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Middle Pliocene Bovidae from Hominid-bearing sites in the Woranso-Mille area, Afar region, Ethiopia

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Hominid-bearing sites of the northwestern part of the Woranso-Mille research area, dated to between 3.7 and 3.8 Mya, yield 10 species of Bovidae. The evolutionary stages of the most common species fit quite well this radiometric age. The most abundant bovid is a new species of *Aepyceros,* of large size, with upright, lyrated horn-cores; it is clearly distinct from the impalas of younger sites in the same area, and from those sampled at Hadar. A new species of *Tragelaphus* is also common; its horn-cores exhibit reduced anterior keel and antero-posterior compression foreshadowing the most common form at Hadar. A single partial *Ugandax* skull, despite some primitiveness, may fit into the variation range of *U. coryndonae* from Hadar. Other tribes are rare; the virtual absence of reduncines is a major difference from younger sites, but the occurrence of a cephalophine and of *Neotragus* is worth noting. This assemblage unambiguously indicates an environment with a significant component of arboreal vegetation.

Keywords: Artiodactyla, Bovidae, Middle Pliocene, Ethiopia, eastern Africa.

INTRODUCTION

A number of fossil vertebrate localities have recently been discovered by a team led by one of us (Y.H-S.) in the Woranso-Mille (WORMIL) area, about 45 km north of Hadar in the lower Awash Valley, Afar region, Ethiopia (Fig. 1). Work at WORMIL began in 2002, and has yielded abundant mammalian faunas, together with crucial hominid remains (Haile-Selassie *et al.*, in press.). There are about 25 groups of vertebrate localities, among which five, including some of the most significant in terms of paleoanthropological discoveries, are now chronometrically dated to between 3.57 ± 0.014 and 3.82 ± 0.18 (Deino *et al.*, in press; Haile-Selassie *et al.* 2007; Haile-Selassie *et al.,* in press). These are Am-Ado (AMA), Aralee Issie (ARI), Makah Mera (MKM), Mesgid Dora (MSD) (collectively referred to as AAMM), all dated to between 3.7 and 3.77 Ma, and the slightly younger Korsi Dora (KSD), dated to the *c.* 3.5 Mya period. These five localities are situated in the northwestern part of the Woranso-Mille study area. They are older than all Hadar localities, but their ages correlate with the base of the Basal Member of the Hadar Formation (Wynn *et al.* 2008). In the early 1970s, some fossils were collected by the International Afar Research Expedition (IARE) from two localities (AL-99 and AL-100) in the same area, then called 'Ahmado'; they are presently housed in the National Museum of Ethiopia (NME). Although it is clear that the fauna from these localities is earlier than that of Hadar, the geographic and stratigraphic locations of these two localities remain too uncertain for precise correlation.

All of the bovid material studied below consists of cranial parts; very few postcranial elements of this family have been collected. Authors of family-group names follow Grubb (2001). Measurements are in mm. In descriptions, the tooth-row is taken to be horizontal. Upper teeth are in upper case, lower teeth are in lower case.

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SYSTEMATIC PALEONTOLOGY

Family Bovidae Gray, 1821
Subfamily Bovinae Gray, 1821
Tribe Tragelaphini Blyth, 1863

Genus *Tragelaphus* Blainville, 1816

Type species. Tragelaphus scriptus (Pallas, 1766), living bushbuck.

Diagnosis. Medium to large tragelaphines with spiralled horn-cores inserted close together and having an anterior keel and sometimes a strong postero-lateral one. Small to medium-sized supra-orbital pits, which are frequently long and narrow; occipital surface tending to have a flat top edge and straight sides (Gentry 1985).

***Tragelaphus saraitu* sp. nov.**, Figs 2A–E, 3, Table 1

Holotype. MSD-VP-5/2, a braincase with complete horn-cores, but lacking the cranial base, from Mesgid Dora, Woranso-Mille area, lower Awash valley, Ethiopia, 3.7–3.8 Ma (Fig. 2A).

Referred material. About 15 frontlets and horn-cores, plus numerous teeth from ARI, MKM, KSD, and MSD. A few specimens from AMA are perhaps also of this species.

Derivatio nominis. The species name 'saraitu' means kudu in the local Afar language.

Diagnosis. A *Tragelaphus* with horn-cores that are long and slender, divergent by about 90° at the base, inserted upright, strongly spiralled (almost a complete whorl), so that their lower part is strongly curved backwards, and their lowermost part is straight or slightly curved outwards (but never shows decreasing divergence). The tips are more or less parallel. The basal cross-section is intermediate in size between that of *T. moroitu* from the earliest Pliocene of the Middle Awash and that of the most common *Tragelaphus* species of Hadar; it is moderately compressed antero-posteriorly (index *c.* 0.8), with a change in outline curvature antero-laterally that may be called a keel higher

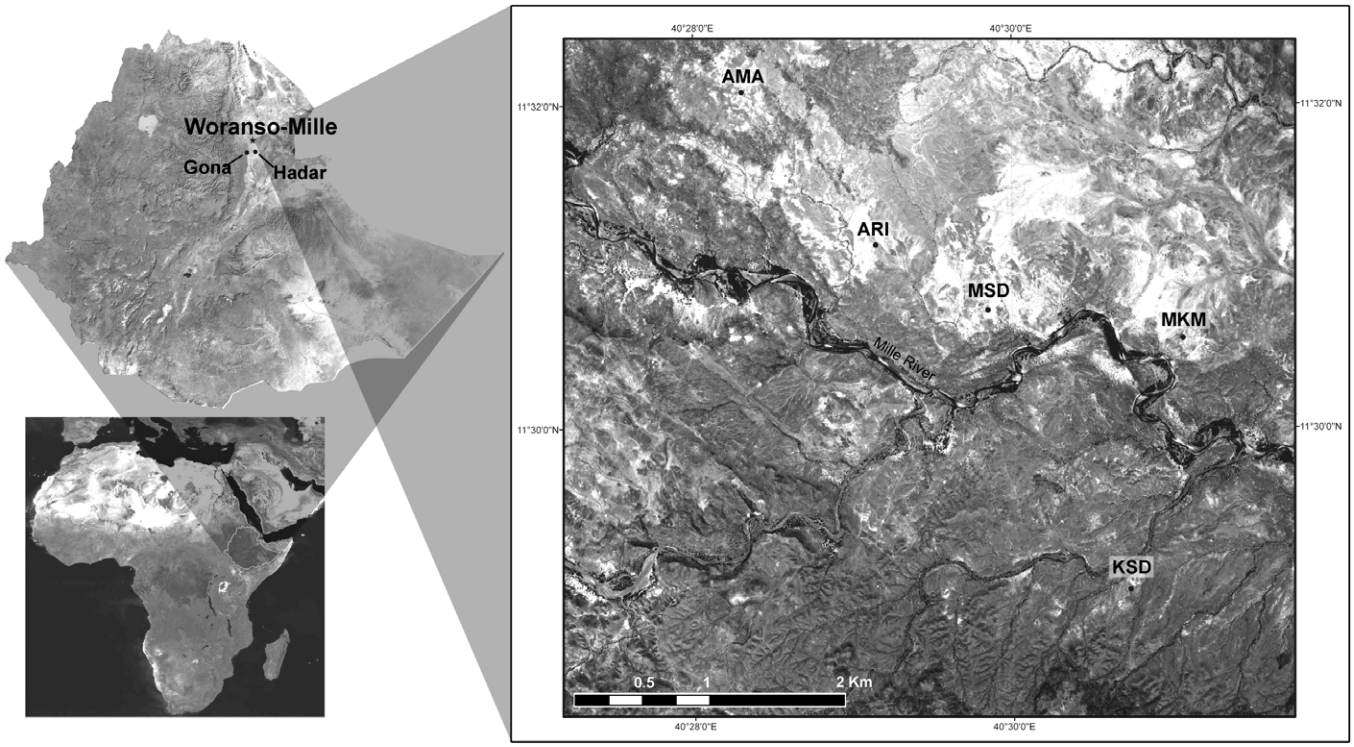


Figure 1. Location map showing major collection areas at AAMM. AMA = Am-Ado; ARI = Aralee Issie; MSD = Mesgid Dora; MKM = Makah Mera; KSD = Korsi Dora.

up, and a moderate postero-lateral keel that usually becomes more acute upwards. The occipital is trapezoidal rather than semi-circular, but with rounded upper border, and no transverse ridge above it. Lower p4 usually with an open lingual wall.

Description. The main features of this species are listed in the diagnosis. The holotype (Fig. 2A) is the only specimen with complete horn-cores, but other frontlets and horn-cores can be assigned to the same species with confidence, on the basis of their measurements, and degree of horn-core divergence, upright insertion, curvature, and cross-section shape (Fig. 3). The horn-cores of ARI-VP-3/62 share the same morphology, but are clearly more slender than the others although they are long and therefore adult; we tentatively include this specimen in the same species. Measurements are given in Table 1.

The only cranial base is that of the braincase MSD-VP-1/20 (Fig. 2C), which is certainly fully adult, as its horn-core measurements are among the largest of this species. The *foramen ovale* is circular. The basioccipital is long, as in other tragelaphines, but the anterior tuberosities are weak for this tribe, close to each other, and extend posteriorly as long ridges on either side of a very narrow central groove. No specimen includes any part of the face, although MSD-VP-8/7 has a small but well-preserved supra-orbital foramen (SOF) The damaged foramina of ARI-VP-3/62 were also likely small.

Teeth are identified on the basis of the absence of another medium to large *Tragelaphus* at these localities, but the occurrence of such another species in slightly younger sites of the WORMIL area precludes definite assignment of every tragelaphine tooth to *T. saraitu.* In any case, even if a few of them in fact belong to another species, the characters mentioned in the diagnosis would remain valid: of seven specimens of p4, five have the paraconid and metaconid separated down to the cervix, whereas the other two have a complete wall, but only one of them (ARI-VP-4/7, Fig. 2D) is in early wear, the other being much worn. The usual lack of contact between paraconid and metaconid of p4 is more like the Hadar *Tragelaphus* than like the Omo *T. nakuae,* in which more than half of the p4s are closed lingually (Gentry 1985). The mean length of seven m3s is 31 mm (range = 28–34). The lengths of three lower molar series are: 69.5 (MKM-VP-1/168), 71.3 (MSD-VP-2/161, Fig. 1E), and 74 (MSD-VP-2/44).

Comparisons. By the general course and cross-section of its horn-cores, *Tragelaphus saraitu* is reminiscent of the modern nyala (*T. angasi*), sitatunga (*T. spekei*), mountain nyala (*T. buxtoni*) and bongo (*T. euryceros*). It averages larger than the former two (the difference is greater for the teeth than for the cranium), and slightly smaller than the latter two. The nyala differs in its less spiralled, less divergent and more inclined horn-cores; those of the sitatunga differ by the same two latter characters, but their degree of spiralling is about the same as in *T. saraitu.* Those of the bongo have very weak basal divergence, and this divergence decreases from the very base, in contrast to all other species. A possible resemblance with *T. saraitu* is the presence of horns in females, as no hornless skull is known from AAMM, but this could also be due to preservation bias against hornless skulls. The mountain nyala, endemic to Ethiopia, has much more uprightly inserted horns than the other above-mentioned living species (thus resembling *T. saraitu* in this feature) but they are strongly spiralled and with re-approaching tips.

Tragelaphus saraitu can also be compared to several Pliocene eastern and South African species:

The poorly known *Tragelaphus* from the early Pliocene of

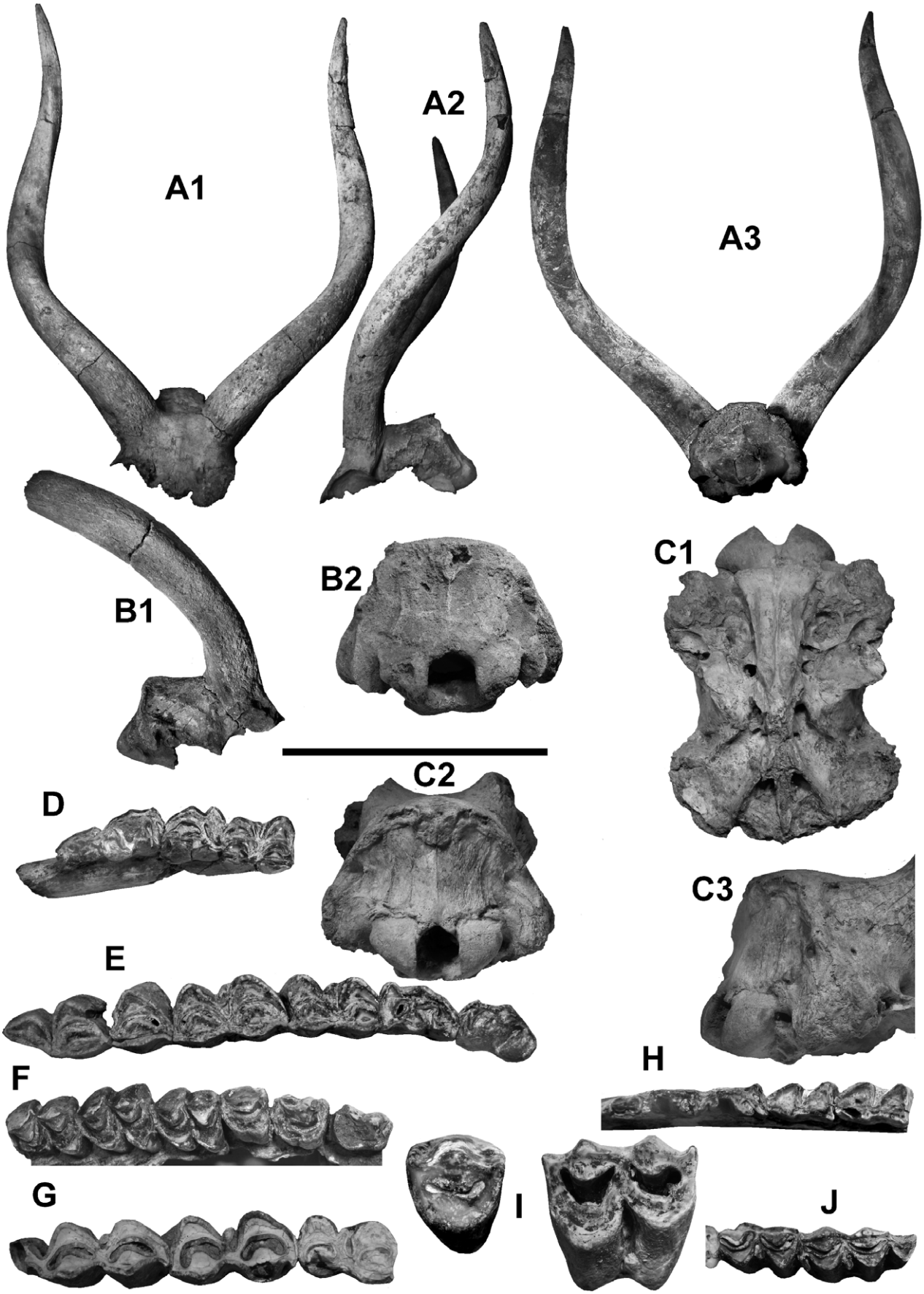


Figure 2. **A–E**, *Tragelaphus saraitu*. **A**, holotype frontlet and brain-case, MSD-VP-5/2, in (**A1**) front view, (**A2**) lateral view, and (**A3)** posterior view; **B**, brain-case, ARI-VP-3/22, in: **B1,** lateral view, and **B2,** occipital view; **C**, brain-case, MSD-VP-1/20, in (**C1**) ventral view, (**C2**) occipital view, and (**C3)** oblique right lateral view; **D**, lower tooth-row p2–m1, ARI-VP-4/7; **E**, lower tooth-row p3–m3, MSD-VP-2/161; **F**, *Tragelaphus* sp., upper tooth-row P2–M3, KSD-VP-1/9; **G**, *cf. Hippotragus* sp., lower tooth-row m1–m3, MKM-VP-1/62; **H**, *Neotragus* sp., lower tooth-row p3–m2 and roots of p2, MKM-VP-1/93; **I**, *Cephalophus* sp., upper P4, ARI-VP-1/370, and upper molar, ARI-VP-1/197; **J**, Reduncini gen. et sp. indet., m2–m3, MSD-VP-1/43. Scale = 30 cm for Fig. A, 15 cm for Figs B,C, 5 cm for Figs D–G and J, 2.5 cm for Figs H–I.

Table 1. *Tragelaphus saraitu* – measurements of the most complete specimens.

	HC APD	HC Transv.	Length along anterior curve	Width over pedicles	Width over middle of supra-orbital foramina	Minimum width over temporal fossa	Minimum width of braincase	Width over mastoids	Bicondylar width	Occipital height	Width over post. tuber. of basiocc.
ARI-VP-1/148	43.6	53.5	600	–	–	–	–	–	–	–	–
ARI-VP-3/22	51	54.3	–	–	–	60	95	128	–	66	49.5
ARI-VP-3/62	35.6	46.3	–	112	*c.* 46	–	–	–	–	–	–
MSD-VP-1/20	48.5	64.3	–	130	–	61	97	131.6	69.3	62.5	47.5
MSD-VP-3/12	41.5	56.4	–	122.5	–	–	–	–	–	–	–
MSD-VP-5/1	45	52.5	–	123	–	–	–	–	–	–	–
MSD-VP-5/2	43.7	55.7	580	120	–	50	92	124	71	60	–

Figure 3. Cross-sections of *Tragelaphus saraitu* horn-cores. Scale bar = 5 cm.

Langebaanweg in South Africa (Gentry 1980) is smaller, and has horn-cores without antero-posterior compression, and an anterior keel which is stronger on average, and is not shifted laterally.

Tragelaphus kyaloi from the Pliocene of Kenya (Harris 1991, 2003; Harris *et al.* 2003; this name was originally spelled *kyaloae* but, being based on a male name, its genitive is *kyaloi*) is smaller, has an incipient transverse ridge across the top of the occipital, the tips of the horn-cores re-approach closely (as in *T. buxtoni*), and on the type-specimen at least (Haile-Selassie *et al.* 2009, fig. 9.10), the horn-cores have a much more rectangular basal cross-section. Although this species has been reported from several sites (East and West Turkana, Kanapoi, and Lothagam), it has not been described in great detail. Nevertheless, its type, which comes from strata not much younger than *T. saraitu,* is sufficiently distinct for specific identity to be ruled out.

Tragelaphines are rare at Laetoli. A frontlet of doubtful stratigraphic provenance (Gentry 1987, in review) was illustrated by Dietrich (1942, fig. 154) as *T.* cf. *buxtoni*; it is certainly larger than *T. saraitu* (basal perimeter 20.5 cm according to Dietrich), and has less spiralled horn-cores that are correlatively more inclined, and wholly lack an anterior keel. Although probably a member of the same broad group, this Laetoli species is certainly distinct.

Tragelaphus moroitu from the latest Miocene/earliest Pliocene of the Middle Awash (Haile-Selassie *et al.* 2009) is much smaller than *T. saraitu* (Fig. 4) and has less divergent horn-cores that are clearly more primitive in their strong anterior keel and thus slight to moderate antero-posterior compression (index A–P/transverse = *c.* 0.85 instead of 0.8). There is no doubt about the distinctness at species level, but the overall similarity of the horn-cores suggests a phyletic relationship (see below).

Tragelaphus nakuae from the Turkana basin (Gentry 1985; Harris *et al.* 1988; Harris 1991) is larger than *T. saraitu,* has a strong transverse ridge across the top of the occipital, and its horn-cores are very compressed antero-posteriorly (A–P/transverse = *c.* 0.70), less divergent, less spiralled

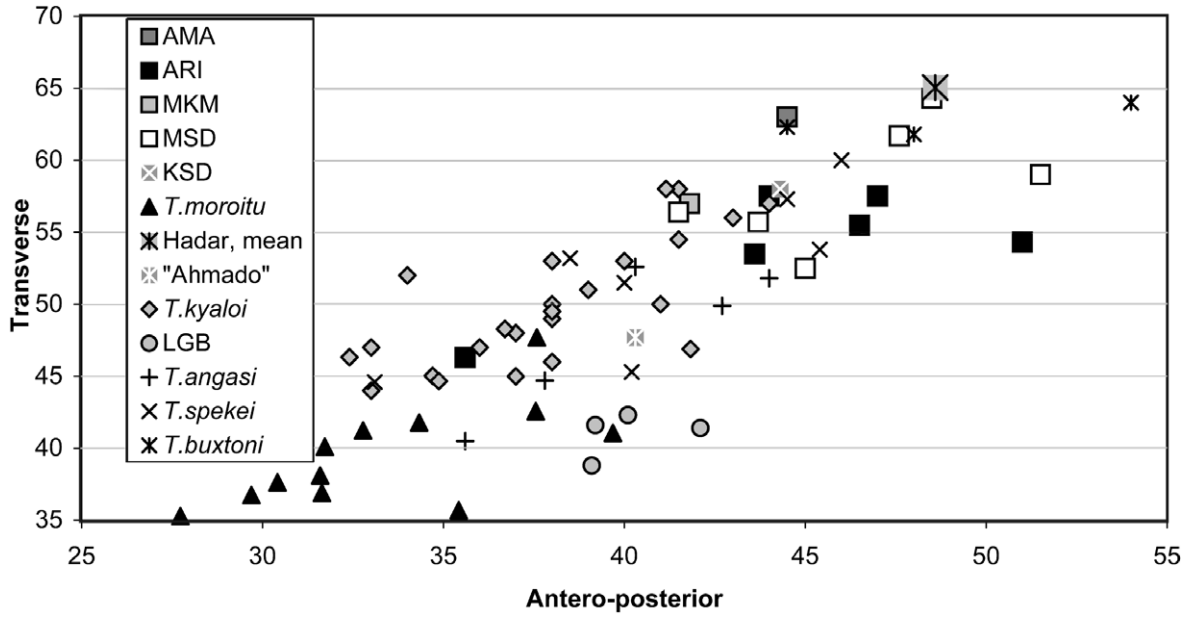


Figure 4. Plot of basal diameters of *Tragelaphus* horn-cores.

(they describe a simple curve in anterior view, and are more or less straight in lateral view), and much more inclined backwards. At Omo, more than half of the *T. nakuae* p4s have a complete lingual wall (Gentry 1985, p. 136).

The *Tragelaphus* aff. *nakuae* from Hadar (Gentry 1981) is similar to the Turkana species, but on average its horn-cores are slightly less compressed (Fig. 4; A–P/transverse = *c.* 0.75), more spiralled, and the braincase is longer with a weaker supra-occipital ridge. In these respects, it is intermediate between *T. saraitu* and *T. nakuae,* but the low inclination of the horn cores in lateral view is more like the latter species, and distinction of the common Hadar *Tragelaphus* from *T. nakuae* is perhaps not necessary. We do not see much difference between the Hadar form and the slightly younger one from Shungura upper member B, as most of the features listed by Gentry (1985, p. 133) for the latter are also found at Hadar, and the differences do not exceed intra-specific variability. We believe that the succession *T. saraitu* (AAMM) – *T.* aff. *nakuae* (Hadar) – *T. nakuae* (Omo) is a single anagenetic lineage, but it could be marked by phases of stasis and more rapid evolution. The ancestors of *T. nakuae* would thus be 'normal' tragelaphines, implying that the boselaphine-like features of this species were secondarily acquired.

Haile-Selassie *et al.* (2009) view *T. moroitu* from the latest Miocene earliest Pliocene of the Middle Awash as a likely ancestor of *T. kyaloi,* and it now seems that it could be ancestral to *T. saraitu* as well.

***Tragelaphus* sp.**

KSD-VP-1/9 is a complete upper tooth series too small to belong to *Tragelaphus saraitu* (length P2-P4 = 31.6; length M1–M3 = 40.5). The only specimen from AAMM small enough to match these upper teeth is ARI-VP-1/327, a slightly incomplete m3 (length = *c.* 18.8). No horn-core from AAMM is small enough to go with these teeth.

There is no small *Tragelaphus* at Hadar or Laetoli, but Gentry (1985) described small horn-cores from Shungura Mb C that he assigned to *Tragelaphus* ?*pricei,* a species named upon dental remains from Makapansgat by Wells & Cooke (1956). Measurements provided by these latter authors for m3 length (18, 18 and 19 mm) raise the possibility that this species is the same as that from KSD and ARI. *Tragelaphus nkondoensis* Geraads & Thomas, 1994, from Uganda, is also of similar size, so that we will not attempt specific identification for the small tragelaphine remains from KSD and ARI.

Tribe Bovini Gray, 1821
Genus *Ugandax* Cooke & Coryndon, 1970

Ugandax coryndonae Gentry, 2006

Bovini are represented by: MSD-VP-5/7 (Fig. 5A; measurements: Table 2), the posterior part of a cranium with complete left horn-core; MSD-VP-6/5, a mandible with p3–m3 (p4 missing), about 15 isolated teeth, and two astragali.

MSD-VP-5/7 originally consisted of many fragments, but

Table 2. *Ugandax coryndonae* – horn-core and skull measurements.

	HC APD	HC Transv.	Length along anterior curve	Width over pedicles	Minimum width over temporal lines	Length from horn-core to occipital
MSD-VP-5/7	83	71	250	180	71	55
	Width over mastoids	Bicondylar width	Occipital height	Width over post. tuber of basiocc.		
MSD-VP-5/7	190	96	63	62		

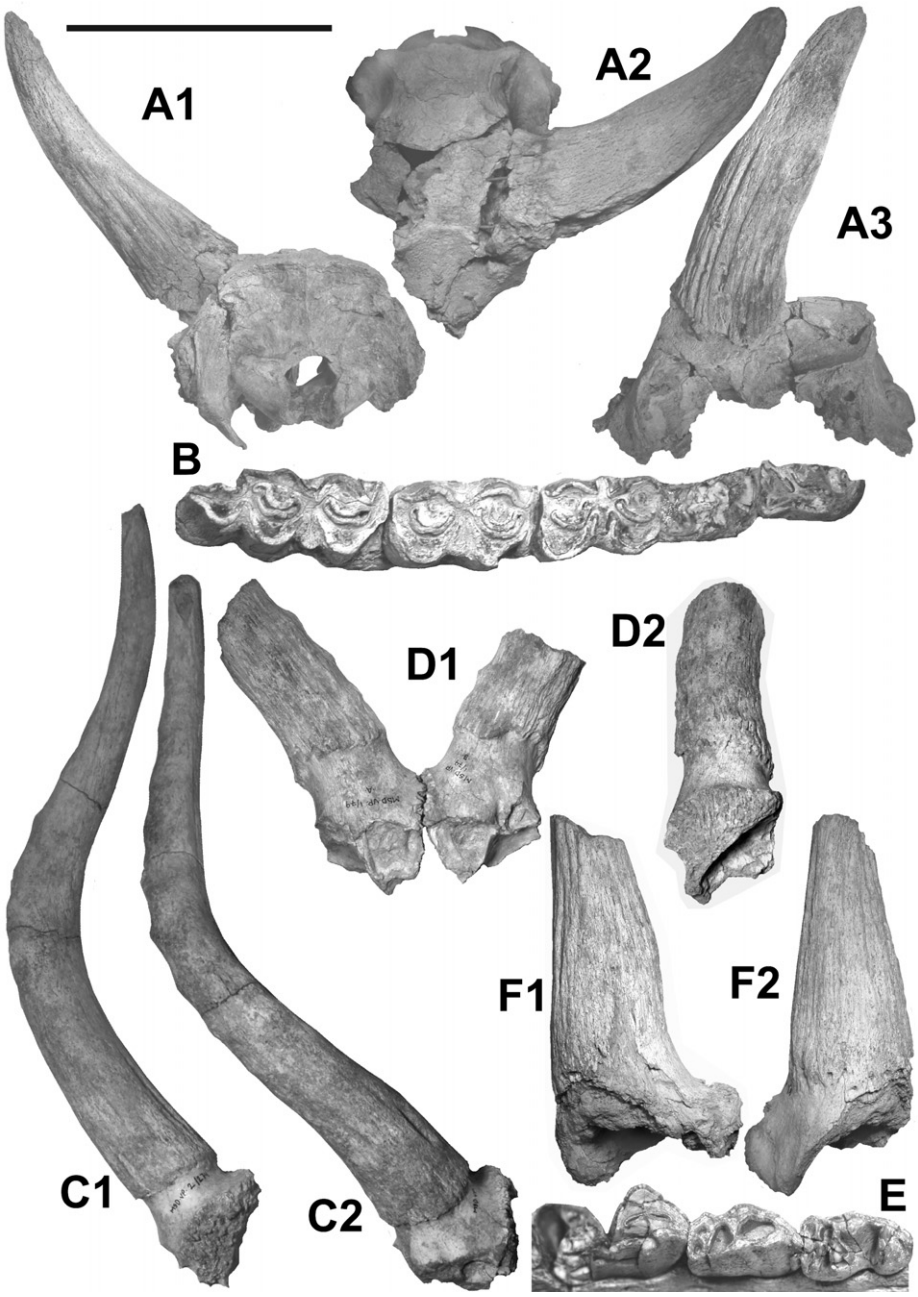


Figure 5. **A, B**, *Ugandax coryndonae*. **A**, brain-case with left horn-core MSD-VP-5/7, in (**A1**) occipital view, (**A2**) dorsal view (**A3**) left lateral view; **B**, right tooth-row p3-m3; **C–E**, *Aepyceros afarensis*. **C**, holotype right horn-core, MSD-VP-2/274, in (**C1**) medial view, (**C2**) anterior view; **D**, frontlet, MSD-VP-1/79: **D1**, anterior view of right horn-core, **D2**, medial view; **E**, lower tooth-row p3-m1, MSD-VP-4/1. **F**, *cf.* '*Damalops*' sp., right incomplete horn-core in (**F1**) anterior view, (**F2**) lateral view. Scale = 20 cm for Fig. A, 10 cm for Figs C, D, and F, 5 cm for Fig. B, 2.5 cm for Fig. E.

has been carefully and accurately reconstructed. The dorsal fronto-parietal surface is transversely flat, but slightly arched antero-posteriorly. Behind the horn-cores, it is limited by strong temporal crests that remain far apart. The brain-case is low and wide, but not extremely so. The occipital has a rather regularly rounded outline, although its top edge is only gently convex. The mastoid region is definitely less expanded laterally than in *Simatherium kohllarseni* from Laetoli (Dietrich 1942, fig. 163; Gentry 1987, pl. 10.3), *U. demissum* from Langebaanweg (Gentry 1980, fig. 8), *U. gautieri* from Kaiso (Cooke & Coryndon 1970, pl. 17B) or than in extant *Syncerus caffer*. The par-occipital processes have a strong inward curvature, as in *S. caffer*.

The horn-core slightly overhangs the anterior part of the temporal fossa. The base of the horn-core is remarkably close to the orbit for a bovine, certainly closer than in the type of *U. coryndonae* from the Denen Dora Mb. of the Hadar Fm (Gentry 2006, fig. 2), but the distance between the horn-core and the occipital is similar, so that the distance between orbit and occipital, i.e. the neurocranium, is shorter. The horn-core is rather short for a bovine, moderately inclined backwards, and moderately divergent from its counterpart at the base (by an angle of about 90°), but this divergence decreases upwards, so that the tips are parallel. The cross-section can hardly be called triangular as all sides, especially the antero-lateral and postero-lateral ones, are well rounded, with no real keel between them. These sides are also covered by deep grooves. Slightly above the base, the postero-lateral side has a flattened,

almost concave surface, as is also often found at Hadar. The frontal bone is slightly inflated in front of the anterior 'keel'.

This skull is closely similar to those of *Ugandax coryndonae* from Hadar (Gentry 2006), but differs slightly in that its horn-cores are inserted not so far behind the orbits and are less inclined backwards. Both characters (which are probably related) denote a more primitive stage for the Mesgid Dora form, in agreement with its earlier age (most *U. coryndonae* specimens at Hadar are from the Denen Dora Mb.), but do not warrant specific distinction, especially as some Hadar specimens look more similar to the Mesgid Dora form than to the type specimen of the species.

The horn-cores of the *Ugandax* sp. from the Middle Awash Late Miocene (Haile-Selassie *et al.* 2009) are remarkable by their strongly triangular cross-section, which makes them less different from boselaphines.

A frontlet from Kanapoi, unfortunately poorly preserved, was assigned to *Simatherium demissum* by Harris *et al.* (2003); its horn-cores certainly had no conspicuous postero-lateral keel, and were more medio-laterally compressed and more divergent, thus making them a poor fit as an ancestor of the Mesgid Dora form. The latter is also very different from the Laetoli *S. kohllarseni,* which lacks keels (Gentry 1987).

On MSD-VP-6/5 (Fig. 5B), the p3 (length = 20.6+) has a narrow metaconid crest (epicristid) extending disto-lingually, but a wide valley remains between it and the paraconid. The molars have strong localized lingual ribs and pinched labial lobes. The length m1–m3 is 90, but this is an overestimate because of gaps between the teeth. MSD-VP-2/139 is an m3 (length = 40.3) showing the same characters. MSD-VP-2/158 is probably a p3 (length = 26); its talonid is narrower than the trigonid, and the metaconid is more transverse, but it is too large for a hippotragine. Upper molars also have pinched lingual lobes.

There is a good deal of variation in the morphology of lower bovine premolars at Hadar, as at Omo (Gentry 1985, fig. 6); even the lower tooth-row AL165-10 from the Sidi Hakoma Mb., that Gentry (1981) had distinguished as more primitive, does not look very different from the other Hadar specimens. A larger sample from AAMM would be needed to discover any evolutionary difference from the Hadar tooth sample, but the differences in horn-core insertion are clear, and suggest that the Hadar form is more derived.

Subfamily indet.
Tribe Reduncini Knottnerus-Meyer, 1907

Reduncini gen. et sp. indet.

Reduncines are extremely rare in the Woranso-Mille area, and only a few teeth have been recovered from the sites considered here. The best specimen is MSD-VP-1/43, a mandible fragment with m2–m3 (Fig. 2J; length of m3 = 22.2). The molars are confidently identified as reduncine due to the presence of a strong goat fold and transversely elongated ectostylid, but they look less mesio-distally compressed than in later forms, the central enamel islands have the shape of an open V, and the labial lobes are not pinched. MKM-VP-1/172 is a p4 (13.5 × 7.6) which is brachyodont for a reduncine but is otherwise typical of this tribe, with transverse talonid cristids and a labially salient hypoconid.

AMA-VP-2/2, ARI-VP-2/74 and MKM-VP-1/6, all lower molars, have a more modern morphology, but the former two have a different facies, and could be derived from slightly younger strata.

The very limited amount of available material prevents any generic assignment, but at least some of the reduncine teeth are more primitive than expected for their age; they are, for example, more primitive than those from the roughly contemporaneous sites of Koro Toro (Geraads *et al.* 2001), and even than those from the earlier site of Kollé (Geraads *et al.* 2009); this confirms that various reduncine lineages evolved at different rates (Haile-Selassie *et al.* 2009; Geraads *et al.* 2009).

Subfamily Hippotraginae Sundevall in Retzius & Lovén, 1845
Tribe Hippotragini Sundevall in Retzius and Lovén, 1845

cf. *Hippotragus* sp.

We assign 10 specimens to this tribe, with various degrees of confidence. The most secure identifications are those of two well-worn p4s, MKM-VP-1/36 and MKM-VP-1/226, both from the right side (length × width = 16.3 × 10.7 and 16.3 × 10.4, respectively). At this wear stage, the parastylid is not distinct from the paraconid that remains separated by a narrow grove extending down to the cervix from a bulbous pillar-shaped metaconid, typical for this tribe. Identification of lower molars, such as those of MKM-VP-1/63 (Fig. 2G) is less straightforward; pinching of their labial lobes is only incipient, ectostylids are high but small, and goat folds are weak and do not reach the top of the crown. None of these features excludes alcelaphines, but when these characters are associated in lower molars, they fit better as hippotragines. The only upper teeth, MKM-VP-1/7, have small but transversely elongated entostyles, and also a hint of pinching of the lingual lobes.

The incomplete horn-core ARI-VP-1/84 is straight in anterior view and moderately curved backwards, but its orientation cannot be determined. It is transversely compressed (basal dimensions = 48 × 37.3), oval in cross-section, with no keel or torsion, no transverse ridges, and a slightly flattened lateral side. There is a single large sinus in the pedicel, and the post-cornual fossa is very shallow. Again, none of these features rules out alcelaphines, but it is so similar to *Hippotragus* or *Tchadotragus* (Geraads *et al.* 2008; Geraads *et al.* 2009) that Hippotragini is a much more likely identification. It is certainly distinct from the straight horn-cores of the species known as *Praedamalis deturi* from Hadar and Laetoli. Other eastern African sites of similar age have yielded few hippotragines. Harris *et al.* (2003) described a horn-core fragment from Kanapoi as *Hippotragus* sp., but it could in fact be reduncine. There are

some specimens from Omo (Gentry 1985) and the Middle Awash Late Miocene (Haile-Selassie *et al.* 2009) that are of similar size, but those from the latter sites were probably shorter.

Tribe Alcelaphini Brooke in Wallace, 1876

cf. *'Damalops'* sp. (new genus Gentry, in press)

Alcelaphines are not common elements in the AAMM localities. There are only three horn-cores, of which only one, MSD-VP-1/8 (Fig. 5F), is reasonably complete and can be oriented. Enough of the frontal bone is preserved to indicate that it was inserted rather uprightly, with little divergence from its counterpart. It is quite short for its basal size, with the antero-posterior diameter quickly decreasing upwards, and is straight in lateral view, but with a slight outward curvature, especially marked on its medial side, in anterior view. The basal cross-section is almost circular (47.6 × 45.7), and the base of the horn-core is lower laterally than medially, but there is no tendency towards a splayed out expansion of this base, as is often seen in specimens from Hadar. The antero-lateral side of the horn-core is convex and there are no transverse ridges. The frontal sinus certainly penetrates into the horn-core, and the post-cornual fossa is virtually absent.

Most alcelaphine dental remains are isolated teeth. Metrics from these specimens suggest that two species coexisted at Mesgid Dora, where an M3 (MSD-VP-2/80: 25.8 × 17) probably belongs to a smaller form than an M1 or M2 (MSD-VP-5/28: 25.3 × 19). Thus, assignment of all specimens to either form is impossible. These dental remains are less characteristic than those of modern alcelaphines. Upper molars may have lingual expansions at the mesio-lingual and disto-lingual corners of the crown, giving the occlusal surface a more rectangular outline than in modern alcelaphines, and this is matched by a tendency to form small goat folds on lower molars, also unknown in modern forms. The lingual wall of the p4 is closed in 5 out of 6 specimens, but open down to the cervix in the longest tooth (MKM-VP-1/175; L = 16.2). It is almost closed in two other teeth, of small size (MSD-VP-2/107; L = 13.3 and MSD-VP-1/63, L = 13.8); they could be p3s, or p4s of the smaller species if two species are really present, but all these measurements are in the range of the '*Damalops*' '*sidihakomae*' from Hadar (Vrba 1997). This advanced stage of lingual closure of p4 compares better with Hadar specimens, where four out of six p4s show lingual closure, than with specimens from Maka and Wee-ee (Vrba 1997) where only one out of four does. No specimen shows whether a p2 was present.

It is unfortunate that alcelaphines are so rare in the AAMM sites, because they probably attest a poorly known early stage in the evolution of the eastern African '*Damalops*', referred to a new genus by Gentry (in press). The single well-preserved horn-core looks much like an alcelaphine frontlet, 1959.233, from Laetoli (Gentry & Gentry 1978, pl. 22, fig. 1) that is considered by Gentry (in review) as close to the Ethiopian *'Damalops*', but both the Mesgid Dora and Laetoli forms differ from later *'Damalops' 'sidihakomae'* in their shorter horns lacking transverse ridges. However, the horn-cores are also relatively long, and with transverse ridges, on a frontlet from Aramis (Vrba 1997). Vrba (1997) also referred frontlet KNM-KP-71 from Kanapoi to this lineage, but this is debatable, because its horn-cores, albeit badly preserved, are smaller but relatively longer.

Subfamily Antilopinae Gray, 1821
Tribe Antilopini Gray, 1821
Genus *Gazella* Blainville, 1816

***Gazella* sp.**

Antilopines are extremely rare in the AAMM sites. From the localities considered here, only the basal part of a horn-core, KSD-VP-1/25, probably belongs to a female *Gazella.* It is a supra-orbital, slightly curved backwards, and has an almost circular cross-section (A–*P* = 20.5, Transverse = 19.6). A few teeth from ARI and KSD also belong to this tribe.

Tribe Aepycerotini Gray, 1872

Genus *Aepyceros* Sundevall, 1847

Type species. Aepyceros melampus (Lichtenstein, 1812), living impala.

Diagnosis. Horn cores little compressed, long and often with transverse ridges. They diverge proximally, then change course in their centre and have more or less parallel distal parts. This lyrated course never becomes strong enough to be spiralled. Females hornless. Frontals hollowed internally and slightly raised between the horn bases, small supraorbital pits. The teeth and limb bones of the living species have a number of unique or distinctive characters (Gentry, in review).

***Aepyceros afarensis* sp. nov.**, Figs 5C–E, Table 3

Holotype. MSD-VP-2/274, a virtually complete left horn-core from Mesgid Dora Vertebrate Locality 2, Woranso-Mille area, lower Awash valley, Ethiopia, 3.7–3.8 Ma (Fig. 5C).

Referred material. Almost 30 horn-cores, mostly basal parts, and numerous dentitions from the localities of Aralee Issie, Makah Mera and Mesgid Dora.

Diagnosis. An *Aepyceros* of large size, matched only by the Laetoli *Aepyceros* and the modern *A. melampus.* Horn-cores with well-marked transverse ridges, very uprightly inserted on long pedicles, almost spiralled, with almost no backward curvature at the base (or even with a slight forward one), but with a strong backward curvature higher up; divergence moderate at the base but increasing for the first few centimetres before decreasing thereafter. The cross-section is but slightly compressed transversely, with its main axis strongly oblique with respect to the sagittal plane, a stronger convexity postero-laterally that never amounts to a keel, but sometimes a longitudinal grove.

Sinuses in the frontal bone are large, but less extensive than in *A. melampus,* not extending high into the pedicle; post-cornual fossa roughly circular, and very deep. Premolar series less reduced than in latter forms.

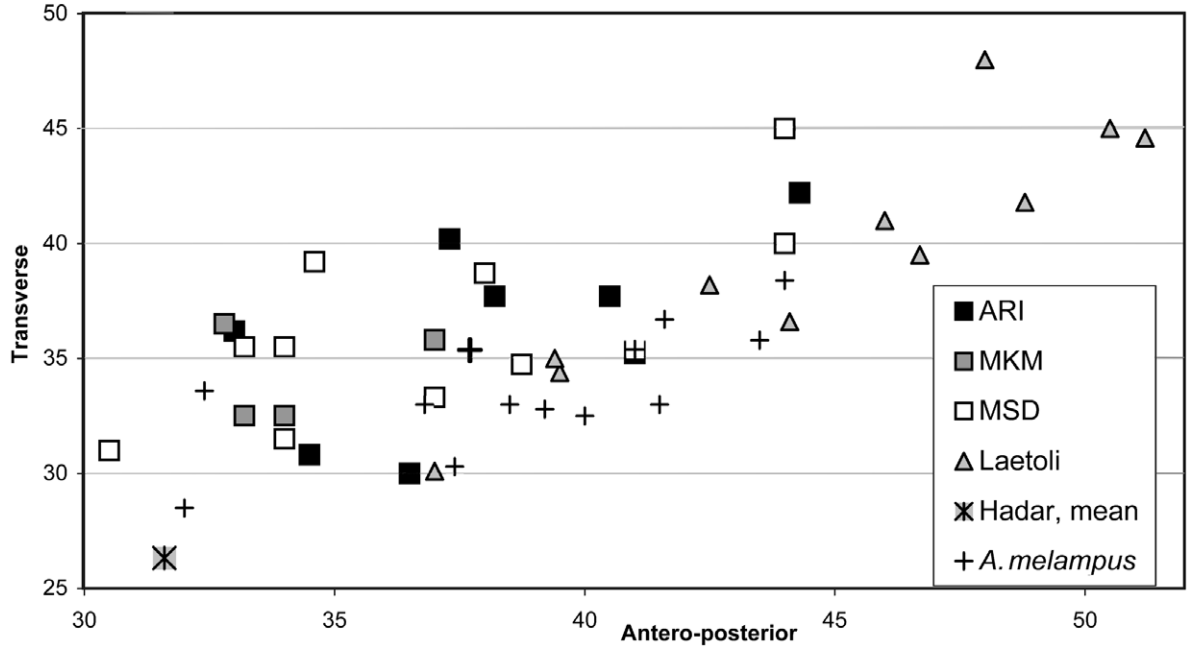


Figure 6. Plot of basal diameters of *Aepyceros* horn-cores. The larger, bold '+' is the mean of 11 specimens (Gentry 1985); they look less compressed than those measured by us, but this is probably only due to a different measurement technique, as the strong inclination of the main axis of the cross-section make them difficult to orientate.

Table 3. *Aepyceros afarensis* – measurements of horn-cores and frontlets.

	HC APD	HC Transv.	Width over pedicles	Width over middle of supra-orbital foramina
ARI-VP-1/44	41	35.2	92	59
ARI-VP-1/214	41	35.3	81	–
ARI-VP-3/172	37.3	40.2	85	–
ARI-VP-2/46	33	36.2	–	*c.* 52
ARI-VP-4/12	44.3	42.2	*c.* 100	–
MSD-VP-1/14	44	45	*c.* 104	–
MSD-VP-1/79	38	38.7	83.5	54
MSD-VP-2/108	33.2	35.5	*c.* 80	–
MSD-VP-2/274	34.7	38.7	*c.* 88.5	–

Table 4. Lengths of premolar row and m3 in *Aepyceros*.

	L p2–p4	L m3
ARI-MSD-MKM	28.6 (MSD-VP-1/19)	23.3 (mean of 9)
A. melampus		
LZMO 1940-1145	23.7	26.1
LZMO 1996-645 (p2 absent in life)	18.2	22.2
LZMO 1962-389	25.0	25.0
A. shungurae holotype	21.3	19.7

Description. The main features of the horn-cores are listed in the diagnosis. The upright insertion (in lateral view, the angle between the posterior border of the horn-core and the fronto-parietal plane is greater than 90°: Figs 5C1, 5D2), lack of clear basal backward curvature, if any, and increasing divergence upwards (Figs 5C2, 5D1), are characteristic enough for horn-core basal parts to be distinguished from other *Aepyceros,* including those from slightly younger sites in the Woranso-Mille area. Measurements are given in Table 3.

A number of teeth also belong to *Aepyceros.* The only complete lower premolar row is MSD-VP-1/19. Its p4 is not unlike that of *Tragelaphus,* but it is smaller than that of *T. saraitu.* In addition, the p2 of MSD-VP-1/19, as inferred from its root, is too small for a tragelaphine. The p4 of this specimen is almost identical to the p4 of MSD-VP-4/1 (Fig. 5E), which is associated with an *Aepyceros* m1. The premolar row is less reduced than in the modern form and than in *A. shungurae* from the Turkana basin (Table 4). No specimen from Laetoli (Gentry, in review) or Lothagam (Harris 2003) is complete enough to estimate this proportion. The four available p4s have only a narrow bridge between paraconid and metaconid that does not reach the top of the crown; the lingual wall is thus less fully formed than in *A. melampus* and the metaconid is less preponderant in its formation. There is only one p4 of *Aepyceros* at Laetoli (Gentry, in review, fig. 5), and it is similar to that of the modern form.

Specific distinctions among Pliocene *Aepyceros* are not easy. *Aepyceros afarensis* differs:

- from living *A. melampus* in its much longer premolar row (although we were able to measure only three specimens of modern impala, the difference is so clear that it can be taken for granted), and in its horn-cores that are less compressed (but some modern specimens may also have an almost circular cross-section; Fig. 6), and more upright (in lateral view, the angle between the posterior border of the horn-core and the fronto-parietal plane never exceeds 90° in the modern form). However, horn-cores are rather similar, and were it not for premolar differences, *A. afarensis* could have been included in *A. melampus*; but of course we know nothing of other possible cranial differences;
- from *A. shungurae* from the Shungura Fm at Omo in its much larger size, more upright insertions and stronger spiralling of the horn-cores;

- from an unnamed species in the same Fm (Gentry 1985, p. 175) in its larger size, much stronger spiralling, much greater basal divergence, and more upright insertion of the horn-cores;
- from the Hadar *Aepyceros* in its much larger size, longer, more spiralled and much more upright horn-cores;
- from the *Aepyceros* of the Upper Laetolil beds (Dietrich 1942, fig. 45; Gentry 1987, pl. 10.8; Gentry, in review) in the more upright insertion of its horn-cores, and in the increasing divergence and lack of clear backward curvature basally. In spite of similar size and geological age, these species are clearly distinct.
- from *A. premelampus* of Lothagam (Harris 2003) in its larger mean size, in the longer pedicles, and presence of transverse ridges and more upright insertions. However, published descriptions of this species are not detailed enough for in-depth comparisons;
- from the rare and poorly known *A.* cf. *premelampus* from the Middle Awash Mio–Pliocene (Haile-Selassie *et al.* 2009) in its larger size, more upright insertion and deeper post-cornual fossa.

Aepyceros afarensis is still very incompletely known, but we prefer to distinguish it at species level because it is clearly, and unexpectedly, distinct from the *Aepyceros* of other Woranso-Mille localities, some of which are probably not much younger, although not yet securely dated. It is also distinct from the *Aepyceros* of the geographically close Hadar Formation at Hadar, including the specimens from the Basal Member, which ranges in age from 3.42 to >3.8 Ma (Wynn *et al.* 2008); however, *Aepyceros* fossils from the Basal Member come from localities sampling its upper part, and are thus certainly younger than the ARI, MKM and MSD ones. *Aepyceros afarensis* therefore appears to have had restricted time and geographic ranges. It adds to the diversity of fossil *Aepyceros,* the evolution of which, far from consisting of a single lineage leading to the modern impala, now appears to have included numerous variations upon a basic pattern.

Subfamily indet.
Tribe Neotragini Sclater and Thomas, 1894
Genus *Neotragus* Hamilton Smith, 1827

***Neotragus* sp.**

Inclusion of this genus in the subfamily Antilopinae has been questioned (Agnarsson & May-Collado 2008), and it is perhaps distinct from other genera recognized as Neotragini.

Description and comparisons. MKM-VP-1/93 (Fig. 2H) is a mandible with p3–m2 (length p2–p4 = *c.* 15), and MSD-VP-5/10 is a mandible with p4, m2 and m3 (length m1–m3 = 24.6; length of m3 = 9.7). They are quite similar in size and morphology, and there is little doubt that they belong to the same taxon, much smaller than *Raphicerus,* which is the most commonly reported 'neotragine'. On p4, the metaconid has a long oblique cristid directed towards the entoconid, itself very long, more or less parallel to the posterior hypoconid cristid, and reaching the disto-lingual corner of the tooth. This tooth is long, but the anterior premolars are shorter, resulting in a relatively short premolar series. The molars are antilopine-like; the third lobe of m3 is not much enlarged. KSD-VP-1/32 is a maxilla with P4-M2 which is of the right size and morphology to go with the above-mentioned mandibles.

These dental remains match in size and morphology those of the living suni of sub-equatorial eastern Africa, *Neotragus moschatus* (which is slightly larger than other species of the genus, and sometimes assigned to a different genus, *Nesotragus*), and we are confident in referring these remains to this genus, which, as far as we know, has never been reported as a fossil. West African forms (*Neotragus s. str.*) are forest dwellers, but *Neotragus moschatus* lives in thick bushes.

Subfamily Cephalophinae Blyth, 1863
Genus *Cephalophus* Hamilton Smith, 1827

***?Cephalophus* sp.**

We tentatively assign to this genus two upper teeth, a premolar (probably P4), ARI-VP-1/370 (9.7 × 11.7), and a molar, ARI-VP-1/197 (14.6 × 14), perhaps of the same individual (Fig. 2), and a lower molar, ARI-VP-3/225 (12.8 × 8.9). The premolar is small compared to the upper molar, quite brachyodont, and has a rounded lingual lobe and a salient labial pillar. The upper molar is less brachyodont, has a small entostyle, rounded but slightly pinched lingual lobes, strongly outbowed labial folds, and no mesostyle. This latter character is the most decisive for inclusion of these 'boödont' teeth in the Cephalophinae. In this subfamily, the mesostyle is small but present in the upper part of the crown, but vanishes in worn teeth. This also occurs in some 'Neotragini', but that group has 'aegodont' teeth, quite unlike these ones. The lower molar also has strong pillars and rounded labial lobes, but no hint of a goat fold, and is therefore definitely not reduncine. These teeth are almost certainly cephalophine, but we are cautious about this assignment, because in the past, specimens referred to *Cephalophus* have more than once been misidentified. This species would be of about the same size as the Laetoli cephalophine (Gentry 1987, in review).

CONCLUSIONS

The distribution of bovid species from the AAMM and KSD localities is given in Table 5. The low diversity at AMA is obviously related to the smaller number of collected specimens, but the high diversity at KSD is worth noting. The other three sites do not differ significantly in terms of their bovid composition.

Figure 7 shows the number of dental and cranial (mainly horn-core) remains found in the AAMM group of localities. As in other eastern African sites, dental remains of Alcelaphini and, to a lesser extent, of Bovini, are relatively more common than horn-cores, while the reverse is true of *Aepyceros* and Tragelaphini. This is doubtless a taphonomic bias due to the horn-cores of the latter groups being solid and more robust, whereas those of the Alcelaphini are more easily broken (in part because of their large basal sinus). Similarly, the robustness of alcelaphine

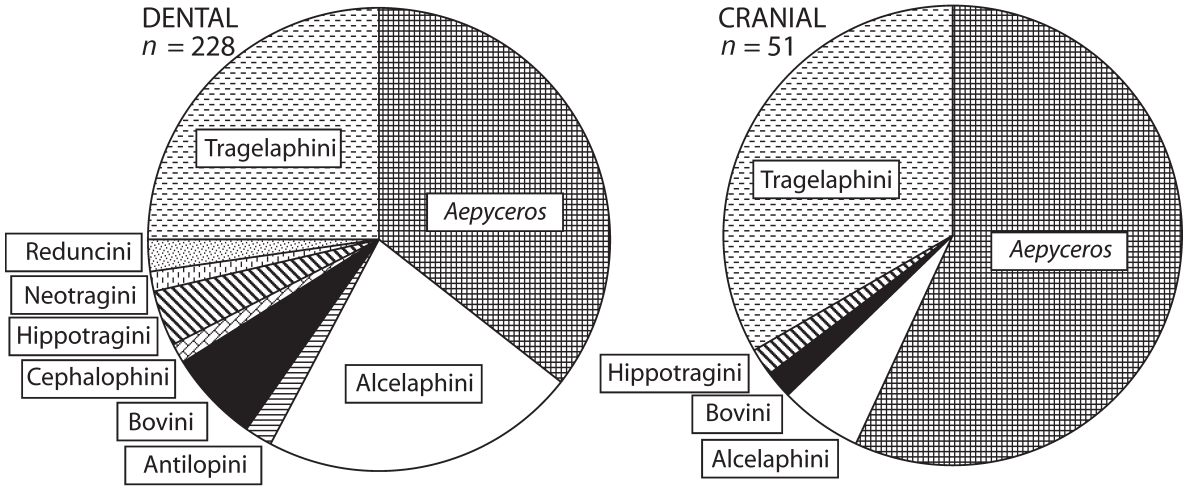


Figure 7. Proportions of the various bovid taxa in the AAMM localities, calculated from the number of identified teeth (**left**) or cranial remains, mostly horn-cores (**right**).

Table 5. Distribution of the various bovid species in the AAMM and KSD localities (the first row gives the total number of bovid cranial and dental remains in each group of localities).

	AMA	ARI	MKM	MSD	KSD
	7	110	77	82	11
Tragelaphus saraitu	*cf.*	+	+	+	+
Tragelaphus sp.		?			+
Ugandax coryndonae	*cf.*	*cf.*	*cf.*	+	
Reduncini gen. et sp. indet.	+	?	+	+	
cf. Hippotragus sp.		+	+	?	
cf. '*Damalops*' sp.		+	+	+	+
Gazella sp.		+		+	+
Aepyceros afarensis		+	+	+	+
Neotragus sp.			+	+	+
?*Cephalophus* sp.		+			

teeth, which preserve better than those of other groups, increases this bias. Therefore, the true relative abundance of the Alcelaphini lies probably between that of their horn-cores and that of their teeth. In any case, it is clear that the AAMM bovid associations are dominated by tragelaphines and impalas, alcelaphines being significantly less common, bovines rare, and other groups virtually absent. The habitat of such an assemblage, very poor in antilopines and reduncines, was certainly neither open savannah nor grassland. Impalas are not very habitat-specific, as they can browse or graze, but usually favour woodland fringes, while tragelaphines are well known to favour bushes and thickets. Their abundance points unambiguously towards a moderate to high degree of vegetation cover, such as dense woodland with bushes, although the presence of alcelaphines implies some clear patches. This inference is compatible with the evidence from other mammalian taxa from these localities.

The slightly younger site of Korsi Dora yielded only 15 identifiable bovid specimens, but the composition of this assemblage differs from the AAMM ones, as it includes four antilopine remains, including the only *Gazella* horn-core, a neotragine, and a maxilla of *Tragelaphus saraitu* and yet another small species of *Tragelaphus*. Sample size is too small to choose between a taphonomic bias and/or a real ecological difference. Further investigation of the KSD-VP-1 assemblage might help in distinguishing between these options.

The bovid fauna cannot contribute to the dating of the AAMM sites as these have been accurately dated by radiometric methods, but it is worth noting that the Bovidae, at least those that are represented by enough material, are clearly distinct from those of the Sidi Hakoma Member of the Hadar Fm, which is only 0.3–0.4 Ma younger. Ancestor-descendant relationships are likely for *Ugandax*, *Tragelaphus* and '*Damalops*', and less likely for the *Aepyceros*. It is noteworthy that none of these taxa remains unchanged, thus demonstrating significant rates of evolution between *c.* 3.5–3.8 Mya.

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ABBREVIATIONS

AAMM Am-Ado + Aralee Issie + Makah Mera + Mesgid Dora
A-P Antero-posterior

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