Pickford, 1983); LT = *Archaeopotamus harvardi* (Lothagam, Kenya) (data partially from Weston, 2003); LUK = Hippopotamidae indet. (Lukeino, Kenya) (data from Coryndon, 1978); WRi = *Hexaprotodon* ? *imagunculus* (Western Rift, Uganda) (data from Faure, 1994); WRk = *Hippopotamus kaisensis* (Western Rift, Uganda) (data from Pavlakis, 1987); A-A = Hippopotamidae indeterminate (Adu-Asa Formation, Ethiopia); ABU = *Archaeopotamus* aff. *lothagamensis* (Abu Dhabi, United Arab Emirates) (data from Gentry, 1999); TM, *Hexaprodoton garyam* "TM" (Toros-Ménalla, Chad). Bracketed numbers are estimated. Measurements are rounded to the nearest mm.

		NK	KEN	LT	LUK	WRi	WRk	A-A	ABU	TM
d4	*n*	**1**		4					1	1
	L	**56**		44–53					44	49
	w	**26**		21–26						27
P1	*n*	**1**	1	4				1		5
	L	**27**	16	26–28				26		23–28
	w	**21**	11	17–23				19		19–23
D2	*n*	**1**								
	L	**32**								
	wd	**19**								
M1	*n*	**1**	1	13	1	3	2	1		21
	L	**46**	25	31–46	45	27–32	36–40	40		36–49
	wm	**(40)**	24	32–46	42	27–30	27	30		31–43

same general range of size as *A. harvardi* and *Hex. garyam* (Table 1).

The morphology of the teeth from Lemudong'o does not exclude with certainty an attribution to any of the following late Miocene to early Pliocene hippopotamids: *A. lothagamensis* (Weston, 2000) from Lothagam, Kenya; *A.* aff. *lothagamensis* from Abu Dhabi, United Arab Emirates (Gentry, 1999); the specimens from Lukeino and Mpesida (Kenya) described by Coryndon (1978); the specimens collected in the Adu-Asa Formation, Middle Awash, Ethiopia (Boisserie and Haile-Selassie, in prep.); aff. *Hip. dulu* (Boisserie, 2004) from the Sagantole Formation, Middle Awash, Ethiopia; *Hex.* ? *imagunculus* (Hopwood, 1926); or, *Saotherium* cf. *mingoz* (Boisserie, 2003) from Kossom Bougoudi, Chad. However, it must be noted that the author has not found a developed endocrista similar to that of M1 KNM-NK 41353 in any of these taxa.

However, linear measurements of the Lemudong'o M1 KNM-NK 41353 clearly exceed the range of variation for the small-sized *Hex.* ? *imagunculus* (Table 1). Additionally, two other possible attributions can be ruled out with some certainty: those to the genera *Kenyapotamus* and *Hippopotamus*. The teeth of the middle to late Miocene *Kenyapotamus* exhibit a simpler, less trilobate wear molar pattern (Pickford, 1983) and are significantly smaller than those of Lemudong'o (Table 1). The latter differ also from the teeth of *Hippopotamus* by their low cuspids and cingula as well as by their wear pattern being more triangular-trilobate rather than trefoliate. The earliest member of this genus is *Hip. kaisensis*, mostly known from Western Rift sites in Uganda (Cooke and Coryndon, 1970; Pavlakis, 1990; Faure, 1994) where it may occur as early as 5.0 Ma (Faure, 1994). Its tooth dimensions are slightly larger than those of Lemudong'o teeth (Table 1).

To conclude, without further material from Lemudong'o, the present evidence does not support a more precise attribution of those hippopotamid remains than to an indeterminate early member of the subfamily Hippopotaminae. However, the dental peculiarities observed in this material (developed endocrista on M1 metacone) may indicate a distinct hippopotamid. It would be particularly interesting to recover more material from this area and time period, given the lack of knowledge of the early history of African Hippopotaminae south of the Equator.

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LATE MIOCENE BOVIDAE (MAMMALIA: ARTIODACTYLA) FROM LEMUDONG'O, NAROK DISTRICT, KENYA

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ABSTRACT

The late Miocene sediments of the Narok District, Kenya have yielded almost 400 fossil specimens representing at least five tribes within the family Bovidae, order Artiodactyla. Most of these fragmentary remains derive from the mudstone horizon at Lemudong'o Locality 1, and compose a tightly geochronometrically controlled six-million-year-old, relatively unmixed faunal assemblage. The more complete craniodental specimens are described here and referred to taxa representing the Aepycerotini, Boselaphini, and Neotragini. There is possibly one new boselaphin species, but it is not named here due to the fragmentary nature of the material (two partial horn cores). The habitat preferences of the Lemudong'o bovid taxa were investigated by "ecomorphological" analysis of the astragali and phalanges. The results clearly indicate that open habitat forms are not represented in this assemblage, and suggest the presence of forest and/or light cover.

Introduction

The Bovidae are one of the more diverse extant mammalian families, with 45 living genera and 137 species (Grubb, 1993a). Much of their evolutionary history is similarly diverse. Bovids first appear in the African fossil record at early Miocene sites such as Gebel Zelten (Libya), Losodok, Rusinga Island, and Songhor (Kenya; Gentry, 1978). By the middle Miocene bovids are one of the more abundant mammals found at the majority of mammalian-dominated fossil localities in Africa (e.g., Fort Ternan, Kenya; Shipman, 1986, p. 195). Bovids are commonly thought to have first arisen in Africa and migrated frequently between Eurasia and Africa during and after the mid-Miocene (Gentry, 1990). Most modern African bovid tribes first appear in the late Miocene, including the endemic Tragelaphini, Hippotragini, Alchelaphini, and Aepycerotini; the migrant Bovini and Ovibovini from Eurasia; and the Reduncini of unknown origin (Harris, 2003). Here we follow the taxonomy of Simpson (1984, p. 586–587; and see Grubb 1993b).

The late Miocene site of Lemudong'o is one of the best geochronologically controlled mammalian-dominated fossil localities from this time period in eastern Africa (Ambrose et al., 2003; Deino and Ambrose, 2007), and it samples a relatively unmixed fauna from a short period of time (Ambrose, Kyule, and Hlusko, 2007; Ambrose, Nyamai et al., 2007). Lemudong'o Gorge is located on the western margin of the East African Rift Valley approximately 100 km west of Nairobi, an area deeply incised by three major river systems. Stratified lavas, air-fall and water-laid tuffs, alluvial, and fluviolacustrine sediments, and paleosols of late Miocene to late Pleistocene age crop out over a ~25 × 50 km area. The stratigraphic sequence at Lemudong'o Locality 1 was formed by sedimentary depositional environments. At the base of the sequence are brown paludal claystones overlain by yellow diatomaceous silts and then sands. Above the sands are claystones with two interbedded yellow-green tuffs. The upper tuff has been dated by ^{40}Ar/^{39}Ar single-crystal laser fusion analyses to approximately 6 Ma (Ambrose et al., 2003, p. 739; Deino and Ambrose, 2007). The majority of the fossils derive from this tuff, and from the underlying clays and sands above the yellow silt.

The fossils from Lemudong'o and the nearby contemporaneous sites of Kasiolei and Enamankewon are generally fragmentary.

Even so, the bovid specimens from these collections yield important insight into the late Miocene evolution and origins of the modern bovid tribes.

Thousands of fossilized bones were collected from the late Miocene deposits in the Narok District, of which approximately 1,300 are identifiable to the family level. Within this subset, 391 (approximately 30%) are identifiable to the family Bovidae. Of these, 73 are craniodental specimens identifiable to tribe, including 6 referred to genus and 2 with recognizable specific affinities. There are 223 postcranial elements identified as Bovidae.

This paper focuses primarily on the taxonomy and habitat preferences of this assemblage. Hence, we describe only the craniodental specimens identifiable to at least tribe and postcranial elements that are relevant to "ecomorphological" or functional interpretations. We then consider the evolutionary implications of the taxa present in the Lemudong'o bovid assemblage as compared to other African sites of similar age, particularly the geographically and temporally close site of Lothagam, Kenya.

The majority of the specimens derive from the mudstone horizon or "speckled tuff" at Lemudong'o Locality 1 (Ambrose et al., 1993; Ambrose, Nyamai, et al., 2007; Ambrose, Kyule and Hlusko, 2007). Exceptions are noted.

Abbreviations

KNM	Kenya National Museum
NK	Narok District, indicates fossils are from localities within this district, including Lemudong'o Localities 1 and 2, Enamankewon Localities 1, 2, and 3, and Kasiolei Locality 1. Locality, when different from Lemudong'o Locality 1, is noted in the text. (See also Appendix 1 in Ambrose, Kyule, and Hlusko, 2007).
LT	Lothagam
Ma	million years ago
AP	anteroposterior horn core dimension at the base
TR	transverse horn core dimension at the base
stdv	standard deviation

Dental abbreviations follow this convention:

RM1	right maxillary first molar
Lp4	left mandibular fourth premolar

Systematic Paleontology

Class MAMMALIA Linnaeus, 1758
Order ARTIODACTYLA Owen, 1848
Family BOVIDAE Gray, 1821
Tribe AEPYCEROTINI Gray, 1872

Remarks

The aepycerotins are small- to medium-sized antelopes with horn cores present only in males. The horn cores are located close together above the orbits and curve backwards. They are fairly rounded in cross-section with a flattened anterior surface and a posterolateral keel. The dentitions are hypsodont and typically lack basal pillars on the molars. Lower molars lack the anterior transverse flanges that are often called goat folds, and the mandibular third molars have a relatively large distal lobe. There is only one known genus within this tribe, represented by the extant impala (*Aepyceros melampus*). Impalas typically inhabit open woodlands, sandy bush country, or acacia savannahs, but are always found close to an open water source (Nowak, 1991, p. 1462).

AEPYCEROS aff. A. PREMELAMPUS Harris, 2003
Figure 1A–B

Referred material

KNM-NK 41349, left horn core; KNM-NK 41458, right horn core and associated vertebral fragments.

Description

KNM-NK 41349 (Figure 1A) is a left partial horn core with frontlet. The pedicel, the superior margin of the orbit, and some portion of the endocranial surface below the pedicel are preserved. The preserved length of the horn core is just over 85 mm. There is no evidence of a frontal sinus; the supraorbital pit is narrow and triangular in shape; and the postcornual fossa is located posterolaterally. The horn core lacks transverse ridges and is oriented straight in anterior view and curved posteriorly in lateral view. In cross section, the horn core is fairly round (AP = 30.9 mm, TR = 29.2 mm) and has only a slight keel formed by longitudinal grooves. This specimen is quite rounded in cross-section for an *Aepyceros*, but this feature is highly variable and is similarly proportioned to other specimens attributed to *Aepyceros* (KNM LT 25953 from Lothagam, for example; Harris, 2003, Table 11.30).

KNM-NK 41458 (Figure 1B) is a right horn core with AP and TR measurements of 30.2 mm and 27.0 mm at the base, respectively. The preserved length of the horn core is 135 mm. The pedicel and most of the horn core are preserved. It has a slight mediolateral compression and deep longitudinal ridges on the posterior surface, providing a slight posterior longitudinal keel. This specimen shows a slight counter-clockwise torsion. The postcornual fossa is located on the posterolateral surface of the pedicel as in KNM-NK 41349. The base is broken such that only a small portion of the orbital ceiling is preserved and shows no evidence of a sinus.

Although the two specimens described above are fragmentary and not entirely typical of the later forms of aepycerotins, they have features that generally align them to impalas. First, these horn cores are long relative to the dimensions at their base. Second, one of these specimens has very slight torsion, and both are quite straight in anterior view, which is expected given that early impalas had very little horn core lyration (e.g., Gentry, 1980, p. 292). However, they are not completely straight as is seen in early gazelles (the Antilopini). Third, the frontal bone appears to have been quite flat in contrast to the rounded frontals of the tragelaphins (kudus). Fourth, the horn cores appear to be longer and more rounded at the base compared to reduncins from deposits older than 5 Ma (Vrba and Haile-Selassie, 2006). And last, the postcornual fossa is very small, sharp, and deep. Therefore, the combination of horn core and frontal characters seen in the two horn cores from Lemudong'o show that these horn cores are likely to belong to Aepycerotini rather than Tragelaphini or Antilopini.

The sizes of these horn cores are also well within the range of variation demonstrated by the Lothagam *A. premelampus* sample (AP mean = 34.9, stdv. = 4.4; TR mean = 30.3, stdv. = 4.2; n = 65; data from Harris, 2003, Table 11.30). However, given the fragmentary nature of the Lemudong'o specimens, their assign-

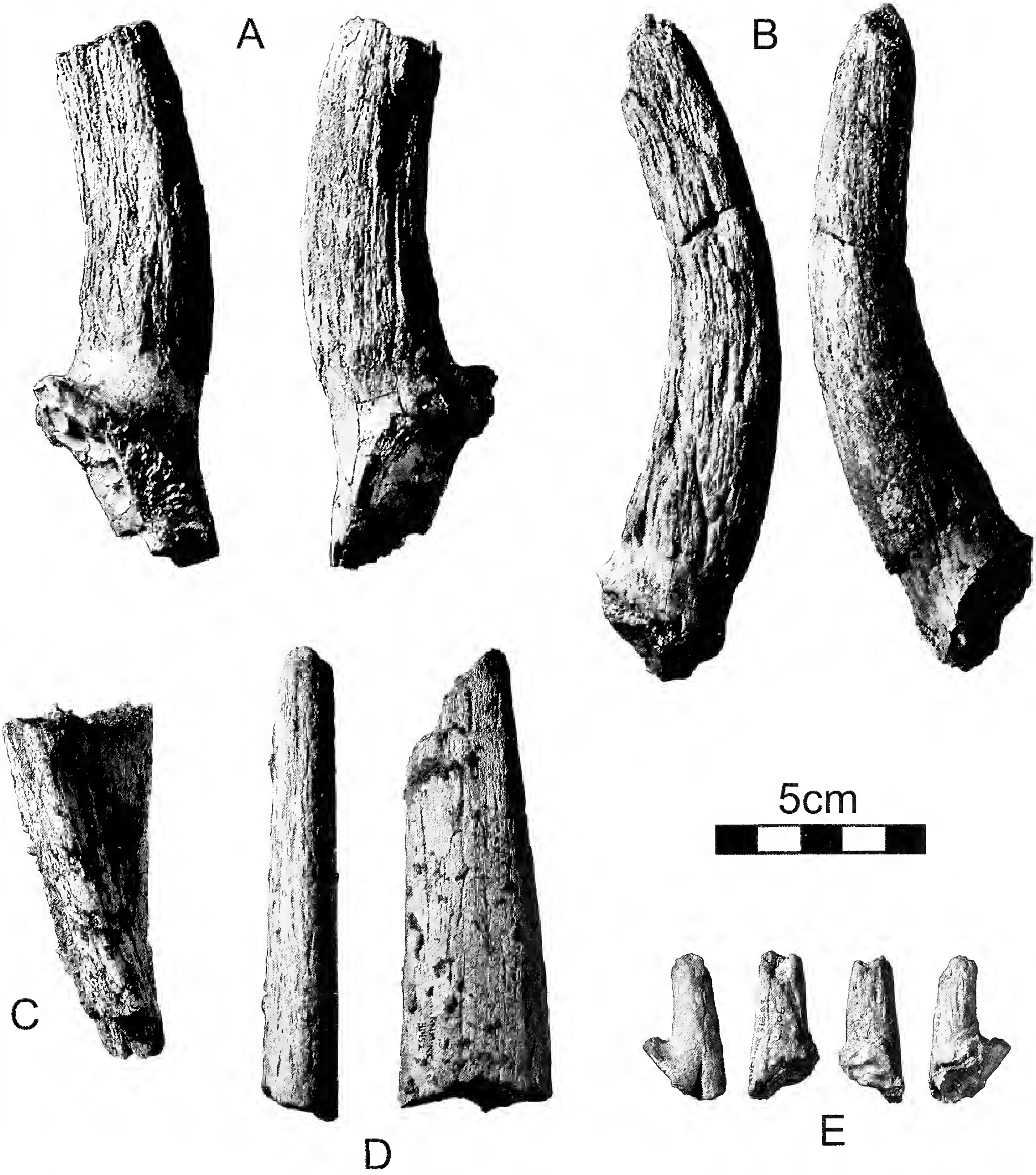

Figure 1. Horn cores from the late Miocene sediments of Lemudong'o and Enamankeon Locality 1. A, KNM-NK 41349, *Aepyceros* aff. *A. premelampus*, partial left horn core in medial and lateral views; B, KNM-NK 41458, *Aepyceros* aff. *A. premelampus*, right horn core in medial and lateral views; C, KNM-NK 45772, *Tragelaphus* sp. partial left horn core; D, KNM-NK 41452, Boselaphini, horn core in anterior and side views; E, KNM-NK 36566, *Madoqua* sp. left horn core in lateral, anterior, posterior, and medial views.

ment to *Aepyceros* aff. *A. premelampus* should be considered tentative.

Tribe Aepycerotini Gray, 1872
Genus and species indeterminate

Referred material

KNM-NK 36562, L & R mandible (m2–3) + isolated m1 & fragments; KNM-NK 36565, Lm2 erupting from mandibular fragment; KNM-NK 36569, L mandible (m1–2); KNM-NK 36576, LM3; KNM-NK 36870, LM3; KNM-NK 36871, Lm1or2; KNM-NK 36873, RM2; KNM-NK 36879, Rm1; KNM-NK 36882, R mandible (m1or2 unerupted); KNM-NK 38314, R mandible (dp4–m2); KNM-NK 40864, half M; KNM-NK 40866, LM3; KNM-NK 40920, LM1or2; KNM-NK 41035, RM fragment; KNM-NK 41132, R mandible (m1–2); KNM-NK 41135, Rm fragment; KNM-NK 41185, L mandible (p3–m2, Rp2–3, m1or2); KNM-NK 41351, Rm3 fragment; KNM-NK 41356, LM2–3; KNM-NK 41357, Lm1or2; KNM-NK41358, Rm3; KNM-NK 41361, R mandible (p3, dp4, m1); KNM-NK 41368, Rm1or2; KNM-NK 41369, L mandible (m1–3); KNM-NK 41373, RP4; KNM-NK 41455, R & L mandible fragments w/(m1–2, m3 erupting); KNM-NK 42324, RM fragment; KNM-NK 42338, Rm1; KNM-NK 42362, Rm3 (2 distal lophs); KNM-NK 42379, Lm3; KNM-NK 42381, LM3; KNM-NK 44798, L mandible (dp4–m1); KNM-NK 44835, Lm1or2; KNM-NK 44897, RM1or2; KNM-NK 44898, RM1; KNM-NK 44900, Lm3 fragment; KNM-NK 44901, Rm1; KNM-NK 45793, RM3; KNM-NK 45833, L maxilla (M1); KNM-NK 45848, Lp3; KNM-NK 45859, Lp3.

Description

The dental and mandibular specimens assigned here to Aepycerotini gen. et sp. indet. all show morphological features that align them more with the Aepycerotini than other bovid tribes. Metrics for complete specimens that are confidently identified to position are presented in Table 1, along with comparative metrics from Lothagam *A. premelampus*. The size variation within the Lemudong'o aepycerotin dental specimens is not contrary to the interpretation that only one species is represented, and that on average, it is dentally slightly larger than *A. premelampus* from Lothagam.

Tribe cf. Aepycerotini Gray, 1872

Referred material

KNM-NK 36888, RM1; KNM-NK 41045, mandibular fragment with associated m fragments; KNM-NK 41184, associated RP4, LM1–2 fragments; KNM-NK 41264, R & Lp3; KNM-NK 41355, RM1-3; KNM-NK 42350, RM fragment; KNM-NK 42382, R mandible (m1); KNM-NK 44899, RM1.

Description

These highly fragmentary dental remains show close affinities with the aepycerotins, but given their preservation and fragmentary nature they are only tentatively attributed to this tribe.

Tribe Tragelaphini Jerdon, 1874

Remarks

The tragelaphins are characterized by spiraling and diverging horn cores with an anterior keel. Extant species include the bongo, nyala, kudu, sitatunga, and the bushbuck (all members of the genus *Tragelaphus*). These are primarily browsing animals that inhabit bush and forest and are almost always found near water (Gentry, 1980, p. 217; Nowak, 1991, p. 1408–1415); the sitatunga is documented as semiaquatic (Nowak, 1991, p. 1409).

Tragelaphus Blainville, 1816
Tragelaphus species indeterminate
Figure 1C

Referred material

KNM-NK 45772, partial left horn core.

Description

KNM-NK 45772 is a superior fragment of a left horn core preserving none of the frontlet or the pedicel. This specimen was found in the sand horizon at the base of the mudstones, and therefore is not part of the fossil assemblage that characterizes the main mudstone horizon. The fragmentary nature of the specimen does not allow precise determination of the degree of divergence from the base or the exact basal AP and TR dimensions (Figure 1C). However, it appears to be very similar in size and morphology to KNM-KP 30156 and KNM-LT 23617. Both of these specimens have been attributed to *T. kyaloae* (Harris, 2003, p. 532; Harris et al., 2003, p. 86). *T. kyaloae* is a medium-sized tragelaphin with a strong posterolateral keel and weaker anterolateral keel. Specific attribution of the Narok specimen is currently impossible since the frontlet is not preserved. Hence, we refer this specimen to *Tragelaphus* sp. indet. until more complete specimens are found.

Tribe cf. Tragelaphini Blyth, 1863

Referred material

KNM-NK 36580, partial left mandible with broken dp3 and dp4; KNM-NK 36868, RM1or2; KNM-NK 36883, left maxilla fragment with M3 erupting; KNM-NK 41156, RM fragment; KNM-NK 41173, Rm3 fragment; KNM-NK 41275, LM1; KNM-NK 41343, Lm fragment; KNM-NK 41459, LM3; KNM-NK 42371, LM1or2; KNM-NK 45821, R. mandible fragment with p2–m3; KNM-NK 45840, Rm3.

Description

These teeth show characters that align them most closely with the Tragelaphini: generally V-shaped buccal lobes on lower molars, relatively large distal lobe on the mandibular third molars, basal pillars that diminish posteriorly along the tooth row, simple central cavities on the lobes of mandibular teeth, and well-developed mesostyles on the maxillary molars. However, early tragelaphin teeth are similar to (although generally smaller in size than) those of boselaphins, as they were not yet morphologically as derived as later tragelaphin dentitions. Therefore, based on the tragelaphin-like dental characters seen in these specimens, we identify them only as cf. Tragelaphini.

Family Bovidae Gray, 1821
Tribe Boselaphini Knottnerus-Meyer, 1907

Remarks

Boselaphins are typically abundant in late Miocene fossil deposits (Gentry, 1999). An anterior keel on the horn core is a consistent feature of all boselaphins (Spassov and Geraads,

Table 1. Dental measurements for Narok Aepycerotini permanent teeth for which position is certain, compared to *A. premelampus* from Lothogam.*

Specimen	Element	MD	BL
KNM-NK 36562	Rm1	14.2	8.5
KNM-NK 36569	Rm1	12.1	5.5
KNM-NK 36879	Rm1	14.4	5.9
KNM-NK 38314	Rm1	14. 5	7.5
KNM-NK 41132	Rm1	14.2	7.8
KNM-NK 41361	Rm1	14.2	7.4
KNM-NK 41369	Lm1	13.2	7.4
KNM-NK 41455	Lm1	13.6	7.4
KNM-NK 42338	Rm1	14.2	8.4
KNM-NK 44798	Lm1	13.8	8.2
KNM-NK 44901	Rm1	14.7	8.3
NK avg. (stdv.)		13.9 (0.7)	7.5 (1.0)
A. premelampus avg. (stdv.)		12.8 (0.7)	7.7 (0.6)
KNM-NK 36562	Lm2	16.9	9.3
KNM-NK 36562	Rm2	16.9	9.3
KNM-NK 36569	Rm2	14.5	5.8
KNM-NK 41132	Lm2	16	8.5
KNM-NK 41369	Lm2	15	8
KNM-NK 41455	Lm2	15.4	6.8
KNM-NK 41455	Rm2	15.4	
NK avg. (stdv.)		15.7 (0.9)	8.0 (1.4)
A. premelampus avg. (stdv.)		14.9 (1.1)	8.6 (0.5)
KNM-NK 36562	Lm3	22.3	7.9
KNM-NK 41351	Rm3		9.9
KNM-NK 41358	Rm3	22.9	10.1
KNM-NK 41369	Lm3	20.1	8.1
KNM-NK 42379	Lm3	21.8	9.6
NK avg. (stdv.)		21.8 (1.2)	9.1 (1.0)
A. premelampus avg. (stdv.)		22.1 (1.3)	8.4 (0.6)
KNM-NK 41185	Lp2	7.9	4.2
A. premelampus		5.9	
KNM-NK 41185	Lp3	11.5	6.2
KNM-NK 41361	Rp3	9.1	5
KNM-NK 45848	Rp3	9.2	5.7
KNM-NK 45859	Lp3	9.3	5. 6
NK avg. (stdv.)		9.8 (1.2)	5.6 (0.5)
A. premelampus avg. (stdv.)		8.5 (0.7)	5.2 (0.4)
KNM-NK 44898	RM1	13.8	12.4
A. premelampus avg.		13.0	11.7
KNM-NK 41356	LM2	17.2	15.3
A. premelampus avg. (stdv.)		14.4 (1.3)	13.7 (0.7)
KNM-NK 36576	LM3	16.3	13.5
KNM-NK 36870	LM3	17.3	
KNM-NK 36873	RM3	15.3	14.3
KNM-NK 40866	LM3	15.6	14.8*
KNM-NK 41356	LM3	17.7	15.9
KNM-NK 42381	LM3	15.6	14.2
KNM-NK 45793	RM3	16.7	13.3
NK avg. (stdv.)		16.3 (0.9)	14.2 (1.0)
A. premelampus avg. (stdv.)		17.9 (1.7)	12.7 (1.5)
KNM-NK 41373	RP4	11.0*	13.3
A. premelampus avg.		10.7	11.5

* Measurements reported in mm; *A. premelampus* data are from Harris (2003, Table 11.31); avg. = average; stdv. = standard deviation; stdv. not calculated for samples with fewer than three individuals; R. = right; L. = left; L = mandibular; M = maxillary molar; p = mandibular premolar; number. indicates tooth position; MD = mesiodistal length; BL = buccolingual width.

2004). This tribe consists of two morphs, the first being from the middle Miocene of Europe and Asia and thought to be related to modern boselaphins. The second morph is represented by the genera *Miotragocerus* and *Tragoportax*, which were common in the middle/late Miocene but extinct by the end of the epoch. This morph is characterized by fairly upright and strongly mediolaterally compressed horn cores (Harris, 2003, p. 536).

Tribe Boselaphini Knottnerus-Meyer, 1907
Genus and species indeterminate
Figure 1D

Referred material

KNM-NK 36531, R. mandible (distal half m2, m3); KNM-NK 36867, fragment of a horn core; KNM-NK 38311, Lm3; KNM-NK 40916, associated M and P fragments; KNM-NK 41372, R &

L M1 or 2; KNM-NK 41452, horn core and associated cranial fragments.

Description

Boselaphins are relatively uncommon at Lemudong'o, in contrast to a number of other fossil sites in eastern Africa. Only two partial horn cores and four dental specimens are identified to this tribe. KNM-NK 36867 is a fragmentary, but clearly mediolaterally compressed, horn core. It is similar in size and morphology to KNM-NK 41452, a fragment of horn core lacking the base (Figure 1D). KNM-NK 41452 is straight on both the dorsal and ventral edges and shows no spiraled or lyrated morphology. This differentiates it from specimens such as KNM-LT 23980 found from the Upper Nawata Formation of Lothagam (Harris, 2003, p. 537) assigned to *Tragoportax* aff. *T. cyrenaicus* (Thomas, 1980). KNM-NK 41452 differs from the Lothagam *Tragoportax* sp. A (KNM-LT 24214, for example; Harris 2003, p. 538) with its lack of upward tapering, and differs from Lothagam *Tragoportax* sp. B in lacking the slight mediolateral bowing seen in specimens such as KNM-LT 195 (Harris, 2003, p. 539).

Given the ontogenetic trajectories frequently documented in bovids (Vrba et al., 1994), the Lothagam *Tragoportax* sp. B may actually represent a juvenile of *Tragoportax cyrenaicus*. However, this does not clarify the affinity of the Lemudong'o specimens since they match neither the juvenile nor the adult morph.

Boselaphins from the western margin of the Middle Awash are relatively diverse and represented by more complete specimens. However, the Middle Awash boselaphin horn cores appear to be different from *T. cyrenaicus*, *Tragoportax* sp. A or *T.* sp. B from Lothagam. KNM-NK 41452 is different from the Middle Awash *Tragoportax* sp. indet. (Haile-Selassie, 2001, p. 281) largely because of the lack of a strong anterior keel on the Narok specimen. Therefore, the two horn core specimens from Lemudong'o might very well represent a new Boselaphini species. However, due to their fragmentary nature, more specimens need to be found to test this interpretation.

Tribe Bovini Gray, 1821

Remarks

Bovini are relatively rare at most late Miocene sites in Africa compared to other large bovids such as the boselaphins. Only two genera, *Simatherium* and *Ugandax*, are usually recognized from this time period. The Bovini become abundant in the Plio-Pleistocene, with the addition of genera such as *Pelorovis*, and *Syncerus* appearing in the fossil record for the first time. Members of this tribe are characterized by large body size, such as the extant Cape buffalo.

Tribe Bovini Gray, 1821
Genus and species indeterminate

Referred material

KNM-NK 45893, LM.

Description

KNM-NK 45893 is an extremely weathered upper molar from Enamankewon Locality 1. Exact measurements could not be taken due to the weathering, but this tooth is similar in size and morphology to the M2 of KNM-LT 475, a right maxillary fragment with dP3–M3 and associated left M2 identified to Bovini gen. and sp. indet. (Harris, 2003, p. 534). However, it is not possible to identify this isolated tooth below the tribe level, and more fossils will need to be recovered before we can provide a more specific taxonomic designation for the bovin from the late Miocene of Narok.

Tribe Neotragini Sokolov, 1953

Remarks

This tribe first appeared approximately 12 Ma (Vrba, 1985) and today consists of at least six genera of dwarfed antelopes (Grubb, 1993a). Due to their small size, they are relatively uncommon in most fossil assemblages. Molecular analyses indicate that this tribe is not monophyletic, suggesting that the shared morphological characters uniting this tribe are probably the result of convergence due to the allometric affects of dwarfism (Matthee and Robinson, 1999). However, here we will follow the paleontological tradition of recognizing the Neotragini, until the morphological and molecular phylogenies are reconciled.

Madoqua Ogilby, 1837
Madoqua species indeterminate
Figure 1E

Referred material

KNM-NK 36566, partial left proximal horn core; KNM-NK 41336, M fragment; KNM-NK 44902, Rm3.

Description

KNM-NK 36566 is the proximal end of a very small left horn core (Figure 1E; AP = 13.8 mm; TR = 13.1 mm). The cross section at its base is circular and the trajectory of the horn core appears to be straight with no evidence of torsion or lyration. This specimen is more likely to belong to the genus *Madoqua* because it is considerably smaller than KNM-LT 38433, a specimen attributed to *Raphicerus* sp. indet. from the Nawata Formation of Lothagam (Harris, 2003, p. 556) and *Raphicerus paralius* from the Quartzose Sand Member of Langebaanweg (Gentry, 1980, p. 300). Moreover, KNM-NK 36566 is also distinct in some cranial morphological features from *Raphicerus*. *R. paralius* has a posterolateral keel and a well-marked postcornual fossa (Gentry, 1980, p. 300), in contrast to the round horn core with no keel and shallow postcornual fossa seen on KNM-NK 36566.

KNM-NK 41336 is a maxillary molar fragment. Its buccolingual dimension is 7.7 mm (mesiodistal not preserved)). KNM-NK 44902 is a Rm3 (buccolingual = 4.8 mm; mesiodistal = 11.6 mm). Both are very small, smaller than all published measurements of the genus *Raphicerus*. However, they do fall within the size range of *Madoqua* from Lothagam (Harris, 2003, p. 556). KNM-NK 44902 is morphologically and metrically quite similar to KNM-LT 177, a right mandibular fragment from the Nawata Formation of Lothagam attributed to *Madoqua* sp. indet. (Harris, 2003, p. 556).

Postcrania

Isolated postcranial elements of the Bovidae are typically of limited utility for taxonomic purposes. However, variation in the morphology of the postcranial skeleton has been shown to correlate with particular locomotor repertoires in bovids (Gentry, 1970; Kappelman, 1988; Köhler, 1993; Plummer and Bishop, 1994; DeGusta and Vrba, 2003, 2005). The study of "ecomorphology" uses such correlations to predict habitat preference (and

Table 2. Results of "ecomorphological" analysis of astragali and phalanges.

Element	Spec. no.	Habitat (%)*	Alternate (%)	Tribe (%)	Alternate (%)	Body wt. (kg)
Astragalus	KNM-NK 41204	F (84%)	L (15%)	Cephalophini (54%)	Neotragini (32%)	23
	KNM-NK 36877	F (48%)	L (45%)	Neotragini (29%)	Antilopini (22%)	29
	KNM-NK 45774	F (48%)	L (24%)	Cephalophini (49%)	Neotragini (23%)	41
	KNM-NK 36533	F (47%)	L (39%)	Neotragini (29%)	Cephalophini (25%)	32
	KNM-NK 36532	L (70%)	F (16%)	Antilopini (37%)	Neotragini (26%)	29
	KNM-NK 41142	L (70%)	F (19%)	Aepycerotini (26%)	Antilopini (23%)	31
	KNM-NK 42323	L (65%)	O (24%)	Aepycerotini (45%)	Antilopini (41%)	42
	KNM-NK 42378	L (63%)	O (25%)	Antilopini (61%)	Aepycerotini (45%)	44
	KNM-NK 41398	L (61%)	F (22%)	Antilopini (27%)	Neotragini (24%)	33
	KNM-NK 36535	L (60%)	F (28%)	Aepycerotini (41%)	Antilopini (21%)	32
	KNM-NK 41348	L (49%)	F (21%)	Reduncini (31%)	Aepycerotini (28%)	55
	KNM-NK 44802	L (46%)	F (43%)	Neotragini (40%)	Cephalophini (23%)	31
	KNM-NK 41384	O (54%)	L (27%)	Antilopini (32%)	Hippotragini (17%)	62
Prox. phx.	KNM-NK 41188	F (66%)	L (32%)	Neotragini (79%)	Aepycerotini (8%)	29
	KNM-NK 45899	H (77%)	F (18%)	Tragelaphini (73%)	Aepycerotini (9%)	40
	KNM-NK 41300	H (45%)	O (37%)	Antilopini (56%)	Aepycerotini (28%)	43
	KNM-NK 41187	L (37%)	F (35%)	Antilopini (45%)	Aepycerotini (18%)	28
Int. phx.	KNM-NK 36950	F (95%)	L (2%)	Tragelaphini (52%)	Cephalophini (45%)	29
	KNM-NK 41179	F (73%)	L (19%)	Cephalopihini (61%)	Aepycerotini (13%)	34
Dist. phx.	KNM-NK 42264	F (71%)	L (28%)	Neotragini (70%)	Antilopini (18%)	15
	KNM-NK 41027	F (61%)	L (36%)	Cephalophini (59%)	Antilopini (33%)	21
	KNM-NK 41198	L (78%)	F (9%)	Antilopini (72%)	Reduncini (21%)	35
	KNM-NK 41339	L (62%)	O (21%)	Antilopini (45%)	Reduncini (39%)	45
	KNM-NK 41246	L (55%)	F (22%)	Reduncini (53%)	Antilopini (35%)	46

* For habitat, F = Forest, H = Heavy Cover, L = Light Cover, O = Open. See DeGusta and Vrba (2003) for details of categories and methods.

Percentages are not indicators of absolute confidence, but indicate confidence relative to alternative possibilities. So if the primary predicted habitat is F (60%) and the alternate is L (30%), the organism is twice as likely to inhabit F as it is L.

thus paleoenvironments) from functional morphology, without the need for specific taxonomic identifications or assumptions of stasis in habitat preference across evolutionary time. Methods have been developed for inferring habitat preference from bovid femora (Kappelman, 1988), metapodials (Plummer and Bishop, 1994), astragali (DeGusta and Vrba, 2003), and phalanges (DeGusta and Vrba, 2005). Given that sufficiently complete femora and metapodials are not preserved at Lemudong'o, we rely here on the methods developed for astragali and phalanges.

The functional morphology of the astragali and phalanges from Lemudong'o Locality 1 was evaluated morphometrically to infer habitat preference and, secondarily, taxonomic affiliation using the methods of DeGusta and Vrba (2003, 2005). Specifically, the astragali and phalanges were measured three times each by a single observer (S. Amugongo) and the mean value used in subsequent analyses. Comparison of the repeated measurements indicates that intra-observer measurement error is within the ranges reported by DeGusta and Vrba (2003, 2005). These measurements were input to discriminant functions, constructed based on modern bovid data, in order to predict both habitat preference and taxonomic affiliation of the individual specimens. Similarly, a regression equation (derived from mixed-sex mean weights) was used to predict, at a broad level, body weight (DeGusta and Vrba, 2003, 2005).

Only specimens that preserved all the necessary metrics can be included in the discriminant analysis, leading to a potential bias if fragmentary specimens differ systematically from more complete specimens. To help account for this, the preserved dimensions of the fragmentary specimens were compared with those of the complete specimens. Except for two fragmentary intermediate phalanges, which are smaller than any complete intermediate phalanges, the incomplete specimens do not alter the range of measurements seen in the complete specimens. Thus, except for those two specimens, the analysis of complete specimens is unlikely to omit taxa present in the more fragmentary remains.

The habitat, tribe, and body weights predicted by the discriminant function analyses of the astragalus and phalanx metrics are given in Table 2. Many of these specimens were recovered during the first few years of collection, and therefore exact stratigraphic provenience is not known. This assemblage must thus be treated as a mix of specimens from the mudstone horizon and the sands below.

For habitat preference, the results show a mix of Forest and Light Cover forms ("light cover" is light bush, tall grass, and hilly areas, DeGusta and Vrba, 2003). However, modern forest and light cover taxa exhibit considerable overlap in their morphologies (DeGusta and Vrba, 2003). As such, these results do not necessarily indicate a mix of those habitats at Lemudong'o, only that this analytical method does not easily discriminate between the two in this case. It is evident, however, that the bovid assemblage does not sample open-country forms, and that at least a few forest-adapted specimens are present (e.g., KNM-NK 36950 proximal and intermediate phalanges, KNM-NK 41204 astragalus). This method has a success rate of approximately 67%–71%, depending on the element (see discussion in DeGusta and Vrba, 2003, 2005). Examination of the probabilities associated with the specific predictions shows that only the two above-mentioned "forest" predictions can be considered significant at $p < 0.05$ (i.e., 95% or greater chance of being correct).

Since the methods of DeGusta and Vrba (2003, 2005) were designed to recover information on habitat preference, the taxonomic results (Table 2) must be considered less robust. Even so, they clearly indicate that a substantial number of the Lemudong'o 1 specimens are morphologically similar to those of modern Antilopini, Cephalophini, and Neotragini. This conclusion is likely due to the generally small size of the

Lemudong'o astragali and phalanges. The predicted body weights (which were generated from mixed-sex means, DeGusta and Vrba, 2003, 2005) range from 15 to 62 kg. Four possible sets of weights are broadly discernable: 15–23 kg, 28-33 kg, 40–44 kg, and then two heavier specimens (55 and 62 kg). Clearly, the bovids sampled in this assemblage were predominately of the smaller, lighter variety (relative to the overall range of size seen in modern African bovids).

Discussion

The Narok late Miocene bovid assemblage is dominated by aepycerotins that are similar in morphology and size to *Aepyceros premelampus* from Lothagam, although this attribution is not conclusive given the fragmentary nature of the Narok specimens. Four other tribes are represented, although these are only represented by a limited number of specimens. For example, the Bovini consists of only one specimen that is from Enamankewon and not from the main fossil horizon (the mudstones) at Lemudong'o Locality 1. Although there are only three specimens referred to *Madoqua*, this is a rather significant proportion given the small size of this assemblage compared to others, such as Lothagam.

At least one new taxon is probably represented in the Narok late Miocene assemblage based on the Lemudong'o Boselaphini horn cores, although a new species is not named due to the fragmentary nature of the specimens. The morphology of these two horn cores is unusual and differs from all known African Boselaphini. Their closest morphological affinities are to species of *Tragoportax* and *Miotragocerus*. These genera first appeared in Africa during the middle Miocene. The fossil record documents their diversification towards the end of the Miocene, but then they appear to have quickly gone extinct (Gentry, 1999). The presence of multiple boselaphin species of the *Tragoportax* morph in eastern African terminal Miocene deposits may not be unexpected, although such diversity and abundance is in sharp contrast to its then relatively sudden extinction. It is also at this time that tragelaphins become more abundant, begging the question of whether or not these shifts in relative abundance were related. Further discoveries are needed to better place these Lemudong'o specimens within the late Miocene evolution and extinction of the known boselaphin genera (*Tragoportax* and *Miotragocerus*), as these are among the last representatives of this lineage (along with those from the Nawata Formation of Lothagam, Harris, 2003; and the western margin of the Middle Awash, Haile-Selassie, 2001; Haile-Selassie et al., 2004).

All of the bovid tribes represented in the Narok late Miocene deposits are also present in the contemporaneous Upper Nawata Formation at Lothagam, Kenya (Harris, 2003). However, there are distinct differences in the proportions of bovid tribes represented at the two sites. The Upper Nawata bovid assemblage appears to have been dominated by Alcelaphini and Reduncini. There is no evidence for these two tribes within the Lemudong'o craniodental assemblage. Hippotragini is also present in the Lothagam Upper Nawata, but absent from Lemudong'o. These suggest that the paleoecology of Lemudong'o Locality 1 differs significantly from the open habitat inferred for the Upper Nawata (Harris, 2003, p. 556), probably by being more forested.

The Ibole Member of the Wembere-Manonga Formation in northern Tanzania dates to 5.5–5.0 Ma (Harrison and Mbago, 1997, p. 16). The Artiodactyla collections from these late Miocene deposits are highly fragmentary, as is the Narok assemblage. The taxonomic identifications for the Manonga Valley fossils are similarly based largely on partial horn cores and isolated teeth (Gentry, 1997). Despite the drawbacks of comparing two such assemblages, there are distinct contrasts in the bovid representations in the Ibole Member and the Narok late Miocene localities. *Kobus* and *Praedamalis* are present in the Ibole Member, but no members of either of these tribes (Reduncini and Hippotragini, respectively) have been recovered from Narok. The Ibole Member sites have also yielded a relatively large number of teeth attributed to *Damalacra* sp. (Gentry, 1997). However, the tribe Alcelaphini is not represented in the Narok assemblage. The Narok bovid assemblage thus appears to sample a more forested habitat than do the Manonga Valley late Miocene deposits.

The fauna from the Quartzose Sand Member of the Varswater Formation at Langebaanweg, South Africa, is similar to faunal assemblages of East Africa dated to between 5.2–4.8 Ma (Haile-Selassie, 2001). Comparison of the Narok bovid assemblage with the Quartzose Sand Member bovid assemblage shows that most of the tribes represented in the Narok were also present in the Quartzose Sand Member, both sites yielding taxa that are not commonly found in contemporaneous eastern African sites (Hendey, 1982). The overall faunal assemblage from the Quartzose Sand Member has been interpreted as having inhabited an area with a relatively warm temperature, high rainfall, and lush vegetation (Hendey, 1982). The similarity between Lemudong'o and Quartzose Sand Member bovid faunas is obviously ecological and not temporal.

The bovid assemblage from the late Miocene deposits of the Middle Awash dated to between 5.8 and 5.2 Ma is more diverse compared to the Narok bovid assemblage. While there is a substantial overlap in terms of the tribes represented at each site, reduncins and antilopins are abundant and diversified in the Middle Awash but are absent from the Narok assemblage. This difference could be explained either from an ecological point of view or due to sampling bias since the sample from the Middle Awash is much larger than the one from Narok. However, the overlap, particularly in the groups that usually inhabit more wooded and forested environments, suggests that there may have been substantial ecological similarities between Narok and the Middle Awash at the time of their deposition.

Since the Oligocene, there have been three major climatic shifts: 33 Ma, 15.6–12.5 Ma, and 2.95–2.52 Ma (Denton, 1999, p. 96). The late Miocene was also a time of significant climate change in Africa marked by an increase in tectonic activity and formation of the Western Rift, the Messinian salinity crisis, global cooling, and an increase in C_4 plants (Cerling et al., 1997). The African fossil record appears to reflect these shifts, with mid-Miocene sites typically being forested (Nesbit Evans et al., 1981, but see Shipman, 1986 for Fort Ternan paleoecology debate) while early Pliocene sites are more open (e.g., Lothagam, Leakey and Harris, 2003). Climatic shifts such as occurred in the late Miocene have been hypothesized as triggers for rapid evolution in the African bovids (e.g., Vrba, 1995, 2000, p. 289–290), an example of punctuated equilibrium in a mammalian lineage (Eldredge and Gould, 1972) in contrast to phyletic gradualism (e.g., Darwin, 1859; Retallack, 1992; Denton, 1999).

The late Miocene bovid assemblage from Narok contributes an interesting data point in our understanding of African bovid evolution, as it sits in this time of transition and appears to sample a light forested or forested habitat, based on our "ecomorphological" analyses. Lemudong'o and Enamankewon are penecontemporaneous with a few other eastern African fossil sites all yielding the earliest occurrences of several genera including

Tragelaphus, *Madoqua*, and *Aepyceros* (Vrba, 2000; Kingston et al., 2002, p. 110). With these new genera existed a previously unknown Boselaphini species, a member of a lineage near the end of its reign.

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PRELIMINARY ASSESSMENT OF THE LATE MIOCENE AVIFAUNA FROM LEMUDONG'O, KENYA

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ABSTRACT

The small collection of avian skeletal remains, including those of an eagle, an owl, and possibly a pheasant, from Lemudong'o provides additional information about terrestrial late Miocene avifaunas in east Africa. Large phasianids are known elsewhere in the Miocene of Africa, but pheasants are naturally absent today from the continent. The presence of two predatory bird species at the locality also is important because they may have acted as bone accumulators for part of the mammalian fauna occurring at the fossil site.

Introduction

Although Miocene avifaunas and fossil specimens are known from across Africa, relatively few of these collections have been described in detail. These faunas include the predominantly aquatic avifauna of the Beglia Formation (Rich, 1972) and Lothagam (Harris and Leakey, 2003), and terrestrial faunas from Morocco (Brunet, 1971) and Arrisdrift, Namibia (Mourer-Chauviré, 2003), in addition to other material (Rich, 1974). Current research in Chad, Libya, and Ethiopia has produced a diversity of avian taxa (Louchart et al., personal communication, 2006). The Lemudong'o avifauna, as with the mammalian fauna, of the African late Miocene has faunal components (apparently including some extant species) present in Africa today, as well as species and clades that no longer occur naturally in Africa. Miocene African bird clades that are now extinct in Africa include large-bodied ostriches that laid aepyornithoid and *Diamantornis* eggs (Senut et al., 1998; Stidham, 2004; Harrison and Msuya, 2005), swans (Louchart, Vignaud, et al., "New swan," 2005), and Idiornithidae (Mourer-Chauviré, 2003). Miocene faunas from Namibia and Morocco appear to include galliforms not present in Africa today (but known in Eurasia), including several phasianids possibly referable to *Phasianus*, *Gallus*, and *Palaeortyx* (Mourer-Chauviré, 2003). With this sparse Miocene record and faunal change, Lemudong'o adds to the puzzle of the history and biogeography of the African avifauna, even though it comprises relatively few bird bones.

Lemudong'o is a set of fossil localities in the Southern Rift Valley in Kenya that are somewhat older than 6 Ma (Ambrose et al., 2003, p. 739; Deino and Ambrose, 2007). That radiometric age determination appears to place Lemudong'o and its avifauna within the *Struthio karingarabensis* ostrich-eggshell biozone (Senut et al., 1998; Stidham, 2004; Harrison and Msuya, 2005). Fossils from Locality 1, where most vertebrate fossils have been collected, were deposited under mostly fluvial and lacustrine settings (Ambrose et al., 2003, p. 739; Ambrose, Nyami, et al., 2007). The Lemudong'o fauna includes a diverse assemblage of mammals and reptiles (Ambrose et al., 2003; Ambrose, Bell, et al., 2007). However, the bird skeletal remains include mostly pedal phalanges and long-bone shaft fragments. Only four bone fragments are identifiable to a taxonomic group within Aves at this time. These specimens appear to be fragments of a species of pheasant, an owl, and an eagle. All measurements were made from casts.

Abbreviations

FMNH = Field Museum of Natural History, Chicago, Illinois; MVZ = Museum of Vertebrate Zoology, University of California, Berkeley, California; KNM-NK = Kenya National Museum (Narok District), Nairobi, Kenya.

Systematic Paleontology

Order Galliformes (Temminck, 1820)
Family Phasianidae Vigors, 1825
Genus cf. *Phasianus* Linnaeus, 1758

Referred material

KNM-NK 36940 and KNM-NK 41255, proximal right-scapula fragments.

Description

KNM-NK 36940 is the anterior end of a right scapula that has a maximum dorsoventral width through the glenoid of 11.2 mm. The glenoid and acromion are preserved, but the scapular shaft is broken obliquely from the posterior end of the glenoid extending dorsoposteriorly. KNM-NK 41255 is the anterior approximately one-third of a right scapula with a maximum dorsoventral width through the glenoid of 11.1 mm. The tip of the acromion is missing. The shaft is broken just posterior to the anteroposteriorly elongate tubercle on the ventral side of the scapular blade. KNM-NK 41255 is slightly smaller than KNM-NK 36940.

Remarks

The two specimens are from two individuals and the slight difference in size between them is probably within the range of sexual size dimorphism present in galliforms. There is no evidence to support these two specimens as representing two species. Based on their size and ordinal identification, these scapulae were originally identified as members of Numidinae (Hlusko et al., 2002, p. 66A). However, careful comparisons with extant skeletal material have changed that identification. Both of the fossil scapulae are larger than comparative elements in *Acryllium vulturinum* (MVZ 155192), *Numida meleagris* (MVZ 124694), and *Guttera plumifera* (FMNH 313049). The fossils also have a ventral tip of the glenoid that is much more pointed than in the Numidinae. The lateral groove separating the acromion from the glenoid (an extension of the triosseal canal) is wider in the fossils than in the Numidinae. The fossils lack the lip on the dorsal edge of the glenoid present in extant guineafowl. The elongate tuber on the ventral surface of the scapular blade is relatively closer to the posterior edge of the glenoid in KNM-NK 41255 than in *Guttera plumifera* and *Numida meleagris*. The tuber is a similar size and in a similar position in the fossil and *Acryllium vulturinum*. Comparisons with *Phasianus* indicate very similar morphology between the fossil specimens and extant pheasant species. For example, *Phasianus colchicus* (MVZ 84651) has the same pointed ventral aspect of the glenoid, the wide groove between the glenoid and acromion, and an acromion that is widest (projecting laterally) dorsally and narrows ventrally in anterior view that are present in the fossils. The fossils lack the pneumatic foramen present in *Pavo*. At present, the morphology appears to support placement within the Phasianidae and possibly within *Phasianus* rather than with Numidinae or other extant African galliform clades ("*Francolinus*"). The identification of fossil pheasants in Kenya may not be unique in Africa (see below).

Order Falconiformes Sharpe, 1874
Family Accipitridae Vieillot, 1816

Referred material

KNM-NK 41004, a proximal right carpometacarpus.

Description

KNM-NK 41004 is broken just distal to the point where the major and minor metacarpals separate distally. The proximal face of the extensor process is damaged. The flexor process is broken. The maximum proximal-distal length of the trochlea is 14.9 mm and the dorsoventral depth through the proximal end of the trochlea is 9.2 mm.

Remarks

Overall the fossil's morphology is generally similar to *Pandion* and other falconiforms except that it is larger and differs in details of the morphology. Comparisons with *Pandion*, *Sagittarius*, *Accipiter*, *Buteo*, *Aquila*, and *Circus* appear to reject allocation to those genera. The distal end of the carpal trochlea with large ridges at the distal end is similar to *Haliaeetus*. The specimen is also similar in size to *Haliaeetus* and *Aquila*. With these comparisons, it appears that the fossil should be allocated to the Accipitridae (not Pandionidae or Sagittariidae), and is probably from a large eagle (i.e., not a hawk) and possibly from a fish eagle. Refinement of the identification of this specimen will require further work.

Order Strigiformes Wagler, 1830
Family cf. Strigidae Vigors, 1825

Referred material

KNM-NK 41489, a distal right ulna.

Description

KNM-NK 41489 is broken a little proximal to the end of the intercondylar sulcus. The carpal tuber is damaged just above its base. A small chip is missing from the distal edge of the intercondylar sulcus. The distal width (with carpal tuber broken) is 5.8 mm, and the depth through the dorsal rim of the intercondylar sulcus is 7.5 mm.

Remarks

KNM-NK 41489 was compared to nearly every order of neognathous bird. Several characters present in the fossil appear to allocate it with owls: the presence of a lateral trochlear ridge that extends much further proximal relative to the medial ridge (almost two times greater in length than the medial ridge); the proximal end of the lateral trochlear ridge is displaced medially and is nearly centered (mediolaterally) on the ventral face of the ulna; the lateral ridge of the trochlea is larger (extending further ventrally) than the medial ridge, but the medial ridge extends further distally and is the distal tip of the ulna; and in distal view, the dorsal margin of the ulna forms a rounded point laterally, and medially this dorsal margin is concave adjacent to where the carpal tuber was. The combination of those characters is consistent with the identification of the fossil as an owl. An area, proximal to the base of the carpal tuber (anterior surface), that is slightly concave and that is bounded dorsally by a slight ridge separating the concave area from an adjacent relatively flat area on the dorsal surface, appears to be present among owls only in the Family Strigidae. It is absent in *Tyto alba* and *Phodilus*. The fossil is approximately the size of *Asio flammeus*, *Strix fulvescens*, and *Strix woodfordi* (Ambrose et al., 2003, p. 741), is smaller than *Bubo africanus*, and is much larger than *Glaucidium* and *Aegolius*.

Aves indeterminate

Referred material

KNM-NK 40898A, an ungual phalanx; KNM-NK 40898B, a humeral shaft fragment; KNM-NK 41244, the proximal end of a radius; KNM-NK 41476A, the proximal end of an ungual phalanx; KNM-NK 41476B, an ungual phalanx; and KNM-NK 44801, a pedal phalanx missing the distal end.

Description

KNM-NK 40898A is 11.6 mm long. The proximal diameter of KNM-NK 41244 is 3.8 mm. KNM-NK 41476B is 8.7 mm long. KNM-NK 44801 has a maximum preserved length of 23.2 mm, a proximal width of 8.2 mm, and a proximal depth of 8.9 mm.

Remarks

These bones and fragments lack distinctive morphology for them to be identified at this time beyond Aves. The one possible exception to this is KNM-NK 44801. With further comparison it might be identified as a falconiform and possibly accipitrid. It has distinctive, flattened, medial and lateral surfaces that are absent in owls, falcons, *Buteo*, and *Aquila*. The other specimens are all from taxa smaller than the pheasant, eagle, and owl described above and indicate additional taxa of birds at Lemudong'o. The small size of these elements could indicate their allocation to Passeriformes, Piciformes, or Coraciiformes, but the ungual phalanges lack any distinctive morphology to identify them to a lower taxonomic level at this time.

Discussion

Lemudong'o preserves one of the few late Miocene avifaunas of Africa. The Lemudong'o avifauna is roughly equivalent in age to that of the Upper Member of the Nawata Formation (McDougall and Feibel, 2003) and its taxa *Struthio* cf. *karingarabensis*, *Pelecanus*, *Anhinga* cf. *rufa*, *Leptoptilos* cf. *crumeniferus*, a heron, a duck, a rail, and a bustard (Harris and Leakey, 2003; Harrison and Msuya, 2005). Lemudong'o is intermediate in age between the Miocene avifaunas from Chad and Ethiopia (Louchart et al., personal communication, 2006). The dominance of terrestrial (rather than aquatic) bird taxa at Lemudong'o is similar to Arrisdrift, Namibia (Mourer-Chauviré, 2003) and Beni Mellal, Morocco (Brunet, 1971). In general, these terrestrial avifaunas have specimens similar to Eurasian taxa. Other Miocene African (aquatic) avifaunas can appear to be very similar (at the generic level) to those present in Africa today, but also exhibit Eurasian links (Louchart et al., personal communication, 2006). These avifaunas with genera present in Africa today include: Rusinga Island, Kenya with a flamingo (*Phoenicopterus aethiopicus*) (Harrison and Walker, 1976), a stork (*Ciconia minor*), a goshawk (*Accipiter* cf. *tachiro*), and a francolin (Harrison, 1980); Beglia Formation, Tunisia with an ostrich, a cormorant (*Phalacrocorax* cf. *littoralis*), an anhinga (*Anhinga* cf. *pannonica*), a whalehead stork, and a marabou stork (*Leptoptilos richae*) (Rich, 1972; Louchart, Vignaud, et al., "Extinct stork," 2005); Toros Menalla area, Chad with anhingas (*Anhinga* cf. *melanogaster* and *Anhinga* cf. *pannonica*), a heron (*Ardea* sp.), a stork (*Ephippiorhynchus* sp.) and a finfoot (*Helopais* cf. *personata*) (Louchart et al., personal communication, 2006); Adu Asa Formation, Ethiopia with a grebe (*Podiceps* sp.), cormorants (*Phalacrocorax* cf. *carbo* and *Phalacrocorax* sp.), anhinga (*Anhinga* cf. *melanogaster*), a heron (*Ardea* sp.), and spur-winged goose (*Plectropterus* sp.) (Louchart et al., personal communication, 2006); and Maboko Island with a stork (*Ciconia* sp.) and a bustard (cf. *Chlamydotis undulatus*) (Harrison, 1980). These aquatic-dominated avifaunas contain members of families, genera, and in some cases specimens identical to species present in Africa today. However, swans (Louchart, Vignaud, et al., "New swan," 2005) and the finfoot *Helopais* cf. *personata* (Louchart, Mourer-Chauviré, et al., 2005) are extinct in Africa today. This parallels the avifaunas that have a larger proportion of terrestrial birds that also contain species in clades that presently do not occur in Africa. These include the occurrence of *Gallus* at Beni Mellal (Brunet, 1971) and possibly Arrisdrift, and the records of other phasianids similar to *Palaeortyx* and *Phasianus* at Arrisdrift (Mourer-Chauviré, 2003). The terrestrial birds of the African Miocene, in particular the galliforms, differ significantly from those found in present day Africa, as demonstrated by the presence of taxa similar to Miocene African specimens in Eurasia (*Phasianus*, *Gallus*, and *Palaeortyx*). In addition, the fossils of *Pavo* in the early Pliocene of Africa (Louchart, 2003; Pickford et al., 2004) add to the distinctiveness of the late Neogene African avifauna and indicate significant changes in avifaunal make-up since the end of the Miocene in Africa. In an unpublished manuscript, Louchart et al. (personal communication, 2006) discuss the biogeographic links among the birds of North and East Africa with Europe and the Oriental Region of Asia. The Lemudong'o phasianids at present appear to support this biogeographic affiliation. The links between Africa and Eurasia are present in aquatic and terrestrial avian taxa distributed across the Pelecaniformes, Galliformes, Ciconiiformes, and Gruiformes. The potential presence of Eurasian taxa in avifaunas in Morocco, East Africa, and Namibia appear to indicate that avifaunal changes potentially would have been pan-African, and not just regional extinctions or emigrations.

The current absence of aquatic bird taxa at Lemudong'o in spite of its largely fluvial and lacustrine nature is unusual. As noted above, terrestrial Miocene avifaunas are uncommon in Africa. However, the avian sample size is small from Lemudong'o and further fieldwork may yet produce aquatic birds. Even with that potential bias, the presence of an eagle and an owl at Lemudong'o may indicate proximity of the fossil sites to a nest or roost, and it is potentially important for the interpretation of the mammalian faunal assemblage. Both birds were predators and both would have included mammals in their diet. With the large number of small mammals in the fossil deposit, a taphonomic contribution provided by the diurnal and nocturnal carnivorous component of the Lemudong'o avifauna cannot be ruled out. Bone breakage patterns and skeletal element compositions should be examined to determine if they are consistent with modern predatory bird bone accumulations.

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SNAKES FROM LEMUDONG'O, KENYA RIFT VALLEY

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ABSTRACT

We examined snake fossils collected through 2003 from Lemudong'o Locality 1 in Kenya. Taxonomic identifications were made based on derived apomorphic features preserved in the fossils. The disarticulated and sometimes fragmentary nature of the fossils themselves, combined with the relatively few apomorphic characters of vertebrae, restricted our ability to diagnose the fossils to fine-scale taxonomic levels. Identified specimens represent at least two taxa. Specimens diagnosable as members of Pythoninae are most common, but a single specimen records the presence of a colubroid snake in the fauna.

Introduction

The Lemudong'o Locality 1 is situated in the southern Rift Valley, approximately 100 km west of Nairobi, Kenya (Ambrose et al., 2003). Snake specimens collected through 2003 from Lemudong'o consist of a relatively small number of incomplete and broken vertebrae. We adopted an apomorphy-based approach to the identification of these elements. Although this is not a common approach for Neogene paleoherpetologists, the decreased reliance of phenetic similarity in favor of apomorphy yields more readily testable taxonomic identifications (Head, 2002; Bell et al., 2004) and reduces the potential for circularity of arguments that are based, at least in part, on the modern geographic distributions of taxa (Bell and Gauthier, 2002). When applied to many (but not necessarily all) isolated snake vertebrae, one consequence of this approach is a reduced taxonomic resolution relative to identifications derived from more traditional approaches. This is a result of several factors, including inadequate exploration of vertebral apomorphies for species-level resolution in snakes (apomorphies for higher-level systematic categories of snakes were only recently explored and identified [see Head, 2002; Bell et al., 2004]) and considerable ontogenetic and intracolumnar variation in vertebral morphology which limits recognition of apomorphic characters for isolated elements.

Methods

Our identifications were made from high-quality, detailed casts of the original fossils housed in the National Museums of Kenya, under the general locality designation Lemudong'o Locality 1. The casts were prepared by Leslea Hlusko. We compared these specimens with extant specimens of snakes in the collections at the University of Texas at Austin and the United States National Museum (Smithsonian Institution) in Washington, D.C. Vertebral apomorphies were derived, with some modification, from those discussed and illustrated by Head (2002).

Paleontology

Most squamate skeletal elements are represented by broken fragments. We were able to identify 14 specimens, representing at least two taxa. Numerous characteristics that diagnose Alethinophidia permit identification of these specimens as members of that group of snakes, although not all characters are preserved on all specimens. These diagnostic features include the presence of synapophyses with strongly differentiated dia- and parapophyseal articular facets, paired and symmetrical sub-central foramina, presence of an expanded condylar rim, approximately circular cotylar-condylar margins, a well-developed haemal keel, sub-central paralymphatic fossae on more posterior precloacal

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vertebrae, and a prominent posterior median notch of the neural arch.

Systematic Paleontology

Alethinophidia Nopcsa, 1923
Subfamily Pythoninae Fitzinger, 1826
Genera and species indeterminate

Description

Four specimens (KNM-NK 41363, KNM-NK 41415, KNM-NK 41440, and KNM-NK 44829) are diagnosed as Pythoninae by a combination of characters including the presence of a triangular neural canal, a straight interzygapophyseal ridge, and tall zygosphene, and the absence of paracotylar foramina. Individually, these characters are not apomorphic for pythonines (for example, a straight interzygapophyseal ridge is also present in many boine and additional taxa, e.g., Kluge, 1988; Rage and Albino, 1989), however, their combined presence occurs only within pythonines among Neogene taxa. Seven vertebral fragments catalogued under number KNM-NK 40892 display the same character combination with the exception of the triangular neural canal, which is not preserved in these specimens. We also refer these to Pythoninae. Two additional specimens are only tentatively referred to Pythoninae. One of these (KNM-NK 41329) consists only of a centrum and a small portion of the neural arch. The second (KNM-NK 41226a) is a poorly preserved and somewhat fractured centrum with a small portion of the arch. Both specimens demonstrate at least a suggestion of a straight interzygapophyseal ridge.

Remarks

The specimens compare better in both size and shape with extant large-bodied *Python* than other pythonine genera. Among extant African taxa, the Lemudong'o specimens are most similar to *Python sebae*; however, we refrain from using geographic proximity in taxonomic determination for the aforementioned reasons (see also Bell et al., 2004).

Colubroidea Oppel, 1811
Genus and species indeterminate

Description

Specimen KNM-NK 40897 is an isolated vertebra identified as an indeterminate colubroid snake. Assignment to Colubroidea is based upon the combined presence of paracotylar foramina and a well-developed neural spine that extends onto the zygosphene anteriorly. A wide, well-developed haemal keel is present and a distinct hypapophysis is suggested, but if originally present, it is broken and missing.

Discussion and Conclusion

Higher-order taxonomic composition of the Lemudong'o record is identical to the rest of the African Neogene record: pythonine and colubroid taxa were described previously from the early Miocene of Namibia (Rage, 2003), early and middle Miocene of Kenya (Madden, 1972; Rage, 1979), middle Miocene of Morocco (Hoffstetter, 1961; Rage, 1976), late Miocene and Pliocene of Chad (Brunet et al., 2000; Vignaud et al., 2002) and Uganda (Bailon and Rage, 1994), Pliocene of Morocco (Bailon, 2000), and Pliocene and Pleistocene of Tanzania (Rage, 1973; Meylan, 1987). Although this record does not increase the taxonomic diversity of the African fossil snakes, it contributes to our understanding of snake evolution in Africa, because it is part of a fossil record the quality and density of which was only recently recognized.

The evolutionary history of African snakes is poorly understood relative to other continents. Patterns of endemicity and estimations of divergence timings are difficult to elucidate among extant taxa (e.g., Gravlund, 2001), and histories of immigration and emigration are controversial (Underwood and Stimson, 1990; Kluge,1993). Reports of derived snakes from the early Late Cretaceous of Sudan (Rage and Werner, 1999) suggested radically different divergence timings and biogeographic patterns than previously considered. Given the comparative paucity of the African fossil record, documenting the snakes of Lemudong'o is important in building a dataset for reconstructing evolutionary patterns and processes in African snakes.

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