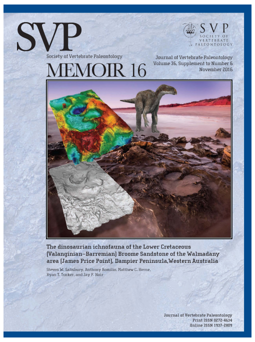

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ARTICLE

LATE PLIOCENE BOVIDAE FROM LEDI-GERARU (LOWER AWASH VALLEY, ETHIOPIA) AND THEIR IMPLICATIONS FOR AFAR PALEOECOLOGY

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ABSTRACT—Fossil bovids are described from the late Pliocene site of Ledi-Geraru, mainly from the Gurumaha and Lee Adoyta sedimentary packages (2.8–2.6 Ma). Finds include taxa already known from the slightly older Hadar Formation, such as the buffalo *Ugandax coryndonae*, the bongo-like *Tragelaphus rastafari-nakuae* lineage, an alcelaphin resembling *Parmularius pachyceras*, and a large impala. Differences from Hadar include the abundance of *Kobus sigmoidalis*, the absence of *K. oricornus*, and the presence of *Tragelaphus gaudryi* and probably also *Menelikia lyrocera*. The fossil bovids from Ledi-Geraru are mainly comparable to those known from contemporaneous assemblages in the Turkana Basin. *Menelikia* and *T. gaudryi* are characteristic of the Turkana Basin, and these are probably their first records from the Afar. A new species of *Beatragus* is also named. A well-preserved skull and skeleton of a fossil wildebeest from the Ogoyta sediments (<2.4 Ma) bears a mosaic of advanced and conserved traits that illuminate the evolution of the *Connochaetes* clade prior to the divergence of its two extant species. Taxonomic abundance, as well as functional analyses of postcranial elements, indicates that the ancient landscape at Ledi-Geraru was primarily made up of open habitats such as seasonal grasslands, with minor components of woodlands and wetlands. This contrasts with most localities from the Hadar Formation, which record more covered habitats. Comparisons with older Afar faunas indicate that environmental changes to drier and more open habitats were part of a long-term trend that goes back to at least 4 Ma, if not earlier.

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

The fossil sites of the Awash Valley, Ethiopia, have produced late Miocene to Pleistocene faunas, including human ancestors. To the north and east of Hadar lies the fossiliferous Ledi-Geraru area (Fig. 1), which was first explored in the 1970s by the International Afar Research Expedition (IARE). Since 2012, the Ledi-Geraru Research Project (LGRP) has explored the Lee Adoyta Basin, which lies in the eastern Ledi-Geraru area, with the goal of locating fossiliferous sediments in the 3.0–2.5 Ma time range (DiMaggio et al., 2015; Villmoare et al., 2015). This time frame has been a recurrent focus for hypotheses causally linking faunal (including human) evolution with global climate change (e.g., Vrba, 1985, 1995; deMenocal, 2004, 2011).

Knowledge of the 3–2.5 Ma interval in eastern African has relied mainly on the Turkana Basin, namely, Members B and C of the Shungura Formation, the Lomekwi Member of the Nachukui Formation (West Turkana), and the Tulu Bor and Lower Burgi members of the Koobi Fora Formation (East Turkana). Little is known about faunal change in the 3–2.5 Ma interval in the Afar Basin because sediments of this age are not common. Here we describe the fossil bovids of Ledi-Geraru, which alone account for ~50% of the LGRP fossil collection. The ecological diversity of this clade of large herbivores makes them a great proxy for paleoenvironmental reconstruction (Vrba, 1980; Greenacre and Vrba, 1984; Bobe and Eck, 2001). Besides describing new fossil material, our analyses aim to shed new light on the timing and magnitude of evolutionary change in the Afar region with respect to the paleoclimate record.

The majority of the Lee Adoyta Basin fossil assemblages derive from four overlying fault blocks (Fig. 1; see DiMaggio et al., 2015, for details). The Bulinan block is 10 m thick, with a tuff dated to 2.84 Ma four meters above its base. The Gurumaha block is 21 m thick with a tuff dated to 2.82 Ma and sediments in normal polarity. The Lee Adoyta fault block is 22 m thick with a basal tuff at 2.67 Ma and encompasses the Gauss-Matuyama polarity reversal at 2.581 Ma (DiMaggio et al., 2015). The Ogoyta fault block is younger and not yet well constrained.

MATERIALS AND METHODS

Fossil Collection

All fossils with LD numbers were collected as surface finds during paleontological surveys of the Lee Adoyta exposures except

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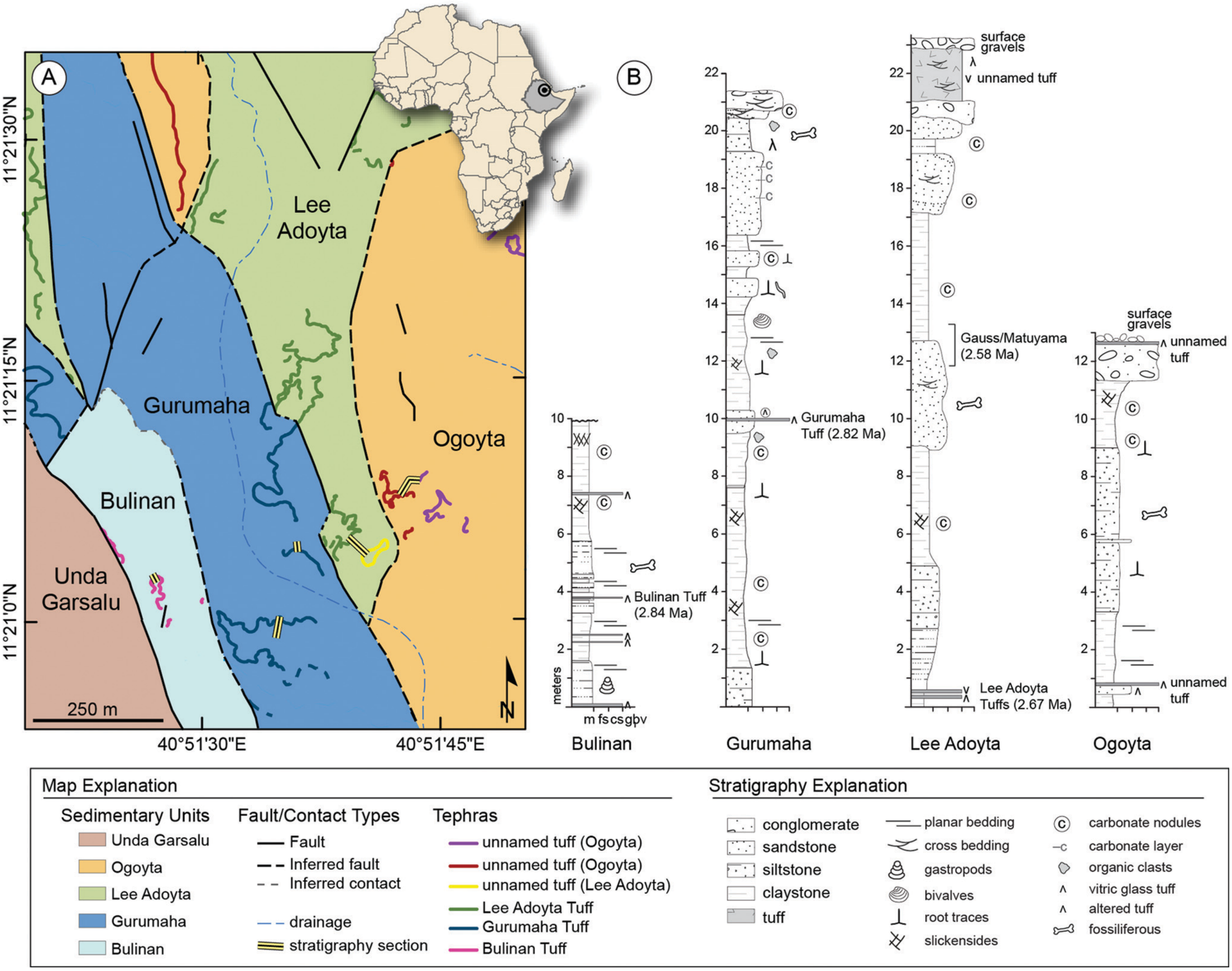

FIGURE 1. **A**, geologic map of the Lee Adoyta region in the Ledi-Geraru project area showing sedimentary units, tephra deposits, and faulting patterns. Note that the 'Garsalu' sedimentary package in DiMaggio et al. (2015) is now called the Ogoyta. **B**, stratigraphic sections from four fault blocks showing the position and age of tephras and the sedimentary context of fossils from Lee Adoyta (modified from DiMaggio et al., 2015). Courtesy E. DiMaggio.

for the LD 390-1 *Connochaetes* skull and skeleton, which was excavated in situ. The LGRP followed a 100% collection strategy for all material that was identifiable to the family level, including even very fragmentary remains. All specimens described here are listed in online Supplementary Table S1, and all measurements are given in online Supplementary Tables S2–S7.

Horn Core Torsion

In descriptions of horn core torsion, heteronymous and homonymous refer to spiraling that is anticlockwise or clockwise, respectively, in the right horn core as perceived from the base up. Extant bovids with heteronymous torsion include tragelaphins (*Tragelaphus* spp.), as well as addax (*Addax nasomaculatus*), blackbuck (*Antilope cervicapra*), and markhor (*Capra falconeri*). Extant species with homonymous torsion normally have less well-developed spiraling and include springbok (*Antidorcas marsupialis*), some populations of Grant's gazelle (*Nanger granti*), and many species of goats (*Capra* spp.) and sheep (*Ovis* spp.).

Analytical Methods

Postcranial Functional Morphology—Barr (2014) examined the relationship between astragalar dimensions and habitat in African bovids while controlling for phylogenetic effects (i.e., non-independence of morphology between closely related species due to shared evolutionary history). We used a modified version of his discriminant function (provided to us by Barr) that allows for use with just his five 'informative' measurements (i.e., those that have high habitat and low phylogenetic signals) on 18 measurable astragali from Ledi-Geraru. We also scored eight proximal phalanges, six intermediate phalanges, and two distal phalanges according to the verified discrete characters of DeGusta and Vrba (2005).

Species Diversity and Tribal Relative Abundances—Data on number of bovid specimens assigned to species and tribal levels were taken from the literature for Aramis (4.4 Ma; White et al., 2009), Asa Issie (4.1 Ma; White et al., 2006), and Woranso-Mille (3.77–3.5 Ma; Geraads et al., 2009). Species data for Hadar (3.5–2.9 Ma) come from Geraads et al. (2012), whereas tribal counts were taken by us. For tribal counts, we ignored indeterminate tribal affiliations (e.g., '?Antilopini') as well as Neotragini, Caprini (including Ovibovini), and Cephalophini because these are all rare and some are of very small size, meaning that they are subject to different preservation and collection biases than larger mammals. Species diversity was calculated using both conservative and relaxed taxonomies, which either excluded or included 'cf.' generic and specific designations. Results are very similar, and here we report the relaxed version. Rarefied species richness was calculated for all assemblages using the smallest number of specimens identified to species in a collection, which was 15 (for the Lee Adoyta assemblage). The Shannon diversity index, a measure of both species richness and evenness, was also calculated for each assemblage. Neither rarefied richness nor Shannon diversity was correlated with sample size (Spearman's rank correlation, $p = 0.5$). All diversity analyses were performed in R using the 'vegan' package (Oksanen et al., 2013).

Analyses of bovid relative abundances for paleoecological reconstruction at African sites have become common in the literature since Vrba's (1974, 1980) pioneering work. Taphonomic work has also since demonstrated that comparisons within a single broad clade (e.g., vertebrates vs. invertebrates) and a single broad depositional facies (e.g., terrestrial fluvial deposits) yield a single 'taphonomic domain,' considered fair for intersite comparisons of ratios, trends, etc. (see review by Behrensmeyer et al., 2000). Here, as in previous work, we take taphonomic biases such as preservational and collecting biases to be minimal. Our reasoning is that frequency data such as relative abundance patterns are robust to sampling intensity; Rift Valley fossil sites have broadly similar depositional environments (fluvial, lacustrine); the taxa compared (bovids) all have similar skeletal structure, implying consistency of preservation, recovery, and identification; these bovids are large in size (mostly >20 kg), minimizing biases against small taxa; and collecting strategies by the collecting teams at the different sites are broadly similar, focusing particularly on the recovery of fragmentary but diagnostic cranial remains.

Hypsodonty Ratios—Hypsodonty ratios were calculated in two ways: as crown height divided by length and as crown height divided by width. This was done for lower third molars that were unworn or in early wear stages (prior to fusion of the enamel ridges of the four main cusps). Crown height was measured on lingual surfaces as the greatest distance from the enamel-dentine junction to the tallest cusp. These we measured from the Ledi-Geraru and Hadar collections (National Museum of Ethiopia), Kanapoi and Lothagam (National Museums of Kenya), and the Kohl-Larsen Laetoli collections (Museum für Naturkunde, Berlin). From the literature we obtained measurements for Harrison's Laetoli collections (Gentry, 2011) and Langebaanweg and the Sterkfontein type site (both Gentry, 1980, with raw data kindly provided by A. Gentry). The majority of specimens from the Kohl-Larsen sites (namely, 'Vogelfluss' and 'Garussi') were probably collected from the Upper Laetolil Beds (Harrison and Kweka, 2011; F.B., pers. observ.), but there is a chance of mixing from the older Lower Laetolil and the younger Upper Ndolanya beds (preservational differences practically preclude anything younger). Data on extant alcelaphin hypsodonty were obtained from Janis (1988; raw data kindly provided by C. Janis). In this data set, age, but not dental wear stage, was recorded. In order to avoid lower hypsodonty values as a result of tooth wear, we selected only the most hypsodont 50% of individuals aged between 2 and 4 years old. For comparison, oryx (*O. leucoryx*) and buffalo (*Syncerus caffer*) have similar life spans to alcelaphins (12–20 years in the wild, data variable), and in both these species the lower m3 erupts and remains in early wear stages between about 2 and 5 years of age (Kingdon, 1982:7; Ancrenaz and Delhomme, 1997). All raw data are given in Table S7.

Abbreviations

Institutional Abbreviations—**A.L.**, 'Afar Locality,' specimens collected by the International Afar Research Expedition (IARE) and Hadar Research Project, housed in the National Museum of Ethiopia, Addis Ababa, Ethiopia; **GAM-VP**, specimens from sites at Gamedah in the Middle Awash, housed in the National Museum of Ethiopia; **KNM**, specimens housed in the National Museums of Kenya, Nairobi, Kenya; **HWK EE**, site HWK EE at Olduvai Gorge, Tanzania; **LD**, specimens collected from the Lee Adoyta region by the Ledi-Geraru Research Project (LGRP), housed in the National Museum of Ethiopia, Addis Ababa, Ethiopia; **MfN** or **MB. Ma**, specimens housed in the Museum für Naturkunde, Berlin, Germany; **NHM**, specimens housed at the Natural History Museum, London; **Omo**, specimens from the Shungura Formation, housed at the National Museum of Ethiopia.

Anatomical Abbreviations—**AP**, anteroposterior length; **DAP**, anteroposterior diameter; **DT**, transverse diameter (perpendicular to DAP); **M** or **m**, molar tooth, upper (M) or lower (m); **P** or **p**, premolar tooth, upper or lower; **R** or **L**, right or left; **T**, transverse width.

All Ledi-Geraru fossils are housed at the National Museum of Ethiopia, Addis Ababa, under the Authority for Research and Conservation of Cultural Heritage.

SYSTEMATIC PALEONTOLOGY

ARTIODACTYLA Owen, 1848
BOVIDAE Gray, 1821
BOVINAE Gray, 1821
BOVINI Gray, 1821
UGANDAX Cooke and Coryndon, 1970
UGANDAX CORYNDONAE Gentry, 2006

Referred Specimen—Gurumaha: LD 285-3, R and L horn cores with conjoined frontals.

Description and Comparisons—Horn core and pedicel (Fig. 2A) located above the posterior orbit; basal horn core cross-section triangular, becoming more circular distally; anterior keel well developed, continuing down the pedicel and frontal almost to the level of the supraorbital foramina; anteromedial pedicel swollen; frontals between the supraorbital foramina concave; supraorbital foramina moderately large, round to oval in shape; frontal bones very thick at midline, with extensive frontal sinuses reaching into the pedicel and probably to the basal horn core limit. Horns moderately divergent, slightly inclined, with weak medial curvature in anterior view, and a straight posterior edge in side view. Midline frontoparietal suture deeply indented anteriorly. Temporal lines just behind the horn cores very prominent ridges; dorsal surface of frontal concave. Postcornual fossa absent. Measurements given in Table 1. In both size and morphology, LD 285-3 is a match for specimens of *Ugandax coryndonae* from the Hadar Formation (Gentry, 2006).

Discussion—*Ugandax coryndonae* is perhaps the best known Plio-Pleistocene African bovin, represented by a large number of specimens from Hadar (Gentry, 2006; Geraads et al., 2012) and Woranso-Mille (Geraads et al., 2009). A single specimen from the Hata Member of the Middle Awash may extend the younger limit of this species to 2.5 Ma (Bibi, 2009). *Ugandax* probably gave rise to *Syncerus* (Gentry, 2006), although the earliest records of *Syncerus* may overlap those of this species (see next entry).

SYNCERUS Hodgson, 1847
cf. *SYNCERUS*

Referred Specimens—Lee Adoyta: LD 61-1, cranial parts with right horn core, three upper molars, braincase fragments; LD 242-2, R and L horn core basal.

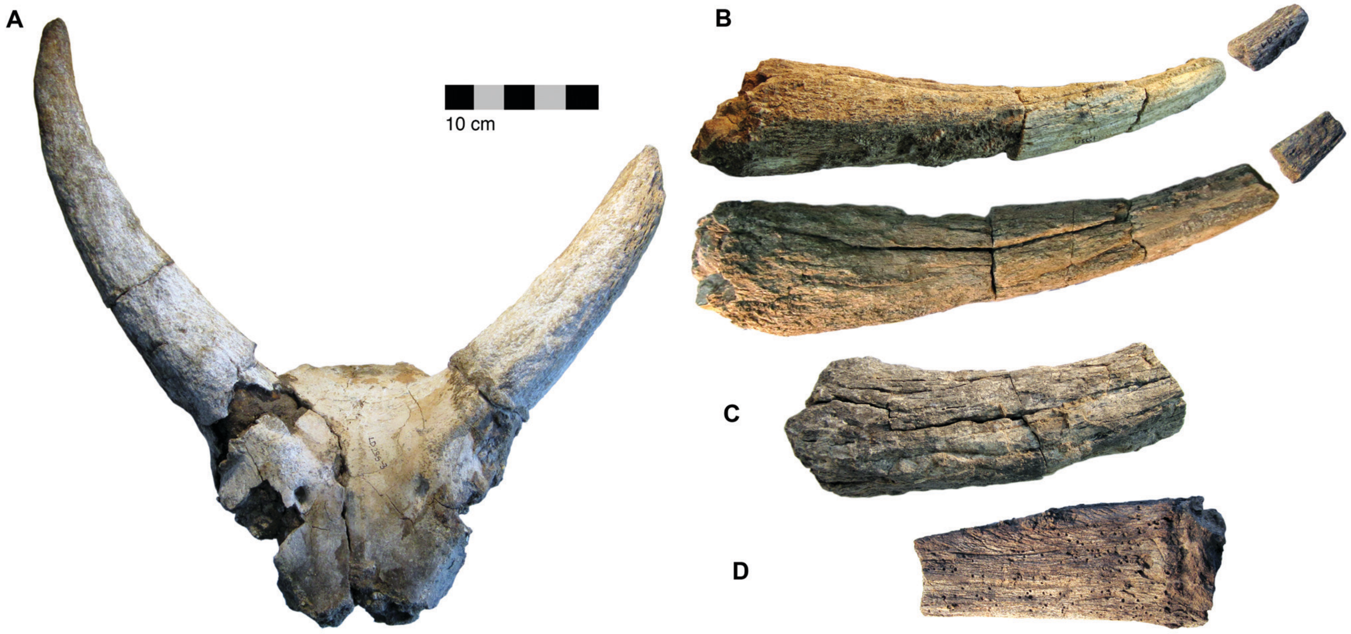

FIGURE 2. Bovini. **A**, *Ugandax coryndonae*, LD 285-3, partial cranium with horn cores. **B**–**C**, cf. *Syncerus*. **B**, LD 61-1, left horn core in anterior (top) and medial (or dorsal) (bottom) views; **C**, LD 242-2, left horn core in anterior view. **D**, Bovini cf. *U. coryndonae*, LD 302-7, indeterminate basal (?right) horn core (?ventral view).

Description—Two horn cores suggest the presence of at least a second bovin species (Fig. 2B–C). The LD 61-1 horn core would have been quite long (>400 mm, preserved length) and probably widely divergent (estimated 120°). It is straight in anterior view, with faint posterior curvature in medial (= dorsal in case of high divergence) view, with some mediolateral (= dorsoventral) compression, a sharp anterior keel, a lateral (= ventral) keel located far posteriorly, and a flat posterior surface. It appears to be from the right side, which results in the presence of weak heteronymous torsion. The left horn core fragment of LD 242-2 is the most complete piece of this specimen. It exhibits strong heteronymous torsion, posterior curvature of both anterior and posterior edges, and a triangular section with three keels. Anterior and lateral keels are sharpest, whereas the posterior keel is weak and rounded. The lateral keel is located far anteriorly, with a flat anterior surface between it and the anterior keel. Almost no compression is present in these specimens.

Comparisons—The presence of keels, flat surfaces, a triangular cross-section, weak curvature, and heteronymous torsion ally these specimens with *Ugandax* and *Syncerus* (although these in fact are all primitive features for Bovini). They are differentiated from those of *Pelorovis* (*P. turkanensis, P. oldowayensis*), which bear no keels, are rounded at the base, strongly curved anteriorly, and with homonymous torsion. They are also differentiated from the type horn of *P. kaisensis*, which is much larger, straighter, bears no keels, and has a rounded cross-section (Geraads and Thomas, 1994). LD 61-1 may differ from *Ugandax coryndonae* in a direction towards *Syncerus* in the greater divergence, apparently broader and more flattened medial (dorsal) surface, greater mediolateral (dorsoventral) compression of the horn core above the base, and weaker medial (dorsal) curvature. Also, in LD 61-1, the anterior edge seems weakly curved posteriorly whereas the posterior edge (although broken) is straight. In *U. coryndonae*, both anterior and posterior edges tend to follow a similar course, being either weakly curved backwards (as in the holotype A.L. 194-1) or relatively straight (LD 285-3). At over 400 mm (the preserved length of the horn core, including a fragment previously numbered 'LD 553-1'), the LD 61-1 horn core is longer than most specimens of *U. coryndonae*, which do not often surpass 300 mm in length.

Gentry (1985) compared Shungura Member C *Syncerus* horn cores with those of *Syncerus acoelotus*, named from the much younger Olduvai Bed II, but later (Gentry, 2010) referred them to *Simatherium shungurense*. We reexamined some of the Shungura material (e.g., Omo 18-1967-114, Omo 18-1961-415) and prefer Gentry's early (1985) opinion. These horns were probably widely divergent, with well-developed mediolateral (dorsoventral) compression, a flattened medial (dorsal) surface, three keels with the posterior keel sharpest and lateral (ventral) keel located far anteriorly, a flat anterior surface and a wide posteroventrally facing surface, a posteriorly curved anterior outline and straight posterior outline, and only very slight medial (dorsal) curvature. They are intermediate in length between the two illustrated specimens from Olduvai (Gentry and Gentry, 1978:pls. 2, 4, fig. 2) but differ in having a posterior edge that is straight rather than posteriorly curved. They differ greatly from horns of *Simatherium shungurense*, which are much longer, more slender, and more rounded than those of *Ugandax* and *Syncerus acoelotus* (Geraads, 1995).

TABLE 1. *Ugandax coryndonae*: measurements (mm) of LD 285-3, partial cranium.

Basal horn core DAP	67.5 R, 66.6 L
Basal horn core DT	64.7 R, 60.0 L
Horn core length	290 R, 220+ L
Basal divergence	80°
Inclination against braincase	70°
Distance across basal horn cores	245
Distance between basal horn cores	140
Distance between supraorbital foramina	79.1
Distance across dorsal orbits	210e

+, preserved dimension of a broken specimen; **e**, estimate.

Specimen LD 61-1 differs from the Shungura Member C specimens in the location of the lateral (ventral) keel, which is at the posterior limit of the horn core, resulting in a flat posterior surface in LD 61-1 in contrast to a flat anterior surface in *Syncerus*. Furthermore, the anterior keel is sharper than the posterior one, and LD 61-1 has less mediolateral (dorsoventral) compression and medial (dorsal) flattening. In all these features, LD 61-1 remains closer to *U. coryndonae* or other primitive Bovini. Unfortunately, the pedicel and frontal anterior to the horn core are not preserved, preventing comparison with the basal anterior keel 'bulging' or the long continuation of the anterior keel rugosity down the pedicel that are typical of *U. coryndonae*. Specimen LD 242-2 fits the Shungura *Syncerus* horn cores in some features but differs in the lack of a straight posterior border in dorsal view, in less dorsoventral compression, and in the much stronger torsion and probably much greater length. It provides another suggestion of a *Syncerus*, but one that doesn't match either LD 61-1 or the Shungura *Syncerus* well.

Discussion—These two fragmentary specimens differ from each other, and it is very likely that they do not belong to the same species. The best we can say is that they are both unlikely to be *U. coryndonae* and therefore suggest the presence of a second bovin species at Lee Adoyta. Both specimens bear some similarity to early *Syncerus*, but differences preclude a match with the better-known Shungura material.

BOVIN, gen. et sp. indet.

Referred Specimens—Gurumaha: LD 15-1, L lower molar fragment; LD 156-2, R lower m1 or m2; LD 274-1, lower m1 or m2 fragment; LD 302-7, R? horn core basal; LD 302-8, R lower m1 or m2; LD 304-48, L lower p3 or p4 fragment; LD 392-1, molar fragment; LD 483-3, L upper M2; LD 509-1, R upper maxilla fragment M2–M3; LD 698-1, L upper M1 or M2; LD 709-1, R lower molar fragment.

Lee Adoyta: LD 32-1, L lower p3 or p4; LD 116-1, R and L mandibles fragmentary, with alveoli but no teeth; LD 533-1, R upper molar fragment; LD 560-1, L upper molar fragment; LD 574-1, L lower mandible p4–m3.

Description and Comparisons—The teeth are assigned to Bovini based on their large size and the presence of complex enamel ridges and large basal pillars. They might all be of *U. coryndonae*, and overall size is similar to the teeth of this species at Hadar.

Specimen LD 302-7 (Fig. 2D) is a basal horn core that may also be of *U. coryndonae*. Orientation relies on a sliver of temporal fossa that lines up well with that of a right horn core of *Ugandax* rather than *Syncerus*.

Two proximal phalanges are probably Bovini based on their large size (LD 137-1, LD 291-1). These have roughened medial surfaces, indicative of 'forest' or 'heavy cover' habitats (DeGusta and Vrba, 2005). Two large astragali may also be bovin (LD 71-1, LD 324-5).

TRAGELAPHINI Blyth, 1863
TRAGELAPHUS Blainville, 1816
TRAGELAPHUS GAUDRYI Thomas, 1884

Referred Specimens—Gurumaha: LD 341-3, L lower p4; LD 503-1, L horn core midsection; LD 604-1, L lower mandible fragment m1–m3; LD 668-7, R horn core basal. Lee Adoyta: LD 72-1, L horn core basal.

Diagnosis—(Revised following Gentry, 1985.) A tragelaphin of medium size, horn cores with mediolateral compression, strong and helical heteronymous torsion completing more than a single whorl (i.e., ≥360°), a sharp anterior keel, a rounded medial surface with a posteromedial edge that may sometimes be a keel, and slightly flattened anterolateral and posterolateral surfaces with a posterolateral keel that is located far anteriorly. The posterolateral keel is variably present basally but is normally sharp at midsection and distally. The resulting basal horn core cross-section (which is normally consistent a fair way up) is of a rounded and medially inflated triangular to quadrangular shape.

In these horn core characters, *T. gaudryi* is differentiated from almost all tragelaphin species, because these species normally exhibit a triangular cross-section with anteroposterior compression (if any at all) and are normally accompanied by a sharp posterolateral keel and a weaker anterior keel. The greater kudu (*T. strepsiceros*), its probable ancestor *T. lockwoodi* from Hadar (Bibi, 2009; Reed and Bibi, 2011), and the lesser kudu (*T. imberbis*) are the only other tragelaphins with mediolateral compression, greater than a whorl of torsion, and the anterior keel sharpest. The first two of these kudus are mostly larger than *T. gaudryi*, but there is some overlap in size, and with fragmentary specimens it is difficult to differentiate a large *T. gaudryi* from a small *T. strepsiceros* or *T. lockwoodi*. This is especially true of horn core midsections missing the base, or juvenile specimens. The tragelaphin that comes closest to the horn core morphology of *T. gaudry* is the lesser kudu *T. imberbis*. Horn cores of *T. gaudryi* (especially from Shungura Member G and younger) are difficult to distinguish from *T. imberbis*, and the two species probably form a single lineage (Gentry, 1985, 2010).

Description—LD 72-1 and LD 668-7 (Fig. 3A–B) are both slightly weathered such that the anterior and posterolateral keels are discernible but not prominent. The anterior keel is better developed, and the surface between it and the posterolateral keel forms the flattest part of the horn core. The posterolateral keel originates quite anteriorly along the horn core base in LD 668-7, although perhaps more posteriorly in LD 72-1. The anteromedial corner is inflated outwards such that the horn core has a rounded to quadrangular cross-section. Heteronymous torsion is well developed, with marked lateral divergence above the base. Specimen LD 72-1 preserves a curved length of ~20 cm, with about 90° of torsion preserved; this could have easily reached 360° or more when complete. Mediolateral compression is strong throughout. Specimen LD 503-1 is a horn core midsection that is not very indicative on its own but matches the features shown by the other two specimens. Teeth assigned to this species are done so on the basis of size (smaller than the next species).

Comparisons—Distinguishing a large *T. gaudryi* from a small and primitive *T. strepsiceros* is not straightforward. The three horn core specimens from Ledi-Geraru do not fit among the known samples of *T. lockwoodi* from Hadar, nor among those of early *T. strepsiceros* from Hata and Koobi Fora. They are differentiated from *T. strepsiceros* and *T. lockwoodi* by their smaller size and less rounded basal cross-sections, with more flattened posterolateral surface, and retention of stronger posterolateral and posteromedial keels at the base. They are slightly larger than horns of extant *T. imberbis* and match in size and shape specimens of *T. gaudryi* from the Shungura Formation (Gentry, 1985). Resemblance may be closer to specimens from Members E and F (such as Omo 58-1968-2301; Fig. 3C) rather than those from older or younger intervals.

Discussion—*Tragelaphus gaudryi* was first named from Ain Jourdel in Algeria (Thomas, 1884), but it is best known from Shungura Formation Members B–H (Gentry, 1985). Horn cores of *T. gaudryi* from Member G and younger levels are difficult to distinguish from those of *T. imberbis*, the extant lesser kudu, and this appears to represent in situ phyletic evolution (Gentry, 1985).

Neither *T. gaudryi* nor *T. imberbis* has been securely recorded from any other fossil sites (Gentry, 2010). The *T.* aff. *gaudryi* from Hadar (Geraads et al., 2012) is not closely related (see Supplemental Data 1). Vrba (1995:appendix 27.2) recorded *T. gaudryi* from the Middle Awash site of Gamedah. We examined this specimen (GAM-VP-1/15); it is large and the weakness of the horn core keels at the base and the more oval and mediolaterally compressed basal cross-section is a better fit for a small *T. strepsiceros*.

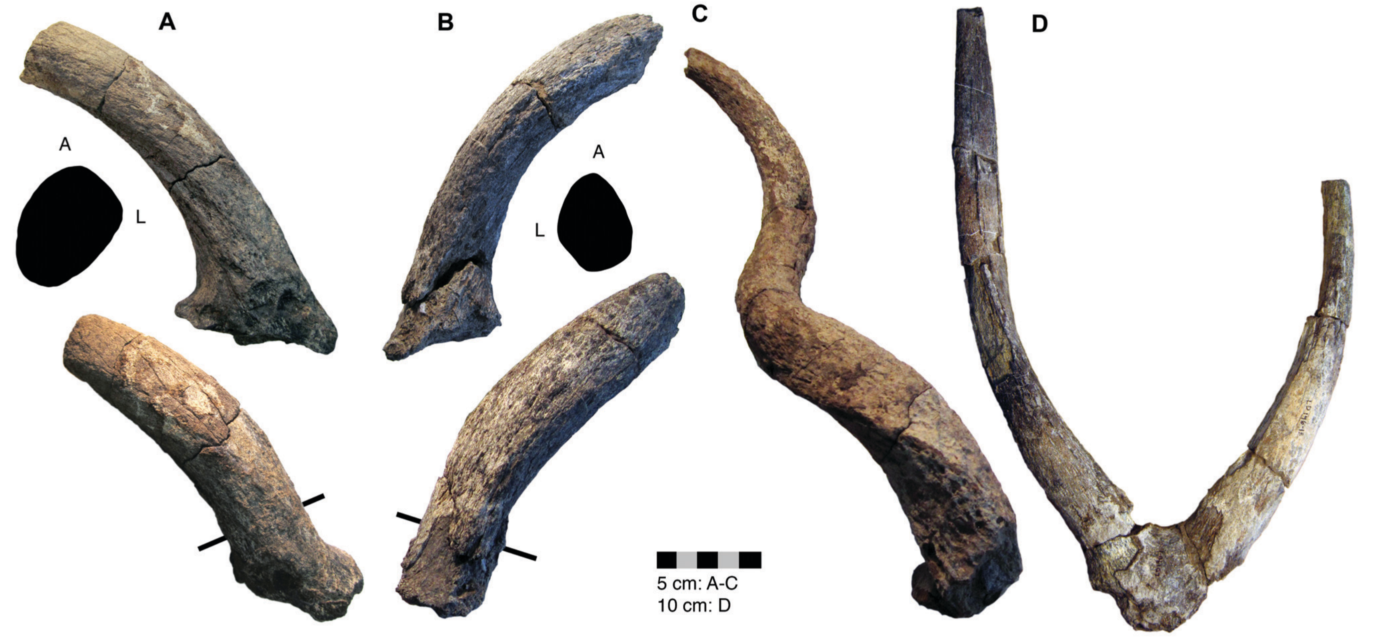

FIGURE 3. Tragelaphini. **A**–**B**, *Tragelaphus gaudryi*. **A**, LD 668-7, right horn core in lateral (top) and anterior (bottom) views; **B**, LD 72-1, left horn core. Lines mark location of cross-sections drawn to scale, with A and L denoting anterior and lateral sides. **C**, *Tragelaphus gaudryi*, Omo 58-1968-2301, left horn core from the Shungura Formation (Member E/F) in anterior view. **D**, *T. rastafari* or *nakuae*, LD 196-1, frontlet with horn cores.

In contrast, the greater kudu *T. strepsiceros* is widely recorded from eastern and southern African sites (Gentry, 2010) but is rare in the Shungura Formation. Its probable ancestor, *T. lockwoodi*, is so far known only from the Afar (Reed and Bibi, 2011), and perhaps the earliest records of *T. strepsiceros* are also in the Afar (Hata Member, Middle Awash; Heinzelin et al., 1999; Bibi, 2009). Accordingly, one would have expected the greater kudu lineage to be present at Ledi-Geraru, rather than *T. gaudryi*. These specimens therefore come as some surprise.

Despite morphological similarities, molecular evidence indicates that the lesser and greater kudus are not sister species (Willows-Munro et al., 2005; Hassanin et al., 2012). Any similarities in their horns must therefore have been acquired independently. The fossil record of the *T. lockwoodi-strepsiceros* and *T. gaudyri-imberbis* lineages appears to support this view.

TRAGELAPHUS RASTAFARI Bibi, 2011, or *T. NAKUAE* Arambourg, 1941

Referred Specimens—Gurumaha: A.L. 70-12, R and L horn cores left basal, right midsection; LD 94-1, R horn core midsection near base; LD 108-1, L horn core basal; LD 140-1, R horn core midsection; LD 143-1, L horn core midsection; LD 147-1, R cranium with horn core; LD 148-2, R horn core distal; LD 182-8, R lower m1 or m2; LD 196-1, R and L frontals with horn cores almost complete; LD 304-44, upper molar fragment; LD 341-2, L horn core basal; LD 346-5, R lower molar fragment; LD 450-1, L horn core distal fragment; LD 483-8, L upper M1; LD 483-10, upper molar fragment; LD 489-2, R lower m1; LD 646-1, L lower p3; LD 702-1, R upper M3. Lee Adoyta: LD 186-1, L horn core midsection; LD 205-1, R horn core distal; LD 259-1, L mandible with m2–m3.

Description and Comparisons—These horn core fragments, best represented by LD 196-1 (Fig. 3D), are of a large tragelaphin with spiraling of probably three-quarters of a whorl when complete, triangular cross-section with anteroposterior compression, and a strong posterolateral keel and a weaker anterior keel. The length and slenderness of the horn cores matches either *Tragelaphus rastafari*, known from ~3.8 to 2.8 Ma, or its descendant *T. nakuae*, specifically specimens from 2.8 to 2.3 Ma (Bibi, 2011). Specimens of *T. nakuae* younger than about 2.3 Ma have shorter horns that only spiral about half a whorl (~180°), with wide bases and rapid narrowing distally. The main distinguishing feature between *T. rastafari* and early *T. nakuae* is the presence of a prominent transverse torus in the supraoccipital area in *T. nakuae*, which can be extremely large in specimens younger than 2.3 Ma. However, the supraoccipital region is not preserved among the Ledi-Geraru remains, so we cannot be certain of the specific identity. Dental specimens are assigned to this lineage based on their large size.

ANTILOPINAE Gray, 1821
REDUNCINI Knottnerus-Meyer, 1907
KOBUS A. Smith, 1840
KOBUS SIGMOIDALIS Arambourg, 1941

Referred Specimens—Gurumaha: LD 97-1, L horn core basal with frontlet; LD 110-3, L horn core midsection; LD 110-7, R horn core basal with frontlet; LD 266-2, horn core distal; LD 267-1, R horn core basal; LD 381-1, L horn core basal; LD 387-1, R? horn core basal; LD 707-4, L horn core basal; LD 708-1, R horn core basal. Lee Adoyta: LD 324-6, horn cores two midsections; LD 584-1, horn core distal. Unknown: LD 119-1, R horn core basal and midsection (non-conjoining).

Description—These horn cores arise above the orbit, are compressed mediolaterally, with weak to moderate posterior curvature basally. The approach to a straight midsection with weak medial curvature can be seen in LD 97-1. The lateral surface is flattened, there is a variably expressed posterolateral ridge or keel, and transverse ridges are prominent. The anteroposterior long axis of the basal horn core is weakly rotated to the sagittal plane. Pedicels are short, and the horn core–pedicel transition is very prominent (a common feature of reduncins). Fine longitudinal grooving covers the horn core, with wider grooves on the posterior surface. Postcornual fossa small and deep. The best specimens are LD 97-1 and LD 110-7 (Fig. 4A–B). The former

FIGURE 4. Reduncini. **A**–**B**, *Kobus sigmoidalis*. **A**, LD 110-7, right basal horn core, lateral (left) and anterior (right) views; **B**, LD 97-1, left basal horn core, anterior and lateral views. **C**–**D**, cf. *Menelikia lyrocera*. **C**, LD 659-1, right basal horn core in medial (at left) and anterior views; **D**, LD 661-2, left basal horn core in anterior and lateral views.

bears a well-fused interfrontal suture that is very weakly raised. Breaks on the left side show the frontal sinuses ending just anterior to the supraorbital foramen (in LD 381-1, the sinuses may reach the anterior edge of the horn core). The supraorbital foramen is large, set in a large teardrop-shaped fossa, and set far from the midline (as in waterbuck or lechwe, and unlike kob).

Comparisons—These horn cores are distinguished from most specimens of *Kobus kob* in having larger basal size, stronger mediolateral compression, less flattening of the posterior surface, and less posterior curvature basally. They differ from *Kobus ellipsiprymnus, K. oricornus*, and *K. ancystrocera*, all of which have much weaker basal posterior curvature if any. They further differ from *K. oricornus* (abundant at Hadar), which has a rounded to anteroposteriorly compressed base and weak to absent transverse ridges (Geraads et al., 2012). They differ greatly in basal compression, curvature, and ridges and divergence and inclination from the Chadian *K. korotorensis* and *K. tchadensis* (Geraads et al., 2001). Rather, they resemble horns of *K. sigmoidalis* (and its probable descendants the extant lechwe, *K. leche*, and waterbuck, *K. ellipsiprymnus*).

The type specimen of *K. sigmoidalis*, a frontlet with complete left and right horn cores, is named from 'Bourillé' in the Shungura (Arambourg, 1941), which probably correlates with lower Member G (Heinzelin, 1983). The Lee Adoyta horn cores appear shorter, with more posterior basal curvature and less enlarged fossae around the supraorbital foramina than the holotype and specimens of *K. sigmoidalis* from Member G, the Upper Burgi Member, Olduvai Bed I, and the KBS Member (Gentry and Gentry, 1978; Gentry, 1985; Harris, 1991). In these features, they are more like a horn core from the lower Tulu Bor (Harris, 1991: fig. 5.22). Further comparison is needed with the handful of early records of *K. sigmoidalis* from the Moiti, Kataboi, Lokochot, Tulu Bor, and Upper Lomekwi Members (~4–2.5 Ma) at East and West Turkana (Harris et al., 1988; Harris, 1991).

Discussion—*Kobus sigmoidalis* is abundant at Lee Adoyta, but absent from Hadar, whereas *K. oricornus* is abundant at Hadar and absent from Lee Adoyta. This may reflect the younger age of Lee Adoyta, because the same pattern in the Shungura Formation (Members B and C; Gentry, 1985) suggests a possible regional replacement of one species by another around 2.8 Ma. Vrba (2006) believed that *K. sigmoidalis* could be descended from *K. basilcookei* from the 4.4 Ma Lower Aramis Member of the Middle Awash. Its evolution might therefore have occurred in situ in the Afar, except for the conspicuous absence of *K. sigmoidalis* from Hadar (Geraads et al., 2012). Otherwise, in the Afar, *K. sigmoidalis* has previously been noted in the faunal list from the 2.5 Ma Hata Member of the Middle Awash (Heinzelin et al., 1999). It is recorded as possibly present (but rare) in the Boolihinan (~1.7–1.5 Ma) and Dark Paleosol (~1.4–0.9 Ma) beds at Gona (Everett, 2010), although differentiating this species from its descendant, the living waterbuck *K. ellipsiprymnus*, becomes difficult after about 2 Ma (Gentry, 1985).

MENELIKIA Arambourg, 1941

Generic Diagnosis—(Revised following Gentry, 1985.) A medium- to large-sized reduncin (about the size of a large lechwe) distinguished from *Kobus, Redunca*, and all other known reduncins most clearly by the presence of expanded frontal sinuses (thick frontals, longer pedicels), homonymous horn core torsion, small supraorbital foramina with simple opening lacking a deep fossa, frontal between the supraorbital foramina flatter and less depressed downwards, postcornual fossa shallow or absent, transverse ridges less developed, often very weak or absent proximally, and weak to moderately developed distally. The horn core anteroposterior axis is rotated to the sagittal plane. In anterior view, the horns are weakly divergent at the base (ca. 20° in *M. lyrocera*) but strongly divergent (approaching

160°) at their midsections. Horn core surfaces bear longitudinal grooving along the entire horn core, but unlike *Kobus* and *Redunca* this is typically most developed (wider and deeper grooving) on the anterior rather than the posterior surface. The horn core–pedicel junction can be quite rugose and prominently raised, especially in *M. lyrocera*. Nuchal ridges more pronounced and anterior tuberosities not quite as large and not splayed outwards as in *Redunca* and *Kobus*.

MENELIKIA LYROCERA Arambourg, 1941
cf. *MENELIKIA LYROCERA*

Diagnosis—A species of *Menelikia* differing from *M. leakeyi* by horn cores with more pronounced homonymous torsion, stronger posterior curvature, and greater divergence above the base; horns become shorter in later representatives (especially <2 Ma); enlarged horn core bases exhibiting little or no compression; and frontal sinuses more developed, in some individuals completely hollowing out the pedicels (resembling the alcelaphin condition).

Referred Specimens—Gurumaha: LD 659-1, R? basal horn core; LD 661-2, L? basal horn core.

Description—Specimens LD 661-2 and LD 659-1 (Fig. 4C–D) were surface finds 8 m apart and very likely derive from the same individual. These are large horn cores with weak mediolateral compression and pronounced homonymous torsion, curving posteriorly at the base then laterally above. The basal break in LD 661-2 preserves a sliver of smooth surface, indicating that the pedicel was hollow. Transverse ridges are present on what are presumably the anterior and anterolateral surfaces, and these are well developed and widely spaced. Both specimens lack keels or flattening of any surface and exhibit fine longitudinal grooving on the posterior surface and deep and wide grooves on the anterior surface. The anterior horn core is also marked by a thick rugose surface, clearest in LD 659-1.

Comparisons—The LD 661-2 and LD 659-1 horns differ from those of *Kobus* spp. (including *K. sigmoidalis*) in having a lateral surface that is not flattened, posterolateral keel absent, and the presence of expanded frontal sinuses entering the pedicel. There is no good match among alcelaphins. Even by switching the siding of the specimens, the torsion and curvature cannot be made to match horns of *Beatragus* or *Connochaetes* or *Parmularius* species. All these features, however, agree with *Menelikia*, and in particular *M. lyrocera*. The rugose anterior horn core surface is also very well matched by numerous specimens of this species from Shungura Member G. In the majority of *M. lyrocera* specimens, the frontal sinuses end anterior to the pedicel, but in a few they extend into the pedicels right up to the horn core base, as seen in LD 661-2. The development of sinuses, the strong torsion and curvature, rapid diminution of size from the base, and large size are all a good match with *M. lyrocera*, but not *M. leakeyi*, which retains more of a *Kobus*-like morphology. The two LD specimens are a good match in both size and morphology with horn cores of *M. lyrocera* from the Turkana Basin (Gentry, 1985; Harris, 1991). Given their fragmentary nature, however, we prefer to wait for further specimens before being certain of the presence of *Menelikia* in the Afar.

Discussion—*Menelikia lyrocera* is an extinct reduncin antelope that is well documented from the Turkana Basin and has otherwise only been recorded from Kaiso in Uganda (Geraads and Thomas, 1994). The new LD horn cores (probably from a single individual) may extend this taxon's range into the Afar. The rarity of *Menelikia* relative to *Kobus* may have been due to differing habitat preferences. Modern reduncins have strong affinity to wetland habitats, and Spencer (1997) proposed that *Menelikia* may have depended on edaphic grasslands that remained wet year-round, with a lower tolerance for seasonality than extant *Redunca* and *Kobus*. It is conceivable that perennial wetlands were far less widespread or stable in the Afar than in the Turkana Basin (especially along the Omo River), and that the final extinction of *Menelikia* was driven by increased aridity and seasonality.

REDUNCINI, gen. et sp. indet.

Referred Specimens—Gurumaha: LD 182-3, R upper M1 or M2; LD 278-1, L upper M1 or M2; LD 283-2, R lower m1 or m2; LD 293-1, L mandible with m1; LD 304-67, L lower m1 or m2; LD 315-10, R upper molar fragment; LD 335-2, R lower m1 or m2 fragment; LD 377-1, L lower m1 or m2; LD 382-1, L lower p4, m2, m3; LD 437-1, lower molar fragment; LD 447-5, L lower m3; LD 483-1, R lower m3 partial; LD 483-2, R lower molar fragment; LD 487-1, lower mandible m1. Lee Adoyta: LD 70-1, R upper molar fragment; LD 90-1, L mandible with m1–m3; LD 249-1, L lower mandible with p4–m1. Ogoyta: LD 375-1, L lower mandible with maxillary fragment.

Description and Comparisons—These dental remains are all of similar size and likely belong to *K. sigmoidalis*. They are smaller than specimens from Turkana attributed to *K. sigmoidalis* (Harris, 1991) and to living *K. ellipsiprymnus* and rather fall within the size range of living *Kobus leche*.

ALCELAPHINI Brooke in Wallace, 1876
BEATRAGUS Heller, 1912

Generic Diagnosis—(Modified from Gentry and Gentry, 1978; Vrba, 1997.) Alcelaphins of medium to large size. Most clearly distinguished by horn cores that are long, arise above or just behind the orbit, have their maximum diameter moderately to strongly angled to the midfrontal suture, diverge strongly from the base, with weak heteronymous torsion, weak to well-marked transverse ridges, and end in elongated tips that are relatively straight and with divergence moderate to absent. Other features that may not be unique to *Beatragus*: moderately to greatly prominent nuchal crests; and basioccipital with continuous and raised longitudinal ridges connecting prominent anterior and posterior tuberosities, and a wide valley in between. Greatly reduced second premolars, lower p2 usually absent in *B. hunteri*, and perhaps in fossil species as evidenced by *B. whitei* (= *B. antiquus remotus*) from Ahl al Oughlam (Geraads and Amani, 1998; Gentry, 2010).

Type Species—*Beatragus hunteri* (Sclater, 1889). No known fossil record besides a single reported specimen from Lainyamok (Potts and Deino, 1995).

Other Species—*Beatragus antiquus* Leakey, 1965: Olduvai Bed I (Leakey, 1965), Shungura Formation Member G (Gentry, 1985), Koobi Fora Formation Upper Burgi, KBS, and Okote Members (Harris, 1991). *Beatragus whitei* Vrba, 1997: Matabaietu in the Middle Awash (Vrba, 1997), and from Ahl al Oughlam (= *B. antiquus remotus*) (Geraads and Amani, 1998; Gentry, 2010).

BEATRAGUS VRBAE, sp. nov.

Alcelaphini sp. (in part) Gentry, 1981:23.
Beatragus sp. Geraads, Bobe, and Reed, 2012:191.

Diagnosis—A large alcelaphin, larger than *B. hunteri* and about the size of a hartebeest, distinguished from living and fossil *Beatragus* species in the more extreme rotation of the basal horn core long axis such that it is almost perpendicular to the interfrontal suture, the slightly recurved (rather than very straight) distal portions, the extreme prominence of the nuchal and median crests, and the deeper hollowing of the occipital surfaces in between. It is further distinguished from *Beatragus whitei* and *B. antiquus* in smaller size, shorter and more compressed horn cores that are much less divergent, arising up and outwards rather than diverging strongly from the very base, with a more oval basal cross-section, slight flattening of the anterior-facing surface, no basal swelling, and inferior temporal lines that draw together very closely on the braincase. In these features, the new species may be more like the living hirola, *B. hunteri*.

Holotype—LD 60-1, frontlet with complete left and right horn cores and most of a braincase (Fig. 5A–E).

Other Referred Specimens—A.L. 94-1, fragment of left posterior braincase (labeled A.L. 94-1a), left frontlet with almost complete horn core (A.L. 94-1b), and a right horn core about two-thirds complete (A.L. 94-1c) (Fig. 5F–H). Found in association with the holotype but not certainly from the same individual are LD 60-6, a weathered distal radius fragment missing its distal epiphysis; LD 60-4, a right calcaneum with epiphyses fused; and LD 60-9, a lumbar vertebra missing both centrum epiphyses. LD 697-1 is a horn core in many non-conjoining fragments that may be of this species—flattening of one side, if lateral, would make it from the right side.

Age and Distribution—Type and paratype collected from fossiliferous horizons of the Lee Adoyta fault block, which are constrained to between 2.67 and 2.58 Ma (DiMaggio et al., 2015). Currently known only from the Awash Valley.

Etymology—Named for Elisabeth S. Vrba, for her pioneering work on bovid paleontology, mammalian paleoecology, and evolutionary theory.

Description and Comparisons—In this species, the long axis of the basal cross-section is oriented almost perpendicular to the skull midline, and this is taken to be homologous with an anteroposterior axis that has been strongly rotated medially. In the following descriptions, designations of horn surface or direction indicate the current anatomical direction in the species, but parentheses indicate the homologous horn surface or direction if these are considered to be medially rotated horn cores.

Metrics are given in Table 2. In both LD 60-1 and A.L. 94-1, the horn cores arise above or just behind the orbit, with a basal long axis strongly rotated to the sagittal plane, moderately divergent above the base, sigmoidal in course, and with long and straight distal ends. Horn core cross-section is oval and quite symmetrical with weak to moderate compression basally, and round with weak to no compression at midsection and distally; the anterior (lateral) horn core surface is slightly flatter than the posterior (medial) surface; weak and widely spaced transverse ridges are present along the horn core's length, but are clearest on the medial-facing (anterior) surface at midsection and distally; longitudinal grooving is present all around the horn core surface, with deeper and wider grooves on the medial-facing (anterior) surface. Keels absent. Heteronymous torsion is present, but only barely, not amounting to greater than 15° along the entire horn core.

The horns in A.L. 94-1 are more rounded at their bases than in LD 60-1 but are still anteroposterioly (mediolaterally)

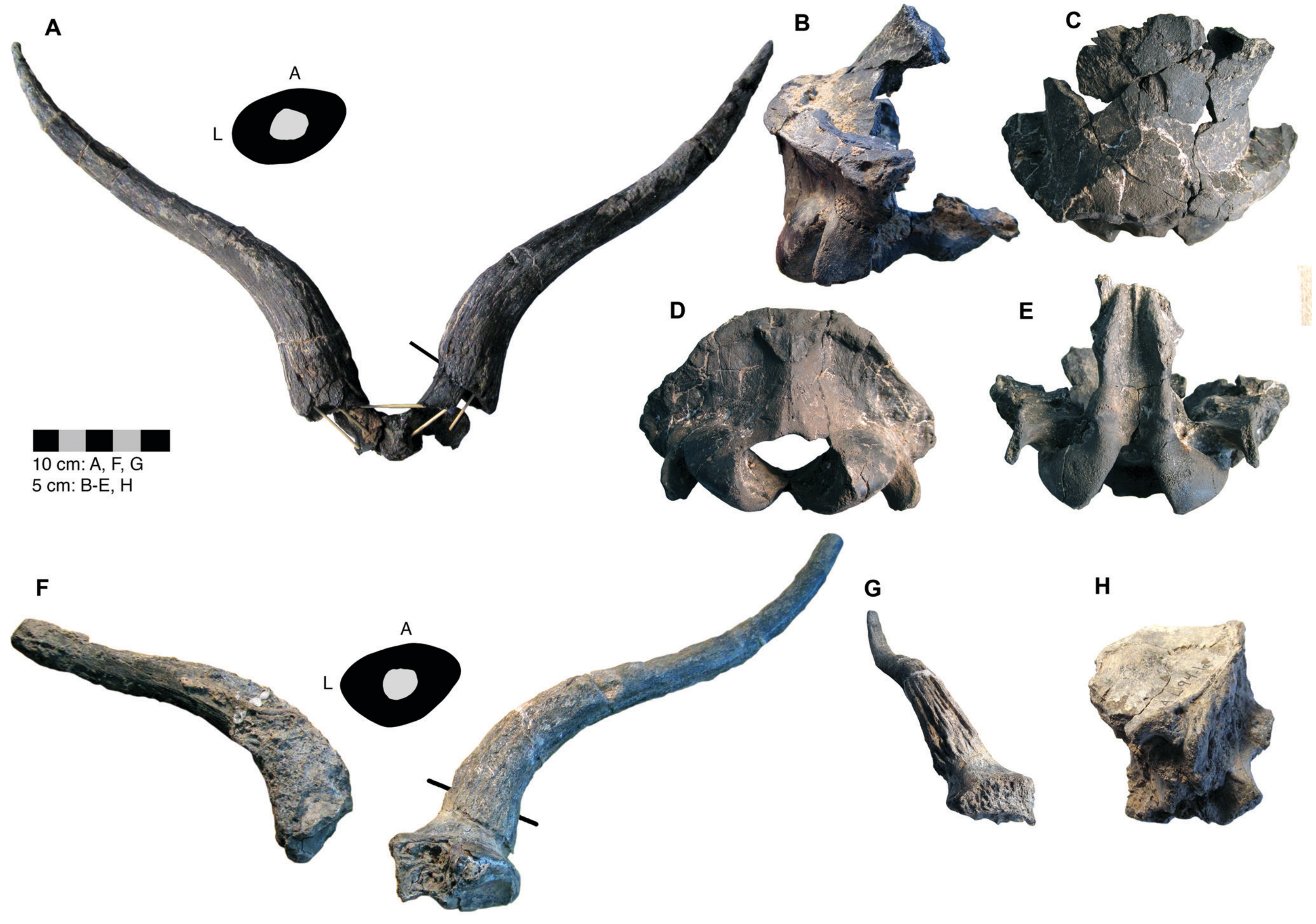

FIGURE 5. *Beatragus vrbae*, sp. nov. **A**–**E**, LD 60-1 (holotype), horn cores and partial braincase. **A**, horn cores in anterior view; braincase in **B**, right lateral, **C**, dorsal, **D**, posterior, and **E**, ventral views. **F**–**H**, A.L. 94-1, horn cores and partial braincase. **F**, horn cores in anterior view. **G**, left horn core in medial view. **H**, braincase in left lateral view.

TABLE 2. *Beatragus vrbae*: measurements (mm) of LD 60-1 (holotype) and A.L. 94-1.

Dimension	LD 60-1 (type)	A.L. 94-1
DAP	50.6 L, 50c R	54.3 L, 54.4 R
DT	42.1 L, 43.8 R	45.8 L, 45.0 R
Horn core length	380 L, 370 R	375+ L
Basal divergence	60°	60°e
Distance between basal horn cores	60.5	72.6
Distance across basal horn cores	142	145
Frontal thickness at midline between horns	24.2	29.3
Distance across posterior tuberosities	29.6	—
Distance across anterior tuberosities	30.6	—
Distance across occipital condyles	77.8	—
Distance across mastoids	130.4	—
Height from basioccipital to supraoccipital	67.5	—
Height from dorsal edge of foramen magnum to supraoccipital	44.0	—
Distance of frontoparietal midline to occipital plane	62c	—
Angle of occipital to dorsal braincase	125°	100–130e

+, preserved dimension of a broken specimen; **c**, approximate; **e**, estimate.

compressed, with the long axis of the cross-section oriented almost perpendicular to the skull midline. Transverse ridges are very weak, and much clearer on A.L. 94-1 than LD 60-1. Pedicels are short, with the horn core base higher medially (anteriorly) than laterally (posteriorly). Specimen A.L. 94-1 preserves an alcelaphin-like postcornual groove. The frontals are greatly expanded, with sinuses reaching the frontoparietal suture, and hollow, smooth-walled pedicels. The A.L. 94-1 frontal is very thick at the midline between the horn cores (29 mm), probably more so than LD 60-1. The frontoparietal suture runs along the base of the posterior edge of the horn cores. What is preserved of the frontal anterior to the horn core suggests a strongly flexed skull, as is typical in alcelaphins.

The braincase (i.e., the parietals) is quite short, as is typical for alcelaphins, but with a straight dorsal profile and lacking the parietal boss or raised feature seen in *B. hunteri* and *B. antiquus* (Vrba, 1997). Attachment surfaces for temporal musculature are quite deep, and the inferior temporal lines approach quite closely. In LD 60-1, the temporal lines approach to about the width of the foramen magnum, whereas the superior temporal lines are prominent with a long midline contact. Associated with this development of the temporal muscle area are prominent nuchal ridges that slightly overhang the occipital plane and a sharp median nuchal crest with deep depressions to either side. The occipital is low and wide, rounded dorsally; mastoids are wide and flattened and enclosed within the nuchal crest area.

The supraoccipital is triangular and relatively short and wide. The frontoparietal suture is indented anteriorly at the midline (unlike most Alcelaphini including *Damalborea* and *B. hunteri*, but like *B. whitei*). The braincase is short; in alcelaphins, the distance from the midline frontoparietal suture to the nuchal plane is about 40–70% of braincase width across the mastoids (49% in LD 60-1), whereas this value is much higher for most other tribes.

The basicranial fragment in A.L. 94-1 preserves a broken hollow bulla that is large, as in most alcelaphins, and smaller than in *Kobus* or *Redunca*. The temporal lamina (vaginal process) draws close to the bulla posterolaterally but remains weakly separated from it. In both specimens, the anterior tuberosities are slightly larger than the posterior tuberosities and of equal width apart. Narrow longitudinal ridges extend between the anterior and posterior tuberosities; these weaken midway, with a wide and smooth valley along the midline.

In isolation, the horn cores of LD 60-1 (more so than A.L. 94-1) might be mistaken for those of *Kobus sigmoidalis*. Gentry (1981) had also noted that the internal braincase sulci of A.L. 94-1 may be more like Reduncini than Alcelaphini. However, the greatly expanded frontal sinuses with hollow pedicel, postcornual groove (preserved on A.L. 94-1), frontals relatively flat anteriorly and high above the level of the orbits between the horn cores, relatively short parietals, flattened mastoid enclosed entirely in the occipital plane, deep occipital depressions, very prominent dorsal and median nuchal crests, and only moderately sized anterior tuberosities and quite thin longitudinal ridges flanking a wide and smooth median basioccipital valley are features unlike Reduncini and indicative of Alcelaphini. Some specimens of *Menelikia lyrocera* possess unstrutted, smooth-walled pedicel hollowing that is similar to the alcelaphin condition, but the horn cores in this and earlier species (*M. leakeyi*) are very different from those in *B. vrbae. Menelikia* also has sharp and prominent nuchal ridges, although these are not as developed as in *B. vrbae* and other fossil alcelaphins. Such morphology is better approached, but not quite matched, by *Beatragus antiquus, B. whitei*, and '*Damaliscus*' *eppsi* (Harris, 1991:fig. 5.53). The strongly defined temporal and nuchal muscular attachments, with prominent nuchal ridges and closely approaching temporal lines, is a characteristic feature of the Lee Adoyta species and probably reflects well-developed neck and chewing musculature.

The distal radius fragment LD 60-6 is missing its distal epiphysis and has a distal shaft width of ∼44 mm. The calcaneum LD 60-4 is of the right side, has epiphyses fused, and is of length 107.2 mm. The lumbar vertebra LD 60-9 has both epiphyses missing and is of centrum length 42.8 mm; with epiphyses it would have been around 47 mm. These three specimens have the same preservation and correspond in size to the type cranium, and the sequence of epiphyseal fusion fits that of a young adult bovid (Reitz and Wing, 1999). It is very likely that they all belong to the same individual as the holotype; however, caution is warranted, because tooth fragments too large to be the same species and some non-bovid specimens were also found in association.

The development of the horns, thickness of the frontals, and fusion of the braincase sutures all indicate that both referred cranial specimens are of young adult to adult age. The possibility that these represent juveniles of another *Beatragus* species can further be excluded by the shape of the horns, which are well developed and arise upright and with low basal divergence. No further ontogenetic changes to these horns could transform them into those of any other species. Similarly, the new specimens cannot be attributed to females of already known alcelaphin species. Extant alcelaphins show low levels of sexual dimorphism, whereby female horns are the same shape as those of males, although typically more slender and slightly shorter. The unique shape of the horns of the new specimens precludes them from being females of any other known species.

Discussion—The new *Beatragus* from Ledi-Geraru is roughly contemporaneous with *B. whitei*, from 3 to 2.5 Ma in the Middle Awash (Vrba, 1997) and ∼2.5 Ma at Ahl al Oughlam (Geraads and Amani, 1998). *Beatragus antiquus* is known from slightly younger deposits in the Turkana Basin and Olduvai and may be descended from *B. whitei* (Vrba, 1997). *Beatragus vrbae* would be a sister taxon to the *whitei-antiquus* lineage. The similarities of *B. vrbae* to the living hirola, including smaller size and an upwardly arising basal horn core, may simply be plesiomorphic for the genus, rather than indicative of any close relationship.

The hirola is today a critically endangered species, with a restricted (probably relict) range on the Somali-Kenyan border area, where it persists in semiarid habitats. In contrast, the genus *Beatragus* was much more widespread during the Plio-Pleistocene. Kingdon (1982) suggested that the restricted geographic range of the extant species is the result of competition with the more successful hartebeest (*Alcelaphus buselaphus)*, which emerged within the last 1 Ma (Flagstad et al., 2001).

The horns of *Beatragus, Alcelaphus, Connochaetes, Damalborea, Megalotragus*, and *Oreonagor* share many derived features in common, morphologically separating them from *Damaliscus, Parmularius*, and *Awashia* (Vrba, 1997; O'Brien et al., 2016). Mitogenomic phylogenies, however, nest *Damaliscus* deep inside the alcelaphin clade and consistently align *Beatragus* with *Alcelaphus* and *Damaliscus* to the exclusion of *Connochaetes* (Hassanin et al., 2012; Steiner et al., 2014), implying that the shared morphological features of *Connochaetes, Alcelaphus*, and *Beatragus* must be either plesiomorphic or convergent. This seems unlikely from a morphological perspective and further phylogenetic investigation, incorporating both morphological and molecular (including nuclear DNA) data, is needed to resolve the issue.

CONNOCHAETES Lichtenstein, 1812

Generic Diagnosis—Large alcelaphins with low, wide skulls, and broad muzzles; horn cores inserted wide apart and behind the orbits, strongly divergent in earlier species, emerging transversely or forwards in later species, and with weak homonymous torsion. Frontoparietal suture indented centrally; frontal between orbits weakly domed; strongly projecting orbits; zygomatic not thickened under anterior orbit; preorbital fossae absent or shallow without an upper rim; posterior suture of nasals indented centrally; greatest width of nasals lying anteriorly; broad palate; premaxillae greatly expanded laterally; anterior tuberosities of basioccipital more localized than in *Alcelaphus* and *Damaliscus*; auditory bullae large and inflated; occipital surface faces backwards rather than laterally; early forms with strong median occipital crest, extant without; premolar rows very short with p2 absent; metapodials short with metacarpals slightly shorter than metatarsals (modified from Gentry and Gentry, 1978; Vrba, 1997).

CONNOCHAETES GENTRYI Harris, 1991

Connochaetes sp. Gentry and Gentry, 1978:365, pl. 15.
Connochaetes sp. Gentry, 1985:166.
Connochaetes, sp. nov., Harris, Brown, and Leakey, 1988:97, figs. 51–56.
Connochaetes gentryi Harris, 1991:192, fig. 5.49.
Connochaetes gentryi DiMaggio et al., 2015:1358.

Species Diagnosis—A species of *Connochaetes* about the size of a small *C. taurinus* or large *C. gnou*, distinguished from both living species in horn cores arising less posteriorly behind the orbits, arising more vertically at their base (more developed basal stem), and diverging posterolaterally and without a pronounced ventral dip in their course. Parietals less reduced. Strong median occipital and nuchal crests. Metapodials only slightly shortened.

Referred Specimen—Ogoyta: LD 390-1 (= LD 162-15), partial skeleton excavated in situ, including a fairly complete skull with both horn cores, atlas, axis, cervical vertebrae 3–4, three thoracic vertebrae, four lumbar vertebrae, sacrum, pelvis, a number of ribs, both scapulae, left and right humeri, left and right radii, right metacarpal, left femur, tibia, and metatarsal, podials including calcaneum, astragalus, and cubonavicular, and several proximal, intermediate, and distal phalanges.

Description—The skull LD 390-1 (Fig. 6) is fairly complete, including a complete right horn core, mostly complete but non-articulating left horn core, cranium missing anterior maxilla and premaxilla, and mandible broken at the gonials and anterior

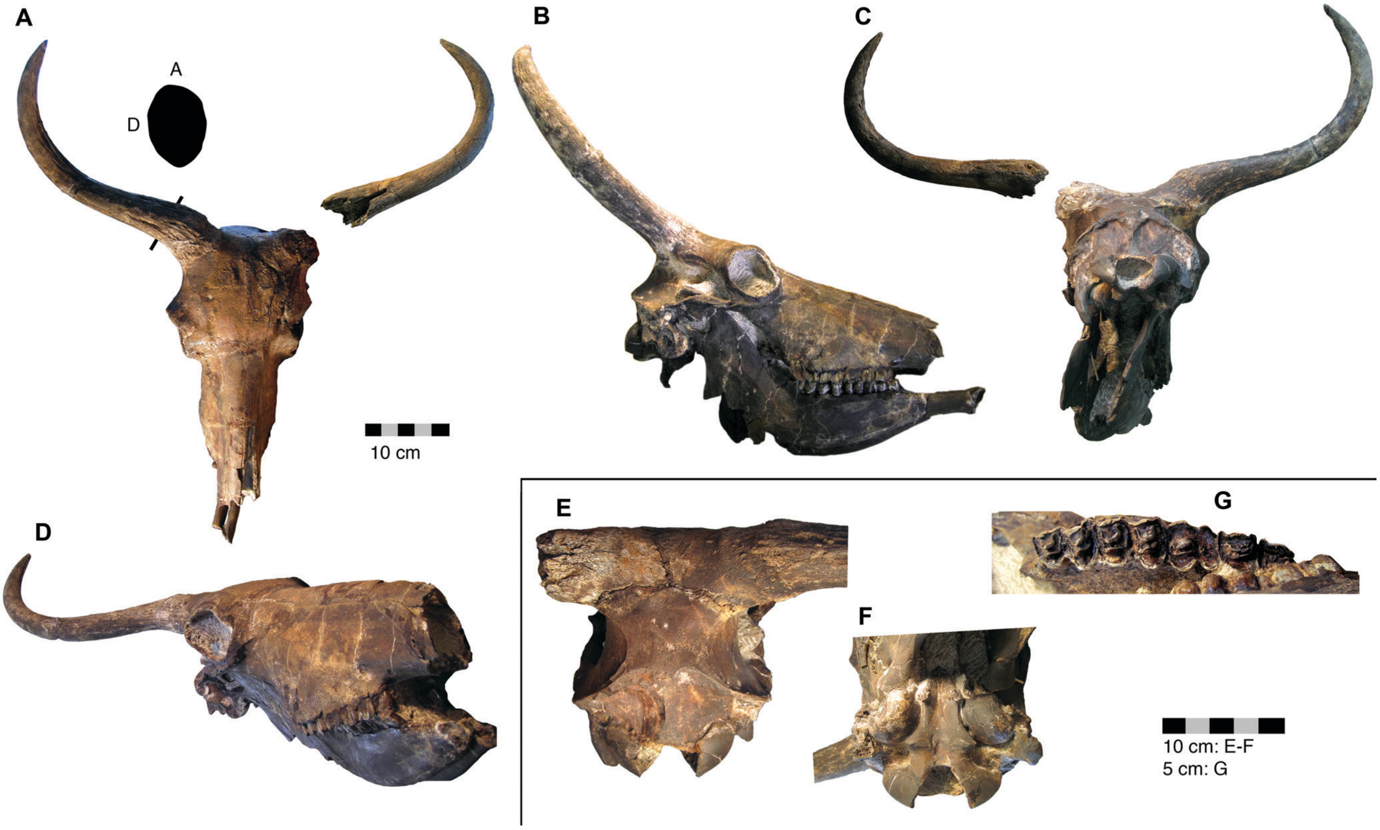

FIGURE 6. *Connochaetes gentryi*, LD 390-1, skull in **A**, dorsal, **B**, right lateral, **C**, posterior, **D**, anterolateral, **E**, posterodorsal, and **F**, ventral views. **G**, left upper tooth row.

portions (complete up to mental foramina). The age of LD 390-1 was adult, as indicated by third molars in middle wear and fused epiphyses on the vertebrae and long bones. Temporal lines are quite prominent and wide apart; the parietals are flat and quite smooth, without a parietal boss; the supraoccipital is anteroposteriorly short and in the same plane as the parietals; the nuchal lines and the median nuchal keel are prominent; the occipital is low and wide, with its surface mainly facing posteriorly; the mastoid is broad and quadrangular, located entirely in the occipital (posterior) plane; there is no large fossa or groove on the mastoid; the paroccipital process (preserved on left side) is tall and quite straight, and contacts the posterolateral edge of the auditory bulla; the bullae are large and inflated; the temporal lamina (vaginal process) is fused to the bulla anteriorly and free posteriorly; the anterior tuberosities of the basioccipital are prominent but not large, with a sharp posterior edge; the posterior tuberosities are prominent, sharp-edged, and larger than the anterior tuberosities; the basioccipital midline is a wide ‘U’-shaped valley with no median crest except just anterior to the anterior tuberosities; the orbits protrude laterally and are widest posterodorsally; the zygomatic is not dorsoventrally expanded beneath the anterior orbital rim; the lachrymal (preorbital) fossa is very shallow; the face is elongated (the anterior orbit lies just behind the posterior edge of M3); the infraorbital foramen is located above anterior P3, lying in a small shallow fossa; the premaxilla ascending ramus articulates with the nasals; the palatal ridges remain quite far apart; P2 is present, but reduced; the teeth are very hypsodont, and typically alcelaphin, perhaps with less anteroposterior constriction of the molar central cavities than in extant alcelaphins; cementum is absent or was thin; palate lateral indentations reach just behind M3 (median indentation in matrix); the posterior edge of the maxilla with a very sharp crest; the nasal aperture is taller than wide; the nasal-frontal suture is broad, anteriorly indented at midline; p2 is absent; the gonial angle (left side) is broken but probably not prominent (alcelaphin condition); horn cores with sigmoidal shape, expanded base, diverging strongly laterally slightly above the base, then recurving medially in their distal parts, dorsoventrally compressed in midsection, becoming rounded distally, and inflated with a more oval and less compressed shape basally; transverse ridges absent; the horn core surface is quite smooth, with fine striations ventrally in the basal half; the postcornual groove is wide and shallow (alcelaphin condition).

Comparisons—Specimen LD 390-1 matches KNM-ER 287, the holotype cranium of *C. gentryi* (Harris, 1991), in skull, horn core, and dental proportions and is an almost equally good match with the type cranium of *C. africanus*, NHM M14688 (Table 3 and discussed below). Specimen LD 390-1 is slightly larger than both KNM-ER 287 and NHM M14688 (and within the range of *C. taurinus*) and differs from other Koobi Fora and Nachukui specimens assigned by Harris (1991) to *C. gentryi* in having less pronounced lateral curvature of the horn core above the base and a less developed vertical basal stem. The basal horn core is the last to develop in ontogeny, so this morphology should be variable at different ontogenetic stages and between males and females. Specimen LD 390-1 is an adult, so the lesser development of the basal stem might indicate that it is a female, but its large size would better suit a male individual.

Postcranial elements fit general alcelaphin morphology (e.g., Gentry and Gentry, 1978:fig. 23). Lengths of the humerus, radius, femur, and tibia (Supplementary Table S4) are larger than those in *C. gnou*, and within the size range of *C. taurinus* (measurements in Brink, 2005). This matches the larger size of the LD 390-1 cranium relative to those of the *C. gentryi* and *C. africanus* types. A defining apomorphy of living wildebeest is a reduction in the length of the metapodials relative to the other long bones, and a greater reduction of the metacarpals relative to the metatarsals, particularly in *C. gnou* (Brink, 2005). In LD 390-1, the metacarpals are reduced in length, but less so than in *C. gnou* and *C. taurinus*. Metacarpal to metatarsal proportions, however,

TABLE 3. Measurements (in mm) of fossil *Connochaetes* crania: the new skull LD 390-1 (*C. gentryi*), the type cranium of *C. gentryi*, and the type cranium of *C. africanus* (includes data from Leakey, 1965; Gentry and Gentry, 1978; Harris, 1991).

Dimension	LD 390-1	*C. gentryi* type KNM-ER 287	*C. africanus* type NHM M14688
Ventral skull length (premaxilla to occipital)	420e [360+]	410	[270+]
Horn core curved length	360 (R), 370 (L)	[245+ R]	[130++]
Frontoparietal midline to occipital	57.5	55	62.1
Posterior postorbital bar to occipital	112c	110	110
Width across dorsal orbits	185 preserved, 195e	174	154
Horn core divergence in anterior view	~160°	almost 180°	almost 180°
Horn core base DAP × DT	56.3 × 47.8 (R) NA × 43.3 (L)	53 × 54 (R) 53 × 57 (L)	—
Horn core basal circumference	175 (R)	160 (R), 170 (L)	—
Outer distance across horn core bases	~180	170	144
Inner distance between horn core bases	~100	71	102c
Anterior orbit to tip of premaxilla	270–300e	250	—
Anterior orbit to occipital	170	165	150e
P2–M3	111.4 (R)	96e	—
M1–M3	72.6 (R)	65	62.5 (L), 63.8 (R)
m1–m3	82.2 (R)	—	—
Internal palatal width at M2	—	48	50
Angle between parietals and anterior frontals (craniofacial flexion)	115°	125°	120e°
Distance across mastoids	142.0	139	135.4
Distance across occipital condyles	87.3	85	74.5c
Distance from basioccipital to supraoccipital	83.2	76	62.9
Distance from top of foramen magnum to supraoccipital	60.0	52	—
Width across posterior tuberosities	43.6	41e	34.0
Width across anterior tuberosities	28.8	34e	26.1
Distance from posterior to anterior tuberosities	37.2	42.9	34.9
Bulla maximum length	40.0 (R)	34	—
Width at closest approach of palatal ridges	17.3	14	—
Distance between supraorbital foramina	78.8	76	86.7
Width across premaxillae	—	78	—

+, preserved dimension of a broken specimen; **c**, approximate; **e**, estimate.

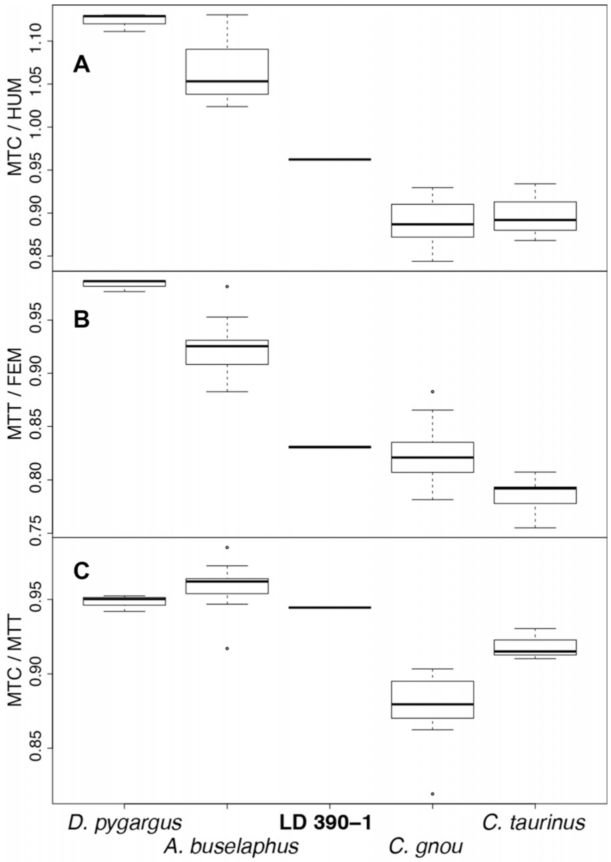

FIGURE 7. Limb bone proportions in Alcelaphini and the fossil *Connochaetes gentryi* specimen LD 390-1. Extant wildebeest have short metapodials, with metacarpals shorter than metatarsals. LD 390-1 exhibits metacarpal (**A**) and metatarsal (**B**) shortening approaching that in extant wildebeest but retains metacarpal to metatarsal proportions (**C**) similar to those in other Alcelaphini (ancestral condition). Extant species data from Brink (2005).

remain similar to those of *Damaliscus* and *Alcelaphus* (presumably the ancestral condition) rather than the reduced state in *C. taurinus*, or the more extremely reduced state in *C. gnou*. Specimen LD 390-1 therefore exhibits an intermediate condition in which the metapodials are reduced, but less so than in both living wildebeest species (Fig. 7).

Discussion—Although more primitive than extant species in several respects, *C. gentryi* already possessed several important hallmarks of living wildebeests. The narrow face, shortened premolar row, wide premaxilla, and reduced metapodials are features suggesting that this species shared similar dietary and behavioral habits with its living congeners (e.g., Spencer, 1997). Although the premaxillae are not preserved in LD 390-1, the type cranium KNM-ER 287 shows that in this species they were of the same absolute width as in both *C. taurinus* and *C. gnou* (Brink, 2005:table 23).

The broad muzzle of living wildebeest is an adaptation for obligate grazing, namely, for specialized cropping of mats of low-lying fresh green grass, particularly the kind growing shortly after the end of the dry season (Estes, 2014). Wildebeest are so dependent on this vegetational type that some (eastern African) populations migrate long distances, tracking rainfall in a constant search for fresh grass growth. This contrasts with the narrow premaxillae and much more selective feeding styles of *Alcelaphus* and *Damaliscus*, which can feed in grass stands of varying heights. The morphology of *Connochaetes gentryi* therefore indicates the presence of lawns of freshly sprouted grass, and perhaps the climatic seasonality (or fire) that produces them today. Unfortunately, the exact age of LD 390-1 is uncertain, so the vegetational and climatic inferences associated with the presence of a wildebeest at Ledi-Geraru cannot be related to the Gurumaha and Lee Adoyta faunas. The Ogoyta fault block is younger than 2.6 Ma (= Garsalu in DiMaggio et al., 2015:fig. 3). Elsewhere, the earliest appearance of *C. gentryi* is in the Upper Lomekwi Member in the Turkana Basin (~2.6 Ma; Harris et al., 1988).

However, numerous features of the cranium and postcranium, such as the anterior origin and lack of ventral dip in the horns, and the only moderately reduced metapodials, indicate that *C. gentryi* is less derived than extant wildebeest and phylogenetically basal to the most recent common ancestor of *Connochates taurinus* and *C. gnou*, as shown by Vrba's (1997) analysis.

Another early Pleistocene wildebeest species, *Connochaetes africanus*, was named by Hopwood (1934) on a cranium from Bed II (~1.7–1.2 Ma) at Olduvai Gorge. Gentry (2010:fig. 38.16) referred a second specimen to this species, HWK EE II 2315, also from Olduvai Bed II. Otherwise, the many specimens of *Connochaetes* from Olduvai Beds I and II were treated separately by Gentry and Gentry (1978) and later referred to a new species, *C. gentryi*, by Harris (1991), the type of which came from the Upper Burgi Member (~1.9 Ma).

Both Gentry and Gentry (1978) and Vrba (1997) proposed that a shorter face, more strongly sloping nasals, shorter, more divergent horn cores, and a less developed preorbital fossa distinguish *C. africanus* from *C. gentryi* and placed the former on the lineage leading to extant *C. gnou*. This was recently supported by the analyses of O'Brien et al. (2016), based largely on the same character differences.

After examining the new skull LD 390-1, the types of both *C. africanus* and *C. gentryi*, and a sample of extant *C. taurinus* and *C. gnou* skulls, we find the differences between the two early Pleistocene species unconvincing. The type cranium of *C. africanus* has broken horns, with no indication of these having been shorter than those in the type of *C. gentryi* or in LD 390-1. In anterior view, they are all of similar divergence. It is true that the horns pass more backwards in the *C. africanus* type, but this can easily be accommodated within the range of variation of a single species today, particularly considering that in alcelaphins both sexes carry horns, and that in wildebeest small differences in the development of the basal-most portion of the horn core (the last to develop in growth) can have large influences on the orientation of the rest of the horn. The HWK EE II 2315 horn core referred to *C. africanus* (Gentry, 2010) is long and of similar divergence and shape to those of *C. gentryi*. The *C. africanus* cranium does have a slightly shorter face with a more posteriorly placed M3, but the differences are minor compared with the range of variation observed within extant *C. taurinus*, or with the differences between *C. taurinus* and *C. gnou*, in which the face is much more noticeably shortened. All three crania also have similar degrees of facial-cranial flexion (Table 1). Both extant wildebeest species exhibit a preorbital fossa that is less developed than in *Alcelaphus buselaphus* and *Damaliscus* spp. This feature is also highly variable among sexes and age stages of modern wildebeest, and we interpret the flatter lachrymal surface in the *C. africanus* type as falling within the range of variation of a single species. The type cranium of *C. africanus* is also about the same size as the type of *C. gentryi* (Table 3), with upper molar row lengths within the range of variation of living *C. gnou* (66.3 ± 3.1, n = 3, specimens at MfN).

There is further (circumstantial) evidence against an exclusive affinity of *C. africanus* with extant *C. gnou*. From an ecological perspective, it is highly unlikely that two wildebeest species of such similar size and morphology coexisted at Olduvai, one of these (*C. africanus*) represented by just two specimens. Today, *C. gnou* and *C. taurinus* differ significantly in both size and skeletal morphology, and still their natural ranges hardly overlap. Brink's (1993, 2005) study of fossil wildebeest material from Cornelia-Uitzoek (~1–0.7 Ma) in South Africa suggests that the differentiation of the *C. gnou* lineage from an ancestral (*C. taurinus*–like) morphology occurred around this time. This suggests a younger (~1 Ma) minimum age for the divergence of the blue and black wildebeests than previously proposed (Vrba, 1997). Short mitochondrial branch lengths between *C. taurinus* and *C. gnou* (Hassanin et al., 2012; Bibi, 2013; Steiner et al., 2014) also support a recent divergence scenario.

On this basis, we suggest that *C. gentryi* Harris, 1991, and *C. africanus* (Hopwood, 1934) be synonymized, leaving a single early Pleistocene wildebeest species from which both living wildebeest could be descended. In that case, the name *C. africanus* (Hopwood, 1934) would have priority.

PARMULARIUS Hopwood, 1934
PARMULARIUS aff. *PACHYCERAS* Geraads et al., 2001

Referred Specimen—Lee Adoyta: LD 223-1, L? horn core basal.

Description and Comparisons—Specimen LD 223-1 (Fig. 8A) is the same taxon as '*Parmularius* cf. *pachyceras*' from Hadar (Geraads et al., 2012), best represented there by A.L. 241-1, a right horn core from the DD2 Member (previously '?Alcelaphini sp. C'; see online Supplementary Data 1). The Hadar and Ledi-Geraru specimens are different enough from the Chadian material on which *P. pachyceras* is based for us to believe that a designation of aff. (rather than cf.) is more appropriate. The Hadar and Ledi-Geraru *Parmularius* aff. *pachyceras* is characterized by relatively short horn cores arising close to the midline, with stout bases, weak basal swelling medially, tapering quite rapidly above the base, with pronounced posterolateral curvature that gets weaker distally, weak anterior recurvature distally (e.g., A.L. 192-10), transverse ridges present but weak (variable), and a well-defined posterolateral edge (not quite a keel). Longitudinal grooving is deep and wide on the anteromedial horn core surface, and the horn core to pedicel transition is much lower down laterally. Basal cross-section is quite round, weakly compressed anteroposteriorly, with a rounded anterior surface, a slightly flattened posterior surface, and an expanded posterolateral corner. Siding and orientation of LD 223-1 is not clear, but comparison with Hadar A.L. 241-1 suggests that LD 223-1 is from the left side based on the descent of the horn core surface and the strong lipping of the horn core–pedicel junction on the lateral surface.

These horn cores are similar to those of *Parmularius ambiguus* from the early middle Pleistocene of Algeria (Geraads, 1981) and *P. pachyceras* from the late Pliocene of Chad (Geraads et al., 2001) in overall size and shape, especially in the very robust bases, rapid diminution above the base, weak posterior flattening, broad longitudinal grooving on the anterior surface (*P. ambiguus* at least), and a further dip of the lateral horn core surface. The Hadar and LD species differs from *P. ambiguus* in lacking the greatly raised and united pedicels, and from both *ambiguus* and *pachyceras* in the posterolateral (rather than posterior) direction of horn core curvature, in lacking a pronounced backward bend slightly above the horn core base, and in weak anteroposterior (rather than mediolateral) horn core compression. *Parmularius pachyceras* is also reported to have no postcornual fossa, whereas a postcornual groove is present (although weak) in A.L. 241-1. On account of these differences, the Hadar and LD specimens appear to represent a separate, although related, species.

DAMALBOREA Gentry, 2010
cf. *DAMALBOREA* sp. A in Geraads et al., 2012

Referred Specimens—Bulinan: LD 263-1, R? horn core basal. Gurumaha: LD 336-1, L frontlet with basal horn core fragment; LD 368-1, R horn core basal with frontlet.

Description and Comparisons—Specimen LD 263-1 (Fig. 8B) is small. Part of the hollow pedicel is preserved at the proximal break. Basal cross-section is very round, without compression or flattening, and no transverse ridges. Fine parallel striations run longitudinally along what is presumably the posterior surface. The most distinctive (and enigmatic) feature is the presence of a weak but clear keel, presumably originating on the anterior surface, and the presence of torsion (heteronymous if this were a right horn) that is close to the horn core axis and that probably

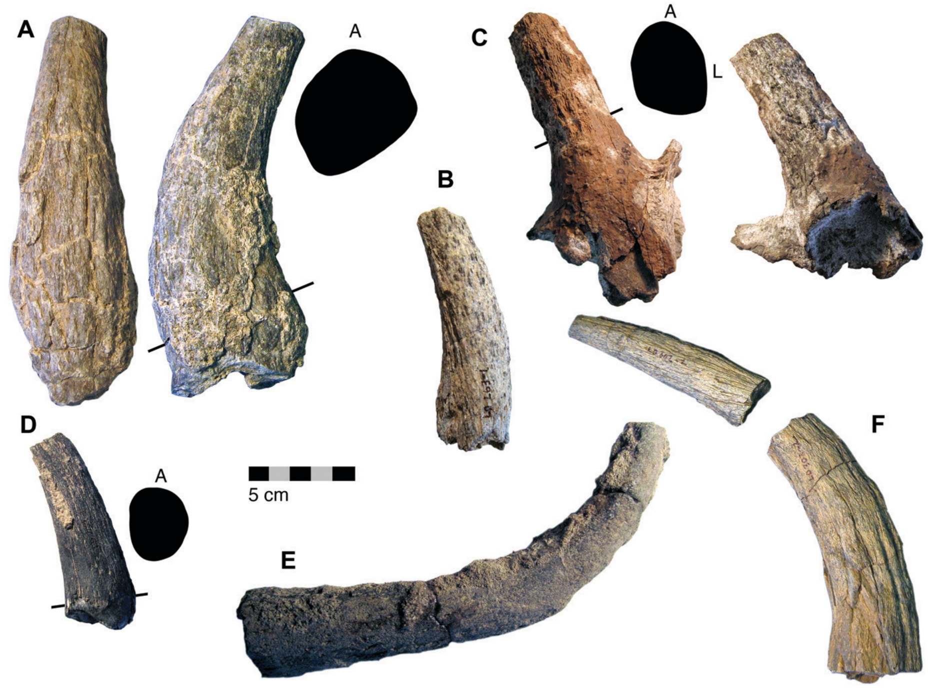

FIGURE 8. Alcelaphini. **A**, *Parmularius* aff. *pachyceras*, LD 223-1, ?left horn core, in anterior (left) and ?lateral (right) views. **B**–**C**, cf. *Damalborea* sp. A. **B**, LD 263-1, basal horn core, side indeterminate; **C**, LD 368-1, frontlet with right horn core base in anterior (left) and right lateral (right) views. **D**, cf. *Damaliscus* sp., LD 239-1, basal horn core, side indeterminate. **E**–**F**, Alcelaphini indet. **E**, LD 242-1, horn core basal and midsection, side indeterminate; **F**, LD 302-2, left horn core, non-conjoining basal and distal fragments.

did not exceed half a whorl (180°) when complete (135° is preserved).

Specimen LD 368-1 (Fig. 8C) is quite straight, arises above the orbit, is quite upright and not very inclined to the frontal just behind, with only very weak mediolateral compression basally that gets slightly stronger distally, expanded frontal sinuses, and a hollow pedicel. There is no sign of basal horn core swelling, but the posterolateral corner is eroded and any weak swelling there would not be preserved. Transverse ridges and the postcornual fossa seem to be absent, but these may have been eroded away. The dorsal surface of the frontal behind the horn core is depressed. The LD 368-1 horn core resembles *Oryx* in the apparent straightness and weak mediolateral compression of the horn core. However, in LD 368-1, this arises very close to the midline and exhibits marked divergence (about 40°), with pronounced orbital protrusion producing a large distance between the lateral horn core and the orbital edge, and the frontal between the horn cores being slightly raised above the level of the orbits. These features are very different from the widely inserted and little-divergent horns of *Oryx* (including *Praedamalis*; Gentry, 2010), which arise off low-lying frontals. In these features, LD 368-1 is more like an alcelaphin than a hippotragin, although not as derived as *Parmularius* or *Alcelaphus*.

The LD 336-1 frontlet is larger than the other two specimens and from what is preserved shows a basal horn core with round cross-section, arising very close to the midline and of similar basal divergence to LD 368-1.

These three specimens are very poorly preserved and may not be conspecific. Collectively, they signal the presence in the Lee Adoyta Basin of an alcelaphin species characterized by small size and horn cores that are relatively straight basally, arising close to the midline, with short pedicels, and divergence right from the base (best seen in LD 368-1). They resemble smaller specimens of *Damalborea* known from Aramis, Maka, and Hadar (Vrba, 1997; Gentry, 2010; Geraads et al., 2012) and possibly Woranso-Mille (Geraads et al., 2009) and the Laetolil beds (Gentry, 2011).

DAMALISCUS Sclater and Thomas, 1894
cf. *DAMALISCUS* sp.

Referred Specimens—Gurumaha: LD 311-2, horn core midsection very close to base. Lee Adoyta: LD 239-1, L? horn core basal and midsection.

Description and Comparisons—Specimen LD 311-2 has weak posterior curvature, an oval, symmetric cross-section, pronounced mediolateral compression, rounded anterior and posterior surfaces, and a smooth horn core surface without pronounced longitudinal grooving. It lacks major flattening of either the medial or the lateral surface, basal swelling, torsion, keels, lateral curvature, and transverse ridges. Traces of a smooth-walled, hollow pedicel are present in the proximal break. It is probably not *Hippotragus*, which is not so strongly mediolaterally compressed and is also much larger. In basal dimensions, LD 311-2 is much smaller than the Olduvai *D. niro*, but within the range of specimens from the much younger Florisbad locality (Gentry and Gentry, 1978:fig. 27).

Specimen LD 239-1 (Fig. 8D) is also mediolaterally compressed and posteriorly curved, with hollow pedicels, and no ridges, keels, or torsion. There is some flattening of one side (lateral if from the left side), and swelling or bulging of the opposite side. Size is much smaller than LD 311-2 and similar to extant bontebok *(D. pygargus)*.

Differences in size and morphology indicate that the two LD specimens are probably not conspecific. They differ from *Parmularius* in greater mediolateral compression and lack of basal swelling. Small size, strong mediolateral compression, and posterior curvature suggest referral to a *Damaliscus*-like alcelaphin. *Damaliscus* spp. tend to have greater flattening of medial and lateral surfaces, often some indication of transverse ridges, the widest part of the horn core set anteriorly, and possibly even posterolateral basal swelling (Gentry and Gentry, 1978), all features lacking in these specimens.

ALCELAPHINI, gen. et sp. indet.

Referred Specimens—Bulinan: LD 506-1, R upper M1 or M2. Gurumaha: LD 12-1, L upper M1 or M2; LD 105-1, L lower m1 or m2; LD 130-1, L mandible with m3; LD 182-5, L mandible with p4; LD 191-1, molar fragment; LD 268-1, R upper M1 or M2; LD 269-2, lower molar fragment; LD 302-2, L horn core basal and distal fragments (non-conjoining); LD 302-6, horn core fragment; LD 305-5, R mandible with m2 frag, m3; LD 305-20, molar fragment; LD 307-1, R mandible with p4–m2; LD 308-3, R lower m1 or m2; LD 308-9, lower molar fragment; LD 314-25, molar fragment; LD 314-29, L upper P3; LD 320-1, R lower molar fragment; LD 332-1, L upper M1 or M2; LD 336-2, L mandible with m3; LD 338-1, molar fragment; LD 347-1, upper molar fragment; LD 350-2, R lower molar fragment; LD 351-1, R lower m1 or m2; LD 353-2, R mandible with p4 frag; LD 355-1, L mandible with m1–m2; LD 356-1, R upper M1 or M2; LD 358-1, R mandible with two molar frags; LD 380-1, L lower m3 partial; LD 382-2, R upper M1 or M2; LD 382-3, R lower m1 or m2; LD 385-1, L upper M1 and M3; LD 393-3, L lower mandible molar fragments; LD 474-1, R lower mandible m3 fragment; LD 477-2, L lower m3; LD 478-2, R lower m3 partial; LD 483-7, L lower m1 or m2 partial; LD 488-1, molar fragment; LD 499-3, lower molar fragment; LD 508-1, R lower m1 or m2; LD 671-3, R lower mandible p3–p4; LD 689-1, R lower m3 partial; LD 695-1, upper molar fragment; LD 707-5, molar fragment; LD 710-1, molar fragment. Lee Adoyta: A.L. 72-12, R mandible with p4–m3. A.L. 83-9, lower molar fragment. A.L. 87-3, L lower m3 partial. A.L. 94-3, R mandible with m2–m3; LD 1-1, molar fragment; LD 25-3, R lower molar fragment; LD 25-5, R lower m1; LD 40-1, molar fragments; LD 49-1, upper molar fragment; LD 66-1, R upper M3; LD 67-1, L upper M1 or M2; LD 73-2, R upper molar fragment; LD 88-1, L lower molar fragment; LD 89-1, L lower molar fragment; LD 201-1, R upper M3; LD 217-1, L lower molar fragment; LD 227-2, L upper M3; LD 231-1, R upper M1 or M2; LD 242-1, horn core basal and midsection; LD 325-2, R upper M1 or M2; LD 331-1, L lower molar fragment; LD 353-3, upper molar fragment; LD 367-1, lower molar fragment; LD 616-1, R lower p4. Ogoyta: LD 42-2, upper molar; LD 246-1, L lower m3 partial; LD 330-1, L upper M3; LD 593-1, L upper M3; LD 609-1, molar fragment. Unknown: A.L. 71-1, R lower m3 partial.

Description and Discussion—Dental specimens are identifiable as alcelaphin, but not further. Size range (e.g., lower third molar AP: 28.6–32.3 mm, n = 7) is within the range of living *Alcelaphus, Beatragus, Damaliscus lunatus*, and *Connochaetes gnou* (lower m3 length in the *C. gentryi* skull LD 390-1, for comparison, is 36.9 mm). There is no clear evidence for a very small alcelaphin as at Hadar (Alcelaphini sp. B in Geraads et al., 2012) or at younger sites (e.g., unnamed small alcelaphin from Olduvai; Gentry and Gentry, 1978). The Ledi-Geraru alcelaphins also lack the very large-bodied *Megalotragus isaaci*, known from younger sites such as Olduvai (Gentry and Gentry, 1978) or Koobi Fora (Harris, 1991).

Specimen LD 242-1 is the basal half of a long and slender horn core of indeterminate siding (Fig. 8E). It is straight basally then curves strongly some distance above. The cross-section is weakly compressed basally and quite round distally. Transverse ridges are absent, torsion is absent, and the horn core surface lacks any major grooving. At the proximal break is the remnant of a smooth-walled and hollow pedicel. There is no swelling or recurvature of the horn core at the base. It resembles certain long and slender horn cores attributed to *Connochaetes* such as from Melka Kunture (Geraads, 1979) or Olduvai (Gentry and Gentry, 1978:pl.16, fig. 2) but lacks the enlargement and compression of the basal horn core.

Specimens LD 302-2 (Fig. 8F) and LD 302-6 are probably not conspecific, but both show a large pedicel sinus, relatively symmetric cross-section, no clear basal swelling, no torsion, strong curvature, and large and widely spaced transverse ridges. The LD 302-2 horn core has one flattened surface, which if lateral, would indicate siding as left, and a weak posterolateral keel. It differs from *Beatragus vrbae* in the strong transverse ridges, lack of deep longitudinal grooving, and no indication of any anterior recurvature distally. It may be similar to the possible ?*Damaliscus* described above, or a small *Parmularius*.

AEPYCEROTINI Gray, 1872
AEPYCEROS Sundevall, 1847
AEPYCEROS sp.

Referred Specimens—Gurumaha: LD 267-2, L horn core midsection; LD 305-4, L horn core midsection; LD 350-10, R horn core basal; LD 388-1, R lower m1 or m2; LD 460-2, L upper M3; LD 669-1, L horn core basal; LD 703-2, R horn core basal. Lee Adoyta: A.L. 87-1, R lower m3; LD 54-1, R and L horn cores right basal, left distal; LD 204-1, R horn core basal; LD 252-1, L horn core basal; LD 260-1, L mandible with m3 frag; LD 550-1, L horn core; LD 591-1, L upper M1 or M2 fragment. Ogoyta: LD 172-1, R upper M1 or M2; LD 636-1, horn core basal.

Description and Comparisons—Specimen LD 54-1 (Fig. 9A) is the most complete specimen. It is of a small impala, about the size of *Aepyceros shungurae* or the smallest individuals of extant *A. melampus*, and the length and completeness of lyration of the horns and the thick frontals all indicate an adult individual. The horns are slender with a rounded cross-section, no compression, a weak posteroexternal keel, and a slightly flattened area between the posterolateral keel and the medial surface. Heteronymous torsion is present but very weak, lyration is well developed, and prominent and widely spaced transverse ridges dip medially. The frontal sinuses are expanded but end above the orbit and do not reach into the pedicel. The frontal is thick and in between the horn cores is higher than the level of the orbits. The postcornual fossa is large and deep. Horn core LD 252-1 is also of a small, slender-horned impala. It matches LD 54-1 in size and morphology, but in LD 252-1 the frontal sinuses penetrate into the pedicel up to the base of the horn core. The remaining three referred specimens are of larger size. In LD 204-1, the frontal sinuses also extends into the pedicel, and it also shows the strong transverse ridges, posterolateral keel, posteromedial flattening, lack of compression, and very weak torsion characteristic of this impala. Specimen LD 305-4 is a midsection fragment that exhibits greater mediolateral compression than the others.

The absence of significant horn core compression in most specimens is a little different from most fossil and living impalas, and similar to some specimens of *Aepyceros afarensis* from the Pliocene of Woranso-Mille (Geraads et al., 2009). The LD 54-1 individual probably did not have the same degree of uprightness of the horns as in *A. afarensis* (≥90° in that species). *Aepyceros afarensis* is otherwise only differentiated by its much longer premolar rows, and these are unknown in the Ledi-Geraru impala. Pliocene *Aepyceros dietrichi* from Laetoli was a much larger species (Gentry, 2011). The closest comparison is with the fossil impalas at Hadar and in the Turkana Basin. In basal horn core dimensions, the Ledi-Geraru impala matches larger specimens of *Aepyceros datoadeni* from Hadar but differs from this species (especially the type specimen) in longer horn cores and more pronounced lyration and torsion. The Lee Adoyta Basin impala may belong to the same variable lineage as at Hadar, or it may be referable to *A. shungurae*, which it also matches in basal horn core size.

Discussion—Fossil impalas of the Plio-Pleistocene were never very morphologically diverse (Vrba, 1984), and the difficulty of distinguishing among several very similar extinct *Aepyceros* species makes the assignment of fragmentary material difficult. Impala are rare in the Lee Adoyta Basin, accounting for less than 10% of specimens identified to tribe, in contrast to almost 25% at Hadar or Member C of the Shungura Formation.

?ANTILOPINI Gray, 1821
PARANTIDORCAS Arambourg, 1979
cf. *PARANTIDORCAS LATIFRONS* Arambourg, 1979

Referred Specimen—Gurumaha: LD 359-1, R horn core basal with frontlet.

Description and Comparisons—A horn core about the size of *G. thomsonii*, with homonymous torsion, strong mediolateral compression, gradual posterior curvature, no keels, and no transverse ridges (Fig. 9B). Basal cross-section fairly symmetric, with

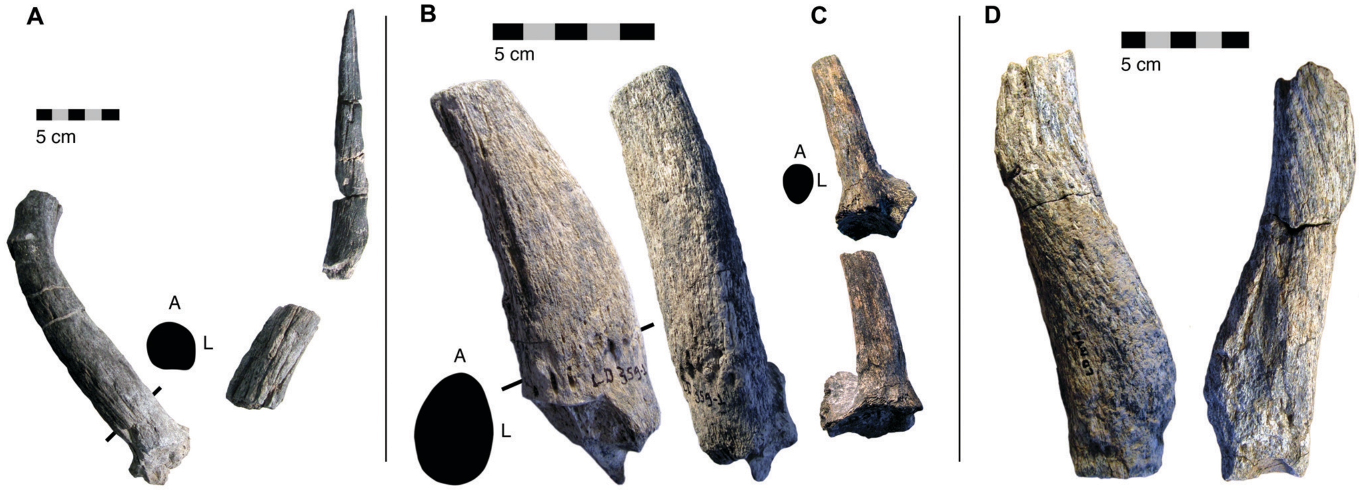

FIGURE 9. *Aepyceros* and ?Antilopini. **A**, *Aepyceros* sp., LD 54-1, right and left horn cores in anterior view. **B**–**D**, ?Antilopini, gen. et sp. indet. **B**, cf. *Parantidorcas*, LD 359-1, right horn core in lateral and anterior views; **C**, cf. *Gazella*, LD 34-2, right horn core and frontlet in anterior (top) and lateral (bottom) views; **D**, LD 107-1, (right?) horn core of cf. *Antilope* in anterior(?) and posterior(?) views.

no flattening of either side, widest diameter central, anterior edge narrow (but not keeled), and posterior edge rounded. Basal horn core long axis may have been slightly rotated medially, but this is not certain. The horn core arises above the orbit, on a short pedicel, and appears quite strongly inclined backwards. The horn core surface is marked by longitudinal grooves, fine on the lateral surface, wider on the medial surface, and widest on posterior surface. Along the preserved length of 95 mm, about 25° of homonymous torsion is present. The supraorbital foramen is partially preserved and located just beneath the anterior horn core edge. It opens straight down into the orbit and widens ventrally. It may have been associated with a triangular-shaped fossa as is common in antilopins. The frontal seems quite thick at the break just lateral to the midline. The frontal sinuses are not expanded (no sign of them in this specimen).

Of similar size and compression to horn cores of extant *G. thomsonii*, but this and the fossil *G. praethomsoni* are more flattened laterally, bear a posterolateral keel, and lack torsion. Horn cores of *G. janenschi* are smaller, much less compressed, and also lack torsion. *Antidorcas* spp. exhibit homonymous torsion and no lateral flattening, but LD 359-1 is more compressed and lacks the extensive frontal sinuses, basal swelling, and strong backward bend of these species.

Parantidorcas latifrons from Ain Boucherit and Ain Brimba (Arambourg, 1979), dated to between 3 and 2 Ma (Gentry, 2010; Sahnouni et al., 2011), may come closest. Basal size is similar, but LD 359-1 is more compressed, has stronger posterior curvature, and perhaps weaker torsion. *Parantidorcas latifrons* may have a much sharper anterior edge, or keel. Low pedicels and multiple parallel grooves along the posteromedial surface are additional similarities.

?ANTILOPINI Gray, 1821
GAZELLA de Blainville, 1816
cf. *GAZELLA*

Referred Specimen—Lee Adoyta: LD 34-2, R horn core basal with frontlet, and podial.

Description and Comparisons—The specimen LD 34-2 (Fig. 9C) comes from a small gazelle-like antelope with a horn core that is large for the size of the frontal, quite straight with only weak posterior curvature, a posterior keel and a weak anterior keel, weak to moderate divergence, mediolaterally compressed throughout, with its basal long axis oriented parallel to the sagittal plane, arising above a large orbit, inclined about 60° to the dorsal frontal, and located quite far from the midline. It is preserved for 37 mm but was probably originally much longer, because in the length preserved it hardly narrows. Torsion is absent; transverse ridges are absent. There is no clear flattening of the medial or lateral horn core surface, although the lateral surface is slightly less convex than the medial surface. Maximum horn core width is anterior to the center. The pedicels are high, and the horn core ventral limit is only slightly lower posteriorly than anteriorly. A postcornual fossa is not present, although there is a poorly defined shallow fovea lower down than expected. The frontal sinuses are not expanded.

Specimen LD 34-2 is larger than *Madoqua* spp. and lacks the anteroposterior compression and very short horns of these species. It is in the size range of *Raphicerus, Ourebia*, or *Oreotragus* but differs in the stouter horn, lacking weak anterior curvature and tapering less along its length, and the absence of a clear postcornual fossa.

In horn core size and the weak posterior curvature it is perhaps closest to *Gazella* sp. at Kanapoi (Harris et al., 2003:fig. 31; Geraads et al., 2013), although the mediolateral compression may be greater. Otherwise, LD 34-2 is much smaller than most other fossil and extant *Gazella*, such as *G. pomeli, G. setifensis, G. vanhoepeni, G. psolea, G. thomasi, G. janenschi*, and *G. praethomsoni*. It also lacks the lateral flattening, pronounced mediolateral compression, and strong posterior curvature of *G. praethomsoni* and *G. thomsonii* and further differs from *G. janenschi* in the greater mediolateral compression, much more upright horn cores, lack of lateral flattening, and lack of pronounced posterior curvature. It is similar to *G. harmonae* from Hadar, and possibly also Olduvai, Laetoli, and the Omo (Geraads et al., 2012), in the weak posterior curvature and lack of lateral flattening, but LD 34-2 is much smaller and exhibits greater horn core compression.

?ANTILOPINI Gray, 1821
ANTILOPE Pallas, 1766
cf. *ANTILOPE* sp.

Referred Specimen—Gurumaha: LD 107-1, R? horn core basal.

Description and Comparisons—Specimen LD 107-1 is the basal 15 cm of a very straight horn core with strong torsion (heteronymous if specimen is a right) that is tight around the central axis, lacking transverse ridges, and with a wide and deep groove on one surface and a hollow pedicel (Fig. 9D). Among antilopins, *Antidorcas* has variable homonymous torsion as well as pedicel sinuses, but so does the reduncin *Menelikia*. The great degree of torsion combined with straightness in LD 107-1 is unlike these taxa but resembles *Antilope* from the Omo (Gentry, 1985). The horn core LD 107-1 is larger and lacks the sharp and straight posterolateral keel of the Shungura *Antilope*, and probably also the expanded frontal sinuses. The base is broken, and the exact basal morphology and cross-sectional outline is not observable.

BOVIDAE, gen. et sp. indet.

A large number of cranial and postcranial specimens are identifiable as bovid, but no further. These are listed in Supplementary Table S1.

DISCUSSION

Paleoecology

Taxonomic Composition—Living African bovid tribes are strongly associated with particular vegetational habitats, and their relative abundances reflect differing habitat proportions and amounts of woody cover and precipitation (Greenacre and Vrba, 1984). Alcelaphini are the most abundant tribe at Ledi-Geraru, making up >40% and >50% of the Gurumaha and Lee Adoyta assemblages, respectively (Fig. 10A). Today, alcelaphins are grazers that inhabit open grassland habitats. Enamel stable carbon isotope evidence (Cerling et al., 2015) indicates that alcelaphins were consistently among the most dedicated grazers in herbivore communities going back over 4 Ma, and this is confirmed by the consistency of morphological traits such as tooth crown shape and height. A slightly higher proportion of alcelaphins and lower proportion of tragelaphins in the Lee Adoyta suggests a greater representation of open habitats there than in the older Gurumaha assemblage, but these differences are small. The more interesting comparison is with older Pliocene assemblages in the Afar.

Examining the abundance of bovid tribes at Afar middle to late Pliocene sites reveals that major environmental changes took place during this time (Fig. 10A). Assemblages at 4.4–4.1 Ma (Aramis, Asa Issie) record mainly wooded habitat signals, as indicated by an overwhelming dominance of tragelaphins. Thereafter, at Woranso-Mille (3.7 Ma), tragelaphins are largely replaced by aepycerotins, which also indicate wooded habitats, but a large increase in alcelaphins reflects significantly increased representation of open habitats. Proportions of

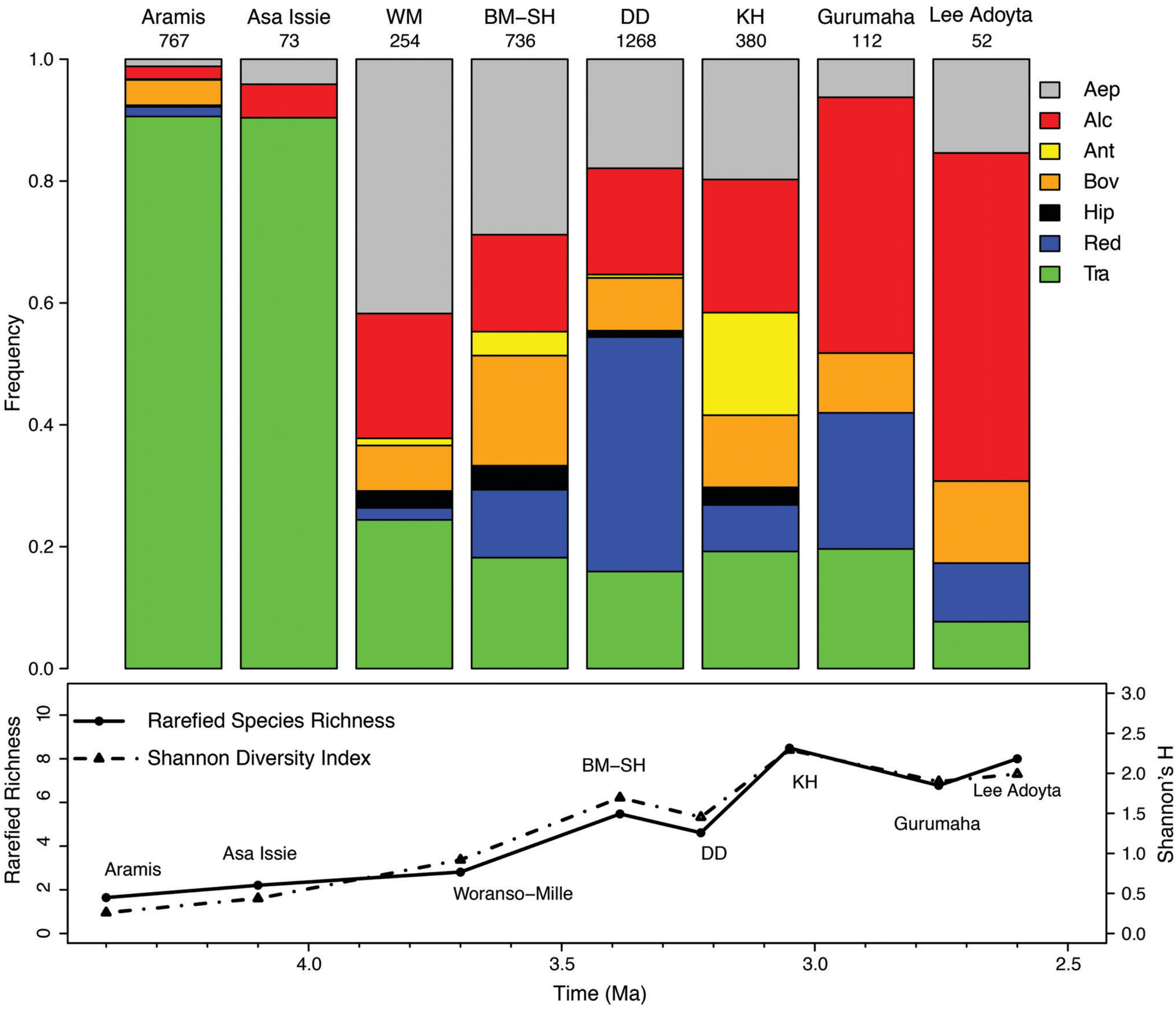

FIGURE 10. Diversity of bovid tribes (above) and species (below) in the middle to late Pliocene of the Afar (based on all identified specimens). Increasing proportions of Alcelaphini and decreases in Tragelaphini and Aepycerotini reflect more open habitats over time. This is accompanied by increasing species diversity, which probably reflects greater habitat heterogeneity. **Abbreviations: BM-SH**, basal to Sidi Hakoma members; **DD**, Denen Dora Member; **KH**, Kada Hadar Member; **Wor-Mil**, Woranso-Mille. Numbers below site names are the number of specimens identified to tribal level. See Materials and Methods for data sources.

aepycerotins decrease over time, and both aepycerotins and tragelaphins reach their lowest frequencies in association with a large increase in alcelaphins between the upper Hadar (e.g., DD, KH) and the Ledi-Geraru (Gurumaha, Lee Adoyta) assemblages. Increasing species diversity over this time (Fig. 10B) probably reflects increasing habitat heterogeneity at local scales (Geraads, 1994), in combination with increased representation of species-rich Alcelaphini and decreases in species-poor Aepycerotini and Tragelaphini. Increases in alcelaphin abundance, and by inference open grassland habitats, are particularly pronounced between 4.1 and 3.8 Ma (Asa Issie to Woranso-Mille), and again at ~2.9 Ma, between the Kada Hadar Member of the Hadar Formation and the Gurumaha assemblage at Ledi-Geraru. Such changes towards drier and more open habitats appear to have been regional in extent, as a recent community-level analysis of dental traits found evidence for a decrease in precipitation over the Turkana Basin shortly after 4 Ma (Fortelius et al., 2016), and Bobe et al. (2007) recorded increasing proportions of arid-adapted bovids in the West Turkana sequences between about 3.5 and 3 Ma.

That the Ledi-Geraru faunas derive from more open and possibly drier habitats than most of those at Hadar is in agreement with the community-level analyses of DiMaggio et al. (2015) and the analyses of giraffids by Rowan et al. (2016). The bovid data, however, also show that the paleoenvironmental changes leading up to Ledi-Geraru times may be viewed as part of a long-term trend of increasing aridity and reorganization of faunal communities since at least ~4 Ma, rather than the result of a major climatic and faunal reorganization at ~2.9 Ma. Long-term changes to eastern African environments may have been driven by the progressive drop in global temperature leading up to the end of the ‘Pliocene Warm Period’ around 3 Ma (Ravelo et al., 2004; Fedorov et al., 2013), modulated by tectonic drivers, such as regional uplift (Sepulchre et al., 2006) or rift valley subsidence.

Postcranial Functional Morphology—Following Barr (2014) and DeGusta and Vrba (2005), we assigned taxon-free habitat classifications to bovid astragali and phalanges. Out of 18 measurable astragali in the Ledi-Geraru collection, 13 are assignable to a habitat category with >60% probability (Supplementary Table S5). Nine of these are classified as open habitat (e.g., Alcelaphini and Antilopini), two as heavy cover (e.g., *Kobus* spp. and most Tragelaphini), and two as forest (e.g., Cephalophini and some *Tragelaphus* spp.). One of the two 'forest' specimens (LD 324-5) and one of the 'heavy cover' specimens (LD 71-1) are very large and may well be of Bovini, a tribe that was not included in Barr's training set. Otherwise, the large majority of astragali, including that of LD 390-1 (*Connochaetes* skeleton), are classified as open habitat.

We also scored eight proximal phalanges, six intermediate phalanges, and two distal phalanges according to the verified discrete characters of DeGusta and Vrba (2005). Out of eight proximal phalanges, six are likely to be from light cover or open habitats, whereas the two largest (probably Bovini) are likely to be from forest or heavy cover (Supplementary Table S6). Five intermediate phalanges are likely to be from light cover or open habitats, and one is equivocal. The two distal phalanges are assigned to light cover or open habitat. All phalanges from LD 390-1 (*Connochaetes* skeleton) are assigned to open habitat or light cover categories.

The metric and qualitative characteristics of bovid astragali and phalanges therefore confirm the dominance of open habitat taxa in the Ledi-Geraru assemblage, as established taxonomically through the craniodental remains.

Species Turnover—It has been proposed that African faunas experienced elevated origination and extinction (turnover) rates in conjunction with rapid global cooling between 2.9 and 2.6 Ma (Vrba, 1985, 1988, 1995). Numerous studies, however, have failed to record elevated turnover rates among African large mammals at this time (Behrensmeyer et al., 1997; Werdelin and Lewis, 2005; Frost, 2007; Bibi and Kiessling, 2015). The new Ledi-Geraru assemblages provide an opportunity to examine this temporal interval within the Afar Basin. Unfortunately, sample sizes are not large enough to attempt a proper analysis accounting for sampling biases (e.g., Bibi and Kiessling, 2015), and only a rough approach is attempted here. Leaving out indeterminate alcelaphins and antilopins, nine out of 15 species from the Gurumaha and Lee Adoyta blocks are diagnostic enough for comparative purposes. Of these, five (*Beatragus vrbae, Kobus sigmoidalis, Tragelaphus gaudryi*, the possible *Menelikia lyrocera*, and the possible *Syncerus*) are local first appearances not present in the Hadar assemblage. *Kobus sigmoidalis* is known from earlier deposits in the Turkana Basin (Harris, 1991). Four species (*Tragelaphus rastafari-nakuae* lineage, *Ugandax coryndonae, Parmularius* aff. *pachyceras*, and probably the large impala) are, in contrast, all survivors from the older Hadar or even Woranso-Mille faunas. That half or more of bovid species in the Ledi-Geraru collections are new relative to those at Hadar does suggest elevated levels of turnover, particularly considering there seem to be low levels of bovid turnover within the Hadar Formation itself (Geraads et al., 2012:fig. 9). This would provide support for previous claims of increased turnover and faunal dispersal in eastern Africa at this time (Vrba, 1995, 2000; DiMaggio et al., 2015), in contrast to studies that found no evidence for significant turnover between 3 and 2.5 Ma (Behrensmeyer et al., 1997; Werdelin and Lewis, 2005; Bibi and Kiessling, 2015). Further discoveries and larger sample sizes from this interval, especially in the Afar, are needed.

Hypsodonty—Extant herbivores with tall tooth crowns are mainly grazers, and hypsodonty itself is an adaptation that provides dental longevity against abrasive diets including tough plant matter or dirt (Fortelius et al., 2002; Damuth and Janis, 2011). The mean hypsodonty of large herbivore communities has also been shown to correlate with aridity (Fortelius et al., 2002; Eronen et al., 2010). In the African record, the most common hypsodont bovids are the Alcelaphini, extant species of which are grazers in highly seasonal grassland habitats. As discussed above, alcelaphins often form a major proportion of both the abundance and species diversity of fossil herbivores at Plio-Pleistocene sites. Tracing the evolution of hypsodonty in Alcelaphini may therefore provide clues as to the chronological development of grazing behavior as well as its response to increasing aridity (including seasonality) in Africa.

Our expanded Plio-Pleistocene data set (see Materials and Methods) shows slight differences depending on which hypsodonty index is used (Fig. 11A, B). This is probably related to small sample sizes, but also possibly to discrepancies in measuring tooth width, which in bovids varies along the length of the crown. Regardless, both data sets agree that alcelaphin hypsodonty had reached modern levels by 3.7 Ma or even earlier and changed little after that (Fig. 11). As Gentry (1980) showed, alcelaphins from Langebaanweg at 5.1 Ma were lower-crowned than extant alcelaphins (Wilcoxon tests, $p < 0.0001$), but already significantly more hypsodont than extant tragelaphins ($p < 0.0001$). Perhaps as early as Kanapoi (4.1 Ma, low sample size), but certainly by Upper Laetolil (3.7 Ma) and Hadar (3.5-2.9 Ma) times, alcelaphin hypsodonty had become significantly greater than at Langebaanweg ($p < 0.05$) and indistinguishable from that of extant species ($p > 0.1$). Alcelaphin hypsodonty at Ledi-Geraru is no different from that at older sites such as Laetoli and Hadar ($p > 0.05$) or that of extant alcelaphins ($p > 0.7$).

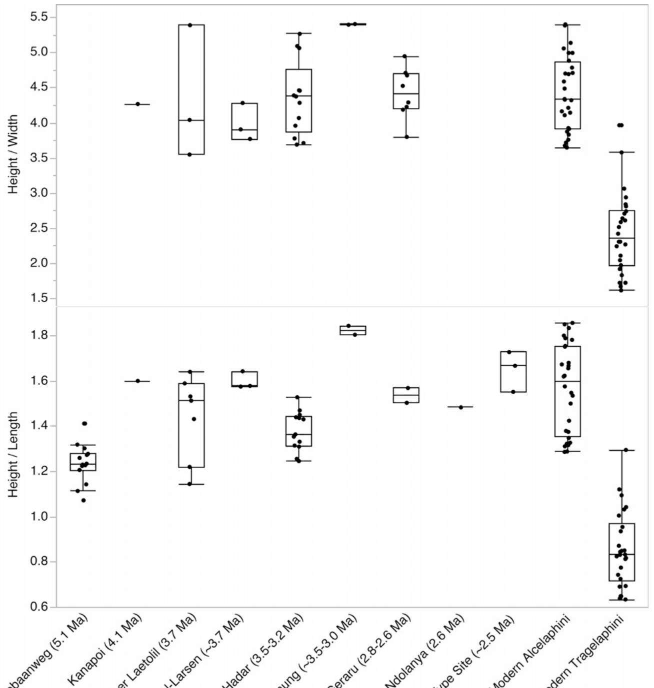

FIGURE 11. Hypsodonty of alcelaphin lower third molars from African Pliocene sites compared with values for extant alcelaphins (hypsodont grazers) and tragelaphins (mesodont browsers). Unworn or little worn crown height is divided by width (above) or length (below). Alcelaphins were already hypsodont by ~5 Ma and had reached modern-like values by ~4 Ma. Laetoli KL refers to the Kohl-Larsen collections in Berlin, specimens believed to come from the Upper Laetolil Member. UL and UN refer to the Upper Laetolil and Upper Ndolanya members in Gentry (2011). Extant species data from Janis (1988); see Materials and Methods for other data sources.

TABLE 4. Faunal list and number of specimens by fault block for Ledi-Geraru as well as possible match (X) with species from the Hadar Formation (Geraads et al., 2012).

Taxon	Hadar	Bulinan	Gurumaha	Lee Adoyta	Ogoyta	Unknown
Species						
Ugandax coryndonae	X	—	1	—	—	—
cf. *Syncerus*		—	—	2	—	—
Tragelaphus rastafari/nakuae	X	—	18	3	—	—
Tragelaphus gaudryi		—	4	1	—	—
Aepyceros	X	—	7	7	2	—
Beatragus vrbae		—	—	2	—	—
Connochaetes gentryi		—	—	—	1	—
Parmularius aff. *pachyceras*	X	—	—	1	—	—
cf. *Damalborea* cf. sp. A (Geraads et al., 2012)	?	1	2	—	—	—
cf. *Damaliscus*		—	1	1	—	—
Kobus sigmoidalis		—	9	2	—	1
cf. *Menelikia lyrocera*		—	2	—	—	—
cf. *Antilope*		—	1	—	—	—
cf. *Gazella*		—	—	1	—	—
cf. *Parantidorcas* cf. *latifrons*		—	1	—	—	—
Tribe						
?Antilopini		—	2	1	—	—
Aepycerotini		—	7	7	2	—
Alcelaphini		2	47	28	6	1
Bovini		—	11	7	—	—
Reduncini		—	25	5	1	1
Tragelaphini		—	22	4	—	—

These preliminary data suggest that the main selective forces leading to the evolution of hypsodonty in Alcelaphini—for example, increasing reliance on grass—were in place prior to 4 Ma, in the early Pliocene or even late Miocene. If the evolution of taller-crowned teeth was driven by increased exploitation of more arid habitats and the consumption of greater quantities of C_4 grass, then alcelaphins must have been among the earliest African large herbivores to do so. Stable carbon isotope analyses support this view, showing that this bovid tribe has been feeding in C_4 grasslands in both the Afar and Turkana basins since at least 4.4 Ma (White et al., 2009; Cerling et al., 2015), if not since the late Miocene (Cerling et al., 2003; Uno et al., 2011). This contrasts with stable isotope and morphological data in other African large mammals. Elephantids, for example, show large increases in hypsodonty around ~4 Ma and only reach modern-like values after 2 Ma (Lister, 2013). In suids too (notochoeres and metridiochoeres), it appears that major increases in hypsodonty took place much later, after 2.7 Ma (Cooke, 2007).

Biochronology—With the exception of the wildebeest *Connochaetes gentryi*, which is younger, the bovid fauna from Ledi-Geraru is a match for what might be expected from faunas post-dating the Hadar Formation and contemporaneous with Shungura Member C (i.e., 2.9–2.5 Ma). The presence of *Tragelaphus gaudryi*, possibly *Menelikia lyrocera*, a possible *Syncerus*, and the absence of *Kobus oricornus* and commonness of *K. sigmoidalis* are the main indicators in this regard. Although they derive from the older sedimentary packages, *T. gaudryi* and the probable *M. lyrocera* may be a better match for Shungura specimens younger than 2.4 Ma. The bovin *Ugandax coryndonae* is well recorded from middle to late Pliocene sites in the Afar, and the *T. rastafari-nakuae* lineage is common in both the Afar and Turkana basins. Unfortunately, not enough of the latter is preserved to identify the species. According to Bibi (2011), the age of the assemblage (particularly the Lee Adoyta fault block) would make *T. nakuae* the more likely assignment.

Biogeography

Both *Tragelaphus gaudryi* and *Menelikia lyrocera* are almost entirely unknown from outside the Turkana Basin. The new fossil remains from Ledi-Geraru, although hardly complete specimens, may be the first records of both of these species in the Afar. This would increase biogeographic linkages (and decrease potential endemism) between the Afar and Turkana basins. The rarity of both these species in the Afar in comparison with their relative abundance, particularly in the Shungura Formation, likely reflects different habitat distributions (drier Afar environments), rather than the presence of any major biogeographic barriers between these two regions.

CONCLUSIONS

Fossil bovids recovered from 2.9–2.5 Ma strata in the Lee Adoyta Basin represent a minimum of 15 bovid species (Table 4). These are the buffaloes *Ugandax coryndonae* and a possible early *Syncerus*, the large bongo-like *Tragelaphus rastafari/nakuae*, the small kudu *T. gaudryi, Kobus sigmoidalis* (probable waterbuck ancestor), probably the reduncin *Menelikia lyrocera, Beatragus vrbae* (a new hirola species), *Connochaetes gentryi* (an early wildebeest), a *Parmularius* species, two more indeterminate alcelaphins, an impala, and three indeterminate small antelopes. Alcelaphins are by far the most abundant and diverse tribe, indicating the dominance of open habitats (namely, grasslands) at Ledi-Geraru. This is confirmed by taxon-free analysis of postcranial remains.

The Ledi-Geraru assemblage is slightly younger than the well-studied Hadar Formation (3.5–2.9 Ma). A rough assessment of species turnover suggests the possibility of increased turnover between these two collections. There is also evidence for increased opening of habitats or aridity at this time, although these ecological changes may also be viewed as part of a much longer-term trend of increasing aridity and associated faunal change going back to at least 4 Ma, if not the late Miocene. A compilation of hypsodonty data in Alcelaphini, for example, indicates that the major increases in dental crown height took place in the early Pliocene or earlier.

In the interval between 3 and 2.5 Ma, the origin of the genus *Homo* (Villmoare et al., 2015), Oldowan stone tool technology (Semaw et al., 1997), and a large faunal turnover pulse (Vrba, 1995, 2000) have been documented. Links have previously been drawn between all three of these events and rapid global cooling and African aridification. Much of this framework remains in place, but the bovid fossil record favors placing these evolutionary events within a larger context of environmental change over several million years, rather than as the result of a sudden and rapid climatic shift shortly after 3 Ma.

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