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Denis Geraads, René Bobe

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1 Ruminants (Giraffidae and Bovidae) from Kanapoi

2

3 Denis Geraads ^{a, b, *}, René Bobe ^{c, d}

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5 ^a Sorbonne Universités - CR2P-MNHN, CNRS, UPMC-Paris 6 - CP 38, Muséum National
6 d'Histoire Naturelle, 8 rue Buffon, F-75231 Paris Cedex 05, France;

7 ^b Max Planck Institute for Evolutionary Anthropology, Department of Human Evolution,
8 Deutscher Platz 6 - D-04103 Leipzig—Germany

9 ^c Departamento de Antropología, Universidad de Chile, Santiago, Chile

10 ^d Institute of Cognitive & Evolutionary Anthropology, University of Oxford, Oxford, UK

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12 * Corresponding author.

13 *E-mail address:* denis.geraads@mnhn.fr (D. Geraads)

14

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16

17

18 **Abstract**

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

27

28

29

30 **Introduction**

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

43

44 **Systematic paleontology**

45 *Family Giraffidae* Gray, 1821

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

48

49 Genus *Giraffa* Brisson, 1762

50 *Giraffa jumae* Leakey, 1965

51

52 KNM-KP 58739 (Fig. 1H) is a short horn whose base is very incomplete but shows
53 that it was inserted above a cranial sinus. It is distinctly more conical than in the modern
54 giraffe *Giraffa camelopardalis*, but some ossicones of *G. jumae* from Hadar, such as AL 291-
55 1 (Geraads, 2013b), display the same conical shape. It also resembles the horn from
56 Langebaanweg that Harris (1976b) chose as the paratype of his *Sivatherium hendeyi*, but is
57 much too conical to belong to this genus (Q.B. Hendey pers. comm. to D.G., 1984); it could
58 belong to *G. jumae* as well. Tooth measurements of the mandible KNM-KP 30450 described
59 by Geraads et al. (2013a) are slightly above the observed maxima for the modern giraffe
60 *G. camelopardalis* (length of m3 = 47.7 vs. 37.5 – 46, $N = 36$). Several other teeth and limb-
61 bones are of a similar large size, but most of them are within the range of the modern form;
62 surprisingly, no astragalus is large enough to belong here. A species distinction from
63 *G. camelopardalis* would not be strongly supported on a size basis alone, but the p3 of KNM-

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

76

77 *Giraffa pygmaea* Harris, 1976a

78

79 Geraads et al. (2013a) revised the identification of the smaller giraffe of Kanapoi,
80 which was called *Giraffa stillei* by Harris et al. (2003). KNM-KP 59918 (Fig. 1I) is an
81 incomplete, weathered ossicone of small size. Its apical end forms a terminal knob, as in
82 males of the modern form, showing that it belongs to a small-size species rather than to a
83 female. It does not significantly differ from ER-656, paratype of *Giraffa pygmaea* (Harris,
84 1976a:Pl. 9–10).

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

94 This very small *Giraffa* is less rare at Kanapoi than in younger sites; Geraads et al.
95 (2013b) surmised that this might be because *G. pygmaea* evolved into *G. stillei*, but late
96 Miocene potential ancestors of *Giraffa* are large, and it is perhaps instead the diminutive size
97 of *G. pygmaea* that is derived.

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

103

104 Genus *Sivatherium* Falconer and Cautley, 1836

105 *Sivatherium* cf. *hendeyi* Harris, 1976b

106

107 Harris et al. (2003) identified the species on the basis of a partial horn KNM-KP
108 30449, but the quickly decreasing diameters show that it was far too short for *Sivatherium*,
109 and it is in fact certainly a bovid horn-core (see below). The only new specimen is KNM-KP
110 59920, a short, massive first phalanx; it is stouter than in *Giraffa* and the proximal articulation
111 is broader relative to its antero-posterior diameter, which matches the broad distal metapodials
112 of *Sivatherium*. Still, the only unequivocal specimens of *Sivatherium* are the incomplete upper
113 molar KNM-KP 32551 and the tooth fragments KNM-KP 30227; this taxon is thus extremely
114 rare at Kanapoi.

115

116 Remarks. The enamel $\delta^{13}\text{C}$ of fossil *Giraffa*, except for a single outlying value at Lee Adoyta
117 (Rowan et al., 2016), shows that this genus consistently remained a browser during the whole
118 Pliocene, and Kanapoi is no exception. By contrast, the diet of *Sivatherium* in Africa, long
119 debated, rather abruptly changed during the Pliocene, from browser to almost pure grazer,
120 even though this change looks diachronous in the Turkana and Afar basins (Rowan et al.,
121 2016). Sample size is low at Kanapoi, but the $\delta^{13}\text{C}$ values (Supplementary Online Material
122 [SOM] Fig. 1) indicate a browser, or at most a mixed-feeder, certainly far less distinct from
123 *Giraffa* in its diet than in later sites.

124

125 *Family Bovidae* Gray, 1821

126 Description and comparisons

127 Subfamily Bovinae Gray, 1821

128 Tribe Tragelaphini Blyth, 1863

129 Genus *Tragelaphus* Blainville, 1816

130 *Tragelaphus* cf. *kyaloi* Harris, 1991

131

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

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

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

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

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

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

198

199 Tribe Bovini Gray, 1821

200 Genus *Simatherium* Dietrich, 1941

201 *Simatherium* sp.

202

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

207 On the mandible KNM-KP 96 (Harris et al., 2003:Fig. 23B-C), the metaconid almost
208 completely closes the lingual valley of p4; it is less expanded in KNM-KP 51008 and KNM-
209 KP 56877 (which probably represent both sides of the same individual), but on the average it
210 is stronger than in the more recent Hadar and Woranso-Mille *Ugandax coryndonae* (Gentry,
211 2006; Geraads et al., 2009b, 2012) and earlier Kuseralee Member of the Middle Awash
212 (Haile-Selassie et al., 2009:Fig. 9.8), confirming that they belong to different lineages.

213 However, the phylogeny of African Bovini remains poorly known and, as noted by Geraads et
214 al. (2013a), nothing supports the identification of the Kanapoi bovin with the Langebaanweg
215 'S'. *demissum*, which Gentry (2011) moved to *Ugandax*.

216

217 Sub-family Antilopinae Gray, 1821

218 Tribe Reduncini Knottnerus-Meyer, 1907?

219 Reduncini? gen. et sp. indet.

220

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

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

228

229 Tribe Hippotragini Sundevall in Retzius and Lovén, 1845

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

231

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

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

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

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

251

252 Tribe Alcelaphini Brooke in Wallace, 1876

253 Genus *Damalacra* Gentry, 1980

254 *Damalacra harrisi* Geraads, Bobe and Manthi, 2013a

255

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

264

265 Genus *Damalborea* Gentry, 2010?

266 *Damalborea?* n. sp.

267

268 The occurrence of this taxon at Kanapoi is mostly based upon the frontlet KNM-KP
269 71, identified as *Damalacra* cf. *neanica* by Harris et al. (2003), but revised and discussed by
270 Geraads et al. (2013a). KNM-KP 58588 could be another horn-core of the same taxon. It
271 lacks the base, but has an oval cross-section whose diameters quickly decrease upwards,
272 showing that it was short. Geraads et al. (2013a) observed that this species is probably also
273 present at Aramis and Laetoli. We tentatively include it in the genus *Damalborea*, best known
274 from Hadar; it is certainly different from its two known species (Vrba, 1997; Gentry, 2010;
275 Geraads et al., 2012) but remains too poorly known to be named.

276

277 Alcelaphini gen. et sp. indet.

278

279 Geraads et al. (2013a) regarded the horn-core pieces KNM-KP 30418 and KNM-KP
280 30633 as distinct from the two above mentioned species, and noted that the mandible KNM-
281 KP 31733 is too large to match the horn-cores in size, so that a total of four alcelaphin species
282 might be present. Other alcelaphin dentitions are of homogeneous size, with m3 lengths
283 ranging from 27.5 mm to c. 31 mm ($N = 7$), but we do not know whether they represent one
284 species or two (or more) similar-sized ones.

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

288

289 Tribe "Ovibovini" Gray, 1872?

290 Genus et sp. indet.

291

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

299

300 Tribe Aepycerotini Gray, 1872

301 Genus *Aepyceros* Sundevall, 1847

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

303

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

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

322

323 Tribe Raphicerini Grubb, 2001 ?

324 Genus *Raphicerus* H. Smith, 1827 ?

325 *Raphicerus?* sp.

326

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

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

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

344

345 Tribe Cephalophini

346 Gen. et sp. indet.

347

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

357

358 Tribe Antilopini Gray, 1821

359 Genus *Gazella* Blainville, 1816

360 *Gazella* sp.

361

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

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

380

381 *Gazella cf. janenschi* Dietrich, 1950

382

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

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

404

405 Genus indet., aff. *Dytikodorcas* sp.

406

407 Geraads et al. (2013a) revised the identification of the braincase with right horn-core
408 KNM-KP 29277 identified as *Aepyceros* by Harris et al. (2003:Fig. 28) and tentatively
409 assigned it to the Antilopini, especially because of its complicated frontoparietal suture (Fig.
410 1E), but it is certainly distinct from the most common antilopins of Africa, *Gazella*, and
411 *Antidorcas*. Very few other representatives of this tribe have been identified in this continent.
412 The horn-cores from Omo Shungura Member C identified as *Antilope* aff. *subtorta* by Gentry
413 (1985) are smaller and more twisted. The horn-core of KNM-KP 29277 resembles those of
414 '*Prostrepsiceros*' *libycus* Lehmann and Thomas, 1987 from Sahabi, although they differ in the
415 lack of a longitudinal groove and the presence of faint transverse ridges. *Prostrepsiceros* is a
416 late Miocene genus best known from the Eastern Mediterranean, and Bouvrain and Bonis
417 (2007) tentatively reassigned the Sahabi species to their new genus *Dytikodorcas*, whose type-
418 species is from the latest Miocene of Greece. Inclusion of the Kanapoi form in the
419 *Prostrepsiceros-Dytikodorcas* group remains tentative, but if this group is indeed close to the
420 ancestry of *Antilope* (Gentry, 2008), the occurrence of one of its members at Kanapoi is
421 plausible.

422

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

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

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

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

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

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

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

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

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

484 Abundance data are presented in Table 1; total numbers by tribe are fairly reliable, but
485 some of the numbers of specimens at lower taxonomic levels are estimates. These data allow
486 the computation of diversity indices (Table 2) using the software PAST (Hammer et al.,
487 2001). The comparison with indices based upon bovid cranial remains of other African sites
488 (Geraads, 1994:Figs. 1 and 2) show that both Shannon H" and Brillouin indices have
489 moderate values at Kanapoi, below those reached around the Plio-Pleistocene boundary. This
490 could be because of less favorable conditions, because the African Bovidae had not yet
491 reached the climax of their diversity, or merely because the great number of *Tragelaphus* horn
492 cores, perhaps a taphonomic bias (they are more robust than those of the alcelaphins),
493 decreases the value of these indices at Kanapoi.

494 Ecological interpretations have often been drawn from the relative abundance of bovid
495 tribes and a correspondence analysis allows visualizing their proximity to the main East
496 African sites of this time period (Fig. 5). However, no obvious pattern emerges from this
497 analysis. Probably because all sites are constrained within a relatively short period (from c.
498 5.2 Ma for the Kuseralee Member to c. 3 Ma for Shungura Member B), time is not a major
499 factor. Axis 1 may reflect a South-North gradient, although this could merely be due to the
500 open conditions at Laetoli and Kantis (which are also at a greater altitude). Kanapoi clearly
501 differs from these southern sites, but also differs from most Turkana localities in the low
502 abundance of reduncins and dominance of *Tragelaphus* and *Aepyceros*, attesting to a large
503 proportion of bush or arboreal cover, and resembling instead in this regard the Ethiopian sites
504 of Aramis and Woranso-Mille. Still, despite these variations in bovid proportions, all these

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

507

508 **Conclusions**

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

520

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530

531

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640 complete mitochondrial genomes. *Biochem. Syst. Ecol.* 48, 136–143.
641

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

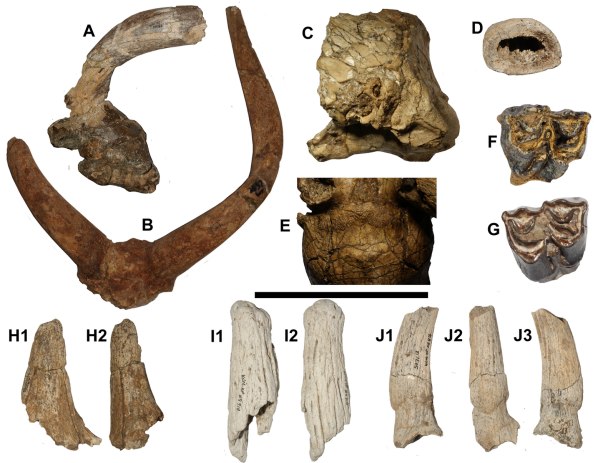
659 Figure 3. Sketch-drawing comparing the cranial profile of a 'normal' *Tragelaphus*
660 (*Tragelaphus spekei*) with that of *Tragelaphus kyaloi* (based upon KNM-KP 58836).

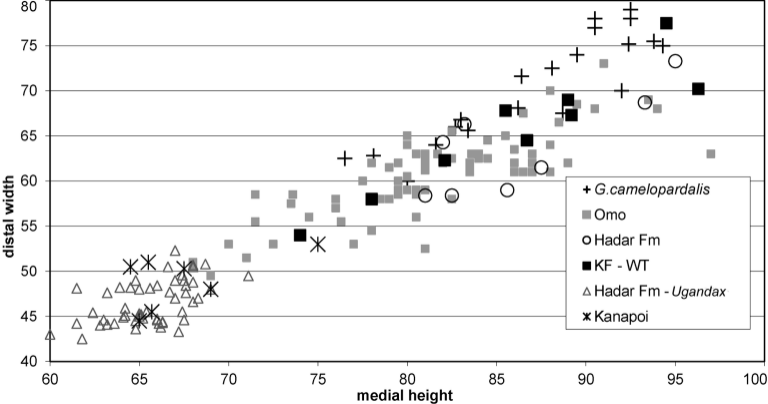
661

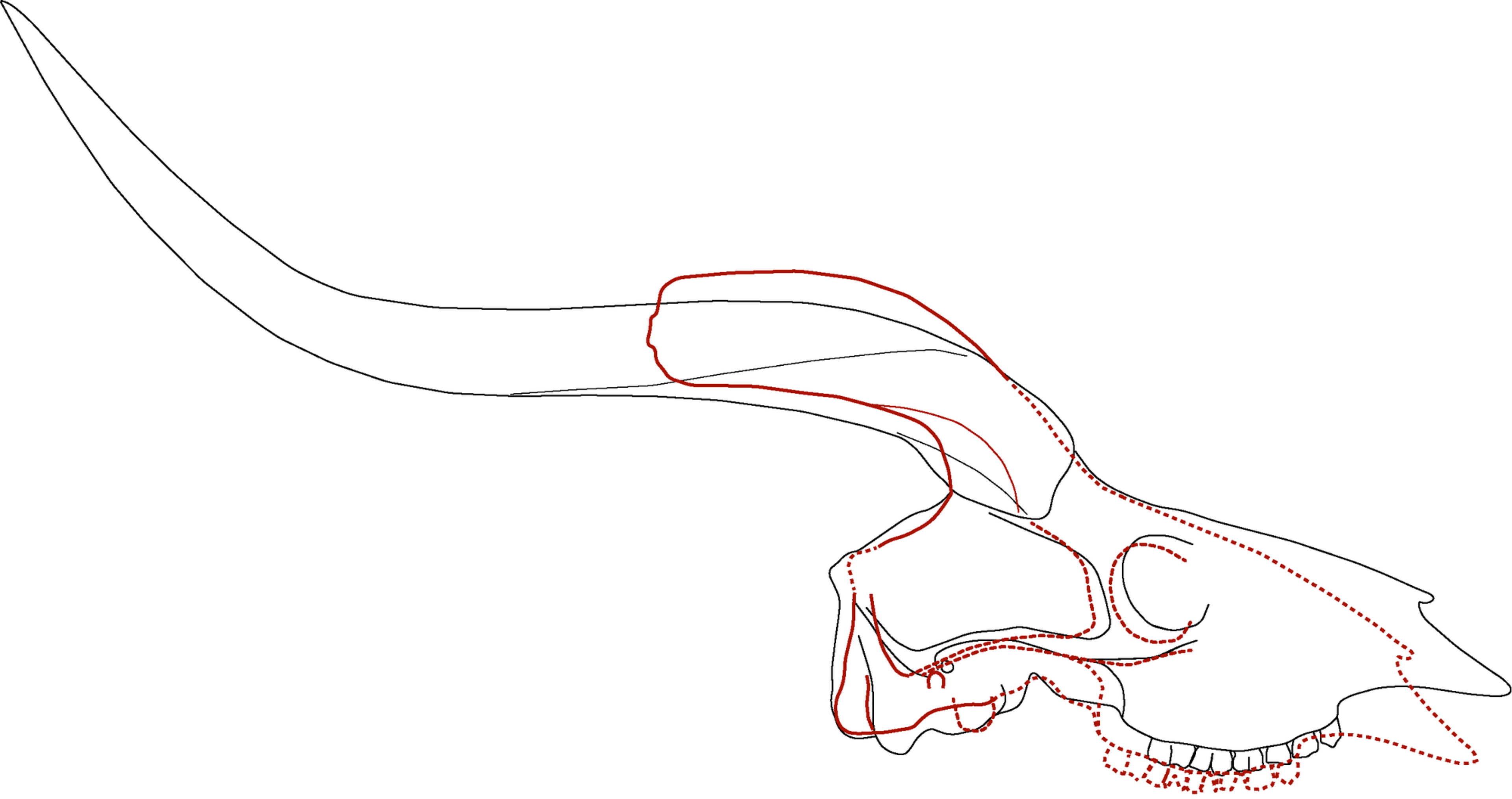
662 Figure 4. Plot of antero-posterior vs. transverse diameters of *Tragelaphus* horn-cores. Note
663 the wide range of measurements at Kanapoi.

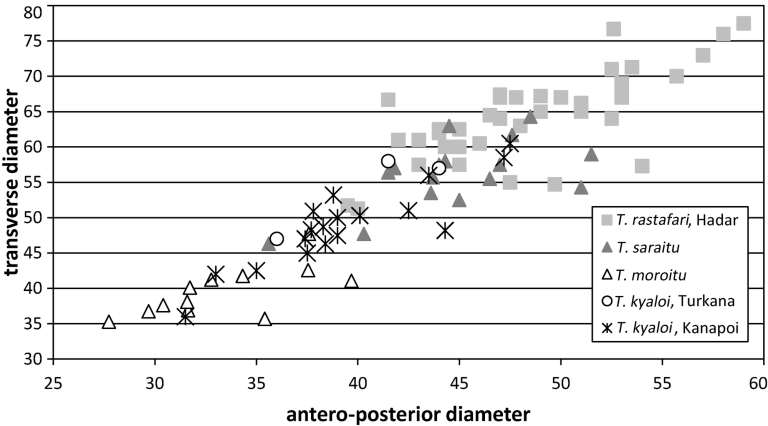
664

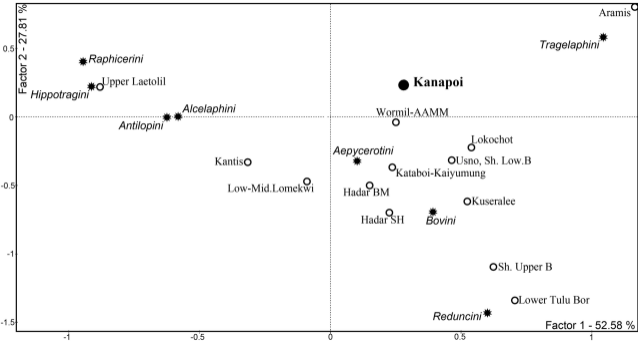
665 Figure 5. Correspondence analysis of the main African bovid tribes (excluding the rare
666 Boselaphini, Cephalophini, and *Brabovus*) and major East African Lower and Middle
667 Pliocene sites (data in SOM Table 3).











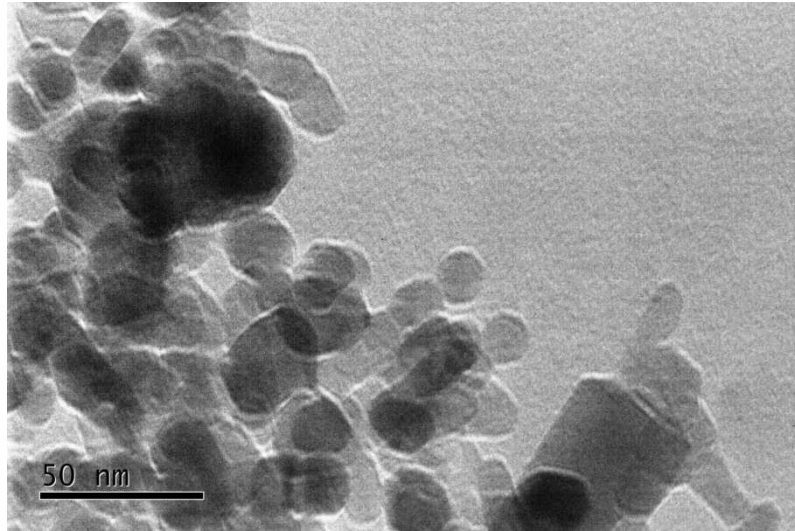


Figure 2.

Table 2. Some of the commonly 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 |