

KIRTLANDIA

The Cleveland Museum of Natural History

December 2007

Number 56:163–172

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

LESLEA J. HLUSKO

Department of Integrative Biology
University of California, 3060 Valley Life Sciences Building,
Berkeley, California 94720-3140
hlusko@berkeley.edu

YOHANNES HAILE-SELASSIE

The Cleveland Museum of Natural History, 1 Wade Oval Drive,
Cleveland, Ohio 44106-1767

AND **DAVID DEGUSTA**

Department of Anthropological Sciences
Stanford University, Building 360, 450 Serra Mall, Stanford,
California 94305-2117

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 lo-

calities 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 $\sim 25 \times 50$ 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 $^{40}\text{Ar}/^{39}\text{Ar}$ 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 Kasiolai 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 lryation (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-

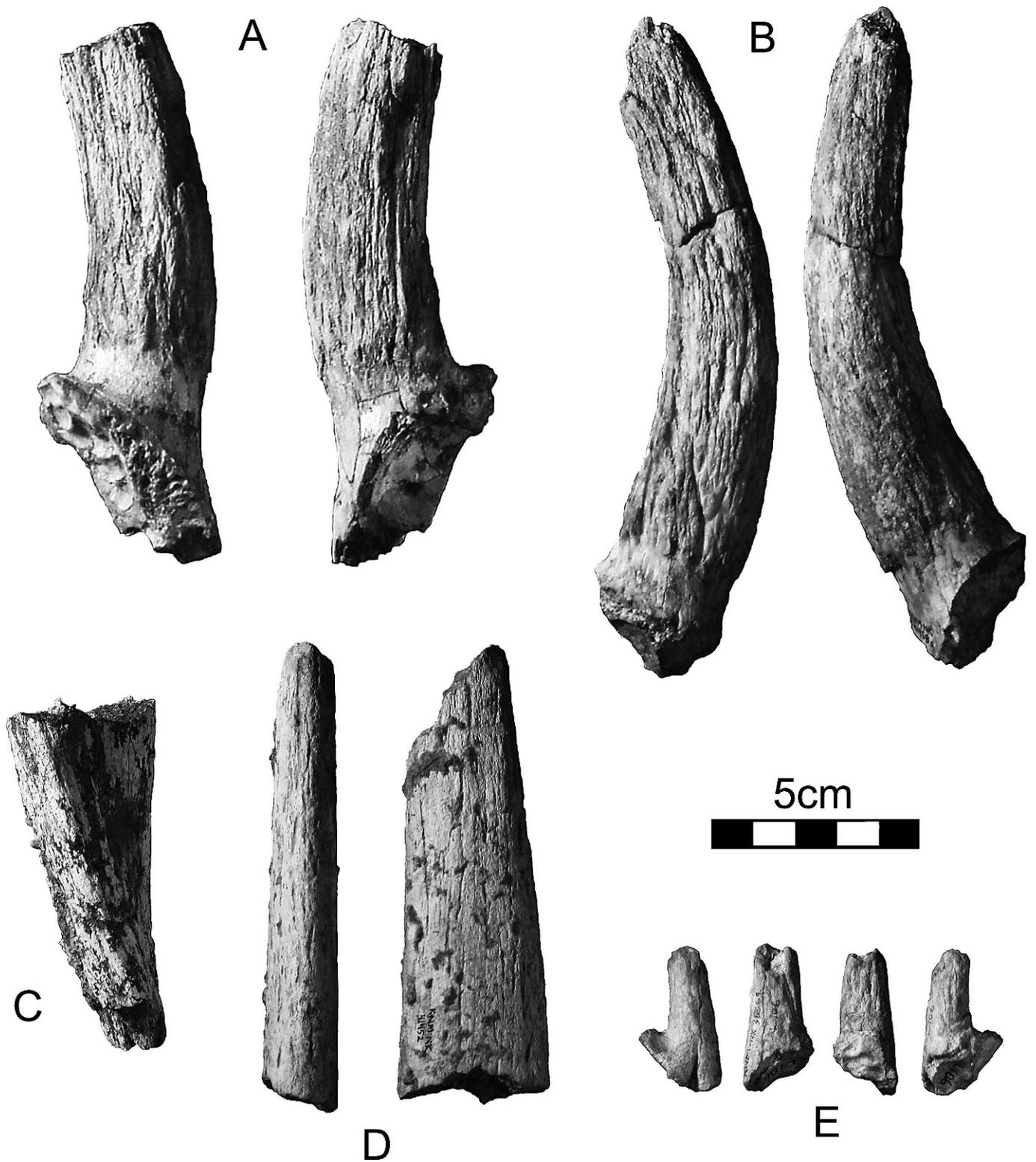


Figure 1. Horn cores from the late Miocene sediments of Lemudong'o and Enamankeon Locality 1. A, KNM-NK 41349, *Aepyceros* aff. *A. premelampus*, partial left horn core in medial and lateral views; B, KNM-NK 41458, *Aepyceros* aff. *A. premelampus*, right horn core in medial and lateral views; C, KNM-NK 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-NK 41358, 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 lophes); 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. kyaloe* (Harris, 2003, p. 532; Harris et al., 2003, p. 86). *T. kyaloe* 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)
<i>A. premelampus</i> 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)
<i>A. premelampus</i> 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)
<i>A. premelampus</i> avg. (stdv.)		22.1 (1.3)	8.4 (0.6)
KNM-NK 41185	Lp2	7.9	4.2
<i>A. premelampus</i>		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)
<i>A. premelampus</i> avg. (stdv.)		8.5 (0.7)	5.2 (0.4)
KNM-NK 44898	RM1	13.8	12.4
<i>A. premelampus</i> avg.		13.0	11.7
KNM-NK 41356	LM2	17.2	15.3
<i>A. premelampus</i> 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)
<i>A. premelampus</i> avg. (stdv.)		17.9 (1.7)	12.7 (1.5)
KNM-NK 41373	RP4	11.0*	13.3
<i>A. premelampus</i> 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 liration. 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 (9%)	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%)	Cephalophini (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 C₄ 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.

Acknowledgments

We would like to express our appreciation to the Office of the President, Kenya, for authorization to conduct research in Kenya; the Archaeology and Palaeontology Divisions of the National Museums of Kenya for staff assistance and facilities; the Maasai people for permission, access, and assistance. Many thanks to S. Kigamwa Amugongo for measuring the postcranial specimens, E. Vrba for advice and assistance, and helpful reviews by D. Geraads and J. Harris. Financial support was provided by the L.S.B. Leakey Foundation, the University of Illinois Center for African Studies and Research Board, National Science Foundation grant SBR-BCS-0327208 and the National Science Foundation HOMINID grant Revealing Hominid Origins Initiative BCS-0321893.

References

- Ambrose, S. H., C. J. Bell, R. L. Bernor, J.-R. Boisserie, C. M. Darwent, D. Degusta, A. Deino, N. Garcia, Y. Haile-Selassie, J. J. Head, F. C. Howell, M. D. Kyule, F. K. Manthi, E. M. Mathu, C. M. Nyami, H. Saegusa, T. A. Stidham, M. A. J. Williams, and L. J. Hlusko. 2007. The paleoecology and paleogeographic context of Lemudong'o Locality 1, a late Miocene terrestrial fossil site in southern Kenya. *Kirtlandia*, 56:38–52.
- Ambrose, S. H., L. J. Hlusko, D. Kyule, A. Deino, and M. A. J. Williams. 2003. Lemudong'o: a new 6ma paleontological site near Narok, Kenya Rift Valley. *Journal of Human Evolution*, 44:737–742.
- Ambrose, S. H., M. D. Kyule, and L. J. Hlusko. 2007. History of paleontological research in the Narok District of Kenya. *Kirtlandia*, 56:1–37.
- Ambrose, S. H., C. Nyamai, E. Mathu, M. D. Kyule, and M. A. J. Williams. 2007. Geology, geochemistry, and stratigraphy of the Lemudong'o Formation. *Kirtlandia*, 56:53–64.
- Blainville, H. M. D. 1816. *Prodrome d'une nouvelle distribution du règne animal*. Bulletin des sciences par la Societe Philomatique de Paris.
- Blyth, E. 1863. *Catalogue of the Mammalia in the Museum of the Asiatic Society of Bengal*. Asiatic Society, Calcutta, India.
- Cerling, T. E., J. M. Harris, B. J. MacFadden, M. G. Leakey, J. Quade, V. Eisenmann, and J. R. Ehleringer. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature*, 389:153–158.
- Darwin, C. 1859. *On the Origin of Species by Natural Selection*. Murray, London. 502 p.
- DeGusta, D., and E. Vrba. 2003. A method for inferring paleohabitats from the functional morphology of bovid astragali. *Journal of Archaeological Science*, 30:1009–1022.
- DeGusta, D., and E. Vrba. 2005. Methods for inferring paleohabitats from the functional morphology of bovid phalanges. *Journal of Archaeological Science*, 32:1099–1113.
- Deino, A., and S. H. Ambrose. 2007. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Lemudong'o late Miocene fossil assemblages, southern Kenya Rift. *Kirtlandia*, 56:65–71.
- Denton, G. H. 1999. Cenozoic climate change. p. 94–114. *In* T. G. Bromage and F. Schrenk (eds.), *African Biogeography, Climate Change, & Human Evolution*. Oxford University Press, New York.
- Eldredge, N., and S. J. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism. p. 82–115. *In* J. J. M. Schopf (ed.), *Models in Paleobiology*. Freeman, Cooper, & Co, San Francisco.
- Gentry, A. W. 1970. The Bovidae (Mammalia) of the Fort Ternan fossil fauna. p. 243–323. *In* L. S. B. Leakey and R. J. G. Savage (eds.), *Fossil Vertebrates of Africa vol. 2*. Academic Press, London.
- Gentry, A. W. 1978. Bovidae. p. 540–572. *In* V. J. Maglio and H. B. S. Cooke (eds.), *Evolution of African Mammals*. Harvard University Press, Cambridge, Massachusetts.
- Gentry, A. W. 1980. Fossil Bovidae (Mammalia) from Langebaanweg South Africa. *Annals of the South African Museum*, 79:213–337.
- Gentry, A. W. 1990. Evolution and dispersal of African Bovidae. p. 195–227. *In* G. A. Bubenik and A. B. Bubenik (eds.), *Horns, Pronghorns, and Antlers: Evolution, Morphology, Physiology, and Social Significant*. Springer-Verlag, New York.
- Gentry, A. W. 1997. Fossil ruminants (Mammalia) from the Manonga Valley, Tanzania. p. 107–135. *In* T. Harrison (ed.), *Neogene Paleontology of the Manonga Valley, Tanzania*. Plenum Press, New York.
- Gentry, A. W. 1999. Fossil pecorans from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. p. 290–316. *In* P. J. Whybrow and A. Hill (eds.), *Fossil Vertebrates of Arabia*. Yale University Press, New Haven.
- Gray, J. E. 1821. On the natural arrangement of vertebrate animals. *London Medical Repository*, 15:296–310.
- Gray, J. E. 1872. *Catalogue of the ruminant Mammalia (Pecora, Linnaeus) in the British Museum*. Trustees of the British Museum, London.
- Grubb, P. 1993a. Family Bovidae. p. 393–414. *in* D. E. Wilson and D. M. Reeder (eds.), *Mammal Species of the World: A Taxonomic and Geographic Reference*. Smithsonian Institution Press, Washington.
- Grubb, P. 1993b. Review of family-group names of living bovines. *Journal of Mammalogy*, 82:372–388.
- Haile-Selassie, Y. 2001. Late Miocene mammalian fauna from the Middle Awash Valley, Ethiopia. Unpublished Ph.D. thesis, University of California, Berkeley. 425 p.
- Haile-Selassie, Y., G. WoldeGabriel, T. D. White, R. L. Bernor, D. Degusta, P. R. Renne, W. K. Hart, E. Vrba, S. Ambrose, and F. C. Howell. 2004. Mio-Pliocene mammals from the Middle Awash, Ethiopia. *Geobios*, 37:536–552.
- Harris, J. M. 2003. Bovidae from the Lothagam succession. p. 532–558. *In* M. G. Leakey and J. M. Harris (eds.), *Lothagam: The Dawn of Humanity in Eastern Africa*. Columbia University Press, New York.
- Harris, J. M., M. G. Leakey, and T. E. Cerling. 2003. Early Pliocene tetrapod remains from Kanapoi, Late Turkana Basin, Kenya. *In* J. M. Harris and M. G. Leakey (eds.), *Geology and Vertebrate Paleontology of the Early Pliocene Site of Kanapoi, Northern Kenya*. Natural History Museum of Los Angeles County, Contributions in Science, No. 498(24 December): 39–113.
- Harrison, T., and M. L. Mbago. 1997. Introduction: paleontological and geological research in the Manonga Valley, Tanzania. p. 1–32. *In* T. Harrison (ed.), *Neogene Paleontology of the Manonga Valley, Tanzania*. Plenum Press, New York.
- Hendey, Q. B. 1982. *Langebaanweg: A Record of Past Life*. South African Museum, Rustica Press (Pty.) Ltd., Wynberg, Cape. 71 p.

- Jerdon, T. C. 1874. *The Mammals of India: Natural History*. John Wheldon, London. 335 p.
- Kappelman, J. 1988. Morphology and locomotor adaptations of the bovid femur in relation to habitat. *Journal of Morphology*, 198:119–130.
- Kingston, J. D., B. F. Jacobs, A. Hill, and A. Deino. 2002. Stratigraphy, age and environments of the late Miocene Mpesida Beds, Tugen Hills, Kenya. *Journal of Human Evolution*, 42:95–116.
- Knotnerus-Meyer, T. 1907. Über das Tränenbein der Huftiere: Vergleichend-anatomischer Beitrag zur Systematik der rezenten Ungulata. *Archiv für Naturgeschichte*, 73:1–152.
- Köhler, M. 1993. Skeleton and habitat of recent and fossil ruminants. *Münchener Geowissenschaftliche Abhandlungen*, 25:1–88.
- Leakey, M. G., and J. M. Harris. 2003. *Lothagam: The Dawn of Humanity in Eastern Africa*. Columbia University Press, New York. 688 p.
- Linnaeus, C. von 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tenth Edition. Laurentii Salvii, Holmiae, Stockholm. 824 p.
- Matthee, C. A., and T. J. Robinson. 1999. Cytochrome b phylogeny of the family Bovidae: resolution within the Alcelaphini, Antilopini, Neotragini, and Tragelaphini. *Molecular Phylogenetics and Evolution*, 12(1), 31–46.
- Nesbit Evans, E. M., J. A. H. Van Couvering, and P. Andrews. 1981. Palaeoecology of Miocene sites in western Kenya. *Journal of Human Evolution*, 10:99–116.
- Nowak, R. M. 1991. *Walker's Mammals of the World*. Fifth edition, Volume 2. Johns Hopkins University Press, Baltimore, p. 643–1629.
- Ogilby, W. 1837. On the generic characters of the ruminants, December 13, 1836 meeting. *Proceedings of the Zoological Society of London*, 1836:131–139.
- Owen, R. 1848. Description of teeth and portions of jaws of two extinct anthracotheroid quadrupeds (*Hyopotamys vectianus* and *Hyopotamys bovinus*) discovered by the Marchioness of Hasting in the Eocene deposits on the N.W. coast of the Island of Wright, with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London*, 4:103–141.
- Plummer, T. W., and L. C. Bishop. 1994. Hominid paleoecology at Olduvai Gorge, Tanzania, as indicated by antelope remains. *Journal of Human Evolution*, 27:47–75.
- Retallack, G. J. 1992. Middle Miocene fossil plants from Fort Ternan (Kenya) and evolution of African grasslands. *Paleobiology*, 18:383–400.
- Shipman, P. 1986. Paleoecology of Fort Ternan reconsidered. *Journal of Human Evolution*, 15:193–204.
- Simpson, C. D. 1984. Artiodactyls, p. 563–587. *In* S. Anderson and J. K. Jones, Jr. (eds.), *Orders and Families of Recent Mammals of the World*. John Wiley & Sons, New York.
- Sokolov, I. 1953. Opyt estestvennoi klassifikatsii polorogikh (Bovidae) [Natural classification of Bovidae], *Trudy Zoologicheskogo Instituta. Akademiya Nauk SSSR*, 14:1–295.
- Spassov, N., and D. Geraads. 2004. *Tragoportax* Pilgrim, 1937 and *Miotragocerus* Stromer, 1928 (Mammalia, Bovidae) from the Turolian of Hadjidimovo, Bulgaria, and a revision of the late Miocene Mediterranean Boselaphini. *Geodiversitas*, 26(2), 339–370.
- Thomas, H. 1980. Les bovidés du Miocène supérieur des couches de Mpesida et de la Formation de Lukeino (district de Baringo, Kenya), p. 82–91. *In* R. E. F. Leakey and B. A. Ogot (eds.), *Proceedings of the 8th Pan-African Congress of Prehistory, Nairobi 1977*. International Louis Leakey Memorial Institute for African Prehistory, Nairobi.
- Vrba, E. S. 1985. African Bovidae: evolutionary events since the Miocene. *South African Journal of Science*, 81:263–266.
- Vrba, E. S. 1995. On the connections between paleoclimate and evolution, p. 24–45. *In* E. S. Vrba, G. H. Denton, T. C. Partridge, and L. H. Burckle (eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven.
- Vrba, E. S. 2000. Major features of Neogene mammalian evolution in Africa, p. 277–304. *In* T. C. Partridge and R. R. Maud (eds.), *The Cenozoic of Southern Africa*. Oxford University Press, New York.
- Vrba, E. S., and Y. Haile-Selassie. 2006. A new antelope, *Zephyreduncinus oundagaisus* (Reduncini, Artiodactyla, Bovidae), from the Late Miocene of the Middle Awash, Afar Rift, Ethiopia. *Journal of Vertebrate Paleontology*, 26:213–218.
- Vrba, E. S., J. R. Vaisnys, J. E. Gatesy, R. DeSalle, and K.-Y. Wei. 1994. Analysis of paedomorphosis using allometric characters: the example of reduncini antelopes (Bovidae, Mammalia). *Systematic Biology*, 43(1), 92–116.