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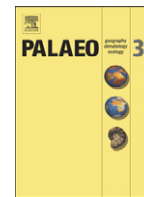
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New perspectives on middle Pleistocene change in the large mammal faunas of East Africa: *Damaliscus hypsodon* sp. nov. (Mammalia, Artiodactyla) from Lainyamok, Kenya

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ABSTRACT

The middle Pleistocene fossil mammal assemblage from Lainyamok in the southern Kenya rift has previously been considered the oldest (330–392 ka) African mammal community consisting entirely of extant species, with the dominant bovid tentatively attributed to the southern African blesbok (*Damaliscus* cf. *dorcas*). We show that the blesbok-like fossils from Lainyamok belong to an extinct species, described here as *Damaliscus hypsodon* sp. nov. The *D. hypsodon* hypodigm includes the previously unnamed small alcelaphine material known from late Pleistocene sites elsewhere in Kenya and Tanzania. Its dental anatomy, together with an ecomorphological analysis of its postcrania, indicates that *D. hypsodon* grazed in open and arid grassland environments. Although Lainyamok is no longer represented entirely by extant species, the absence of species common earlier in the middle Pleistocene of East Africa suggests substantial faunal turnover between 500 and 400 ka. *Damaliscus hypsodon* persisted in East Africa until the end of the Pleistocene and its extinction can be attributed to a loss of arid grassland environments at the onset of the Holocene. The fossil evidence from southern Kenya suggests that the development of the taxonomically modern large mammal community was a long-term process characterized by the extinction of grazing specialists, with marked turnover occurring between ~500 and 400 ka and near the end of the Pleistocene.

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1. Introduction

Dating to between 330,000 and 392,000 years ago, the faunal assemblage from Lainyamok in the southern Kenya rift (Fig. 1) is regarded as the oldest well-sampled African mammal community consisting entirely of extant species (Potts and Deino, 1995). The absence of extinct taxa typical of earlier East African sites (780,000 to 500,000 years ago), including the suid *Kolpochoerus majus*, the giant cercopithecoid *Theropithecus oswaldi*, the elephantid *Elephas recki*, and the hippopotamid *Hippopotamus gorgops* (Deino and Potts, 1990; Potts and Deino, 1995; McBrearty et al., 1996; Potts, 1998; Geraads et al., 2004; Gilbert and Asfaw, 2008), implies substantial faunal turnover during the middle Pleistocene. At the same time,

Lainyamok is atypical of subsequent late Pleistocene sites in East Africa, here several extinct bovid species (e.g., long-horn buffalo (*Syncerus antiquus*), giant wildebeest (*Megalotragus* sp.), *Rusingoryx atopocranium*, and a small alcelaphine) are well documented and sometimes very abundant (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Harrison and Baker, 1997; Tryon et al., 2010, 2012; Faith et al., 2011).

The dominant bovid at Lainyamok was provisionally identified as having closest affinities with blesbok and referred to *Damaliscus* cf. *dorcas* (Potts et al., 1988; Potts and Deino, 1995), which at the time represented the northernmost record of what is today a southern African taxon (Skinner and Chimimba, 2005). Since then, blesbok-like specimens have been reported from the late Pleistocene of Katanda in the Congo (as *Damaliscus* cf. *dorcas*) (Brooks et al., 1995; see also Gentry, 2010) and the Manonga Valley in Tanzania (provisionally as *D. dorcas*) (Harrison and Baker, 1997). These fossils broadly overlap in time and space with an unnamed extinct alcelaphine of similar size, known from the late Pleistocene at Lukenya Hill (Kenya),

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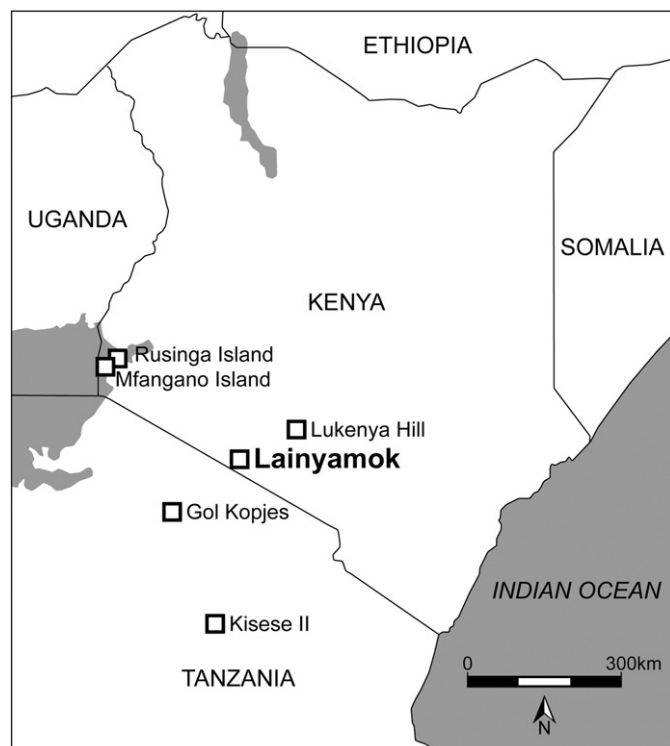


Fig. 1. The location of Lainyamok and other sites yielding remains of *Damaliscus hypsodon*.

Kisese II (Tanzania), Gol Kopjes (Tanzania), and Kenya's Lake Victoria Basin (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Tryon et al., 2010, 2012).

The presence of blesbok together with the absence of extinct forms at Lainyamok raises questions about late Quaternary faunal turnover, including interchange between eastern and southern Africa, and the development of the taxonomically modern large mammal community in East Africa. Here, we offer a new perspective on the Lainyamok mammal community, showing that specimens attributed to *Damaliscus* cf. *dorcas* belong to an extinct species of *Damaliscus* that includes the previously unnamed small alcelaphine. This study provides a formal species description, an evaluation of its dietary and locomotor adaptations, and a discussion of its implications for middle Pleistocene change in the large mammal faunas of East Africa.

2. History of the small extinct alcelaphine

The small extinct alcelaphine was first documented by Marean (1990) in the late Pleistocene deposits (from $\geq 40,000$ to 12,000 years ago) from Lukenya Hill in south-central Kenya, where it is numerically dominant. It was subsequently reported from the late Pleistocene at Kisese II Rockshelter and Gol Kopjes in northern Tanzania (Marean and Gifford-Gonzalez, 1991). Owing to a sample (NISP > 1100) consisting largely of isolated teeth and the lack of a suitably complete type specimen, Marean and Gifford-Gonzalez (1991) did not provide a formal species description. However, their morphological description showed that its teeth are distinguished from extant alcelaphines by the combination of their small size, less complex molar occlusal morphology, simple internal enamel cavities, more rounded buccal walls of the lower molars, absence of the mandibular p2, and hypsodonty index exceeding extant taxa. The occlusal lengths of the teeth overlap with blesbok, but the consistent absence of the p2 (variably present in blesbok) and greater hypsodonty suggest that it is distinct. There are dental similarities between the small alcelaphine and *Damaliscus agelaius* from Olduvai Gorge Beds III/IV (Gentry and Gentry, 1978)

(e.g., simple occlusal morphology and absent p2), although the latter is significantly larger.

In 2009 a modest sample (NISP = 26) of a blesbok-sized alcelaphine was recovered from the late Pleistocene Wasiriya Beds on Rusinga Island (Fig. 1), in Kenya's Lake Victoria Basin (Tryon et al., 2010). These include a mandible lacking an alveolus for the p2 and teeth that are morphologically identical to those of the small alcelaphine from Lukenya Hill. Given the morphological similarities to the Lukenya Hill specimens and the temporal and geographic overlap, Tryon et al. (2010) attributed the Rusinga Island specimens to the same extinct taxon (as cf. *Damaliscus*). Two additional specimens were subsequently recovered from late Pleistocene deposits on the nearby Mfangano Island (Tryon et al., 2012), and the Rusinga Island sample has been expanded to 69 specimens.

The growing sample of small extinct alcelaphine remains prompted a re-examination of *Damaliscus* cf. *dorcas* from Lainyamok. Most of the Lainyamok specimens are complete postcranial elements that are comparable to *D. dorcas*, although the extent to which they can be expected to differ from an extinct alcelaphine of similar size is likely negligible (see e.g., Klein, 1994). The most taxonomically informative specimen from Lainyamok is a nearly complete cranium (KNM-WM 16526). Initial laboratory observations noted morphological features of its maxillary teeth that align it with the small extinct alcelaphine to the exclusion of blesbok (e.g., simple internal enamel cavities, less complex occlusal outlines). Subsequent study revealed features of the horn cores and cranium that sufficiently distinguish it from all extant and previously described fossil species of *Damaliscus* and warrant the description of a new species. Morphological similarities between the Lainyamok sample and specimens of the small extinct alcelaphine from Lukenya Hill, Gol Kopjes, Kisese II, Rusinga Island, and Mfangano Island suggest that they are conspecific. More than two decades after initial reports of the small alcelaphine (Marean, 1990), we provide a formal species description below.

3. Systematic paleontology

Order ARTIODACTYLA Owen, 1848
 Family BOVIDAE Gray, 1821
 Tribe ALCELAPHINI Brooke in Wallace, 1876
 Genus *Damaliscus* Sclater and Thomas, 1894
 Type species *Damaliscus dorcas* (Pallas, 1766)
Damaliscus hypsodon sp. nov.

Holotype: KNM-WM 16526 (Fig. 2), a nearly complete cranium preserving the basal portions (estimated ~60%) of the horn cores and the maxillary dentition. Curated at the National Museums of Kenya in Nairobi.

Hypodigm: includes fossil specimens from Lainyamok previously attributed to *Damaliscus* cf. *dorcas* (Potts and Deino, 1995), the small alcelaphine of Lukenya Hill (Kenya), Gol Kopjes (Tanzania), and Kisese II Rockshelter (Tanzania) (Marean, 1990, 1992; Marean and Gifford-Gonzalez, 1991), and the small alcelaphine of Rusinga and Mfangano islands (Kenya) (cf. *Damaliscus* in Tryon et al., 2010, 2012).

Type locality and horizon. Lainyamok (southern Kenyan rift, 1°48'S, 36°12'E), Khaki 2 layer, 392,000 \pm 4000 years ago.

Age: all known records date to the middle and late Pleistocene.

Etymology: the species name refers to its high crowned teeth, which yield a hypsodonty index greater than any extant African bovid (Marean and Gifford-Gonzalez, 1991).

Diagnosis: a species of *Damaliscus* about the size of *Damaliscus dorcas* or slightly smaller. Its horn cores insert above the back of the orbits and closer together than in other species of its genus, emerging at a more upright angle and with greater posterior curvature than in extant *Damaliscus*, with lateral flattening at the base and moderate mediolateral compression that increases from the base upwards, lacking torsion and without the change in course (lyration) characteristic



Fig. 2. Type specimen (KNM-WM 16526) of *Damaliscus hypsodon*: (A) right lateral view; (B) posterior view; (C) anterior view; (D) anterior surface of horn cores illustrating V-shaped insertion. Scale bars in A and D=5 cm; B and C scaled to the same height as A.

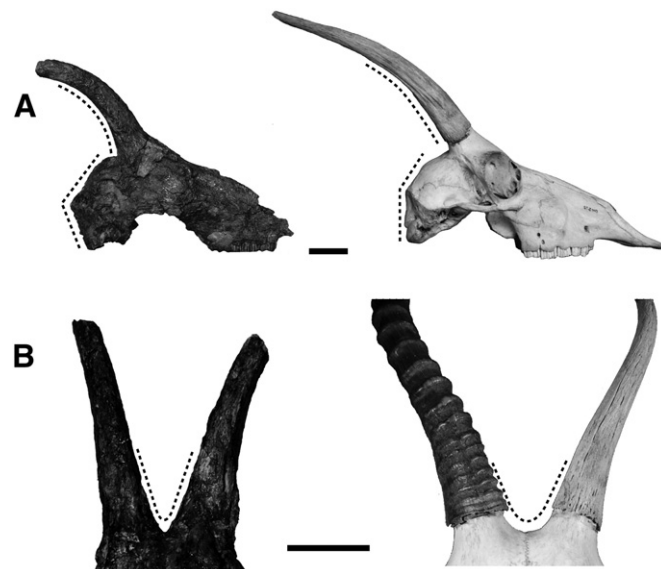


Fig. 3. Some characters distinguishing *Damaliscus hypsodon* from *Damaliscus dorcas*: (A) more acute angle between the occiput and braincase; horn cores that emerge more upright and with a tighter radius of posterior curvature; (B) horn cores that insert closer together and with pedicles that form a distinct V-shaped valley in anterior view. Scale bar equals 5 cm.

of *Damaliscus dorcas*. In anterior view, the valley formed between the horn core pedicles is distinctly V-shaped. The angle between the occiput and the roof of the braincase is more acute than in extant *Damaliscus*. The occlusal morphology of the cheek teeth and internal enamel cavities are simple; lower molars are characterized by rounded buccal walls (hypoconid and protoconid). Mandibular p2s are absent and premolar rows are reduced.

Description and comparisons. The type specimen (KNM-WM 16526) of *Damaliscus hypsodon* is a nearly complete cranium, missing the distal horn cores, the basicranium, and the anterior portion of the face (Fig. 2). Poor surface preservation obscures finer anatomical details (e.g., foramina and sutures), although preservation of the horn cores is good and the maxillary teeth are in excellent condition.

Consistent with its previous attribution to *Damaliscus cf. dorcas*, KNM-WM 16526 resembles *D. dorcas* in most features of the braincase and facial region. However, the frontals of KNM-WM 16526 are slightly depressed into a shallow concavity in front of the horn cores and between the orbits, whereas they tend to be convex in *D. dorcas*. In addition, the angle between the occiput and the roof of the braincase is more acute in KNM-WM 16526 (Fig. 3). There is no indication of a postcornual fossa in the type specimen, although this may be an issue of poor surface preservation.

The horn cores of the type specimen arise above the back of the orbits and are set on relatively short pedicles, with an indistinct junction between the horn cores and the pedicles. They insert close together (Fig. 4) and emerge at an upright angle, curving evenly backward, with no torsion or liration along the preserved length. Transverse ridges are absent, although it is possible that they would be present in the distal-most portions as is sometimes the case in *Damaliscus niro* (Gentry and Gentry, 1978). The horn cores are moderately divergent, with a mutual horn core angle of ~25°. The greatest basal horn core diameter is angled with respect to the sagittal plane, with the anterior surface situated closer to the midline. One of the more striking features is that the valley formed between the horn core pedicles in anterior view is distinctly V-shaped rather than U-shaped (Figs. 2 and 3), a character that distinguishes *Damaliscus hypsodon* from all other species of *Damaliscus* (i.e., it is autapomorphic). Horn cores of *D. hypsodon* are also known from Lainyamok specimen KNM-WM 17386, a partial calvarium preserving the horn core bases and the basicranium. This

specimen confirms the diagnostic horn core morphology of the type specimen.

The maxillary teeth of the type specimen are similar in size to *Damaliscus dorcas*. Relative to extant alcelaphines, the molars are characterized by simple internal enamel cavities and occlusal outlines (Fig. 5). These traits distinguish *Damaliscus hypsodon* from extant *Damaliscus* and suggest that the small alcelaphine specimens from Lukenya Hill, Gol Kopjes, Kiseso II, and the Lake Victoria Basin belong to the same taxon. Both P2s are absent from the type specimen, unlike in modern *Damaliscus dorcas* (present in a comparative sample of 13 individuals), and paralleling the lack of mandibular p2s noted by Mearns and Gifford-Gonzalez (1991) at Lukenya Hill and Gol Kopjes. It is possible that the P2s are lost with increasing ontogenetic age. However, light wear on the M3 of the type specimen (Fig. 5) indicates that the individual is not particularly aged and the P3s lack wear facets on the mesial surfaces, suggesting that the P2s were always absent in this individual. This feature may be diagnostic of the species, although in the absence of additional specimens we remain cautious.

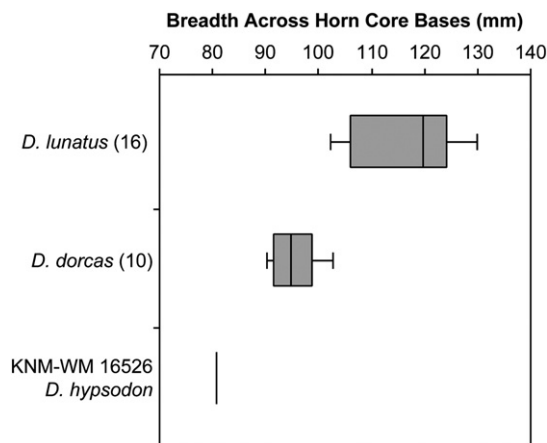


Fig. 4. Breadth across the horn core bases (mm) in extant *Damaliscus* and the type specimen of *Damaliscus hypsodon*. Sample sizes in parentheses.

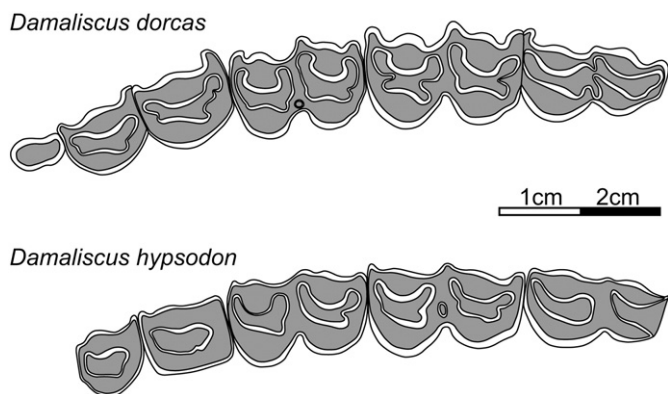


Fig. 5. Occlusal view of the maxillary tooth row of extant *Damaliscus dorcas* and the type specimen of *Damaliscus hypsodon* (KNM-WM 16526).

The mandibular dental sample from Lainyamok consists of a right mandible preserving the p4–m3 (KNM-WM 16532) (Fig. 6). The molars are characterized by simple internal enamel cavities and lingual and buccal walls that are evenly rounded. A break along the ventral margin of the horizontal ramus exposes the roots of the molars and shows them to be very hypsodont. As is the case for the maxillary teeth of the type specimen, this combination of traits further justifies inclusion of the material from Lukenya Hill, Gol Kopjes, and the Lake Victoria Basin in the *Damaliscus hypsodon* hypodigm. The p4 of KNM-WM 16532 is noteworthy in that the paraconid and metaconid are unfused, despite the fact that the tooth is in middle wear. A tendency towards later fusion is also observed in the larger Lukenya Hill sample, whereas the paraconid and metaconid are typically fused in comparably worn blesbok.

Marean and Gifford-Gonzalez (1991) observe that the M3 occlusal length of the small alcelaphine (i.e., *Damaliscus hypsodon*) is nearly identical to that of modern *Damaliscus dorcas*. Nevertheless, it can be shown that the M3 occlusal dimensions of *D. hypsodon* are smaller than in other species of Pleistocene *Damaliscus* when a combination of crown height, occlusal length, and occlusal width is taken into account. In Fig. 7 we plot crown height, to control for changing tooth dimensions as a function of wear, against $(\text{length} \times \text{width})^{1/2}$ of the M3 occlusal surface of fossil *Damaliscus*. The fossil sample includes late Pleistocene *D. hypsodon* from Lukenya Hill and Rusinga Island, late Pleistocene *D. dorcas* from Nelson Bay Cave (South Africa), and mid-Pleistocene *?Damaliscus niro* and *Damaliscus "hipkini"* (*?Damaliscus* sp. nov. of Klein and Cruz-Urbe, 1991) from Elandsfontein (South Africa). Modern blesbok could not be included because the base of the M3 crown in museum specimens is typically masked by alveolar bone, prohibiting crown height measurements. At any given crown



Fig. 6. KNM-WM 16532 in occlusal view (top) and buccal view (bottom). Scale bar = 5 cm.

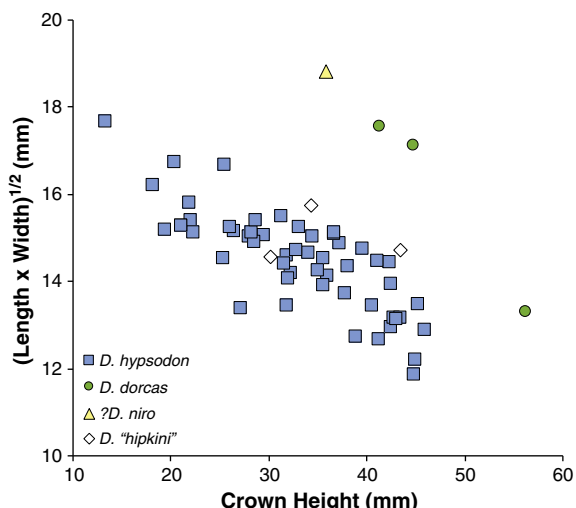


Fig. 7. Plot of crown height against $(\text{length} \times \text{width})^{1/2}$ of the M3 occlusal surface of fossil *Damaliscus* from East and southern Africa.

height, *D. hypsodon* has a smaller occlusal area than Pleistocene *D. dorcas* and *?D. niro* (hence the elevated hypsodonty). There is some overlap with *D. "hipkini"*, although a better sample may show the latter to be larger, as two of the three specimens fall just beyond the upper range of *D. hypsodon*. The difference between our results and those reported by Marean and Gifford-Gonzalez (1991) could reflect either a size increase in fossil *D. dorcas* relative to its living representatives and/or a narrower M3 relative to its height in *D. hypsodon*. The latter is consistent with the greater hypsodonty observed in the Lukenya Hill and Gol Kopjes *D. hypsodon* relative to modern *D. dorcas*.

Damaliscus hypsodon is distinct from all other species of Quaternary *Damaliscus*. Most notably, the V-shaped valley between the horn core pedicles in anterior view (Figs. 2 and 3) is autapomorphic for the genus. *Damaliscus hypsodon* can be distinguished from extant *Damaliscus dorcas* and *Damaliscus lunatus* by its simplified dental morphology (Fig. 5) and the following features of its horn cores: (1) the horn cores insert closer together, (2) emerge more upright, and (3) exhibit greater posterior curvature. The lack of liration in the horn cores further distinguishes *D. hypsodon* from *D. dorcas* whereas the medio-lateral compression is unlike *D. lunatus*.

Several *Damaliscus hypsodon* horn core characters resemble *Damaliscus niro*, which is well known from the Pleistocene of East and southern Africa (Gentry and Gentry, 1978; Brink, 1987; Thackeray et al., 1996; Vrba, 1997; Thackeray and Brink, 2004; Klein et al., 2007). These include upright insertions, even posterior curvature, and lack of torsion. However, the horn cores of *D. hypsodon* exhibit a tighter radius of posterior curvature, are set closer together, and are smaller and more gracile than the smallest fossils of *D. niro*, which are from roughly contemporaneous middle Pleistocene deposits at Florisbad in South Africa (Gentry and Gentry, 1978; Grün et al., 1996; Thackeray et al., 1996; Thackeray and Brink, 2004). Gentry and Gentry (1978) report antero-posterior (AP) basal horn core diameters of Florisbad *D. niro* ranging from ~41 to 53 mm and medio-lateral (ML) diameters from ~32 to 42 mm. Comparable measurements on the type specimen of *D. hypsodon* (AP = 34.4 mm; ML = 28.9 mm) fall below the range of Florisbad *D. niro*. The same is true for KNM-WM 17386 (AP = 38.1 mm; ML = 30.8 mm).

Marean and Gifford-Gonzalez (1991) speculate that the Lukenya Hill specimens, which we include within the *Damaliscus hypsodon* hypodigm, could be a smaller form of *Damaliscus agelaius* from Olduvai Gorge. Horn core morphology, however, suggests a more distant relationship. Unlike those of *D. agelaius*, the horn cores of *D. hypsodon* are less divergent, much more compressed, and with

flattening of the lateral surfaces. The latter two features also distinguish *D. hypsodon* from *Damaliscus strepsiceras*, reported from the early Pleistocene at Melka Kunture in Ethiopia (Geraads et al., 2004b).

A small alcelaphine probably belonging to *Damaliscus* (?*Damaliscus* sp. nov. of Klein and Cruz-Urbe, 1991; *Damaliscus* “hipkini” of Vrba, 1997) is known from the South African middle Pleistocene sites of Cornelia and Elandsfontein (Cooke, 1974; Klein and Cruz-Urbe, 1991; Vrba, 1997). *Damaliscus* “hipkini” bears similarities to *Damaliscus hypsodon*, particularly in terms of its size and horn cores that are moderately divergent, mediolaterally compressed, and with even posterior curvature. The teeth of the South African species are similar in size to *D. hypsodon* (Fig. 7) and the p2 is also absent. However, the horn cores of *D. “hipkini”* differ from *D. hypsodon* by their shorter length, rapid decrease in diameter from base to tip, weaker posterior curvature, greater inclination, and smaller basal dimensions (range of 7 specimens from Elandsfontein: AP basal diameter: 29.3–34.2 mm, ML basal diameter: 21.0–25.6 mm).

4. Paleocology of *Damaliscus hypsodon*

4.1. Hypsodont dentition

The dental anatomy of the small alcelaphine from Lukenya Hill, Gol Kopjes, Kisese II, and the Lake Victoria Basin matches that of *Damaliscus hypsodon* from Lainyamok, to the exclusion of other known extant and fossil species of *Damaliscus*. The morphological similarities, together with geographic and temporal overlap, suggest that they are conspecific. Marean and Gifford-Gonzalez (1991) report a hypsodonty index (HI), defined as m3 crown height divided by m3 width (Janis, 1988), for Lukenya Hill *D. hypsodon* of 5.74, a value that falls solely within the range of extant grazing ungulates inhabiting open grasslands (Janis, 1988; Damuth and Janis, 2011). The level of hypsodonty is extreme, exceeding the HI of all extant African bovids reported by Janis (1988) and surpassing the lower limits of *Equus*. A grazing diet alone does not explain the hypsodont teeth of *D. hypsodon*, as living hypergrazing alcelaphines (consuming >95% C₄ grass) do not exhibit comparable hypsodonty (Janis, 1988). In extant *Equus*, elevated HI values (5.70–8.73) are explained by the fact that they must ingest greater quantities of forage than ruminant bovids of comparable size, owing to their system of hindgut fermentation (Janis, 1988; Damuth and Janis, 2011). High forage intake is unlikely for *D. hypsodon*, however, because its small body size and therefore higher metabolic rate limit it to lower quantities of high-quality food (Bell, 1971; Jarman, 1974; Demment and Van Soest, 1985). Rather, we suggest that its extreme hypsodonty is best explained by (1) feeding on the nutrient-rich grass sward closest to the ground, as opposed to the more fibrous and nutrient-poor middle-to-upper portions of the grass layer, and (2) feeding in arid grassland environments. Both factors will result in the ingestion of large quantities of grit and soil, necessitating extreme hypsodonty to prolong the life-span of the teeth (see also Marean, 1992; Damuth and Janis, 2011). This adaptation to feeding in arid grassland environments is consistent with its association with *Oryx* and *Equus grevyi* at Lainyamok, Lukenya Hill, Kisese II, and the Lake Victoria Basin (Faith et al., in press). Today, these ungulates inhabit arid to semi-arid grasslands and shrublands (Kingdon, 1982).

Our interpretation of the dietary adaptation of *Damaliscus hypsodon* closely parallels Brink and Lee-Thorp's (1992) dietary reconstruction of extinct Bond's springbok (*Antidorcas bondi*) from the late Quaternary of southern Africa. Bond's springbok is both smaller and more hypsodont than the mixed-feeding extant springbok (*Antidorcas marsupialis*) and isotopic evidence indicates a diet dominated by C₄ grasses (Brink and Lee-Thorp, 1992). In light of its small body size and high-quality nutrient requirement, Brink and Lee-Thorp (1992) suggest that Bond's springbok relied largely on newly grown grass shoots, the growth of which was stimulated by

grazing pressure from larger grazing ungulates. Like Bond's springbok, the small-bodied and extremely hypsodont *D. hypsodon* may have also relied on the grazing pressure of larger ungulates to promote new grass growth and expose the more nutrient-rich sward closest to the ground (Faith et al., 2011:705).

4.2. Locomotor adaptation

Antelope (Mammalia: Bovidae) fossils are commonly found in African Pliocene and Pleistocene paleontological and archeological sites. Bovids are among the most useful large mammals for paleoenvironmental reconstruction, as they span a range of body sizes and have varied habitat preferences (Scott, 1985; Kappelman et al., 1997). Here we use discriminant function analysis (DFA) to relate metatarsal morphometrics to habitat preference in modern bovids. Based on this relationship, we develop a mathematical model for predicting the habitat preference of *Damaliscus hypsodon* using measurements from two relatively complete metatarsals recovered from Lainyamok (KNM-WM 15922 and KNM-WM 13754). These specimens were previously attributed to *Damaliscus* cf. *dorcas* on the basis of their morphological similarities (Potts and Deino, 1995). We now attribute them to *D. hypsodon* in light of our reclassification of the diagnostic cranial–dental material.

The discriminant function model presented here links metatarsal morphology to four broadly defined habitat categories: open (grassland, arid country, ecotones bordering open country), light cover (light bush, tall grass), heavy cover (heavy bush, woodland), and forest. These characterizations are based on the frameworks of Scott (1985), Kappelman (1986, 1988, 1991), Kappelman et al. (1997), and Plummer and Bishop (1994) and represent a partitioning of the continuum of African habitat structure from those generally lacking trees and bush to those with a continuous tree canopy. Extant African antelopes were assigned to one of these four habitat preference categories based on modern behavioral observation of these taxa in the wild (assignments follow Plummer et al., 2008). Previous studies using the same or similar habitat classification schemes show that DFA identifies morphological features related to locomotion – not simply phylogeny – in discriminating between antelopes inhabiting different habitat groups (e.g., Kappelman et al., 1997; Plummer et al., 2008).

Fifteen measurements were taken on 321 metatarsals from 37 extant African antelope species housed in the American Museum of Natural History, New York, and the Smithsonian Institution, Washington, DC (Table 1). Measurements were taken on adult animals of both sexes. Wild-shot animals were measured when available; less than 5% of the individuals were zoo specimens, many of which had been wild-caught. These measurements were used to generate ratios reflecting shape. A seven variable quadratic discriminant function model was developed using SYSTAT v. 13 following the variable selection procedure discussed in Plummer et al. (2008). The set of measurements and ratios used in generating our model is presented in Table 2. The success of the model was indicated by multivariate statistics testing the significance of differences among group means, as well as by how well the discriminant function classified specimens of known habitat (Table 3). Model accuracy was tested further using jackknife analysis.

Three discriminant functions were calculated, accounting for 80.6%, 15.9% and 3.5% of the variance, respectively. The resubstitution classification success matrix (Table 3B) demonstrates that the function was effective at predicting habitat membership, with 283 of the 321 specimens being classified correctly (88%). Multivariate means of the different habitat groups were significantly different ($p < 0.0001$) (Table 3C), indicating that the measurements and ratios used here can readily distinguish metatarsals from antelopes with different habitat preferences. Classification success was good across all four habitat groups, and for most species, with only Kirk's dik-dik (*Madoqua kirkii*) and black-fronted duiker (*Cephalophus nigrifrons*) having misclassification rates higher than 50% (Appendix 1).

Table 1
Taxon list and habitat preference category for specimens used in the discriminant function analysis.

| Tribe | Species | Habitat |
|--------------|------------------------------------|-------------|
| Tragelaphini | <i>Tragelaphus euryceros</i> | Heavy cover |
| | <i>Tragelaphus imberbis</i> | Heavy cover |
| | <i>Tragelaphus scriptus</i> | Forest |
| Cephalophini | <i>Tragelaphus strepsiceros</i> | Heavy cover |
| | <i>Cephalophus dorsalis</i> | Forest |
| | <i>Cephalophus leucogaster</i> | Forest |
| | <i>Cephalophus monticola</i> | Forest |
| | <i>Cephalophus natalensis</i> | Forest |
| | <i>Cephalophus nigrifrons</i> | Forest |
| | <i>Cephalophus silvicultor</i> | Forest |
| | <i>Cephalophus weynsi</i> | Forest |
| | <i>Sylvicapra grimmia</i> | Light cover |
| | <i>Madoqua kirkii</i> | Heavy cover |
| Neotragini | <i>Neotragus batesi</i> | Forest |
| | <i>Neotragus moschatus</i> | Forest |
| | <i>Ourebia ourebi</i> | Light cover |
| | <i>Raphicerus campestris</i> | Light cover |
| Antilopini | <i>Antidorcas marsupialis</i> | Open |
| | <i>Gazella granti</i> | Open |
| | <i>Gazella thomsoni</i> | Open |
| Reduncini | <i>Kobus ellipsiprymnus</i> | Heavy cover |
| | <i>Kobus kob</i> | Light cover |
| | <i>Kobus megaceros</i> | Heavy cover |
| | <i>Redunca redunca</i> | Light cover |
| | <i>Redunca arundinum</i> | Light cover |
| | <i>Redunca fulvorufula</i> | Light cover |
| Hippotragini | <i>Addax nasomaculatus</i> | Open |
| | <i>Hippotragus equinus</i> | Open |
| | <i>Hippotragus niger</i> | Open |
| | <i>Oryx gazella</i> | Open |
| Aepycerotini | <i>Aepyceros melampus</i> | Light cover |
| Alcelaphini | <i>Alcelaphus buselaphus</i> | Open |
| | <i>Connochaetes gnou</i> | Open |
| | <i>Connochaetes taurinus</i> | Open |
| | <i>Damaliscus dorcas</i> | Open |
| | <i>Damaliscus lunatus lunatus</i> | Open |
| | <i>Damaliscus lunatus korrugum</i> | Open |
| | <i>Beatragus hunteri</i> | Open |

Resubstitution analysis tests the predictive accuracy of the function with the same data used to create it. In other words, the entire bovid sample was used to generate the discriminant function, and then the accuracy of this function was tested by using it to classify each specimen in the same dataset. The jackknife analysis is a more conservative measure of predictive accuracy, as each specimen in the sample was withheld from generating the discriminant function,

Table 2
Variables used in the discriminant function analysis. See Plummer and Bishop (1994: Fig. 2) for an illustration of all measurements except FOFO, which is the mediolateral (M-L) dimension across the distal end of the metatarsal from the medial trochlear fossa to the lateral trochlear fossa.

| Caliper measurements | Description |
|----------------------|--|
| Log (length) | Log of metatarsal functional length |
| Log (MML) | Log of the midshaft M-L |
| Ratios | |
| LTRO16 | Log DML/log TMLMAX = log (distal articulation M-L)/log (medial trochlea maximum M-L) |
| LFOFO11 | Log DML/log FOFO = log (distal articulation M-L)/log (medial to lateral trochlear fossa M-L) |
| LMID15 | Log DML/log MML = log (distal articulation M-L)/log (midshaft M-L) |
| LMID17 | Log DAP/log MAP = log (distal articulation A-P)/log (midshaft A-P) |
| LMID121 | Log PML/log MML = log (proximal articulation M-L)/log (midshaft M-L) |

and the resultant function was then used to predict the habitat preference of the “left out” specimen. The procedure was carried out 321 times (one for each specimen in the sample), and the summary of the function's predictive success is given in Table 3D. The overall accuracy of the model dropped by just 1%, from 88% to 87%.

When specimens are analyzed by a DFA model, they are assigned probabilities of their membership in one of the predetermined categories in question. These probabilities describe the likelihood that a particular specimen was drawn from a species preferring one of our four habitat classes. The two Lainyamok metatarsals were treated as unknowns, and were assigned to the “Open” habitat category with high probabilities (KNM-WM 15922 = 98.6%, KNM-WM 13754 = 88.2%) (Table 3E).

4.3. Behavior

At Lukenya Hill, which is situated near a topographic trap adjacent to a well-documented historic large mammal migration route, the *Damaliscus hypsodon* mortality profiles from Middle Stone Age and Later Stone Age archeological deposits suggest that people captured entire herds of this extinct alcelaphine (Marean, 1997). It follows that, like some extant alcelaphines, *D. hypsodon* was both gregarious and migratory. Peaks in the age distribution at 12-month intervals (Marean, 1997) further imply that *D. hypsodon* was a seasonal breeder, as is also the case with migratory wildebeest (*Connochaetes taurinus*) (Kingdon, 1982).

5. Discussion

5.1. Biogeographic implications

The large mammal assemblage from Lainyamok can no longer be characterized as a short-lived community consisting of extant East and southern African species. Rather, Lainyamok marks the onset of an equatorial East African community in which *Damaliscus hypsodon* was one of the defining bovids. If we make the parsimonious assumption that the alcelaphine postcrania previously attributed to *Damaliscus* cf. *dorcas* belong to *D. hypsodon*, then *D. hypsodon* is the dominant bovid at Lainyamok. This is consistent with evidence from late Pleistocene localities, which shows *D. hypsodon* to be one of the more common large mammals, if not the dominant taxon (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Tryon et al., 2010, 2012).

Although Lainyamok no longer includes only extant species, it lacks several extinct taxa commonly found earlier in the middle Pleistocene (Potts, 1998). Fig. 8 illustrates the approximate last appearances of extinct middle-to-late Pleistocene mammals in East Africa (from Marean and Gifford-Gonzalez, 1991; Potts, 1998; Geraads et al., 2004a; O'Regan et al., 2005; Lehman, 2009; Tryon et al., 2010; Faith et al., 2011). Seven of the 12 extinct species are not confidently known from East African fossil sites younger than 400 ka. The Kapthurin Formation in Kenya provides the youngest reported *Kolpochoerus majus*, dated to between 543 and 509 ka, in addition to giant baboon (*Theropithecus* cf. *oswaldi*) and *Elephas* (Cornelissen et al., 1990; Deino and McBrearty, 2002; McBrearty and Jablonski, 2005). Together with the 330–392 ka age range for Lainyamok (Potts and Deino, 1995), this implies substantial faunal turnover between ~400 and 500 ka, consistent with the original interpretations of the Lainyamok fauna (Potts and Deino, 1995).

The 400 to 500 ka turnover marks the onset of a unique equatorial East African bovid community, with *Damaliscus hypsodon* and *Rusingoryx atopocranion* known only from this region. Similarly aged southern African sites include some of the extinct taxa found in East Africa (*Megalotragus* and *Syncerus antiquus*) as well as regional species such as Bond's springbok (*Antidorcas bondi*), southern springbok (*Antidorcas australis*), Cape zebra (*Equus capensis*), and a caprine antelope (Klein, 1980; Brink, 1987, 1999). Thus, whereas Lainyamok was

Table 3
Results of metatarsal discriminant function analysis.

(A) Pooled within-class standardized canonical coefficients.

Canonical discriminant functions: standardized by within variances. Asterisks denote the highest values for each variable

| | 1 | 2 | 3 |
|-----------|--------|---------|---------|
| LLENGTH | 1.180* | 0.168 | 0.483 |
| LMML | 0.589 | -2.811* | -0.208 |
| LTRO16 | 0.239 | -2.346* | -0.246 |
| LFOFO11 | 0.028 | 0.679* | -0.136 |
| LMIDI5 | 1.349* | -0.682 | -0.722* |
| LMIDI7 | 0.242 | 0.385 | 0.906* |
| LMIDI21 | -0.163 | -0.441 | -0.144 |
| %Variance | 80.6 | 15.9 | 3.5 |

(B) Resubstitution classification results from quadratic discriminant function analysis (total correct = 88%)

Classification matrix (cases in row categories classified into columns)

| Actual group | Number | Predicted group membership | | | | %Correct |
|--------------|--------|----------------------------|-------------|-------------|--------|----------|
| | | Open | Light cover | Heavy cover | Forest | |
| Open | 136 | 125 | 8 | 3 | 0 | 92 |
| Light cover | 79 | 7 | 69 | 0 | 3 | 87 |
| Heavy cover | 43 | 3 | 0 | 34 | 6 | 79 |
| Forest | 63 | 0 | 4 | 4 | 55 | 87 |

(C) Multivariate statistics testing hypothesis that class means are equal

| Statistic | Value | Approx. F-ratio | DF | p-Value |
|------------------------|-------|-----------------|--------|---------|
| Wilks' lambda | 0.139 | 42.290 | 21/808 | <0.001 |
| Pillai's trace | 1.237 | 31.373 | 21/939 | <0.001 |
| Lawley-Hotelling trace | 3.722 | 54.892 | | <0.001 |

(D) Jackknifed classification results from quadratic discriminant function analysis (total correct = 87%)

| Actual group | Number | Predicted group membership | | | | %Correct |
|--------------|--------|----------------------------|-------------|-------------|--------|----------|
| | | Open | Light cover | Heavy cover | Forest | |
| Open | 136 | 125 | 8 | 3 | 0 | 92 |
| Light cover | 79 | 7 | 66 | 0 | 6 | 84 |
| Heavy cover | 43 | 3 | 1 | 32 | 7 | 74 |
| Forest | 63 | 0 | 4 | 4 | 55 | 87 |

(E) Probability assignments for two Lainyamok metatarsals analyzed as unknowns in the discriminant function model. The DFA model assigned these fossil unknowns to the "open" habitat category with a high probability (> 88%)

| Accession number | pOpen | pLight cover | pHeavy cover | pForest |
|------------------|-------|--------------|--------------|---------|
| KNM-WM 15922 | 0.986 | 0.006 | 0.008 | <0.001 |
| KNM-WM 13754 | 0.882 | 0.108 | 0.007 | 0.003 |

once thought to represent a phase of interchange between southern and East Africa (Potts and Deino, 1995), our taxonomic revision instead implies greater regional distinction. Evidence that blesbok expanded out of southern Africa is now limited to provisionally identified blesbok-like specimens from Katanda (Brooks et al., 1995) and the Manonga Valley (Harrison and Baker, 1997). The assignment of the Lainyamok blesbok to *D. hypsodon* raises the possibility that these

specimens also belong to the same taxon and warrants a re-examination of the *Damaliscus* fossils from these sites. Further north in Ethiopia, late-middle and late Pleistocene faunas are reported as consisting entirely of extant species (Assefa, 2006; Assefa et al., 2008). However, the possibility of a taxonomically modern Ethiopian fauna at this time should be treated with caution, since the known records include very few specimens firmly identified to species, due to high

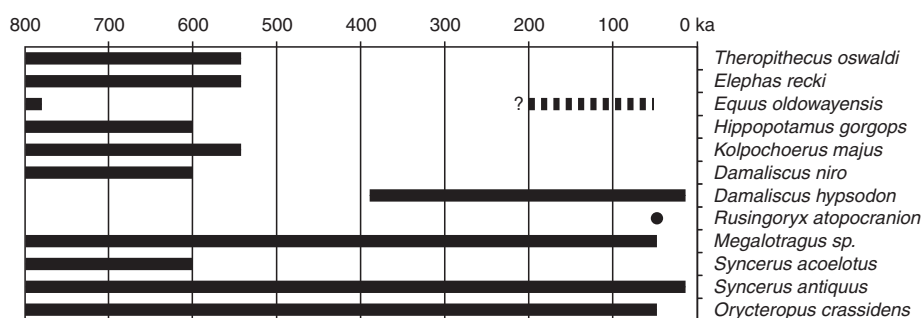


Fig. 8. Approximate last appearances (ka) of extinct middle and late Pleistocene mammals in East Africa. McBrearty (1992) reports a massive equid that is most likely *Equus oldowayensis* (JTF personal observation), from deposits at Simbi with preliminary ⁴⁰Ar/³⁹Ar age estimates of between 200 and 50 ka.

fragmentation and small samples (e.g., most alcelaphine specimens from Porc Epic Cave and the Kibish Formation are identified only to tribe).

Our reclassification of the small alcelaphine material from Lainyamok contributes to a growing literature indicating that a taxonomically modern equatorial East African bovid community did not emerge until the Holocene (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Tryon et al., 2010, 2012; Faith et al., 2011). Although the bovid species found today are well represented in the middle and late Pleistocene records, the numerically dominant taxa are now extinct. For example, *Damaliscus hypsodon* is the dominant bovid at Lainyamok and accounts for 23% of the bovid specimens (NISP) identified to genus or species. The dominance of extinct bovids continues in the late Pleistocene, with extinct taxa accounting for 55% of the bovids from Mfangano Island, 67% from Rusinga Island, and 66% from the Lukenya Hill sites (Marean, 1992; Tryon et al., 2012). In the global context, although the magnitude of African large mammal extinctions over the last 100,000 years is considered small in terms of the number of taxa lost (Barnosky et al., 2004; Koch and Barnosky, 2006), the extinctions dramatically reconfigured the equatorial East African large mammal community by eliminating the dominant bovid taxa. As discussed below, environmental change is likely the driving mechanism.

The dietary and locomotor adaptations of *Damaliscus hypsodon*, together with its paleoenvironmental associations (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Potts and Deino, 1995; Tryon et al., 2010, 2012), indicate a preference for open and dry grassland environments. Similar adaptations and habitat preferences have also been inferred for long-horn buffalo (*Syncerus antiquus*), giant wildebeest (*Megalotragus*), and *Rusingoryx atopocranion* (Klein, 1980; Vrba, 1987; Marean, 1990; Klein, 1994; Tryon et al., 2010; Faith et al., 2011). The last East African records of *D. hypsodon* and *S. antiquus* come from Lukenya Hill, where they disappear at the end of the Pleistocene (Marean, 1992). The Pleistocene–Holocene transition in East Africa was characterized by a marked increase in precipitation (Bonnefille et al., 1990; Taylor, 1993; Bonnefille and Chalieu, 2000; Kiage and Liu, 2006; Wolff et al., 2011). This likely drove the extinction of East Africa's dominant bovids by reducing the distribution of arid grassland environments, allowing moist grass grazers commonly seen today (e.g., *Connochaetes taurinus*, *Equus quagga*) to replace their arid-adapted counterparts (Marean, 1992; Faith et al., 2011). Today, where moist-grass grazers (e.g., plains zebra) and arid-adapted grazers (e.g., Grevy's zebra) overlap, the former outcompete the latter (Rubenstein, 2010), suggesting that in addition to habitat loss, biotic interactions may have also played a role in the extinctions. Although an improved extinction chronology is necessary, these changes may also explain

the extinction of *Rusingoryx* and *Megalotragus*, both known from late Pleistocene deposits in Kenya's Lake Victoria Basin (Tryon et al., 2010, 2012; Faith et al., 2011).

5.2. Emergence of the taxonomically modern East African mammal community

Potts (1998) presented evidence from Olorgesailie (southern Kenya rift) documenting the extinction of formerly abundant large-bodied grazing specialists between 780 ka and 500 ka. These include the Olduvai zebra (*Equus oldowayensis*) (Equidae), *Elephas recki* (Elephantidae), *Hippopotamus gorgops* (Hippopotamidae), and *Theropithecus oswaldi* (Primates). These taxa were survived by closely related extant species characterized by smaller body size and/or more versatile dietary adaptations, including Grevy's zebra (*Equus grevyi*), African elephant (*Loxodonta africana*), hippopotamus (*Hippopotamus amphibius*), and olive baboon (*Papio anubis*). The loss of specialized grazers is attributed to increased climate variability, which favored species capable of persisting across a broader range of environmental conditions (Potts, 1998).

A similar pattern characterizes the subsequent late Pleistocene extinctions within the East African bovid community, with the suite of extinct species characterized by extreme hypsodonty and/or body mass. For example, Fig. 9 plots body mass against the hypsodonty index for *Damaliscus hypsodon*, *Rusingoryx atopocranion*, and extant African bovids (extant data from Janis, 1988). The two extinct alcelaphines define the upper limit of hypsodonty index values, implying a specialized adaptation for grazing in arid environments. We lack comparable estimates of hypsodonty for East African *Megalotragus* and *Syncerus antiquus*, but note that both are the largest of their respective lineages (Alcelaphini and Bovini) and are also characterized (qualitatively) by elevated hypsodonty (Klein, 1980; Vrba, 1987; Marean, 1992).

The extinction of at least four bovids characterized by elevated hypsodonty and/or body mass near the end of the Pleistocene parallels the losses across a range of lineages earlier in time (Potts, 1998). Altogether, this suggests that the development of the taxonomically modern large mammal community in East Africa was a long-term process involving the loss of grazing species adapted to open and arid grassland environments. This pattern may be related to the high-amplitude 100 kyr glacial cycles during the late Quaternary, which would have favored the spread of grazing specialists during glacial phases but also contributed to extinctions in some lineages during deglaciations (e.g., the Pleistocene–Holocene transition).

6. Conclusions

The Lainyamok fossils previously attributed to *Damaliscus* cf. *dorcas* belong to a new extinct species that we designate as *Damaliscus hypsodon*. Included within the *D. hypsodon* hypodigm are the small alcelaphine remains from Lukenya Hill, Gol Kopjes, Kisese II, and the Lake Victoria Basin, and potentially the blesbok-like specimens from Katanda and the Manonga Valley. Ecomorphological evidence implies that *D. hypsodon* was adapted to grazing in arid and open grasslands. The presence of *D. hypsodon* at Lainyamok marks the onset of a regionally distinct equatorial East African bovid community dominated by extinct species, which likely emerged between 500 and 400 ka and persisted until the onset of the Holocene. Our reassessment of the Lainyamok assemblage suggests that the development of the taxonomically modern East African large mammal community was a long-term process characterized by the replacement of grazing specialists by more ecologically flexible extant taxa.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2012.08.005>.

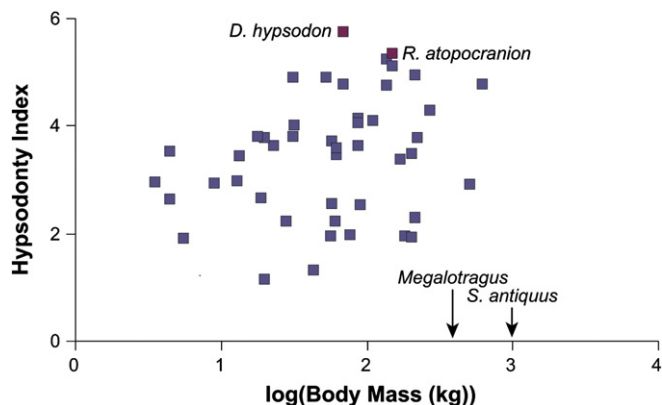


Fig. 9. Plot of body mass (kg) versus hypsodonty index for extant African bovids. The body mass of *Damaliscus hypsodon* is estimated as equivalent to *Damaliscus dorcas* and *Rusingoryx* estimated at ~150 kg. Arrows indicate approximate body mass of *Megalotragus* and *Syncerus antiquus*. Extant data are from Janis (1988).

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