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Ruminants (Giraffidae and Bovidae) from Kanapoi

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Abstract

We update here our recent revision of the Kanapoi ruminants and describe recently collected material. We now regard the occurrence of reduncins as doubtful, we revise the identification of a large raphicerin as being more probably *Gazella*, and we add *Gazella* cf. *janenschi* and the Cephalophini to the faunal list. New material of *Tragelaphus kyaloi* suggests that this species held its head unlike other tragelaphins, and was not an exclusive dedicated browser, but Kanapoi pre-dates the Pliocene change of *Sivatherium*, *Aepyceros*, Alcelaphini, and even Tragelaphini towards more grazing diets. Kanapoi shares several ruminant taxa with sites in Ethiopia and Tanzania, attesting to latitudinal exchanges.

Introduction

The fossils collected at Kanapoi by the Harvard expeditions led by B. Patterson and by the National Museums of Kenya (KNM) expeditions led by M. Leakey were briefly described by Harris et al. (2003), who also figured the most important specimens. Further collecting at Kanapoi since 2003 significantly increased the collections, and an update on the Ruminantia, together with some more figures, were provided by Geraads et al. (2013a). Since then, more material has been found, allowing us to refine the taxonomy; in addition, we add complements regarding the affinities of the various species, as well as their ecological preferences and biogeographic relationships. Collecting during recent years left out only very fragmentary material, but was certainly less exhaustive in earlier years, e.g., isolated teeth are less common; the present day collection includes about 530 ruminant specimens. The material has been extensively compared with that from other late Miocene to early Pleistocene sites from Kenya in the KNM and National Museum of Ethiopia (NME).

Systematic paleontology

Family Giraffidae Gray, 1821

Description and comparisons There are only about 40 specimens in this family, but two species of *Giraffa* can be identified, in addition to *Sivatherium*.

Genus *Giraffa* Brisson, 1762

Giraffa jumae Leakey, 1965

KNM-KP 58739 (Fig. 1H) is a short horn whose base is very incomplete but shows that it was inserted above a cranial sinus. It is distinctly more conical than in the modern giraffe *Giraffa camelopardalis*, but some ossicones of *G. jumae* from Hadar, such as AL 291-1 (Geraads, 2013b), display the same conical shape. It also resembles the horn from Langebaanweg that Harris (1976b) chose as the paratype of his *Sivatherium hendeyi*, but is much too conical to belong to this genus (Q.B. Hendey pers. comm. to D.G., 1984); it could belong to *G. jumae* as well. Tooth measurements of the mandible KNM-KP 30450 described by Geraads et al. (2013a) are slightly above the observed maxima for the modern giraffe *G. camelopardalis* (length of m3 = 47.7 vs. 37.5 – 46, $N = 36$). Several other teeth and limb-bones are of a similar large size, but most of them are within the range of the modern form; surprisingly, no astragalus is large enough to belong here. A species distinction from *G. camelopardalis* would not be strongly supported on a size basis alone, but the p3 of KNM-

KP 30450 is more informative in having a complete lingual wall along the whole crown, rare in the modern form whose p3 is almost always more primitive, but common in *G. jumae* both at Hadar (Geraads et al., 2013b) and Langebaanweg (Harris, 1976b). This confirms that this species is probably not ancestral to the modern form; its possible occurrence in Turkey (Geraads, 1998) raises the possibility of an ancient divergence from the late Miocene Eastern Mediterranean *Bohlinia*. Besides Hadar and the type-locality Olduvai, the species has been reported from several African sites, but this name has uncritically been given to fossil *Giraffa* of large size, and the history of the genus at species level remains poorly understood. If there are really four species of modern giraffes whose East African members diverged about 2 Ma (Fennessy et al., 2016), one would probably expect to find more *camelopardalis*-like fossils in the Pleistocene record, and it is likely that this date, based upon exceedingly old dates for the divergence of the Cetartiodactyla main groups, is over estimated.

Giraffa pygmaea Harris, 1976a

Geraads et al. (2013a) revised the identification of the smaller giraffe of Kanapoi, which was called *Giraffa stillei* by Harris et al. (2003). KNM-KP 59918 (Fig. 1I) is an incomplete, weathered ossicone of small size. Its apical end forms a terminal knob, as in males of the modern form, showing that it belongs to a small-size species rather than to a female. It does not significantly differ from ER-656, paratype of *Giraffa pygmaea* (Harris, 1976a:Pl. 9–10).

Several newly discovered astragali confirm the presence of *G. pygmaea*. No consistent feature seems to distinguish giraffid astragali from those of bovids, but some of these astragali are larger than the numerous astragali of the bovid *Ugandax* from the Hadar Formation. In addition, in at least some of them, the lateral lip of the proximal trochlea is thick and laterally shifted, as in modern *G. camelopardalis*, but unlike in bovins. Their measurements (Fig. 2) are slightly lower than those of other East African *Giraffa* that could belong to either *G. pygmaea* or small *Giraffa stillei*: ST-23825 from South Turkwel, ER-2932 from Koobi Fora, and LT-28646 and LT-25451 from Lothagam. Several astragali from Omo are as small as the Kanapoi ones, but might be bovin.

This very small *Giraffa* is less rare at Kanapoi than in younger sites; Geraads et al. (2013b) surmised that this might be because *G. pygmaea* evolved into *G. stillei*, but late Miocene potential ancestors of *Giraffa* are large, and it is perhaps instead the diminutive size of *G. pygmaea* that is derived.

From an ethological point of view, the sharp distinction between the two *Giraffa* species confirms the observation by Geraads et al. (2013b) that this distinction dwindles in younger sites, contrary to the expectation that character displacement would lead to the opposite, so as to increase niche partitioning and visual recognition. The reasons for this increasing similarity remain unknown.

Genus *Sivatherium* Falconer and Cautley, 1836

Sivatherium cf. *hendeyi* Harris, 1976b

Harris et al. (2003) identified the species on the basis of a partial horn KNM-KP 30449, but the quickly decreasing diameters show that it was far too short for *Sivatherium*, and it is in fact certainly a bovid horn-core (see below). The only new specimen is KNM-KP 59920, a short, massive first phalanx; it is stouter than in *Giraffa* and the proximal articulation is broader relative to its antero-posterior diameter, which matches the broad distal metapodials of *Sivatherium*. Still, the only unequivocal specimens of *Sivatherium* are the incomplete upper molar KNM-KP 32551 and the tooth fragments KNM-KP 30227; this taxon is thus extremely rare at Kanapoi.

Remarks. The enamel $\delta^{13}C$ of fossil *Giraffa*, except for a single outlying value at Lee Adoyta (Rowan et al., 2016), shows that this genus consistently remained a browser during the whole Pliocene, and Kanapoi is no exception. By contrast, the diet of *Sivatherium* in Africa, long debated, rather abruptly changed during the Pliocene, from browser to almost pure grazer, even though this change looks diachronous in the Turkana and Afar basins (Rowan et al., 2016). Sample size is low at Kanapoi, but the $\delta^{13}C$ values (Supplementary Online Material [SOM] Fig. 1) indicate a browser, or at most a mixed-feeder, certainly far less distinct from *Giraffa* in its diet than in later sites.

Family Bovidae Gray, 1821

Description and comparisons

Subfamily Bovinae Gray, 1821

Tribe Tragelaphini Blyth, 1863

Genus *Tragelaphus* Blainville, 1816

Tragelaphus cf. *kyaloi* Harris, 1991

Tragelaphus is by far the most common bovid at Kanapoi, but many specimens are incomplete. The most significant recently collected one is KNM-KP 58836 (Fig. 1A), a braincase with the bases of both horn-cores, unfortunately in bad condition. Together with the previously collected occipital KNM-KP 68 (Fig. 1C), it shows that the Kanapoi *Tragelaphus* has a distinctive cranial morphology, unlike that of other tragelaphins. The horn-cores are inserted very upright on the skull, the angle between their posterior border and the top of the braincase being about 90°, and even more in KNM-KP 58836. The braincase is short and broad posteriorly; the broad occipital is not vertical as in other *Tragelaphus*, but forms with the top of the parietal an angle of about 120° in KNM-KP 58836 (probably less than this in KNM-KP 68, but still certainly more than 90°); KNM-KP 30158 shows that the dorsal frontal profile is more arched between the horn-cores than in other tragelaphins; the paroccipital processes are not directed ventrally, but postero-ventrally (as in alcelaphins). The anterior tuberosities of the basioccipital are long and narrow, with a long, narrow groove in between. All these cranial characters are probably correlated and point to a head posture different from that of other tragelaphins, with a less horizontal forehead (Fig. 3).

The only relatively complete horn-cores are those of KNM-KP 30156 (Fig. 1B), but other specimens conform with their morphology. Those whose basal dimensions can be measured are KNM-KP 58792 (APD = 44.3 × TD = 48.2), KNM-KP 59682 (35 × 42.5), KNM-KP 58725 (33 × 42), KNM-KP 59801 (39 × 47.5), KNM-KP 59802 (31.5 × 36) KNM-KP 59807 (47.5 × 60.5), and KNM-KP 59831 (47.2 × 58.5). The range of variation (Fig. 4) is thus greater than illustrated by Geraads et al. (2013a), but the presence of two species can be rejected because dental size is homogeneous (Geraads et al., 2013). This great variation is comparable to that found in modern tragelaphins that have horns in both sexes (*Tragelaphus eurycerus* and *Tragelaphus oryx*); the fossil *Tragelaphus nakuae* displays a similar large size range (Reed and Bibi, 2011:Fig. 6), and these authors assumed that it also had horned females. It is likely that this was also true of *Tragelaphus kyaloi*, in agreement with the absence of a hornless skull at Kanapoi. The horn cores have a fairly regular curve, diverging by about 80° to 90° at the base, and this divergence somewhat increases upwards and then regularly decreases to the tips, which were relatively close to each other; by contrast, because of the strong basal divergence, the most lateral parts are located far apart. Among modern species, the closest resemblance in course is with the mountain nyala of the Ethiopian highlands, *Tragelaphus buxtoni*. At the base, the keels are variable but generally poorly indicated; the antero-lateral one is no more than a change in outline curvature and almost vanishes upwards. The lateral one is also usually weak. Because of these weak keels, and

because the antero-medial part is often expanded, the section is more quadrangular than triangular (Fig. 1D).

We follow Harris et al. (2003) in relating the Kanapoi *Tragelaphus* to *Tragelaphus kyaloi* Harris, 1991, a species defined at Kosia and about the same age as the Kanapoi specimens (~4 Ma). The species is very poorly represented outside Kanapoi, but the holotype frontlet closely resembles the Kanapoi form in the course (Harris, 1991:Fig.5.7) and cross-section (Haile-Selassie et al, 2009:Fig. 9.10) of the horn-cores. The only visible differences are that, in the type specimen, the anterior tuberosities of the basioccipital are stronger and the parieto-occipital angle looks smaller; given that these differences concern some of the most remarkable characteristics of the Kanapoi form, we now refrain from formally identifying the Kanapoi species with *T. kyaloi*.

The Kanapoi *Tragelaphus* resembles the slightly younger *Tragelaphus saraitu* from Woranso-Mille in the Awash Valley (Geraads et al., 2009b) in its horn-cores that are uprightly inserted and have similar anteroposterior compression, but it differs in having more regularly curved horn-cores with re-approaching tips, a less triangular cross-section with a fainter anterior keel (especially at the base), its slightly longer braincase, lower and broader occipital that makes a greater angle with the top of the braincase in lateral view, and paroccipital processes directed posteroventrally. *T. saraitu*, which might already be present at Mursi (Drapeau et al., 2014), is probably an early member of the *Tragelaphus rastafari-T. nakuae* lineage (Geraads et al., 2009b; Reed and Bibi, 2010; Bibi, 2011), suggesting that the divergence from *T. kyaloi* must be earlier. This was problematic because earlier *Tragelaphus* species are also rather different from *T. kyaloi* (see Geraads et al., 2013a), except perhaps the scarce material from Lothagam; the new material resolves this issue by showing that the characters of *T. kyaloi* are clearly derived. Indeed, the quadrangular cross section of the horn-cores and construction of the braincase are so distinctive that in a phenetic classification, a generic distinction would be warranted.

The cranial flexion of the Kanapoi *T.* cf. *kyaloi*, which implies a muzzle somewhat more inclined ventrally than in browsing tragelaphins, suggests that grasses made up a greater fraction of their diet. Indeed, isotope analyses show that during the whole Pliocene, the tragelaphin diet ranged from browsers to mixed-feeders and even grazers, few of them being strict browsers like modern ones (Cerling et al., 2015); the few available data from Kanapoi also suggest mixed feeding (SOM Fig. 2).

Tribe Bovini Gray, 1821

Genus *Simatherium* Dietrich, 1941

Simatherium sp.

The horn-core KNM-KP 30449 (identified by Harris et al., 2003, as belonging to the giraffid *Sivatherium*) has a rounded cross-section almost devoid of keels, unlike those of *Ugandax* from Uganda (Cooke and Coryndon, 1970) and Ethiopia (Gentry, 2006; Geraads et al., 2009b, 2012; Haile-Selassie et al., 2009); we tentatively identify it as *Simatherium*.

On the mandible KNM-KP 96 (Harris et al., 2003:Fig. 23B-C), the metaconid almost completely closes the lingual valley of p4; it is less expanded in KNM-KP 51008 and KNM-KP 56877 (which probably represent both sides of the same individual), but on the average it is stronger than in the more recent Hadar and Woranso-Mille *Ugandax coryndonae* (Gentry, 2006; Geraads et al., 2009b, 2012) and earlier Kuseralee Member of the Middle Awash (Haile-Selassie et al., 2009:Fig. 9.8), confirming that they belong to different lineages. However, the phylogeny of African Bovini remains poorly known and, as noted by Geraads et al. (2013a), nothing supports the identification of the Kanapoi bovin with the Langebaanweg '*S*'. *demissum*, which Gentry (2011) moved to *Ugandax*.

Sub-family Antilopinae Gray, 1821

Tribe Reduncini Knottnerus-Meyer, 1907?

Reduncini? gen. et sp. indet.

Geraads et al. (2013a) dismissed most of the dental remains assigned to this tribe by Harris et al. (2003) as not belonging here; they were uncertain about the occurrence of this tribe at Kanapoi, and its presence now looks to us even more unlikely.

The only specimens remaining as possible reduncins are the incomplete horn-core KNM-KP 30631 and the lower molar KNM-KP 463 (see Geraads et al. [2013a] for description and discussion), but we will not assert the occurrence of this tribe on the basis of these incomplete pieces.

Tribe Hippotragini Sundevall in Retzius and Lovén, 1845

Genus indet., cf. *Tchadotragus* Geraads et al., 2008

Geraads et al. (2013a) revised some of the identifications made by Harris et al. (2003) and added some Hippotragini to their list. A few new specimens further increase it, but the

Hippotragini remain an uncommon group. The horn core base KNM-KP 56824 is somewhat problematic; its absence of keels and torsion, gentle backward curve, faint transverse ridges, and oval cross-section (basal diameters: 39 × 33) all fit Hippotragini, but the basal sinus looks subdivided, unlike in *Tchadotragus* and modern hippotragins (although struts may be present: Erdbrink, 1988:Pl. 6). It may be that at that time pneumatization of hippotragin pedicles was less extensive than at present; *Saheloryx* Geraads et al., 2008 almost certainly belongs to this tribe, in spite of its solid pedicles.

KNM-KP 56843 (Fig. 1F) and KNM-KP 59763 (Fig. 1G) are two moderately worn upper molars that clearly display their occlusal pattern: they have a central enamel island and a spur in the posterior valley, but the labial pillars are less rounded and the entostyle is weaker than in modern *Hippotragus*. They are distinctly less hypsodont than molars of the Kanapoi bovin. In these features, they resemble more modern *Oryx* and the primitive *Tchadotragus* from Chad (Geraads et al., 2008, 2009a), and characters of the lower teeth match those of *Tragelaphus fanonei* (Geraads et al., 2009a) from the lower Pliocene of Kossom Bougoudi.

On the whole, the Kanapoi hippotragin is at a more primitive evolutionary grade than modern forms and closer to *Tchadotragus*, but formal identification would not be strongly supported.

Tribe Alcelaphini Brooke in Wallace, 1876

Genus *Damalacra* Gentry, 1980

Damalacra harrisi Geraads, Bobe and Manthi, 2013a

No new material definitely attributable to this species has come to light, so that it remains known only by the type-specimen, the braincase with horn-cores KNM-KP 30157 (Harris et al., 2013:Fig. 27). In its long braincase for an alcelaphin and horn-cores with a simple course and no basal swelling, it is a primitive form. Vrba (1997) was the first to observe that it looks morphologically intermediate between the Langebaanweg *Damalacra* Gentry, 1980 and *Parmularius pandatus* Gentry, 1987 from Laetoli, the latter of which is more derived in its less simple horn cores. The Kanapoi form is also intermediate in age and a likely ancestor for *P. pandatus*.

Genus *Damalborea* Gentry, 2010?

Damalborea? n. sp.

The occurrence of this taxon at Kanapoi is mostly based upon the frontlet KNM-KP 71, identified as *Damalacra* cf. *neanica* by Harris et al. (2003), but revised and discussed by Geraads et al. (2013a). KNM-KP 58588 could be another horn-core of the same taxon. It lacks the base, but has an oval cross-section whose diameters quickly decrease upwards, showing that is was short. Geraads et al. (2013a) observed that this species is probably also present at Aramis and Laetoli. We tentatively include it in the genus *Damalborea*, best known from Hadar; it is certainly different from its two known species (Vrba, 1997; Gentry, 2010; Geraads et al., 2012) but remains too poorly known to be named.

Alcelaphini gen. et sp. indet.

Geraads et al. (2013a) regarded the horn-core pieces KNM-KP 30418 and KNM-KP 30633 as distinct from the two above mentioned species, and noted that the mandible KNM-KP 31733 is too large to match the horn-cores in size, so that a total of four alcelaphin species might be present. Other alcelaphin dentitions are of homogeneous size, with m3 lengths ranging from 27.5 mm to c. 31 mm (N = 7), but we do not know whether they represent one species or two (or more) similar-sized ones.

As early as the lower Pliocene, the Alcelaphini were grazers (SOM Fig. 3), and it even seems that this grazing specialization slightly increased during the course of this epoch. The few available isotopic data confirm that they were fully grazers at Kanapoi.

Tribe "Ovibovini" Gray, 1872?
Genus et sp. indet.

The taxon remains known by a single specimen, the partial mandible KNM-KP 66, called aff. *Makapania* sp. by Geraads et al. (2013a:Fig. 4). Members of this certainly polyphyletic 'tribe' are quite rare in the African fossil record; its main East African representatives are *Budorcas churcheri* from Hadar (Gentry, 1996), perhaps *Nitidarcus* from the Middle Awash (Vrba, 1997), and a few remains from Omo. Identification at genus level of the Kanapoi mandible is impossible, especially as dental remains are almost unknown in East Africa, and we now prefer not to suggest affinities with the South African form.

Tribe Aepycerotini Gray, 1872
Genus *Aepyceros* Sundevall, 1847

Aepyceros cf. *afarensis* Geraads, Melillo and Haile-Selassie, 2009

The impala is a common bovid at Kanapoi but, like most other bovids, it is mostly represented by incomplete horn-cores and dental remains. As far as can be ascertained, there is some variation in horn-core torsion and development of transverse ridges, some specimens looking rather primitive, while others are closer to the morphology of the modern *Aepyceros melampus*. The lengths at mid-height of three m3s are 22, 23, and 24.5 mm; they are thus slightly larger than at Hadar (Geraads et al., 2012) and more similar in size to *Australopithecus afarensis* from Woranso-Mille (Geraads et al., 2009b). Surprisingly, they are not smaller than the *Aepyceros* teeth from Laetoli (Gentry, 1987, 2011), although the horn-cores from this site are larger. The variability of horn-core morphology, limited morphological differences between *Aepyceros* species, ambiguous indications provided by size, and the fragmentary nature of the remains prevent definite identification; the one suggested by Geraads et al. (2013a) remains the most likely.

As observed by Cerling et al. (2015), many fossil *Aepyceros* were more grazers than the modern impala. At Kanapoi, this is true of most of the specimens sampled, although two others have low $\delta^{13}C$ values (SOM Fig. 4); these are the ones listed by Harris et al. (2003), but their accession numbers were not provided, so that we could not check the identifications. It is likely, although by no means certain, that they were misidentified (confused with *Tragelaphus*?), and this could also be true of some low values in other sites.

Tribe Raphicerini Grubb, 2001 ?

Genus *Raphicerus* H. Smith, 1827 ?

Raphicerus? sp.

Raphicerus is commonly included in the Neotragini, but this tribe is clearly polyphyletic (e.g., Yang et al., 2013) and it is safer to include it in a less comprehensive clade. Bovids of its size are relatively common at Kanapoi, but are mostly represented by incomplete horn-cores and dental remains. Their identifications are difficult because several small bovids share a rather similar dental morphology and simple, spike-like horn-cores lacking characteristic features. In addition, female horn-cores and dental remains of small gazelles, as well as remains of other tribes (e.g., Cephalophini), may be confused with them. Geraads et al. (2013a) recognized two species at Kanapoi that they called ?*Raphicerus* sp. A and ?*Raphicerus* sp. B; they removed the smaller *Madoqua* from the Kanapoi faunal list. More

material has come to light during the last few years; it confirms the absence of *Madoqua*, but does not improve the distinction between the two or more taxa that are present. All available m3s have a relatively large third lobe, unlike in the modern *Madoqua* and *Rhynchotragus* in which it is reduced or absent.

We tentatively leave in *Raphicerus*?, the smaller taxon represented by some dental remains (SOM Table 1) and at least the incomplete horn-core KNM-KP 49373, which is almost straight, but it now seems to us more likely that the larger one is instead a small species of *Gazella* (see below).

Tribe Cephalophini

Gen. et sp. indet.

KNM-KP 59788 is an upper molar of small size (length = 9.3 mm; width = 8.1 mm) that much differs from those of Raphicerini and Antilopini in its very strong paracone rib and weak mesostyle; however, the latter looks less reduced than in modern *Cephalophus* or than in the very rare fossil representatives of this tribe from Laetoli (Gentry, 1987:Pl. 10.6) or Woranso-Mille (Geraads et al., 2009b:Fig. 2I). Cephalophins are mostly forest-dwellers and are always quite rare in the fossil record. This tooth adds a new taxon to the Kanapoi faunal list and indicates the presence of heavy cover in the surroundings. Size alone is unable to explain the scarcity of this family in the Kanapoi collection compared to other similar-sized bovids, but it may be that other taphonomic factors limited the number of its remains.

Tribe Antilopini Gray, 1821

Genus *Gazella* Blainville, 1816

Gazella sp.

The horn-cores KNM-KP 29264 and KNM-KP 29270 (Harris et al., 2003:Fig. 26) almost certainly belong to the same taxon, as surmised by Geraads et al. (2013a), who tentatively assigned them to the Reduncini, while observing that they differ in important features from other members of this tribe. In addition to the differences that they listed, we observe that none of the teeth recently unearthed at Kanapoi is definitely attributable to the reduncins, and we consequently now favor an alternative identification and regard them as close to *Gazella*. Harris et al. (2003) identified KNM-KP 29264 as *Gazella* sp., but referred KNM-KP 29270 to *Damalacra*.

These horn-cores are remarkable in their virtually straight course, with only a very slight forward curvature in their second half, and in the probably correlated characters of small to moderate transverse compression and tendency towards flattening of the anterior surface. Only KNM-KP 29270 can be oriented and is inserted rather obliquely. Other characters of the frontals are not observable, except that they almost certainly lack sinuses. *Gazella* horn-cores are curved backwards and have a rounded anterior face, and the Kanapoi specimens do not fit within their range of morphological variation. However, their small size, the fact that they do not fit into another tribe, and the occurrence of a number of dental remains of Antilopini whose size matches these horn-cores all support an assignment to this tribe. Small horn cores could be females of the same species (SOM Table 2).

Gazella cf. *janenschi* Dietrich, 1950

The frontlet KNM-KP 29263 that Harris et al. (2003:Fig. 31) identified as *Raphicerus* sp. is certainly of a female *Gazella*, as noted by Geraads et al. (2013a), but the slight backward curvature of the horn-cores is unlike KNM-KP 29264 and KNM-KP 29270, and species identity is unlikely. Its morphology and measurements are similar to those of female *Gazella dorcas* (width over pedicles = 53.2 mm; 47.1–53.5 mm in five female specimens of the modern form). KNM-KP 56816 (Fig. 1J) is the base of a probably male horn-core, of moderate size, little compressed (basal index: 25.3 mm × 21.8 mm), with the maximum diameter located centrally and a slightly flattened lateral surface. The pedicle is distinctly narrower than the horn-core proper, as in a specimen of *Gazella janenschi* from Laetoli (Gentry, 2011:Fig. 15.9B), and other characters of this horn-core, especially the poor transverse compression, also fit this species. However, no other specimen allows us to assess the variation and it is safer not to attempt a formal identification.

Several recently found horn-core pieces resemble KNM-KP 29263. In addition, it now seems more likely that most of the dental specimens assigned by Geraads et al. (2013a) to ?*Raphicerus* sp. B belong instead to *Gazella* (measurements: SOM Table 1). On the partial mandible KNM-KP 56878, which is definitely too small to belong to *Gazella*, the third lobe of m3 has a central valley, showing that the main criterion that Gentry (1980) used to distinguish lower dentitions of *Raphicerus* from those of *Gazella* at Langebaanweg does not work at Kanapoi, leaving size as the only available feature. On this basis, and given the occurrence of a species of *Gazella* of small size, it is more parsimonious to include all specimens larger than *Raphicerus* into this genus.

Genus indet., aff. *Dytikodorcas* sp.

Geraads et al. (2013a) revised the identification of the braincase with right horn-core KNM-KP 29277 identified as *Aepyceros* by Harris et al. (2003:Fig. 28) and tentatively assigned it to the Antilopini, especially because of its complicated frontoparietal suture (Fig. 1E), but it is certainly distinct from the most common antilopins of Africa, *Gazella*, and *Antidorcas*. Very few other representatives of this tribe have been identified in this continent. The horn-cores from Omo Shungura Member C identified as *Antilope* aff. *subtorta* by Gentry (1985) are smaller and more twisted. The horn-core of KNM-KP 29277 resembles those of *'Prostrepsiceros' libycus* Lehmann and Thomas, 1987 from Sahabi, although they differ in the lack of a longitudinal groove and the presence of faint transverse ridges. *Prostrepsiceros* is a late Miocene genus best known from the Eastern Mediterranean, and Bouvrain and Bonis (2007) tentatively reassigned the Sahabi species to their new genus *Dytikodorcas*, whose type-species is from the latest Miocene of Greece. Inclusion of the Kanapoi form in the *Prostrepsiceros-Dytikodorcas* group remains tentative, but if this group is indeed close to the ancestry of *Antilope* (Gentry, 2008), the occurrence of one of its members at Kanapoi is plausible.

Biogeographic and ecological comparisons *T. kyaloi* is most common in Turkana Basin strata chronologically close to the Kanapoi Formation. The holotype, KNM-WT 18673, derives from the lowermost Kataboi Mb of the Nachukui Fm, dating to about 3.9 Ma (this specimen was originally published incorrectly as deriving from the Lokochot Mb). There are several specimens of *T. kyaloi* from the Apak Mb of the Nachukui Fm dated to >4.2 Ma. The species is also relatively common at the top of the Lonyumun Member of the Koobi Fora Formation, about 4 Ma, an interval well sampled at Allia Bay. In higher stratigraphic levels, *T. kyaloi* is rare. Turkana paleolandscapes became dominated by the Moiti floodplain after 3.9 Ma (Feibel, 2011) and the bovid fauna experienced major changes likely as a result of this remodelling of the hydrology of the basin: Reduncini became more common on the east side, while a mix of bovid tribes were co-dominant on the west side of the basin (Bobe, 2011).

In the Omo basin of Ethiopia, the poorly sampled Mursi fauna (Drapeau et al., 2014) has mostly *Tragelaphus* and *Aepyceros*, probably both of different species than at Kanapoi. In the later Usno Fm and in the lower part of the Shungura Fm (Gentry, 1985), these taxa are joined by reduncins, making the assemblage still more different from the Kanapoi one.

Further north, the earliest faunas of Pliocene age are from the Kuseralee Mb of the Sagantole Fm (Haile-Selassie et al., 2009) in the Middle Awash. They document the late survival of boselaphins in East Africa; the most common bovid is the earliest member of the *T. nakuae* lineage, and impalas and various reduncins are present, but there is no alcelaphin. The c. 4.4 Ma faunas of Aramis (White et al., 2009) and other contemporaneous sites have not been studied in detail yet, but the overwhelming majority of bovids at Aramis have been identified as *T. kyaloi*, *Aepyceros* being much less common and all other Bovidae (including reduncins) rare. It is hard to escape the conclusion that such an assemblage attests to a more wooded environment than at Kanapoi, but the lack of detailed study prevents taxonomic comparisons. The *Damalops* sp. of White et al. (2009) and Vrba (1997) is the *Damalborea* of Gentry (2010) and might therefore be identical with one of the Kanapoi alcelaphins, so that taxonomically the Aramis fauna is rather close to that of Kanapoi.

In the c. 3.5–3.7 Ma sites of Woranso Mille (Geraads et al., 2009b), the most common form is an *Aepyceros* probably identical with the Kanapoi one, but both *T. saraitu* and the bovin belong to lineages absent at Kanapoi. Similarities with Kanapoi are a form close to *Damalborea*, as well as the presence of raphicerins, antilopins, and cephalophins, and virtual absence of reduncins.

The Nkondo and Warwire faunas in the Albertine Rift Valley of Uganda (Geraads and Thomas, 1994), probably of early to middle Pliocene age, have bovins, reduncins, and alcelaphins that are hard to identify, an *Aepyceros* perhaps close to the Mursi one, and two tragelaphins of which the larger one is close to *T. saraitu*. They are thus clearly East African in character.

By contrast, Pliocene faunas from Kolle in Chad (Geraads et al., 2009a) sharply differ from East African ones in the absence of tragelaphins. Reduncins are common and the bovin *Jamous* is quite unlike East African forms; the only possible similarity is in the hippotragin *Tchadotragus*, whose identification at Kanapoi is very tentative.

Turning to the south, the site of Kantis near Nairobi (Mbua et al., 2016), dated to c. 3.5 Ma, is unique in being dominated by alcelaphins and impalas that look different from the Kanapoi ones, tragelaphins and reduncins being quite rare. The slightly older fauna of the upper Laetolil Beds, c. 3.6 Ma, includes 15 species (Gentry, 1987, 2011) and shares with Kanapoi a significant number of Raphicerini and *Gazella*, and the virtual absence of Reduncini. The main taxonomic differences are that there is no evidence of *Brabovus* and *Madoqua* at Kanapoi, that the *Tragelaphus* and *Aepyceros* are certainly different (small *Tragelaphus* but large *Aepyceros* at Laetoli), and that no form similar to *Dytikodorcas* is

known from Laetoli. Other differences, in the Hippotragini and Alcelaphini, could largely be explained by the older age of Kanapoi.

No clear biogeographic pattern emerges from these comparisons, as most major taxa range throughout eastern Africa, and the sharp differences between the various sites of the Awash Valley of Ethiopia show that ecological and chronological factors weigh more than geographic ones. In addition, few of the Kanapoi taxa can be identified with enough confidence to draw robust conclusions about their affinities. *T. kyaloi* is unknown south of Kanapoi, but this might be due to the absence of sites of similar age further south; other resemblances with northern sites are the *Aepyceros* and the very tentatively identified cf. *Tchadotragus* and aff. *Dytikodorcas*. On the other hand, *Damalacra harrisi*, *Simatherium* sp., and *Gazella* cf. *janenschi*, together with the virtual absence of reduncins, are similarities with the Laetoli assemblage.

Abundance data are presented in Table 1; total numbers by tribe are fairly reliable, but some of the numbers of specimens at lower taxonomic levels are estimates. These data allow the computation of diversity indices (Table 2) using the software PAST (Hammer et al., 2001). The comparison with indices based upon bovid cranial remains of other African sites (Geraads, 1994:Figs. 1 and 2) show that both Shannon H" and Brillouin indices have moderate values at Kanapoi, below those reached around the Plio-Pleistocene boundary. This could be because of less favorable conditions, because the African Bovidae had not yet reached the climax of their diversity, or merely because the great number of *Tragelaphus* horn cores, perhaps a taphonomic bias (they are more robust than those of the alcelaphins), decreases the value of these indices at Kanapoi.

Ecological interpretations have often been drawn from the relative abundance of bovid tribes and a correspondence analysis allows visualizing their proximity to the main East African sites of this time period (Fig. 5). However, no obvious pattern emerges from this analysis. Probably because all sites are constrained within a relatively short period (from c. 5.2 Ma for the Kuseralee Member to c. 3 Ma for Shungura Member B), time is not a major factor. Axis 1 may reflect a South-North gradient, although this could merely be due to the open conditions at Laetoli and Kantis (which are also at a greater altitude). Kanapoi clearly differs from these southern sites, but also differs from most Turkana localities in the low abundance of reduncins and dominance of *Tragelaphus* and *Aepyceros*, attesting to a large proportion of bush or arboreal cover, and resembling instead in this regard the Ethiopian sites of Aramis and Woranso-Mille. Still, despite these variations in bovid proportions, all these

sites cluster together, testifying to similar environmental conditions, obviously suitable for the closely related hominin species that thrived there.

Conclusions

The Pliocene site of Kanapoi documents at least 16 species of Ruminantia in two families (Giraffidae and Bovidae) with some 300 collected specimens. The Giraffidae include *G. jumae*, *G. pygmaea*, and *Sivatherium* cf. *hendeyi*. *Sivatherium* at Kanapoi is exceedingly rare, known from only a few specimens. Among bovids, Tragelaphini is the dominant tribe, followed by Alcelaphini and Aepycerotini. These three tribes make up almost 75% of the identified Kanapoi bovids. The taxonomic composition of the dominant bovid groups and their stable isotopic signatures indicate a mosaic of wooded and grassy habitats at Kanapoi in the Pliocene. The absence (or rarity) of Reduncini suggests that regularly flooded grasslands were not a major component of the local vegetation. The description of Kanapoi bovids provided here serves as a basis for further paleoecological research at the site of the earliest species of *Australopithecus*.

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642 **Figure legends**

643 Figure 1. A-D) *Tragelaphus kyaloi*. A) KNM-KP 58836, braincase with left horn-core, left
644 lateral view. B) KNM-KP 30156, frontlet in front view. C) KNM-KP 68, posterior part of
645 braincase, left lateral view; note the backwardly directed paroccipital process. D) KNM-KP
646 56829, distal view of right horn-core fragment, showing the outline of the cross-section. E)
647 aff. *Dytikodorcas* sp., KNM-KP 29277, braincase in dorsal view, showing the complicated
648 fronto-parietal suture. F-G) cf. *Tchadotragus* sp. F) Right upper molar KNM-KP 56843. G)
649 Left upper molar KNM-KP 59763. H) *Giraffa jumae*, left ossicone KNM-KP 58739 in H1,
650 lateral, and H2, posterior views. I) *Giraffa pygmaea*, incomplete ossicone KNM-KP 59918 in
651 I1, ?medial, and I2, ?anterior views. J) *Gazella* cf. *janenschi*, left horn-core KNM-KP 56816
652 in J1, lateral, J2, anterior, and J3, medial views. Scale bar = 5 cm for F-G; 10 cm for C-E, I-J;
653 20 cm for A-B, H.

654

655 Figure 2. Plot of distal width vs. medial height in fossil and modern *Giraffa* astragali
656 (although some of the largest ones may belong to *Sivatherium*) and in the Hadar Formation
657 bovin *Ugandax*.

658

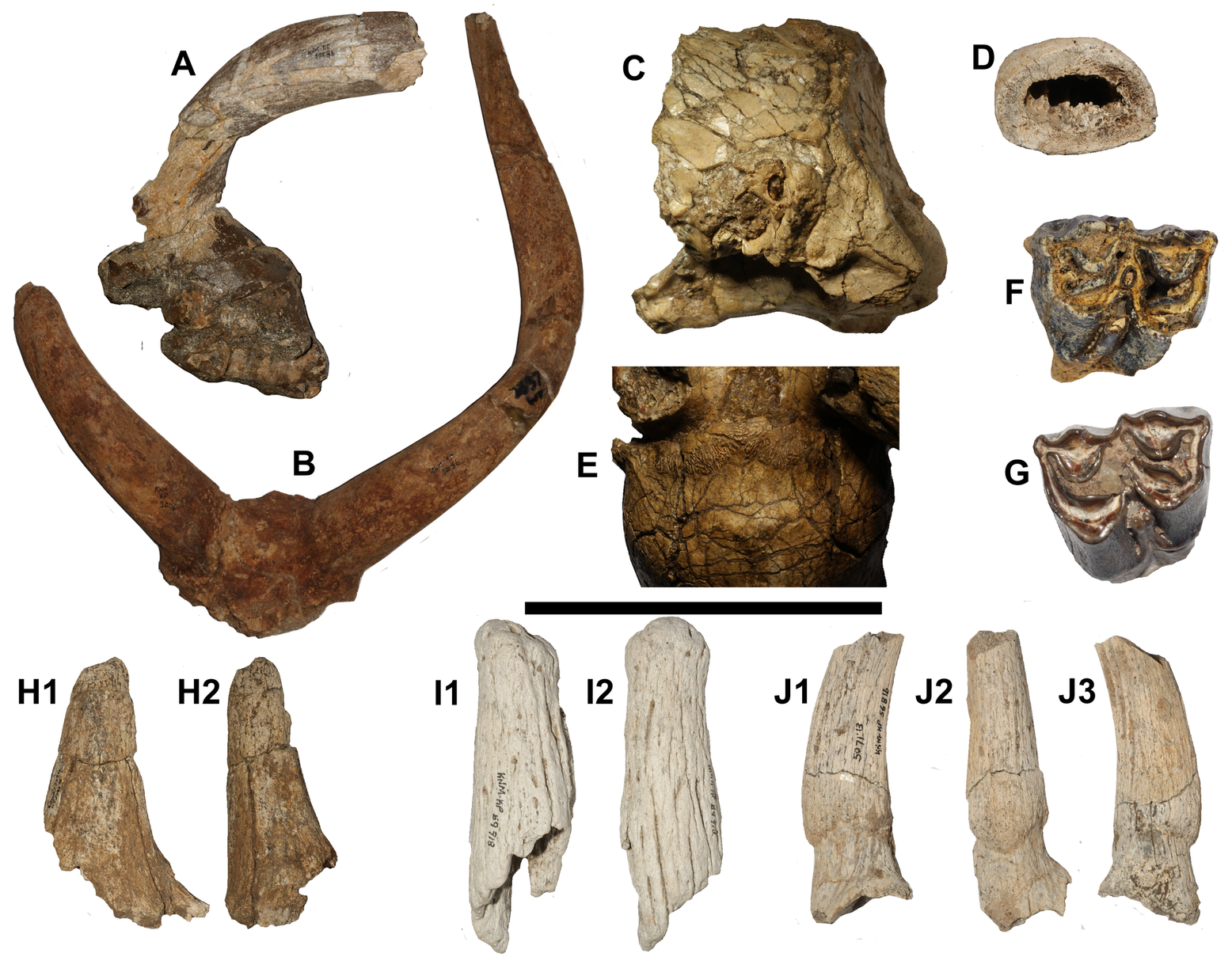
659 Figure 3. Sketch-drawing comparing the cranial profile of a 'normal' *Tragelaphus*
660 (*Tragelaphus spekei*) with that of *Tragelaphus kyaloi* (based upon KNM-KP 58836).

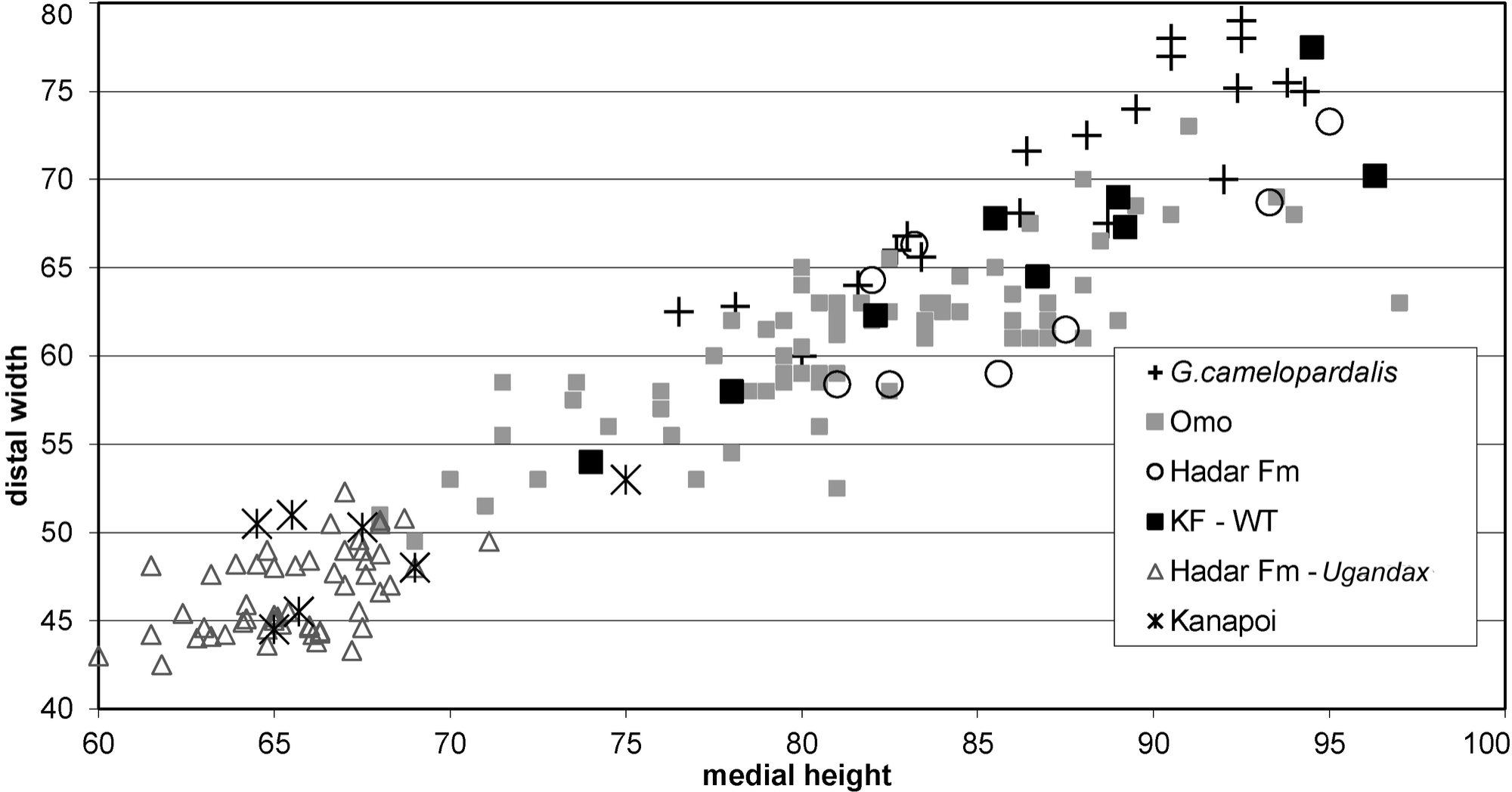
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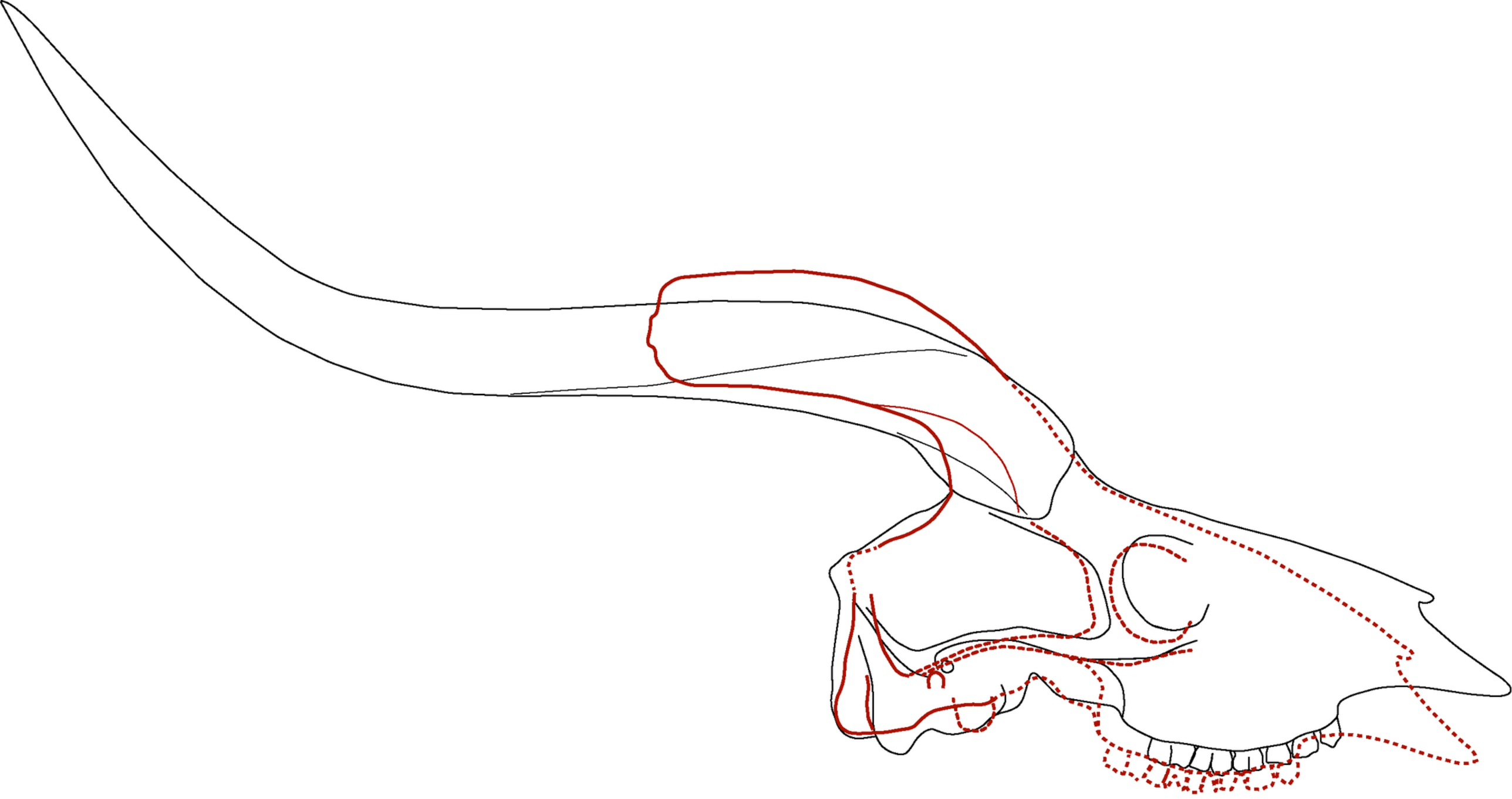
662 Figure 4. Plot of antero-posterior vs. transverse diameters of *Tragelaphus* horn-cores. Note
663 the wide range of measurements at Kanapoi.

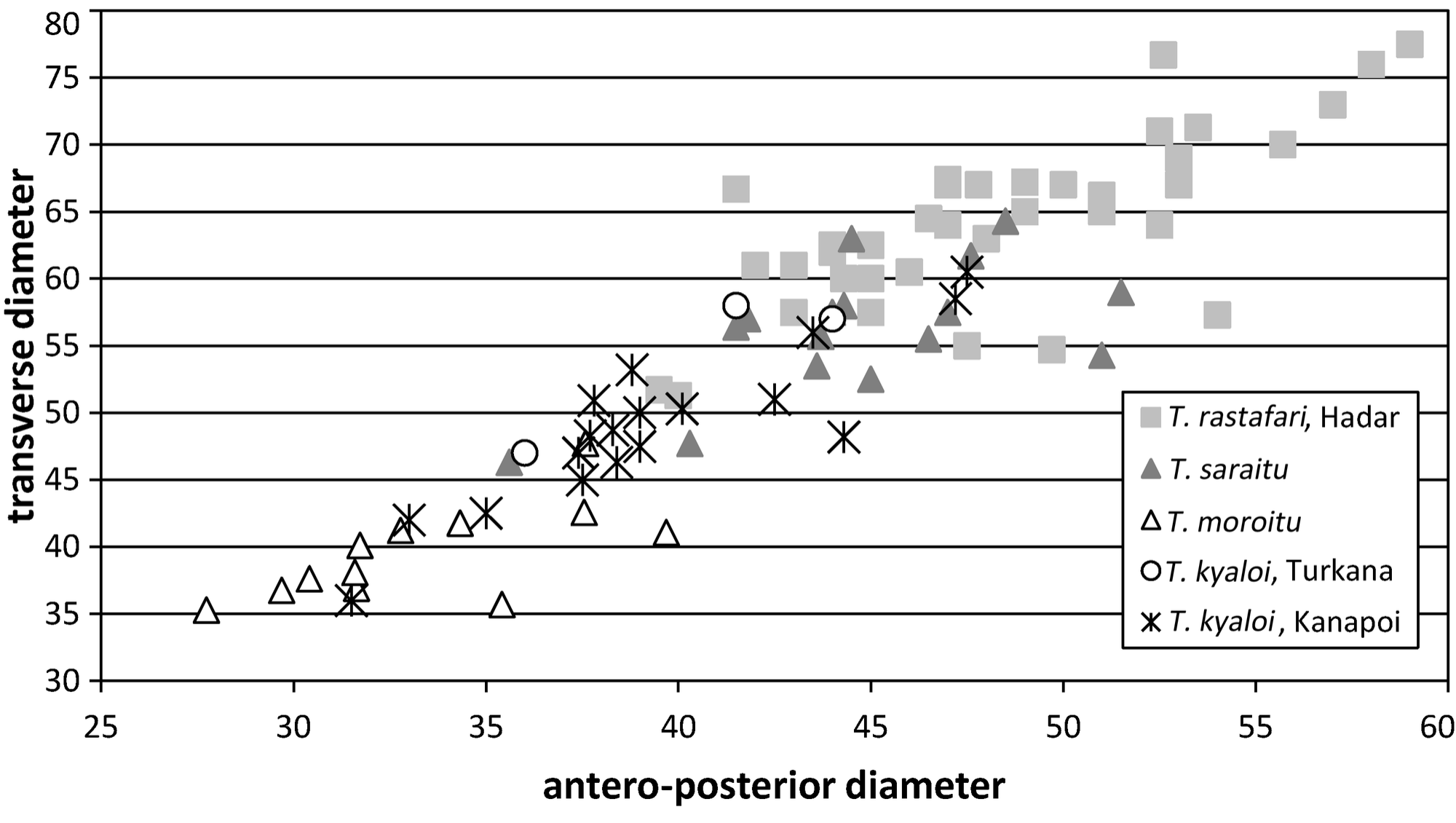
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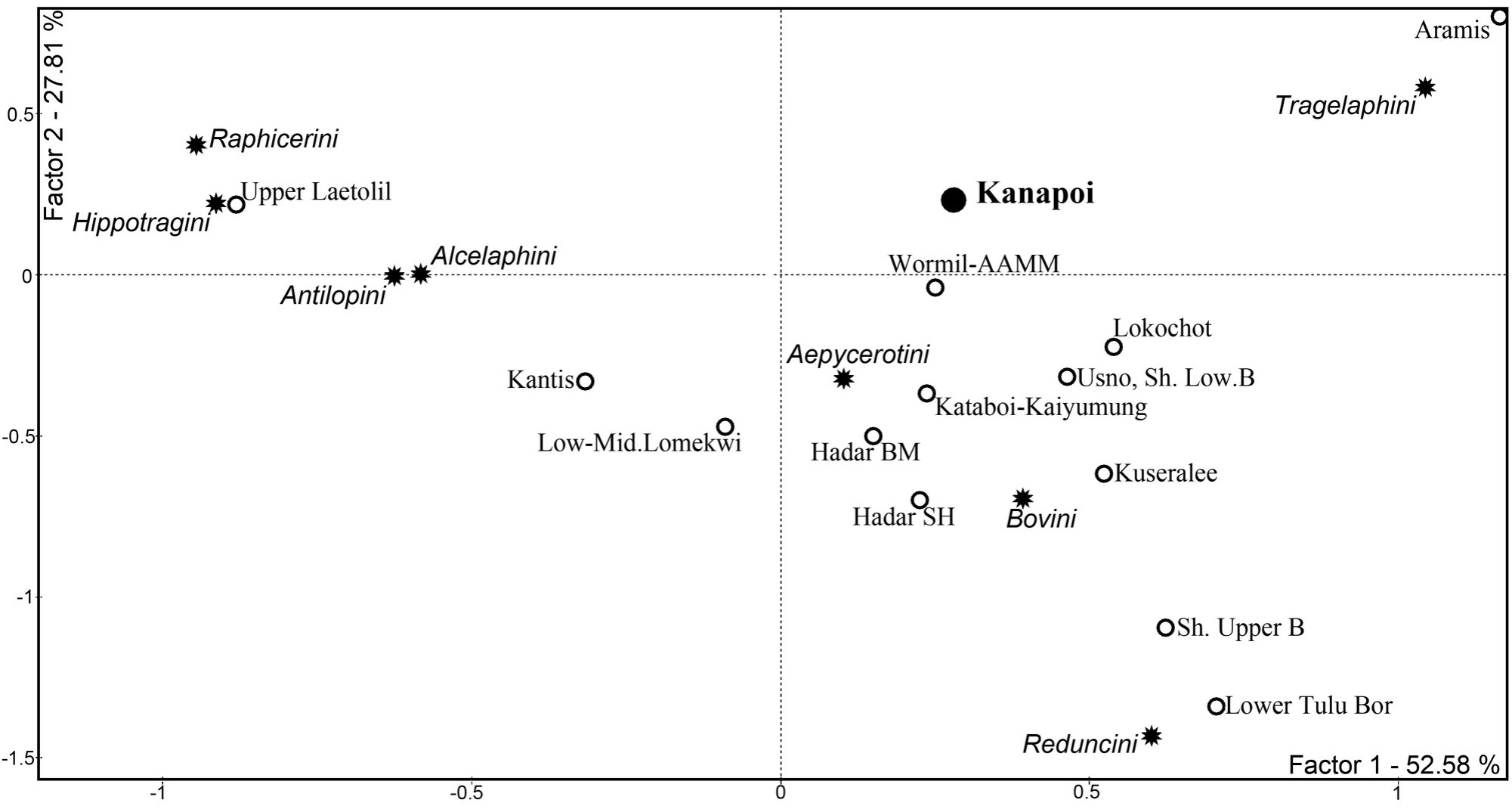
665 Figure 5. Correspondence analysis of the main African bovid tribes (excluding the rare
666 Boselaphini, Cephalophini, and *Brabovus*) and major East African Lower and Middle
667 Pliocene sites (data in SOM Table 3).


A
B
C
D
E
F
G
H1
H2
I1
I2
J1
J2
J3


80
75
70
65
60
55
50
45
40
distal width
60
65
70
75
80
85
90
95
100
medial height
G.camelopardalis
Omo
Hadar Fm
KF - WT
Hadar Fm - Ugandax
Kanapoi




transverse diameter
antero-posterior diameter
80
75
70
65
60
55
50
45
40
35
30
25
30
35
40
45
50
55
60
T. rastafari, Hadar
T. saraitu
T. moroitu
T. kyaloi, Turkana
T. kyaloi, Kanapoi


Factor 2 - 27.81 %
Factor 1 - 52.58 %
Aramis
Tragelaphini
Raphicerini
Upper Laetolil
Hippotragini
Kanapoi
Alcelaphini
Antilopini
Wormil-AAMM
Lokochot
Aepycerotini
Usno, Sh. Low.B
Kantis
Kataboi-Kaiyumung
Low-Mid.Lomekwi
Hadar BM
Kuseralee
Hadar SH
Bovini
Sh. Upper B
Lower Tulu Bor
Reduncini
0.5
0
-0.5
-1
-1.5
-1
-0.5
0
0.5
1

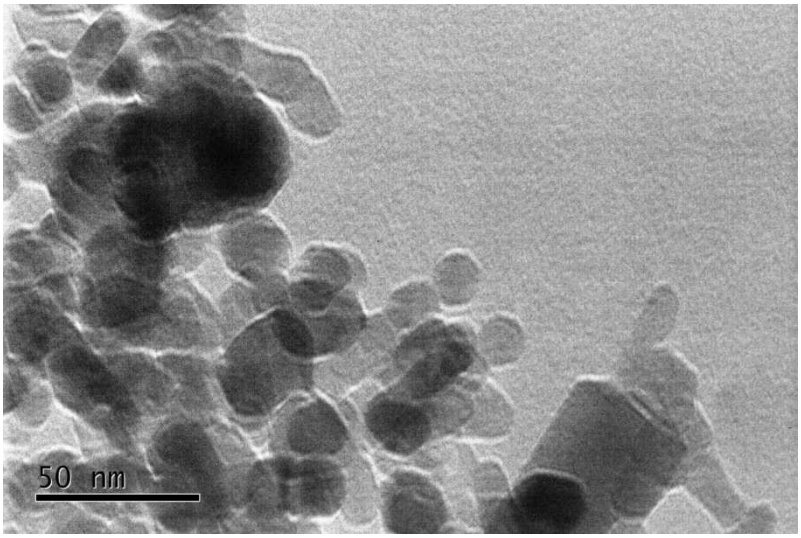


Figure 2.

Table 2. Some of the commmonly used diversity indices computed on all bovid specimens or on cranial pieces only (data in Table 1).

	All specimens	Cranial pieces
Number of taxa	15	12
Number of specimens	396	117
Simpson 1-D	0.798	0.5781
Shannon H"	1.90	1.25
Evenness e^H/S	0.4639	0.3187
Brillouin	1.873	1.212
Fisher_alpha	3.085	3.351