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1 **New ruminants (Mammalia) from the Pliocene of Kanapoi, Kenya, and a**
2 **revision of previous collections, with a note on the Suidae**

3

4 Denis Geraads ^{a, b, *}, René Bobe ^{c, d}, Fredrick KyaloManthi^c

5

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

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

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

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

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13 * Corresponding author.

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

15

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17

18

19 **Abstract**

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

28

29

30

31 **Introduction**

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

44

45 **Systematic paleontology**

46 *Family Giraffidae Gray, 1821*

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

49

50 Genus *Giraffa* Brisson, 1762

51 *Giraffa jumae* Leakey, 1965

52

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

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

77

78 *Giraffa pygmaea* Harris, 1976a

79

80 Geraads et al. (2013a) revised the identification of the smaller giraffe of Kanapoi,
81 which was called *Giraffa stillei* by Harris et al. (2003). KNM-KP 59918 (Fig. 1I) is an
82 incomplete, weathered ossicone of small size. Its apical end forms a terminal knob, as in
83 males of the modern form, showing that it belongs to a small-size species rather than to a
84 female. It does not significantly differ from ER-656, paratype of *Giraffa pygmaea* (Harris,
85 1976a:Pl. 9–10).

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

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

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

104

105 Genus *Sivatherium* Falconer and Cautley, 1836

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

107

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

116

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

125

126 *Family Bovidae* Gray, 1821

127 Description and comparisons

128 Subfamily Bovinae Gray, 1821

129 Tribe Tragelaphini Blyth, 1863

130 Genus *Tragelaphus* Blainville, 1816

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

132

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

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

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

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

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

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

199

200 Tribe Bovini Gray, 1821

201 Genus *Simatherium* Dietrich, 1941

202 *Simatherium* sp.

203

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

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

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

217

218 Sub-family Antilopinae Gray, 1821

219 Tribe Reduncini Knottnerus-Meyer, 1907?

220 Reduncini? gen. et sp. indet.

221

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

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

229

230 Tribe Hippotragini Sundevall in Retzius and Lovén, 1845

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

232

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

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

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

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

252

253 Tribe Alcelaphini Brooke in Wallace, 1876

254 Genus *Damalacra* Gentry, 1980

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

256

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

265

266 Genus *Damalborea* Gentry, 2010?

267 *Damalborea?* n. sp.

268

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

277

278 Alcelaphini gen. et sp. indet.

279

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

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

289

290 Tribe "Ovibovini" Gray, 1872?

291 Genus et sp. indet.

292

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

300

301 Tribe Aepycerotini Gray, 1872

302 Genus *Aepyceros* Sundevall, 1847

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

304

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

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

323

324 Tribe Raphicerini Grubb, 2001 ?

325 Genus *Raphicerus* H. Smith, 1827 ?

326 *Raphicerus?* sp.

327

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

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

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

345

346 Tribe Cephalophini

347 Gen. et sp. indet.

348

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

358

359 Tribe Antilopini Gray, 1821

360 Genus *Gazella* Blainville, 1816

361 *Gazella* sp.

362

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

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

381

382 *Gazella cf. janenschi* Dietrich, 1950

383

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

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

405

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

407

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

423

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

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

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

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

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

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

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

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

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

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

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

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

508

509 **Conclusions**

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

521

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531

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641 complete mitochondrial genomes. *Biochem. Syst. Ecol.* 48, 136–143.
642

643 **Figure legends**

644 Figure 1. A-D) *Tragelaphus kyaloi*. A) KNM-KP 58836, braincase with left horn-core, left
645 lateral view. B) KNM-KP 30156, frontlet in front view. C) KNM-KP 68, posterior part of
646 braincase, left lateral view; note the backwardly directed paroccipital process. D) KNM-KP
647 56829, distal view of right horn-core fragment, showing the outline of the cross-section. E)
648 aff. *Dytikodorcas* sp., KNM-KP 29277, braincase in dorsal view, showing the complicated
649 fronto-parietal suture. F-G) cf. *Tchadotragus* sp. F) Right upper molar KNM-KP 56843. G)
650 Left upper molar KNM-KP 59763. H) *Giraffa jumae*, left ossicone KNM-KP 58739 in H1,
651 lateral, and H2, posterior views. I) *Giraffa pygmaea*, incomplete ossicone KNM-KP 59918 in
652 I1, ?medial, and I2, ?anterior views. J) *Gazella* cf. *janenschi*, left horn-core KNM-KP 56816
653 in J1, lateral, J2, anterior, and J3, medial views. Scale bar = 5 cm for F-G; 10 cm for C-E, I-J;
654 20 cm for A-B, H.

655

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

659

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

662

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

665

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