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1 **A fossil terrestrial fauna from Tobène (Senegal) provides a unique early Pliocene**
2 **window in western Africa**

3
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30

31 ABSTRACT

32 Early Pliocene hominin evolutionary scenarios proposed to date mostly rely on paleontological
33 investigations from eastern Africa. Filling major geographical gaps in the fossil record could
34 potentially invalidate these scenarios and stimulate development of improved theories. Based
35 on published literature, no Pliocene fossil of continental vertebrates have been discovered in
36 Western Africa and the situation is only slightly better in central and northern Africa. Here, we
37 expand the Pliocene vertebrate continental fossil record to western Africa with the description
38 of the Tobène fauna, a new fossiliferous Neogene locality from Senegal. We describe a diversity
39 of large mammals, including at least ten taxa based on fragmentary remains recovered from
40 alluvial channel deposits. Estimation based on weathering events and biochronology suggests
41 an early Pliocene age. Most of these mammalian taxa were widely distributed over the African
42 continent during the early Pliocene. Possible faunal correlations with eastern African localities
43 call for continent-wide paleontological investigations.

44

45 Keywords: Neogene, vertebrate fauna, weathering events, fossil mammals.

46

47 **1. Introduction**

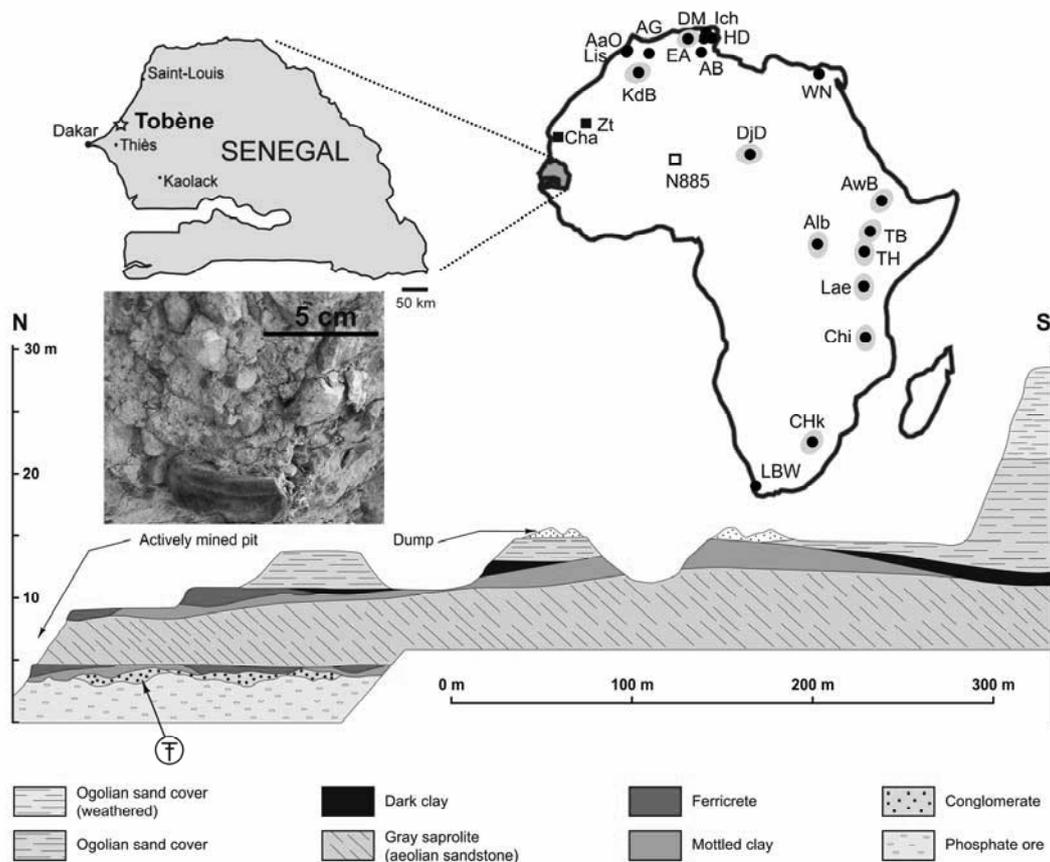
48 Hypotheses on early hominins temporal and spatial distribution across Africa were formulated
49 on the basis of geographically restricted paleontological data. The informal concept of “cradle
50 of humankind” – repeatedly recognized in different regions– perfectly exemplifies how grey
51 areas in the fossil record can bias our understanding of early human history. Although Pliocene
52 localities are common and intensively surveyed in eastern and southern Africa (Werdelin,
53 2010), this time period remains poorly documented in the rest of the continent, notably in
54 northern and central Africa (Arambourg, 1979; Brunet et al., 1995, 1998, 2000; Werdelin, 2010;
55 Zouhri et al., 2017). Researchers however acknowledge important biases in the fossil record
56 when proposing new biogeographic hypotheses or conceptual models (e.g. Joordens et al.,
57 2019), especially the lack of vertebrate remains in western Africa for this time period. Outcrops
58 exploitable for fossil discoveries are rare in this area, mostly due to Cenozoic lateritic
59 weathering, vegetation, and the widespread Quaternary sand cover along the southern fringe of
60 the Sahara (e.g., Michel, 1973; Beauvais et al., 2008).

61 Recent prospections undertaken as part of the PaleoSen project between 2012 and 2015
62 uncovered several vertebrate fossils in the Taïba Ndiaye quarry, Senegal (Fig. 1). Most of these
63 remains were found in limestone deposits embedded in the Lutetian-Bartonian phosphate ore
64 formation, and belonged to marine vertebrates (Hautier et al., 2012, 2014; Vautrin et al. 2019).
65 Remains have also been excavated from the overlying continental deposits intercalated between
66 the Eocene phosphate ore and the Quaternary sand cover in the Tobène pit of the Taïba Ndiaye
67 quarry (Hautier et al., 2014).

68 This paper provides a description of the Tobène site, which hosts the only known
69 Pliocene fauna from Senegal and well-beyond classical African Pliocene faunas, being 2,400
70 km distant from the nearest known Pliocene fossil site of Lissasfa, Morocco (Raynal et al.,
71 1999) and Kossom Bougoudi and Kollé, Chad (Brunet et al. 1998, 2000) (Fig. 1). The Tobène

72 locality, although poor in fossils relative to other Pliocene localities, is key to documenting the
 73 distribution of Pliocene ecosystems in Africa. Its age estimation was based on the combined
 74 study of biochronological markers and lateritic weathering events documented regionally and
 75 dated using geochronology (Beauvais et al., 2008). The taxonomic richness of the locality and
 76 the abundance of carnivorans is encouraging for future discoveries.

77



78

79 Fig. 1 [one and half column]. Location of the Tobène locality (Taïba Ndiaye Quarry), Senegal,
 80 with schematic cross-section of the southern part of the Tobène pit as exposed and investigated
 81 in November 2013 (15°02'15"N 16°48'40"W). The photography shows a tooth remain of
 82 *Deinotherium* SN-Tob-12-03 in situ in the Pliocene conglomerate. The African map shows the
 83 main fossiliferous areas that have yielded Pliocene continental vertebrate faunas (black circle
 84 for isolated locality and grey circles for fossiliferous areas) and the western Neogene localities
 85 that have yielded continental vertebrates (black squares for holocene localities and white square

86 for late Miocene locality). *Abbreviations*. AaO, Ahl al Oughlam; AB, Aïn Brimba; AG, Aïn
87 Guettara; Alb, Albertine rift; AwB, Awash basin; Cha, Chami; Chi, Chiwondo; CHk, Cradle of
88 Humankind; DM, Djebel Melah; DjD, Djurab desert; EA, Eastern Algeria; KdB, Aït Kandoula
89 basin; HD, Hamada Damous; Ich, Garaet Ichkeul; Lae, Laetoli; Lis, Lissasfa; LBW,
90 Langbaanweg; N885: N885 in Niger; TB, Turkana Basin; TH, Tugen Hills; WN, Wadi Natrun;
91 Zt, Zouérate.

92

93 **2. Material and Methods**

94

95 *2.1. Geological context*

96

97 The PaleoSen project is a collaborative framework between Senegalese and French
98 paleontologists from the University Cheikh Anta Diop of Dakar and the Institut des Sciences
99 de l'Evolution of Montpellier. In addition to numerous field expeditions led in Senegalese
100 Paleogene outcrops, three fieldtrips (2012, 2013, and 2015) focused on prospecting the upper
101 part of the Tobène pit in the Taïba Ndiaye quarry, i.e., in strata overlying the exploited
102 phosphate ore (Hautier et al., 2014).

103 During ore exploitation, miners usually extract calcareous blocks from the mined ore as
104 well as blocks from the overlying sterile strata and store them in an open field. Blocks from the
105 barren overburden are mostly made of conglomerates that have consistent sedimentological and
106 petrological characteristics indicative of a common origin. The way the mining company
107 operates for ore exploitation implies that a barren overburden stored area corresponds to a short
108 period of exploitation in a specific part of the exploited open pit. Some of the conglomeratic
109 blocks are fossiliferous (Fig. 1). They are all identified from a common stored area
110 corresponding to one period of exploitation and thus the same mined pit. Detailed field

111 investigations in the Tobène pit (cross-section in Fig. 1) indicate that the conglomerates directly
112 and unconformably overly the phosphate ore. They are laterally discontinuous, suggesting
113 emplacement in alluvial channels that have been partially eroded before sedimentary burial.
114 The material is mostly a heterometric breccia made of reworked elements of the underlying ore,
115 locally preserving a bedding and cross beds underlined by sand layers. Clasts may reach more
116 than 20 cm in size. The most common unsorted and disorganized facies suggests debris flows,
117 torrential and/or colluvial processes have fed the channels. Even if fossil specimens are
118 generally broken, the different fragments are always spatially close to one another (e.g., femur
119 SN-Tob-12-02), indicating a lack of transport after trapping in the sediments. Reworked fossils
120 present in the conglomerates such as Lutetian sharks are easily recognizable by their whitish
121 patina. Only a few conglomerate blocks present non-reworked vertebrate material. They share
122 the same sedimentologic facies, suggesting a single sedimentary event at the origin of the fossil
123 site of Tobène.

124 The conglomerates display various degrees of lateritic weathering and ferruginization,
125 ranging from unconsolidated to a weakly to moderately indurated mottled clay facies (the
126 “lateritoid” phosphate facies of former authors; Tessier, 1952; Pascal and Sustrac, 1989) or
127 even an iron duricrust (ferricrete), in which only the largest clasts are still visible. Field
128 observations indicate that the conglomeratic channels emplaced on a low-relief erosional land
129 surface that developed a weathering profile (Fig. 1), which affected the conglomerates and their
130 substrate. This resulted in a variety of weathering facies depending on the nature of the rocks
131 exposed on the land surface at the time weathering took place (marine phosphate ore or the
132 various overlying detrital materials making the conglomerate unit). This configuration explains
133 the lateral variations in rock units as described/named by the miners in the upper parts of, or
134 above, the main phosphate ore deposit at the scale of a given pit or among pits.

135 The ferricrete-capped land surface exposing the conglomerate was then buried under a
136 sand cover (now sandstones) at least 6-m thick (Fig. 1). Steep oblique parallel stratification in
137 the sandstones suggests an aeolian origin. This cover was then subjected to lateritic weathering.
138 The sands were turned into a saprolite topped by a mottled clay horizon and, in the lower parts
139 of the slightly undulating landscape, by a ferricrete. After a period of organic matter-rich clay
140 sedimentation (dark clays), the weathered landscape was then buried under a thick (>15 m) sand
141 cover. The upper part of that sand cover was slightly weathered and acquired an orange/pinkish
142 color. Those sands are known regionally as the Ogolian aeolian sands (Michel, 1973) deposited
143 during the Last Glacial Maximum between 19 000 and 15 000 BP (e.g., Mulitza et al., 2008).

144

145 *2.2. Fossil materials*

146

147 Fossil remains were found embedded in the conglomerates extracted from the Tobène pit.
148 Hereafter, the fossiliferous Pliocene locality will be designated as Tobène. Vertebrate remains
149 consist of isolated postcranial and dental elements. The material is well preserved, not altered
150 but often broken. It suggests a short but intense transport probably resulting from colluvial
151 processes. Numerous vertebrate remains were excavated among which few are identifiable at a
152 generic level. For mammals, all recognized taxa are represented by only one specimen each.
153 The material is curated in the Geological Department of the University Cheikh Anta Diop of
154 Dakar, Senegal. Material is numbered SN-Tob-year-number for “Senegal-Tobène”. Three
155 specimens were digitized using X-ray microtomography (μ CT): the mandible SN-Tob-12-14,
156 the canine SN-Tob-12-06, and the femur SN-Tob-12-02. The distal extremity of the femur
157 contains four main fragments (the patellar groove, a part of the lateral condyle, the medial
158 condyle, and a part of shaft), which were damaged and displaced post-mortem. 3D surfaces
159 representing these four parts were extracted with Avizo 9.2 (Thermo Fisher Scientific). The

160 four surfaces were positioned in space with MorphoDig software (Lebrun, 2018) in order to
161 retrieve anatomical connection. The virtually restored 3D model of SN-Tob-12-02 has been
162 deposited in MorphoMuseum (Lihoreau et al., in press).

163 Comparisons of this material were made with collections of extant mammals and fossils
164 curated in Montpellier University (UM) in Montpellier, France, under the Authority for
165 Research and Conservation of the Cultural Heritage (ARCCH) in Addis Abeba, Ethiopia, in the
166 National Museums of Kenya (NMK) in Nairobi, Kenya, in the Centre National de la Recherche
167 pour le Développement (CNRD) and in the Département de Paléontologie of N'Djamena
168 University, both in N'Djamena, Chad.

169

170 **3. Systematic paleontology**

171 *3.1. Description of cf. Osteolaemus*

172

173 Class Reptilia Laurenti, 1768

174 Order Crocodylia Gmelin, 1789

175 Family Crocodylidae Cuvier, 1807

176

177 *cf. Osteolaemus*

178

179 3.1.1. Studied material

180

181 Several teeth, mostly of small size, were recovered and are represented by tooth crowns, the
182 root being always broken off (Fig. 2A-J).

183

184 3.1.2. Description

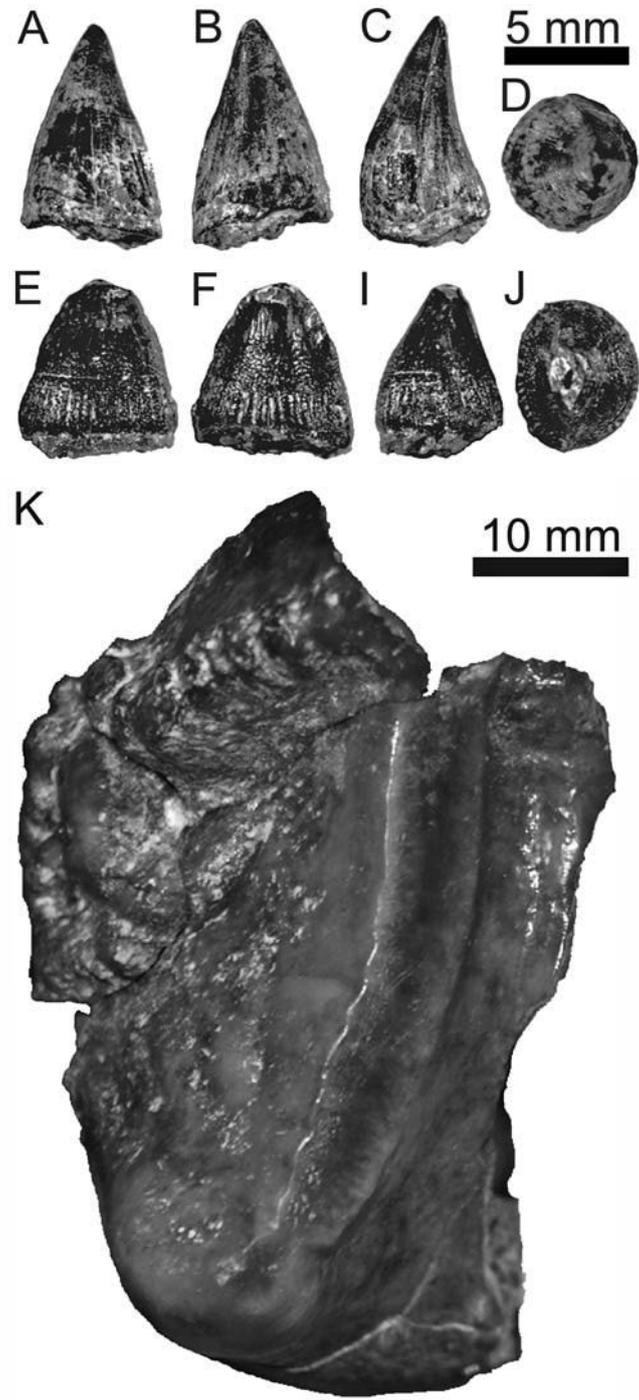
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186 One tooth is substantially larger (SN-Tob-13-07) with a preserved apico-basal length of 29 mm.
187 Its enamel surface is poorly preserved but shows hints of longitudinal ridges over its labial and
188 lingual surfaces. The tooth is conical, slightly curved lingually and bicarinate. The small teeth
189 (SN-Tob-12-10, Fig. 2) are less than a centimeter in apico-basal length and show a distinct
190 morphology with a somewhat bulbous crown. Ornamentation is variable and the enamel can be
191 nearly smooth or marked by longitudinal ridges. In one specimen, the crown-root junction is
192 preserved and is constricted as a collar (Figure 2E). In this specimen, the mesiodistal carinae
193 are ornamented with irregular edges (Figure 2F).

194 This morphology resembles that of the distal tooth row of *Osteolaemus*. But contrary to this
195 genus, they are not button shaped and the apex of the crown is pointed. The morphological
196 variability in our sample most likely reflects tooth positions along the jaw, with mesialmost
197 teeth being conical and distalmost teeth being blunter. Such a heterodonty is indeed most
198 pronounced in *Osteolaemus*, which has bulbous distalmost teeth (compare with Plate I in Prasad
199 and Lapparent de Broin, 2002). *Crocodylus* exhibits some degree of heterodonty too, with distal
200 teeth retaining short crowns. The Tobène locality may have hosted both taxa but an
201 unambiguous identification requires cranial elements or in the case of *Osteolaemus*, the very
202 last distal teeth of the jaw.

203 *Osteolaemus* has been reported on the basis of skull and mandibular material from the Late (?)
204 Miocene Sinda beds of NE Congo (Aoki, 1992), the Late Miocene of Uganda (Pickford, 1994)
205 and from the Pleistocene (?) of Cabinda (Antunes, 1962). Considering the geographic range of
206 the extant genus, encompassing Gambia and Senegal (Eaton, 2010), it would not be surprising
207 to recover it in the fossil record of Senegal. Nevertheless, tooth morphology is poorly diagnostic
208 and in the view of the high crocodylian diversity reported in Neogene localities across Africa

209 (e.g. Delfino, 2008; Brochu et al. 2020), it is too premature to assign the Senegalese teeth to a
210 particular taxon.
211



212
213 Fig. 2. [one column] Isolated teeth from Tobène. A-J: Teeth of Crocodylidae cf. *Osteolaemus*
214 (SN-Tob-12-10) in labial (A, E), lingual (B, F), distal (C, I) and apical (D, J) views. K: fragment
215 of metaloph and postmetaloph of a right M3/ (SN-Tob-12-03) of *Deinotherium bozasi*.

216

217 *3.2. Description of Deinotherium bozasi*

218

219 Class Mammalia Linnaeus, 1758

220 Order Proboscidea Illiger, 1811

221 Family Deinotheriidae Bonaparte, 1845

222 Genus *Deinotherium* Kaup, 1829

223

224 *Deinotherium bozasi* Arambourg, 1934

225

226 3.2.1. Studied material

227

228 A right M3/ (SN-Tob-12-03; Fig. 2K) preserving the metaloph and postmetaloph.

229

230 3.2.2. Description

231

232 Right M3/ largely broken and worn, reduced to an incomplete metaloph concave distally (Width
233 (W)>60mm). The metacone is missing. The postmetacrista is long, crenulated, pointing
234 distomedially and terminating at the midline of the tooth. The distal cingulum is present and
235 constituted of multiple conules of variable size.

236 Concerning size differences (estimated by the width of the metaloph), the Tobène molar
237 globally fits in the lower range of the M3/ from Omo Shungura Formation (Fm.) and Mursi Fm
238 in Ethiopia (pers. obs.; Drapeau et al., 2014: fig.3-2). Harris et al. (2003) looked at size
239 evolution in *D. bozasi* teeth from the Turkana Basin (i.e., Kanapoi, Kenya and Omo Group

240 deposits), and proposed a temporal size gradient, with the oldest ones being smaller than those
241 from younger horizons. The large variation in size amongst contemporaneous sites of the Omo
242 Valley is similar to that observed in the whole temporal sequence of the Turkana basin, which
243 tends to partly contradict this hypothesis. The distal cingulum of the Tobène tooth has large and
244 crenulated postmetacrista and distal cingulum (Fig. 2K), which are variably developed among
245 specimens attributed to *D. bozasi* from the Omo valley (L876-1, L596-19, OMO 29-69-3087,
246 Kib-133-3).

247

248 *3.3. Description of Nyanzachoerus cf. jaegeri*

249

250 Class Mammalia Linnaeus, 1758

251 Order Cetartiodactyla Montgelard, Douzery and Catzeflis, 1997

252 Family Suidae Gray, 1821

253 Subfamily Tetraconodontinae Lydekker, 1876

254 Genus *Nyanzachoerus* Leakey, 1956

255

256 *Nyanzachoerus cf. jaegeri*

257

258 3.3.1. Studied material

259

260 Distolabial fragment of left P4/ metacone (SN-Tob-13-27, Fig. 3A-B).

261

262 3.3.2. Description

263

264 This dental fragment is characterized by a relatively shallow crown (Fig. 3A) and thick enamel
265 displaying (Fig. 3B) a fine wrinkling. These features suggest a suid and, more particularly due
266 to wrinkled enamel (Fig. 3A), a tetracondontine. The cingulum, with a contact wear facet, is
267 high and flattened. It fuses with the wall without reaching the cervix (Fig. 3A), which is curved
268 and apically indented above the cingulum. These features match the morphology of a distolabial
269 fragment of a left P4/.

270 In terms of size, SN-Tob-13-27 appears much larger than in observed specimens of
271 *Notochoerus* from Hadar, Omo, and Middle Awash in Ethiopia (premolars are reduced in this
272 genus), and the groove between the metacone and the paracone (Fig. 3B) is deeper in *No. euilus*.
273 SN-Tob-13-27 is also larger than in early representatives of *Nyanzachoerus* (i.e., *Ny. devauxi*,
274 *Ny. waylandi*, *Ny. tulotos* and *Ny. Khinzir*).

275 In *Nyanzachoerus australis* (e.g., AMH-VP 1/6 and KUS-VP 1/10 from the Middle Awash),
276 the groove between the paracone and the metacone is also better expressed than in SN-Tob-13-
277 27. *Ny. australis* displays higher cusps and cingulum than in SN-Tob-13-27 at an equivalent
278 wear stage, suggesting that the Tobène specimen might be smaller. In *Ny. kanamensis* from
279 Hadar, the cingulum is thicker and not attenuated cervically.

280 Considering its size, its morphology as well as the oblique position and complicated shape of
281 the metacone wear facet, SN-Tob-13-27 would be closer to specimens attributed to *Ny. jaegeri*
282 (e.g., ARA-VP 16/1, SAG-VP 7/122, and GAW-VP 3/300 from the Middle Awash) than to any
283 other observed tetraconodontine specimens. Unfortunately, the P4/ is not preserved on the
284 holotype of this species (Coppens 1971a). Keeping in mind that attributing an isolated tooth is
285 difficult, even more so for such a fragmentary specimen, we tentatively propose an attribution
286 to *Nyanzachoerus cf. jaegeri*.

287

288 3.4. Description of cf. *Giraffa* sp. indet.

289

290 Class Mammalia Linnaeus, 1758

291 Order Cetartiodactyla Montgelard, Douzery and Catzeflis, 1997

292 Suborder Ruminantia Scopoli, 1777

293 Family Giraffidae Gray, 1821

294

295 cf. *Giraffa* sp. indet.

296

297 3.4.1. Studied material

298

299 An ungual phalanx (SN-Tob-12-01, Fig. 3C-E) partially broken at its distal end.

300

301 3.4.2. Description

302

303 The ungual phalanx belongs to a large ruminant. Its dimensions (minimal length (L)=92.8 mm
304 and width (W)=47.1 mm) exceed those of large Bovidae such as *Bos taurus* and the largest
305 known ungual phalanx of Bovidae from Omo and Hadar collections. Its size fits the range of
306 extant *Giraffa* phalanges. Similarly, the morphology of SN-Tob-12-01 recalls Giraffidae rather
307 than Bovidae, notably based on its general proportion (wider than high), the large dorsal part
308 of the proximal facet with prominent dorso-lateral border, the wide distal part on dorsal and
309 plantar views, and the wide and medial articular facet with the sesamoid that is narrower and
310 more central in bovids (Fig. 3D). Unlike bovids, the plantar face is flat, wrinkled and
311 significantly curved, with the distal part larger than the proximal one (Fig. 3C, E). Comparisons
312 with ungual phalanges of fossil giraffids are difficult as this bone is rarely described and specific
313 attribution remains hazardous. The third phalanx is of similar length in extant *Giraffa*, *Giraffa*

314 cf. *stillei* from the Plio-Pleistocene of Omo, an unpublished giraffid from the late Miocene of
315 Toros–Menalla, Chad (TM242-02-03 in CNRD), *Bohlinia* cf. *attica* from the late Miocene of
316 Küçükçekmece in Turkey (Kostopoulos and Sen, 2016), and *Decennatherium* from the late
317 Miocene of Spain (Ríos et al., 2016). The dorso-medial process for the insertion of the toe
318 extensor muscle is more developed than in extant *Giraffa*.

319 Despite a large collection of giraffid from African Pliocene deposits (Harris et al., 2010),
320 no comparison can be established for the third phalanx between *Giraffa* and *Sivatherium*,
321 including the well-known *Sivatherium giganteum* (see Basu et al., 2016). However, the
322 proportions of the phalanx, notably the plantar face and the angle between the plantar face and
323 the articulation, suggest that it belongs to a less massive animal than *Sivatherium* spp, its size
324 being congruent with Giraffinae. SN-Tob-12-01 resembles an indeterminate *Giraffa* specimen
325 from Omo (OMO 66), both in size (L=90 mm, W=45 mm) and morphology. We therefore
326 propose the presence of cf. *Giraffa* in the Tobène locality.

327

328 3.5. Description of cf. *Simatherium demissum*

329

330 Class Mammalia Linnaeus, 1758

331 Order Cetartiodactyla Montgelard, Douzery and Catzeflis, 1997

332 Suborder Ruminantia Scopoli, 1777

333 Family Bovidae Gray, 1821

334 Subfamily Bovinae Gray, 1821

335 Tribe Bovini Gray, 1821

336

337 cf. *Simatherium demissum*

338

339 3.5.1. Studied material

340

341 Left mandible with fragmentary and worn P/4-M/1 and alveolus of P/3 (SN-Tob-12-14, Fig.
342 3I-J).

343

344 3.5.2. Description

345

346 The mandible belongs to a large Bovidae. The lower P/4 lacks its labial part and is strongly
347 worn (Fig. 3I-J). The paraconid and metaconid are not fused and a central valley separates the
348 two cuspids: this condition is known in Hippotragini and early Bovini such as *Ugandax* and
349 *Simatherium* but is absent in most Tragelaphini, Alcelaphini as well as recent African Bovini,
350 *Pelorovis* and *Syncerus* (Gentry, 2006). In Tragelaphini, the metaconid is always projected
351 mesially even if some specimens lack a connection between the paraconid and metaconid. The
352 metaconid is slanted backward and fused with the entoconid (Fig. 3I). The parastylid and
353 paraconid are separated even if largely worn (Fig. 3I). This morphology recalls that of
354 *Simatherium demissum* from Langebaanweg in South Africa (Gentry, 1980; Haile-Selassie et
355 al., 2009). Alongside with the P/4 morphology, the large size of the mandible argues in favor
356 of an early Bovini (Gentry, 1980; Fig. 3J). The Tobène specimen displays a long P/4 (L=24
357 mm), which is larger than in most bovines except for the largest specimen of *S. demissum* from
358 Langebaanweg, an indeterminate Bovini from the Apak Member, Lothagam in Kenya
359 (LT24002; Harris, 2003), and a possible *Simatherium* from the Nkondo Formation, Uganda
360 (NK771'88; Geraads and Thomas, 1994). As in the latter, the mesial valley of SN-Tob-12-14
361 remains open at the base of the crown (Geraads and Thomas, 1994).

362 The M/1 is largely broken and extremely worn; only the lingual wall remains visible.

363 The mesowear is sharp and not blunt (Fig. 3J) as in derived Bovini. No cement is visible on the

364 lingual margin, as in *Simatherium demissum* from Langebaanweg (Gentry, 1980) and *Ugandax*
365 cf. *gautieri* from Lukeino, Kenya (Thomas, 1980). The mesostylid is incipient and the lingual
366 valley is not marked. The remnants of the occlusal surface look simple with a flat lingual border
367 compared to *U. coryndonae* from Hadar and other earliest Bovini. This configuration is due to
368 the bad preservation of the Senegalese specimen because only its crown base is preserved. The
369 M/1 is very long ($L > 30$ mm); it is longer than M/1 of most known Bovini except the largest
370 specimens of *S. demissum* from Langebaanweg (Gentry, 1980). Based on its root insertions, the
371 molar seems to be more brachyodont than other known Bovini. The weak development of
372 cuspid lingual ribs differs from most Bovini but recalls *S. demissum* from the basal Pliocene of
373 South Africa, which is also weakly hypsodont.

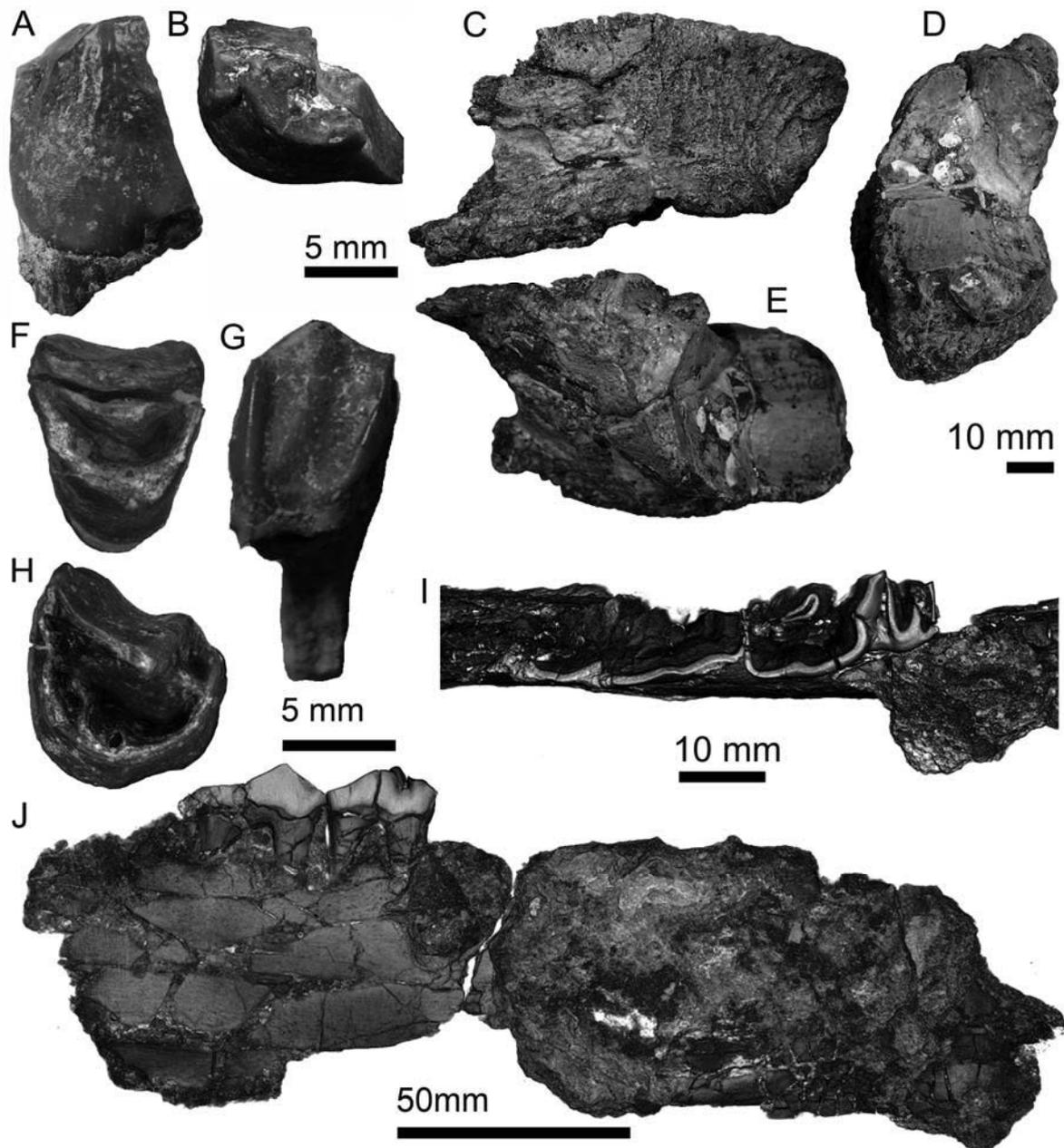
374 Mandibular height below M/1 ($H = 50.5$ mm) is similar to *S. cf. demissum* from Kanapoi
375 and *Ugandax coryndonae* from Hadar. Nevertheless, the few known occurrences of early
376 Bovini do not allow estimating variation in range sizes. The mandibular height below diastema
377 is not measurable due to fossil deformation (Fig. 3J). Lower premolar row length and diastema
378 length in front of P/2 are considered to be more diagnostic (Geraads and Thomas, 1994). The
379 maximum P/2-P/4 length in SN-Tob-12-14 could be estimated around 54 mm, which is not
380 different from early Bovini and even from the extant *Syncerus cafer*. The long diastema (close
381 to 70 mm) is remarkable, and is similar in length to that of *S. demissum* from Langebaanweg
382 and *S. aff demissum* from Kanapoi. In *Ugandax coryndonae*, the diastema is short and
383 systematically shorter than the premolar row length. It is also the case in a mandible from
384 N’Kondo, which led Geraads and Thomas (1994) to propose its attribution to the genus
385 *Ugandax*.

386 Diagnoses of early African Bovini are mainly based on skull and horn morphologies.
387 Differences in the lower teeth of *Simatherium* and *Ugandax* are unclear, but dental variation is
388 often poorly characterized in extinct bovine species due to the material scarcity (Gentry, 2010).

389 The species *Simatherium demissum* has sometimes been attributed to the genus *Ugandax*
390 (Gentry, 2006, 2010; Bibi, 2011) but without clear consensus (Haile-Selassie et al., 2009;
391 Geraads et al., 2013; Geraads and Bobe, 2017). As a matter of consistency, we retain a
392 taxonomic attribution to *Simatherium demissum* pending future taxonomic revisions.

393 The Tobène specimen appears as a plesiomorphic Bovini, considering the morphology
394 of its P/4 and the absence of cement on its molar. Following Gentry (2006), the large teeth of
395 the Senegalese specimen allow an attribution to early Bovini such as *S. demissum* from
396 Langebaanweg. The length of the diastema and of the premolar row is also closer to that of the
397 early Pliocene *Simatherium* from South Africa. We therefore propose a provisory attribution to
398 cf. *Simatherium demissum* as only horn cores material will permit a clear attribution.

399



400
 401 Fig. 3. [double column] Remains of Artiodactyla from Tobène. A-B: Disto-labial fragment of
 402 left P4/ (SN-Tob-13-27) of *Nyanzachoerus* cf. *jaegeri* in labial (A) and occlusal (B) views. C-
 403 E: a complete ungual phalanx of cf. *Giraffa* (SN-Tob-12-01) in plantar (C), proximal (D) and
 404 dorsal (E) views. F-G: Upper right P4/ of a cf. Caprinae (SN-Tob-12-09) in occlusal (F) and
 405 labial (G) views. H: Upper right P3/ (SN-Tob-15-19) of Antilopini indet. in occlusal view. I-J:
 406 3D reconstruction of left mandible with fragmentary and worn P4-M/1 of cf. *Simatherium*
 407 *demissum* (SN-Tob-12-14) in occlusal (I) and lingual (K) views.

408

409 *3.6. Description of Antilopini indet.*

410

411 Class Mammalia Linnaeus, 1758

412 Order Cetartiodactyla Montgelard, Douzery and Catzeflis, 1997

413 Suborder Ruminantia Scopoli, 1777

414 Subfamily Antilopinae Gray, 1821

415

416 Antilopini indet.

417

418 3.6.1. Studied material

419

420 Unworn upper right P3/ (SN-Tob-15-19; Fig. 3H).

421

422 3.6.2. Description

423

424 The P3/ is long with a paracone displaced mesially; the styles are marked but not prominent
425 and the mesial style is shallow and partly overhangs the labial wall to almost reach the paracone
426 rib. A profound groove is visible between this style and the paracone rib. The latter is salient
427 and pinched. The mesial fossa is large and closed distally by a medial crista that joins the
428 postprotocrista to the postparacrista.

429 The tooth is quite small (L=9 mm and W=7.7 mm) with slender cusps and a narrow
430 lingual margin. It belongs to one of the small-size bovid tribes (Antilopini, Caprini,
431 Aepycerotini or Neotragini). Unfortunately, the dentition is not strongly relevant for a specific
432 attribution within these tribes (e.g., Geraads et al., 2012a). Compared with extant species and

433 fossil taxa from Hadar (Geraads et al., 2012a), this tooth clearly differs from Aepycerotini
434 premolars by a larger fossa, a marked labial rib, and less labially developed ribs; from
435 Neotragini premolars by a larger fossa, less prominent mesial style, pinched labial rib of
436 paracone and triangular occlusal shape instead of rectangular; and from Caprini by the presence
437 of a large medial crista that joins the paracone and by being more mesio-distally elongated. It
438 is similar in shape to the Antilopini premolar pattern apart from *Litocranius*, which displays
439 brachyodont teeth. Its size matches with that of large gazelles such as the extant *Nanger granti*
440 (L=9.3 mm and W=8.1 mm), an Antilopini indet. from Hadar (AL 132-3, L=8.2 mm and W=8
441 mm), and *Gazella harmonae* also from Hadar (L=8.5 mm and W=6.9 mm; Geraads et al.,
442 2012a). It is larger than the extant *Eudorcas thomsonii* (L=6.8 mm and W=6.6 mm) and *Gazella*
443 *gazella* (L=7.5 mm and W=6.5 mm) and the fossil *Gazella janenschii* notably specimens from
444 Laetoli, Tanzania (mean L=7.3 mm and mean W=7 mm; Gentry, 2011).

445 Specific and even generic attribution to fossil Antilopini are difficult due to the scarcity
446 of the material and to the fact that dentition is rarely described, figured or even published
447 (Geraads et al., 2009; Haile-Selassie et al., 2009; Geraads et al., 2012a). Several antilopine taxa
448 of similar size can occur in a same formation and only horn cores are diagnostic (e.g., Geraads
449 et al., 2012a). We thus conclude that the P3/ can be attributed to an indeterminate Antilopini
450 genus most probably close to large gazelles such as *Nanger* spp.

451

452 3.7. Description of Caprinae indet.

453

454 Class Mammalia Linnaeus, 1758

455 Order Cetartiodactyla Montgelard, Douzery and Catzeflis, 1997

456 Suborder Ruminantia Scopoli, 1777

457 Subfamily Caprinae Gray, 1821

458

459 Caprinae indet.

460

461 3.7.1. Studied material

462

463 Upper right P4/ (SN-Tob-12-09; Figs 3F-G)

464

465 3.7.2. Description

466

467 The P4/ is bicuspid with crescent cristae. It is wider than long and characterized by a mesially
468 displaced protocone, a large symmetric fossa, weak styles, and slightly pinched paracone rib.

469 A small central fold is visible distally; it forms a small spur (Fig. 3F). The P4/ is small, with
470 slender cusps and narrow lingual margin. It could belong to a tribe of small Antilopinae
471 (Antilopini, Aepycerotini or Neotragini) or Caprinae. It differs from premolars of Aepycerotini
472 by a larger fossa, a marked but not prominent labial rib, less labially protruding styles and a
473 narrower lingual margin. It differs from Neotragini by its larger fossa, less prominent parastyle,
474 pinched paracone labial rib, and a triangular occlusal shape rather than rectangular. Dimensions
475 (L=7.3 mm and W=8.5 mm) are similar to specimens of extant *Gazella dorcas*, but with a
476 weaker style development, and similar to the holotype of *Gazella harmonae* from Hadar
477 (AL444-16, unfigured palate; Geraads et al., 2012a). Differences with *G. harmonae* consist in
478 a slightly larger fossa, the presence of a small central fold and a more slanted disto-lingual
479 margin. It differs from Antilopini by its mesially displaced protocone, its triangular outline with
480 a distolingual flat border and its fossa that is not only mesially distributed but also distally
481 extended.

482 The flat labial wall of the P4/ with developed styles and weak rib resembles that of
483 Caprinae (Fig. 3G). This specimen is however less hypsodont than extant *Ovis* or *Capra*, and
484 its lingual border is not vertical but slanted with the lingual root inclined. On the lingual border,
485 a small enamel bulge is visible at the level of the cervix. The labial face has two style ribs that
486 diverge toward the crown apex (Fig. 3G) whereas these ribs are parallel in extant Caprini.

487 The Tobène specimen differs from the described P4/ of African fossil Caprinae (Bibi,
488 2011) such as *Skouraia helicoides* from the late Miocene of Morocco (Geraads et al., 2012). In
489 most cases, only horn cores are discovered or described in African localities (Vrba, 1997; Bibi,
490 2011; Bibi et al., 2012), which prevents any precise attribution for the Tobène P4/. Caprinae is
491 an Asian subfamily that dispersed repeatedly in Africa during the Pliocene (Gentry, 2010; Bibi,
492 2011; Bibi et al., 2012). Several authors (Bibi et al., 2012; Geraads et al., 2012b) have
493 questioned the existence of putative endemic lineages of African caprines. This question is
494 difficult to address due to the fragmentary nature of the Tobène material. In occlusal view, the
495 Senegalese specimen resembles *Capra dalii* from Dmanisi (Bukhsianidze and Vekua, 2006)
496 but it is less hypsodont. In this regard, it is quite similar to the P4/ of the type specimen of
497 *Capra primaeva* from the Late Pliocene locality of Aïn Brimba, Tunisia (Arambourg, 1979).
498 Indeed, this semi-hypsodont Caprini, sometimes attributed to another genus, *Pseudocapra*
499 *primaeva* (Crégut-Bonnoure and Fernandez, 2018), also exhibits narrow styles on upper teeth,
500 an angular protocone in occlusal view, and a labio-lingual enlargement that confers a concave
501 profil to the lingual face. The Tunisian specimen is however larger (L=10 mm and W=12 mm;
502 Arambourg, 1979) than the senagalese premolar. The difficulty to identify a specific taxon
503 within this subfamily on the sole basis of an isolated tooth leads us to attribute it to an
504 indeterminate Caprinae.

505

506 *3.8. Description of Lutrinae indet.*

507

508 Class Mammalia Linnaeus, 1758

509 Order Carnivora Bowdich, 1821

510 Family Mustellidae Fisher, 1817

511 Subfamily Lutrinae Bonaparte, 1838

512

513 Lutrinae indet.

514

515 3.8.1. Studied material

516

517 Incomplete right femur preserving a fragmentary portion of the proximal part of diaphysis as
518 well as a distal extremity with condyles (SN-Tob-12-02; Fig. 4). Most of the distal epiphysis is
519 broken and the patellar groove is shifted. All fragments were found in association.

520

521 3.8.2. Description

522

523 SN-Tob-12-02 is a femur of a juvenile specimen. Its early ontogenetic stage is assessed through
524 a lack of the lesser trochanter (*i.e.*, only the epiphyseal plate is visible, Fig. 4A) and the presence
525 of a prominent epiphyseal line. The proximal epiphysis is lacking, presumably broken at the
526 level of the femoral proximal epiphyseal plate. A thin portion of the most distal part of the
527 trochanteric crest and the floor of the trochanteric fossa are visible (Fig. 4A). The diaphysis is
528 preserved with the exception of its distal third (Fig. 4A-B). The distal articular surface is well-
529 preserved, but only a minor portion of the lateral condyle articular surface remains (Fig. 4C-E).

530 The femur is robust, short, and wide (Fig. 4). The diaphyseal transverse cross-section is
531 compressed cranio-caudally above the patellar facet (Fig. 4K) and thus differs from that of

532 ungulates, which is squared in transverse cross-section. The cranial extension of the patellar
533 groove and the condyle caudal development are reduced (Fig. 4F) when compared to ungulates.
534 The overall proportions of the femur clearly depart from those observed in primates and most
535 carnivorans, apart from some mustelids. The distal epiphysis is robust and short cranio-
536 caudally, as in mustelids (Lewis 2008). We estimated the length of the femur to a maximal
537 value of 120 mm to calculate the Femoral Robustness Index (FRI), i.e the midshaft cranio-
538 caudal diameter of femur divided by the femur length following Samuels et al. (2013). With a
539 value of 0.108, its FRI falls within the range observed in semiaquatic carnivorans (mean value
540 of 0.09 in Samuels et al. 2013). Based on the 3D reconstruction (Fig. 4C, E, G), we also
541 calculated the Femoral Epicondylar Index (FEI, i.e the epicondylar breadth of the distal femur
542 divided by the femur length in Samuels et al. 2013) with a minimal estimated value of 0.253,
543 which corresponds to the mean value for semi-aquatic carnivorans (0.256 in Samuels et al.
544 2013). Both indices significantly discriminate semi-aquatic carnivorans from other locomotor
545 groups (Samuels et al. 2013). These proportions show a strong resemblance of SN-Tob-12-02
546 with Lutrinae.

547 On the proximal epiphysis, the trochanteric fossa does not reach the level of the lesser
548 trochanter (Fig. 4A, C). The lesser trochanter, even if badly preserved, was likely large and
549 caudally positioned. On the lateral border, the gluteal tuberosities are poorly imprinted with no
550 gluteal tubercle. The shaft is highly platymeric with a distinctive blade-like lateral border (Fig
551 4C, J). This condition is known in Lutrinae, especially in *Aonyx* and *Lontra*. The shaft flares at
552 a more proximal level (Fig. 4G-H) than in terrestrial Mustelidae and rather resembles the
553 condition of Lutrinae.

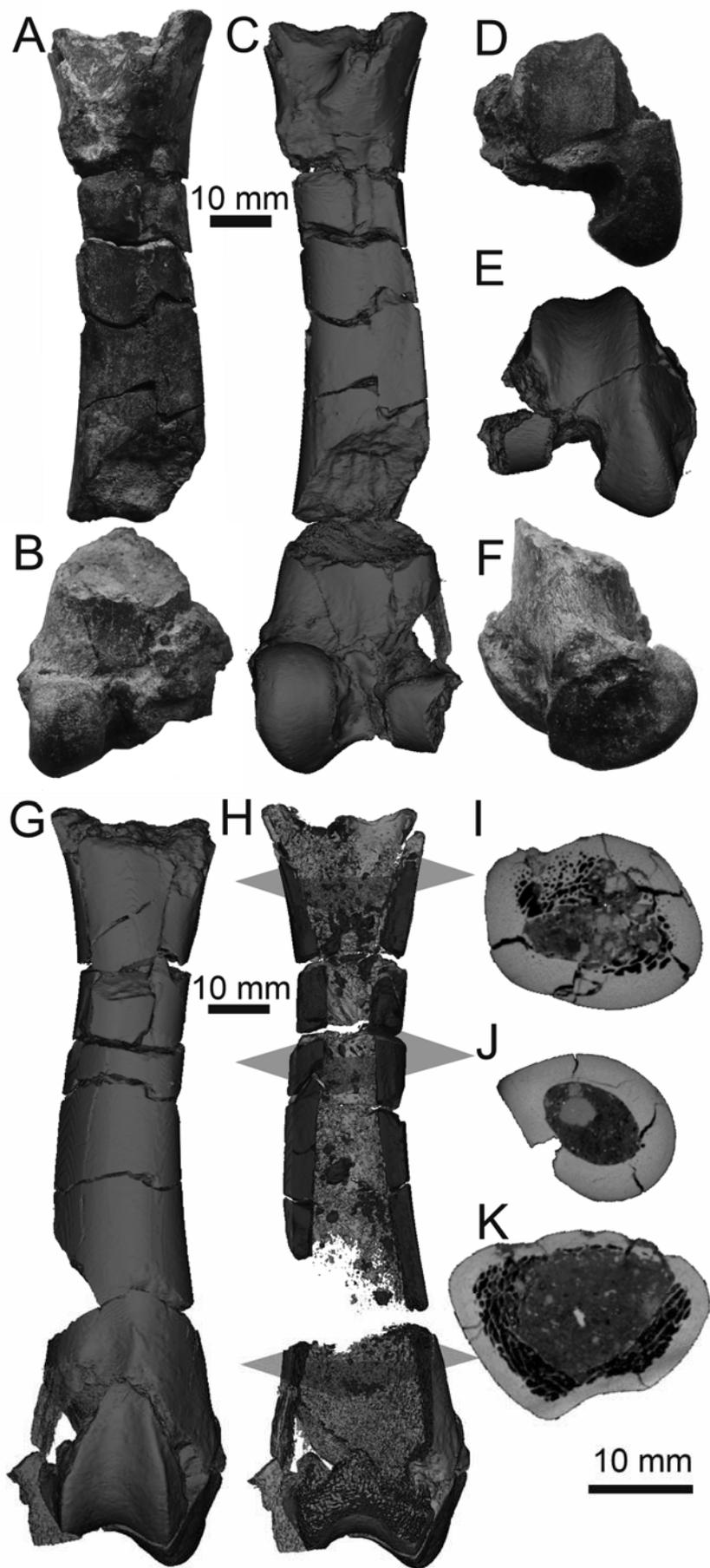
554 The distal epiphysis shows a proximo-distally extended and well excavated patellar
555 groove (Fig. 4D-E, G), which is longer than in terrestrial mustelids. Its proximal end is located
556 above the level of the proximal edge of the condyles. There is a marked sustrochlear hollow

557 (Fig. 4G). In distal view (Fig. 4D-E), the medial patellar lip is cranially projected. We observe
558 a cranio-caudal condylar asymmetry in favour of the medial condyle as in all compared
559 mustelids; it is especially pronounced in Lutrinae including extinct ones (e.g. Lewis 2008;
560 Peigné et al. 2008). The medial condyle of SN-tob-12-02 is characterized by a well imprinted
561 and extensive pit on its medial surface for the medial collateral ligament (Fig4. F), a slight
562 depression medially facing on the caudalo-proximal side for the medial part of *m.*
563 *gastrocnemius*, and a condyle that tapers distally (Fig. 4B-C).

564 The Tobène femur is characterized by an important development of the cortical bone.
565 On longitudinal sections (Fig. 4H), we observed a peculiar thickening near the bone growth
566 center. This distribution of the bone tissue is similar to that described in extant Lutrinae and
567 differs from that of terrestrial mustelids (Houssaye and Botton-Divet 2018). The trabecular
568 network has a larger extension in the diaphysis than in terrestrial mustelids (Fig. 4I, K) and
569 resembles otter trabecular network (Houssaye and Botton-Divet 2018). This microanatomy
570 pattern confirms an attribution of this specimen to the subfamily Lutrinae.

571 The overall dimensions of this femur are congruent with those of large extant otters,
572 such as *Enhydra* and *Pteronura* (Lewis 2008). Its size is very close to that of the African *Aonyx*
573 *capensis*, notably its length, FRI and FEI; it, however, displays larger mid-shaft diameter
574 (Valenciano and Govender 2020). Lutrinae are represented by seven genera in the African fossil
575 record and the systematics of this subfamily is essentially based on dental features (Werdelin
576 and Peigné 2010). Specific or generic attributions of lutrine postcranial materials then entirely
577 depend on associated dental material. Within the group of bunodont lutrine, Lewis (2008)
578 showed that the morphology of the postcranial skeleton is more variable than the dental
579 morphology. Some lutrine femurs have been described from African Mio-Pliocene deposits
580 (Lewis 2008, Peigné et al. 2008, Geraads et al. 2011, Valenciano and Govender 2020). Most of
581 them are larger than the Senegalese specimen, such as *Sivaonyx* from Langebaanweg and Toros-

582 Menalla (Peigné et al. 2008, Valenciano and Govender 2020) and some bunodont lutrines from
583 Hadar, Omo, and West Turkana (Lewis, 2008). There is a tendency of size increase during the
584 Pliocene with the youngest specimens of the bunodont lineage being much larger (Geraads et
585 al. 2011). Only a fossil femur attributed to cf. *Aonyx* sp. from Toros Menalla (Peigné et al.
586 2008) is equivalent in size to Tob-2012-02. Unfortunately, the characters shared by the Chadian
587 specimen and *Aonyx* are not preserved in the Tobène femur. We then propose to assign SN-
588 Tob-12-02 to *Lutrinae* indet.



590 Fig. 4. [one and half column] Incomplete right femur of a Lutrinae indet. from Tobène (SN-
591 Tob-12-02) and its 3D model reconstruction. Caudal (A and B), distal (D) and medial (F) views
592 of the fossil; caudal (C), distal (E), cranial (G) views of the 3D model reconstruction. Coronal
593 section along the proximo-distal axis of the shaft (H) and transverse cross-sections set at
594 proximal (I), midshaft (J) and distal (K) levels.

595

596 *3.9. Description of Mustelidae cf. Mellivorinae*

597

598 Class Mammalia Linnaeus, 1758

599 Order Carnivora Bowdich, 1821

600 Family Mustellidae Fisher, 1817

601

602 Mustelidae cf. Mellivorinae

603

604 3.9.1. Studied material

605

606 Proximal extremity of a right scapula (SN-Tob-15-18; Fig. 5D-F).

607

608 3.9.2. Description

609

610 The glenoid cavity is elliptical (L=13.6 mm and W=9.7 mm), and roughly equivalent in size to
611 that of the European otter. Its elliptical shape is unlike the rounded-one of ungulates (Fig. 5E).
612 Moreover, the scapular neck is very short and robust, a feature also distinct from ungulates (Fig.
613 5D, F). The lateral border is continuous and not depressed above the spine, which recalls
614 carnivorans such as *Felis* or *Genetta*. The coracoid process is not developed on the median

615 portion of the supraglenoid tubercle and the cranial part of the glenoid cavity is not projected
616 (Fig. 5D-F), which contrasts with the condition observed in primates as well as scansorial and
617 arboreal carnivorans (Heinrich and Houde 2006).

618 In lateral view, the glenoid cavity is slightly concave, but less than in terrestrial primates
619 (e.g., *Theropithecus gelada*) or some carnivorans (*Genetta* and *Canis*). The root of the spine is
620 broken but was likely caudally inserted. The cranial border projects abruptly and directly after
621 the neck, revealing a marked scapular notch (Fig. 5D, F), not as gradual as for primates and
622 most of carnivorans. The caudal border is broken just below the spine insertion.

623 Despite its fragmentary nature, the morphology of the glenoid cavity remains similar to
624 that of Mustelidae or Mephitidae such as *Spilogale* (Heinrich and Houde, 2006) and the
625 dimensions are similar to large Mustelidae. It differs from *Meles* and *Lutra* by a weak
626 development of the cranial lip of its glenoid cavity, a lack of coracoid process and a deeper
627 scapular notch. Overall, SN-Tob-15-18 closely resembles the scapula of *Mellivora*, both taxa
628 lacking the coracoid process and the protruding cranial lip of the glenoid cavity. Additionally,
629 the rim of the glenoid cavity is extended in both taxa. The scapular notch of SN-Tob-15-18 is
630 deep as in *Mellivora capensis* (Rose et al., 2014). The overall size of the Tobène specimen is
631 nevertheless smaller than specimens of extant *Mellivora* (OM180 in NMK; not numbered
632 specimens in CNRD). As the preservation state of SN-Tob-15-18 is inadequate for precise
633 taxonomic attribution and given that no scapula of fossil *Mellivora* were described so far, we
634 cautiously attribute this specimen to an indeterminate Mustelidae, probably close, or belonging
635 to, Mellivorinae.

636

637 *3.10. Description cf. Genetta sp.*

638

639 Class Mammalia Linnaeus, 1758

640 Order Carnivora Bowdich, 1821

641 Family Viverridae Gray, 1821

642 Subfamily Genettinae Gray 1864

643

644 cf. *Genetta* sp.

645

646 3.10.1. Studied material

647

648 Distal epiphysis of a right humerus (SN-Tob-12-08, Fig. 5A-C).

649

650 3.10.2. Description

651

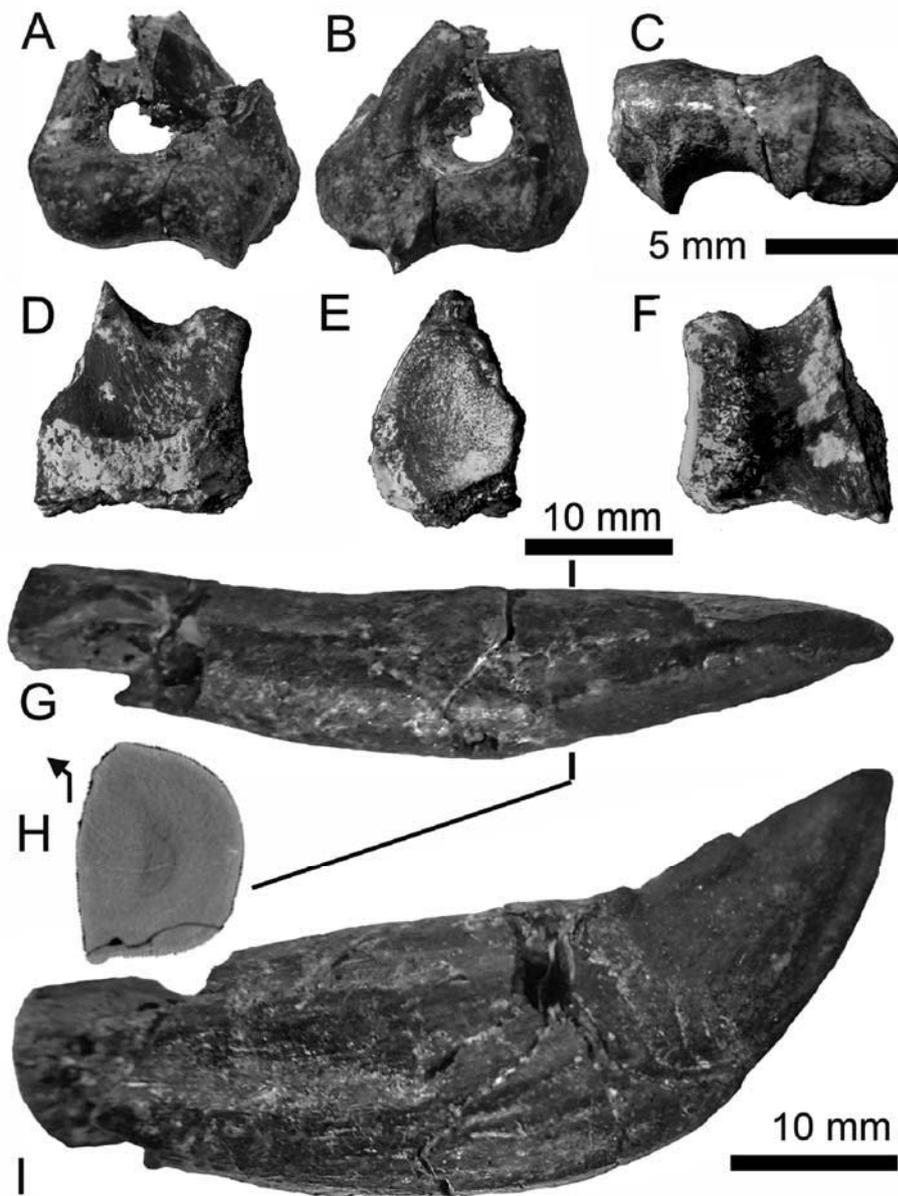
652 The distal fragment displays a biepicondylar breadth of 11.8 mm. It is broken near the olecranon
653 fossa, and only the distal part of the supracondylar foramen is noticeable (Fig. 5A-B). The
654 presence of this foramen supports our taxonomic attribution of SN-Tob-12-08 to a small
655 carnivoran.

656 Felidae and *Civettictis* differ from this specimen by a salient and distally developed
657 medial trochlear keel and by a relatively narrower articular surface. The specimen also differs
658 from similar-sized Mustelidae by an angulate medial epicondyle (flat in *Martes*), an elliptical
659 supracondylar foramen (rounded in *Martes*), a perforation of the olecranon fossa, and an
660 incipient but noticeable zona conoidea (i.e, area between lateral lips of trochlea and capitulum).

661 The Tobène specimen does not resemble carnivoran arboreal walker and climber (following the
662 classes established in Taylor (1974)) due to the weak development of the medial epicondyle
663 and the presence of a shallow zona conoidea (Fig. 5A-C). It also differs from terrestrial species
664 such as *Civettictis* and *Ichneumia* and fossorial species such as *Mungos* that display a deep zona

665 conoidea, which prevents supinatory movements (Taylor, 1974). In regard to substrate and
666 positional behaviors, the specimen SN-Tob-12-08, is a quadruped, with probable mixed
667 substrate preferences like *Genetta*. Viverridae and Herpestidae also present a perforation of the
668 olecranon fossa. Even if uncommon in the sample studied by Taylor (1974), all the specimens
669 of *Genetta genetta* (n=10) observed for the present study display this perforation. In SN-Tob-
670 12-08, the medial lip of the trochlea is straight in cranial view (Fig. 5A), whereas it is slanted
671 in the observed Herpestidae (*Herpestes edwardsi* (UM), *H. ichneumon* and *Ichneumia*
672 *albicauda* (in Taylor, 1974)). The capitulum is larger and less separated from the lateral border
673 of the articulation than in Herpestidae but is similar to *Genetta genetta*. In *Herpestes*, the
674 supracondylar foramen is distally-set and occupies a median position in regard to the axis
675 defined by the medial trochlear keel. In the Tobène specimen, the foramen is separated from
676 the trochlear keel and positioned on the same proximo-distal axis as in *Genetta genetta*.
677 Moreover, the trochlea in *Herpestes* is more cranially projected than the capitulum in distal
678 view, unlike in *Genetta* and the Tobène specimen that both show equivalent cranial projections
679 (Fig. 5C).

680 The Tobène specimen resembles most *Genetta genetta* and displays only slight
681 differences with this species including a smaller size (W=13.1 mm for *Genetta genetta* versus
682 W=11.8 mm for SN-Tob-12-08) and a less cranio-caudally compressed medial epicondyle. Due
683 to the fragmentary nature of SN-Tob-12-08 and the lack of a large humeral comparative fossil
684 sample (especially with other small viverrids), we propose a taxonomic attribution to cf.
685 *Genetta*.



686

687 Fig. 5. [one and half column] Remains of Carnivora from Tobène. A-C: Distal epiphysis of a
 688 right humerus of cf. *Genetta* sp. (SN-Tob-12-08) in cranial (A), caudal (B) and distal (C) views.
 689 D-F: Proximal extremity of a right scapula of a Mustelidae cf. Mellivorinae (SN-Tob-15-18) in
 690 lateral (D), proximal (E) and medial (F) views. G-I: Left lower canine of *Homotherium* sp. (SN-
 691 Tob-12-06) in distal (G) and lingual (I) views, with a cross section at cervix (H). The arrow
 692 indicates the mesio-lingual direction.

693

694 3.11. *Description Homotherium sp.*

695

696 Class Mammalia Linnaeus, 1758

697 Order Carnivora Bowdich, 1821

698 Family Felidae Fisher, 1817

699 Subfamily Machairodontinae Gill, 1872

700 Tribe Homotherini Fabrini, 1890

701 Genus *Homotherium* Fabrini, 1890

702

703 *Homotherium sp.*

704

705 3.11.1. Studied material

706

707 Isolated complete left lower canine with important distal wear (SN-Tob-12-06; Fig. 5G-I).

708

709 3.11.2. Description

710

711 The lower canine is a fang with mesial and distal keels, an enlarged root and, a continuous
712 curvature along the crown-root length (Fig. 5I). This tooth belongs to a large carnivoran with
713 small lower canines, similar in size (comparing sections at cervix) to *Panthera pardus* but one-
714 third smaller in crown height. Indeed, the crown of SN-Tob-12-06 is 24.3 mm in height and the
715 root is 37.7 mm in length. The measured crown linguolabial length is 10.8 mm at cervix and
716 the crown mesiodistal length is 13.7 mm. This small size compared to other carnivorans,
717 together with the compression of the crown associated with a crenulation of the distal keel
718 indicate that it belongs to a Felidae Machairodontinae (Christiansen, 2013). The lingual flank

719 is flat and the labial flank is convex, which clearly differs from the more conical lower canine
720 of *Dinofelis* (Werdelin and Lewis, 2001). The occlusal perimeter of the crown is D-shaped (Fig.
721 5H) and not oval as in *Machairodus* (Antón et al., 2004). It is also considerably smaller than all
722 specimens of *Machairodus aphanistus*, notably regarding the crown height (Antón et al., 2004).
723 A small distal wear facet is present (Fig. 5G). This implies that upper and lower canines occlude
724 in opposition, a characteristic feature of *Homotherium* compared to *Machairodus* following de
725 Beaumont (1975). Two keels are present, one mesio-lingual and one disto-lingual. The latter
726 displays strong crenulation, which differs from that of *Megantereon* (Christiansen and
727 Adolfssen, 2007). Even largely obliterated by wear, the mesial keel is finely serrated and
728 occupies a lingual position contrary to late Miocene Homotherini such as *Amphimachairodus*
729 *giganteus*, which displays a more mesially oriented keel (Morlo and Semenov, 2004).
730 Moreover, the late Miocene machairodontines such as *Amphimachairodus* usually have a larger
731 and less curved lower canine (Salesa et al., 2012). Unfortunately, the lower canine of
732 *Lokotunjailurus* from Lothagam, Kenya, remains unknown (Werdelin, 2003). The association
733 of a flattened, small, and curved lower canine with mesial and distal crenulations is consistent
734 with the description of the genus *Homotherium* (Antón et al., 2014), and congruent with what
735 is expected for a Plio-Pleistocene African Machairodontine (Sardella and Werdelin, 2007).

736 The lower canine fits within the size range of *Homotherium crenatidens* from the early
737 Pleistocene of Kuruksay (Tajikistan) and Liventsovka (Russia) (Sotnikova and Titov, 2009)
738 and in the variation range of *H. latidens* from Incarcál (Spain; Antón et al., 2014).
739 Unfortunately, only one lower canine of *Homotherium* was published in the African fossil
740 record (Geraads et al., 2015). Compared to this specimen of *Homotherium hadarensis* from
741 Dikika (Ethiopia, 3.5-2.9 Ma according to Geraads et al., 2015), the Tobène specimen has a
742 shorter root; it is also slenderer and shows a more pronounced curvature between crown and
743 root in lateral view (Fig. 5F-G). In distal view, the crown is twisted labially with regard to the

744 root as in *H. hadarensis*. In the latter species, the crown apex is twisted lingually unlike SN-
745 Tob-12-06. A small distal crest is observable labially to the main keel but this is probably due
746 to important enamel wear. The root is bilobed with lateral lingual and labial gutters at mid-
747 shape, which are more important than those observed in *H. hadarensis*. Other species of the
748 genus are known from Africa: *H. problematicum* and *H. africanum* (Antón et al., 2014) but no
749 lower canine has been recovered and described for these species. It can be mentioned that *H.*
750 *africanum* from Ain Brimba, Tunisia, (Werdelin and Peigné, 2010) firstly attributed to
751 *Machairodus*, differs from other *Homotherium* by its small size and the retention of some
752 primitive features (Petter and Howell, 1987). An unpublished mandible of *Homotherium* from
753 the locality ARA-VP-1 from the Aramis Member of the Sagantole Formation, Ethiopia (White,
754 pers. comm. 2018) has canines similar in size to those of the Tobène specimen. These canines
755 show comparable crown curvature in lingual view and no crown apex shift in distal view.
756 Postcranial remains of *Homotherium* from Kanapoi are considered to be smaller than in other
757 East African localities (Werdelin and Lewis, 2020), which is also congruent with the small
758 canine of Tobène and Aramis and suggests the existence of a small species of *Homotherium* at
759 least known from the early Pliocene of Africa.

760 Due to the scarcity of the fossil record and to the weak diagnostic support given by a
761 lower canine, we can only conclude on the presence of the felid *Homotherium* sp. in Tobène.

762

763 **4. Discussion**

764

765 *4.1. Age of the fossiliferous conglomerate*

766

767 The age of the Tobène fossiliferous locality is first discussed from the perspective of
768 paleoweathering chronology, then from the perspective of biochronology.

769 Cenozoic climate changes over Sahelian western Africa led to punctuated
770 erosion/weathering history of its landscape. During the Neogene, three main pediment systems
771 (erosion and transportation land surfaces) formed under a dominantly semi-arid climate
772 (Chardon et al., 2018). Each of these surfaces was weathered/duricrusted under seasonally
773 humid climate before a return to semi-arid climate that favored the development of the next
774 pediment (Beauvais and Chardon, 2013). At the Tambao (Northern Burkina Faso) type Sahelian
775 locality, Ar-Ar geochronology of K-Mn oxydes formed in the ferricrete/weathering profile of
776 each pediment allowed bracketing the three Neogene periods of duricrusting under humid
777 climate at ca. 18-11 Ma, 7-6 Ma, and 3 Ma (Beauvais et al., 2008; Fig. 6). More precisely, the
778 youngest weathering episode is constrained between 3.4 Ma and 2.9 Ma (W3 period in Fig.6)
779 and ascribed to the “Low glacis” i.e., the youngest and lowest pediment system in West Africa
780 (Beauvais et al., 2008). As the last pre-Ogolian lateritic weathering episode of regional extent,
781 this period may correspond to the formation of the ferricrete that developed on the fossiliferous
782 conglomerate or to that formed on the overlying aeolian sand unit (Fig. 1). Given the duration
783 of the last weathering period dated in Tambao, the two superimposed duricrusting episodes
784 documented in Tobène may as well have been produced during the 0.5 Ma time laps between
785 3.4 and 2.9 Ma. We therefore propose to correlate the weathered fossiliferous conglomerates
786 and its overlying sandstones with the Low glacis landscape stage recorded over most West
787 Africa (Chardon et al., 2018), before the W3 regional weathering episode (Fig. 6). Those
788 interpretations would be consistent with the fact that, East of the Senegalo-Mauritanian basin,
789 the Ogolian sands (i.e., the youngest formation in the quarry, Fig. 1) are the oldest deposits
790 overlying the youngest of the three West African pediment systems (Michel, 1973). In
791 conclusion, the Tobène fossiliferous locality is therefore proposed to have a minimum age of
792 3.4 Ma (Fig. 6).

793

Class	Order	Family	Subfamily/tribe	Genus/species
Reptilia	Crocodylia	Crocodylidae		<i>cf. Osteolaemus</i>
Mammalia	Proboscidea	Deinotheriidae		<i>Deinotherium bozasi</i>
	Cetartiodactyla	Suidae	Tetraconodontinae	<i>Nyanzachoerus cf. jaegeri</i>
		Giraffidae	Giraffinae	<i>cf Giraffa</i>
		Bovidae	Bovini	<i>cf. Simatherium demissum</i>
			Antilopini	indeterminate
			Caprinae	indeterminate
	Carnivora	Mustelidae	Lutrinae	indeterminate
			<i>cf. Mellivorinae</i>	indet
		Viverridae	Genettinae	<i>cf. Genetta</i>
		Felidae	Machairodontinae	<i>Homotherium sp.</i>

794 Table 1. Faunal list of Tobène.

795

796 Most taxa from the Tobène locality date to late Miocene and were present in Africa
797 during the Pliocene (*Giraffa*, *Deinotherium bozasi*, *Osteolaemus*, large lutrines and large
798 gazelles; Tables 1 and 2). Small carnivorans (close to *Mellivora* and *Genetta*) are well
799 represented in the Pliocene. The earliest occurrence of *Mellivora* is from Langebaanweg and
800 other remains attributed to the genus, even if common in Pliocene localities of Northern Africa,
801 Southern Africa and Eastern Africa (Geraads, 1997; Werdelin and Peigné, 2010), have arguable
802 species determination (Werdelin and Peigné, 2010). These specimens were usually referred to
803 the extant *Mellivora capensis*. Occurrence of *Genetta* spp. is common in the Late Miocene-
804 Pleistocene of Africa. Following Werdelin and Peigné (2010), the earliest fossil remain of the
805 genus that suffers no ambiguity of identification is from Kanapoi, Kenya (4-4.2 Ma).

806 Three specimens from Tobène seem to present affinities with typical forms of early
807 Pliocene African localities considered to belong to the recently defined African Land Mammal

808 Age (AFLMA) Kerian dated from 5.3 to 3.6 Ma (Fig. 6; Van Couvering and Delson, 2020).
809 First, the Tobène suid specimen has a morphology that is more congruent with species of
810 *Nyanzachoerus* known between 5.5 Ma and 3 Ma than with any other African suids. Its tentative
811 attribution to the species *Nyanzachoerus jaegeri*, with a wide geographic distribution in Africa
812 from Tunisia (Coppens 1971a) to, possibly, South Africa (Cooke and Hendey 1992), suggests
813 a more precise age closer to 4 Ma, this species being temporally bracketed between ca. 5 Ma
814 (e.g., Apak Member at Lothagam, Harris and Leakey 2003) and 3.66 Ma (Woranso-Mille, Reda
815 et al. 2019, see Fig. 6). The canine of *Homotherium* is similar to that from ARA-VP-1, Aramis
816 (4.4 Ma; White et al. 2009) and belongs to a small African *Homotherium* possibly also present
817 in Kanapoi (Werdelin and Lewis, 2020). The origin of *Homotherium* is supposed to be nested
818 within African *Amphimachairodus* from the late Miocene-earliest Pliocene (Werdelin and
819 Sardella, 2006; Werdelin and Lewis, 2020). To date, the earliest known *Homotherium* are from
820 Odessa catacombs (Ukraine, 4.2 Ma; Sotnikova and Titov, 2009), Lonyumun Mb, Koobi Fora
821 (4.35-4.1 Ma), and Kanapoi (Kenya, 4.2 Ma; Werdelin and Lewis, 2020). The specimen from
822 Langebaanweg is considered as an advanced *Amphimachairodus* (Werdelin and Sardella,
823 2006). The lower canine from Tobène could represent an unnamed early African form of
824 *Homotherium*, which partially fills the gap with the *Amphimachairodus* lineage. This would
825 therefore constrain the maximum age of Tobène at the first occurrence of *Homotherium* near
826 4.4 Ma (Aramis and Lonyumun Mb, Koobi Fora; Fig. 6). Finally, specimens that resemble the
827 mandible of cf. *Simatherium demissum* from Tobène have been reported from Kanapoi (Harris
828 et al. 2003), even if its species attribution remains uncertain (Geraads et al., 2013; Geraads and
829 Bobe, 2017), and from Kuseralee members of the Sagantole Formation in the Middle Awash
830 (Ethiopia; Haile-Selassie et al., 2009). The material from Tobène could be regarded as an early
831 Pliocene Bovini. Geographically, the closest early Pliocene Bovini attributed to *Simatherium*
832 sp. are from Kossom Bougoudi and Kollé, Chad (Brunet et al., 1998, 2000). Another

853 of the Adu-Asa Formation and Kusarelee Member of the Sagantole Formation, Middle Awash,
854 Ethiopia (Haile-Selassie and WoldeGabriel, 2009); Chi2: Chiwondo Unit 2, Malawi (Bromage
855 et al., 1995); Had: Hadar, Afar region, Ethiopia (Reed, 2008); HD: Hamada Damous, Tunisia
856 (Coppens, 1971b); Ich: Garaet Ichkeul, Tunisia (Arambourg 1979); KB: Kossom-Bougoudi,
857 Chad (Brunet et al., 2000; Lebatard et al., 2008); KL: Kollé, Chad (Brunet et al., 1998; Lebatard
858 et al., 2008); KP: Kanapoi, Kenya (Harris et al. 2003); KT : Koro-Toro, Chad (Brunet et al.,
859 1995); LBW: Langebaanweg, South Africa (Gentry, 1980; Roberts et al., 2011); Lis: Lissasfa,
860 Morocco (Raynal et al., 1999); AaO: Ahl Al Oughlam, Morocco (Zouhri et al., 2017); LLB:
861 Lower Laetolil Beds, Laetoli, Tanzania (Harrison, 2011a, 2011b); MKM: MKM-VP-1, Makah
862 Mera, Woranso-Mille, Afar, Ethiopia (Haile-Selassie and Ryan, 2019); Mur: Mursi, Omo
863 valley, Ethiopia (Drapeau et al., 2014); NK : NKondo Formation, Uganda (Simon et al., 2017).
864 W2 and W3: weathering/duricrusting periods in Tambao, Burkina Faso, after Beauvais et al.
865 (2008). Dark grey and light grey zones are the temporal distributions of the genus *Ardipithecus*
866 and *Australopithecus*, respectively. Time scale is from Hilgen *et al.* (2012).

867

868 4.2. Paleobiogeography and paleoenvironment

869

870 Only few Neogene continental fossiliferous localities are known from western Africa. Most of
871 them correspond to Pleistocene-Holocene deposits, notably from northern Mauritania (e.g.
872 Zouérate and Chami; Coppens et al. 1972; Guérin 1980). A Nigerien locality (unknown precise
873 location, Niger N885) has been dated from the late Miocene (Pickford et al. 2009). All these
874 localities have yielded very few vertebrate remains and their age is clearly different from that
875 proposed for the Tobène locality. At least 35 sub-contemporaneous (lower Pliocene) major
876 fossiliferous localities (or formations) were described in Africa (Werdelin, 2010; see some of
877 them in Fig. 6 and Table 2). Unfortunately, most of the northern African localities from this list

878 are known only from micromammals (Benammi et al., 1996), which precludes comparison with
879 the Tobène fauna. Lissasfa in Morocco (ca. 5.5 Ma) has yielded large mammals but is relatively
880 poor in diversity (Raynal et al. 1999). Another Moroccan locality, Ahl Al Oughlam, is much
881 more diverse but also more recent (about 2.5 Ma; Geraads et al., 2010). Some Pliocene localities
882 in Tunisia have yielded large mammals such as the base of the Hamada Damous (Coppens,
883 1971b), the Garaet Ichkeul and Aïn Brimba (Arambourg, 1979). Those “Villafranchian”
884 localities have been dated close to 4.5 Ma, 3.7 Ma and 2.3 Ma, respectively (Van Couvering
885 and Delson, 2020). However, Sahnouni et al. (2011) proposed an earlier age for Aïn Brimba, at
886 ca. 2.8-3 Ma. Most Pliocene southern African localities consist of karst infillings (Pickford et
887 al., 1994), and only the Langebaanweg locality (5.2-5 Ma; Roberts et al., 2011) can be
888 relevantly compared to the Tobène fauna. Conversely, the East African Rift System is very rich
889 for this time interval, notably *i*) in Ethiopia in the Omo valley (e.g., Mursi Fm.; Drapeau et al.
890 2014) and in the Afar Depression (Sagantole Fm, Hadar Fm. at Hadar, Dikika and Woranso-
891 Mille; Haile Selassie and Woldegabriel, 2009, Reed, 2008, Geraads et al. 2015, Haile-Selassie
892 and Ryan, 2019), *ii*) in Kenya, in the Turkana basin (e.g., Apak Member in Nachukui Fm.,
893 Kanapoi and Allia Bay; McDougall and Feibel, 2003, Harris et al. 2003) and in the Tugen Hills
894 (Mabaget and Chemeron Fm.; Gilbert et al., 2011), *iii*) in Tanzania (Lower Laetolil beds;
895 Harrisson, 2011a,b), *iv*) in Malawi (Chiwondo Unit 2; Bromage et al., 1995), and *v*) in Uganda
896 (Nkondo Fm.; Simon et al., 2017). Finally, Central Africa has yielded some important localities
897 for this time period in Chad (Kossom Bougoudi, Kollo and Koro-Toro; Brunet et al., 1995,
898 1998, 2000).

899 This inventory shows that *i*) large mammalian faunas from the Neogene of Africa are
900 best and mostly known from eastern Africa and that *ii*) western Africa remains a paleontological
901 wasteland for Neogene continental faunas. Considering Pliocene times, western Africa is
902 loosely bounded to the North by the locality of Lissasfa (Casablanca, Morocco at 2,400 km;

903 Raynal. et al. 1999) and to the East by the Kossom Bougoudi and Kollé localities (Djurab erg,
 904 Chad at 3,700 km; Brunet et al., 1998, 2000), i.e. the nearest known early Pliocene mammalian
 905 faunas (Fig. 6).
 906

Tobène	LBW	Chi2	LLB	KP	Mur	KUSM	Ara	MKM	NK	KL	KB	Lis	AaO	AB
<i>Osteolaemus</i>									X					
<i>D. bozasi</i>				X	X	X	X							
<i>N. jaegeri</i>	X	X	X	X	X		X	X	X	X				
<i>Giraffa</i>			X	X	X	X	X	X		X	X			X
Early Bovini (<i>Simatherium</i>)	X	X		X		X	X		X	X	X	X		
Large gazelle			X				X			X	X		X	X
Caprinae	X					X								X
Lutrinae	X		X	X		X	X	X	X		X		X	
Mellivorinae	X					X							X	
<i>Genetta</i>				X		X							X	
<i>Homootherium</i> (small)				X			X	X						X

907
 908 Table 2. Geographic distribution of the taxon retrieved in Tobène in regard to African Pliocene
 909 localities discussed in the text. AaO: Ahl Al Oughlam, Morocco (Zouhri et al., 2017); AB: Aïn
 910 Brimba, Tunisia (Arambourg, 1979); Ara: Ara-VP-1, Aramis, Middle Awash Ethiopia (White
 911 et al., 2009); Chi 2: Chiwondo Unit 2, Malawi (Bromage et al., 1995); KB: Kossom-Bougoudi,
 912 Chad (Brunet et al., 2000; Lebatard et al., 2008); KL: Kollé, Chad (Brunet et al., 1998; Lebatard
 913 et al., 2008); KP: Kanapoi, Kenya (Harris et al., 2003); KUSM: Kuseralee Mb. of Sagantole
 914 Fm., Middle Awash, Ethiopia (Haile-Selassie and WoldeGabriel, 2009, Bibi, 2011); LBW:
 915 Langebaanweg, South Africa (Gentry, 1980; Roberts et al., 2011; Valenciano and Govender

916 2020); Lis: Lissasfa, Morocco (Raynal et al. 1999); LLB: Lower Laetolil Beds, Laetoli,
917 Tanzania (Harrison, 2011a, 2011b); MKM: MKM-VP-1, Makah Mera, Woranso-Mille, Afar,
918 Ethiopia (Haile-Selassie and Ryan, 2019); Mur: Mursi, Omo valley, Ethiopia (Drapeau et al.,
919 2014); NK : NKondo Fm., Uganda (Simon et al., 2017).

920

921 An important result here is an apparent lack of endemism in the Senegalese fauna, at
922 least at generic level. However, this interpretation could be biased by the fragmentary nature of
923 the material preserved in Tobène. Some genera present in the Tobène fauna have a pan-African
924 distribution as early as the early Pliocene: *Mellivora*, *Genetta*, *Homotherium*, and *Giraffa* were
925 present in each of the main fossiliferous regions (Table 2). It is noteworthy that remains
926 confidently attributed to *Giraffa* in Northwestern Africa are only known from Aïn Brimba at
927 the end of the Pliocene (Arambourg, 1979). The species *Deinotherium bozasi* is also present in
928 a large corridor extending from Malawi to Egypt (Sanders et al., 2010). It can now be considered
929 as more widespread given the Tobène occurrence. Its absence from the Pliocene of
930 Northwestern and Central Africa (Chad) could be linked to either relatively drier conditions or
931 to sampling bias, *Deinotherium* being usually rare in fossil communities (except in Omo at
932 Mursi, see Drapeau et al., 2014). However, such absence from localities that yielded numerous
933 proboscidean remains (e.g., Garaet Ichkeul, Aïn Brimba, Koro-Toro) could also be explained
934 by different ecological conditions in the Upper Pliocene of Morocco, as previously proposed
935 by Geraads (2010) based on the absence of both *Deinotherium* and *Giraffa*. In contrast, the
936 presence of *Deinotherium bozasi* in Tobène could suggest biogeographical or environmental
937 affinities with Pliocene East African localities. Whether or not the presence of *Nyanzachoerus*
938 *jaegeri* in Tobène is confirmed, the wide distribution of this species (Reda et al. 2019) is already
939 compelling. Indeed, it was already identified in northern (Tunisia), central (Chad), southern
940 (South Africa), and eastern parts of Africa (Malawi, Tanzania, Kenya, and Ethiopia). For

941 bovids, the comparisons established between the Tobène material and *Simatherium demissum*
942 could imply relation with western and southern Africa. Nevertheless, Bovini (and Antilopini)
943 are usually very diverse in most Pliocene African faunal lists, and the fragmentary condition of
944 the Tobène remains precludes further speculation on ancient geographical distributions. Finally,
945 if confirmed, the possible presence of a caprine could be interesting considering the relative
946 proximity with the Atlas Mountain and southern Europe, even if this bovid group has a complex
947 biogeographical history and is also known from eastern and southern Africa (Bibi, 2011).

948 It would appear infeasible to reliably reconstruct the Tobène paleoenvironment given
949 the limited size of the sample, the uncertain strict isochrony of the specimens, and the colluvial
950 amalgamation of the fossils. Nevertheless, some first-order information may be retrieved. First,
951 carnivorans are well represented and constitute one third of the collected fossils, whereas they
952 are generally less abundant in fossil mammalian communities (e. g., 11% in TM266 (Lefur et
953 al. 2009); near 5% in Aramis (White et al. 2009)). This could indicate taphonomical bias or
954 simply a need to intensify field exploration in this area. The new Senegalese fauna does not
955 seem to characterize a rainforest environment. Indeed, *Homotherium* is considered to have
956 inhabited open environments and to have been more cursorial than other machairodontine felids
957 (Werdelin and Lewis, 2020). *Nyanzachoerus jaegeri* is considered to have been a grazer and
958 could be characteristic of savannah environments (Cerling et al., 2015; Manthi et al., 2017).
959 *Deinotherium* is a leaf-browser throughout the Pliocene (Cerling et al., 2015). It is considered
960 as a closed-habitat species and its abundance in Mursi leads to suggest a mesic refugium in the
961 Omo valley (Drapeau et al., 2014). Thus, the Tobène Pliocene fauna suggests a woodland
962 environment but is not yet sufficiently documented to decipher a paleoenvironmental picture.
963 At first sight, the Tobène fauna differs from that of the pene-contemporaneous Ethiopian
964 locality of Aramis, which is rich in colobines and tragelaphines suggestive of a woodland
965 habitat (White et al., 2009). It also differs from the possibly more open habitat described in

966 Kollé, Chad (3.96 ± 0.48 Ma; Lebatard et al., 2008), which is supported by the presence of
967 rhinocerotids, equids, sivatheres and *Kobus* (Brunet et al., 1998) and by evidence for increasing
968 aridity in Northern Chad at this time (Zazzo et al., 2000; Novello et al., 2017). None of those
969 characteristic mammals have been discovered in Tobène, which might simply be due to the
970 small size of the Senegalese sample. Some differences in the faunal composition between
971 eastern and northern/central African localities (notably for *Deinotherium* and *Giraffa*) were
972 proposed to be linked to more arid conditions in northern/central Africa than in eastern Africa
973 at least during the Late Pliocene (Geraads, 2010). Considering this hypothesis as well as the
974 presence of both *Deinotherium* and *Giraffa* in Tobène, western Africa might display
975 environmental conditions closer to that reconstructed in eastern Africa.

976 So far, Tobène shows more faunal similarities with Kanapoi, Aramis, and Kusarelee
977 Members than with any other studied Pliocene localities (Table 2). Further documentation of
978 the Tobène locality will be critical to validate those relations and reconstruct its
979 paleoenvironment, which has proved pivotal in the discussions around the early evolution of
980 australopithecines in eastern African localities (e.g. Manthi et al., 2020). Considering its
981 temporal, spatial, and environmental assets, Tobène represents an important locality for
982 potential discoveries of western African early hominins.

983

984 **5. Conclusions**

985 Most Sahelian sediments of putative late Cenozoic age are overlain by Quaternary sands that
986 preclude surveys for fossil remains. In Senegal, Pliocene continental sediments are only
987 exposed in mining quarries. The Tobène pit fauna shows that the latest iron duricrusts formed
988 in West Africa in the late Pliocene may cap (and protect) continental strata that have the
989 potential to fill a major gap in our understanding of African fossil faunas. Furthermore, the
990 conspicuous and widespread occurrence of dated Neogene glacial landforms over West Africa

991 and their systematic connections with alluvial terraces should open new perspectives for
992 African vertebrate paleontology.

993 The discovery of the Tobène fauna enabled us to investigate the early Pliocene faunal
994 evolution not only within a few specific areas (e.g. Eastern rift, Djurab desert) but at the scale
995 of the whole African continent. A large part of the African vertebrate history remains unknown,
996 notably during the Pliocene, which is a critical period of the hominins evolutionary history.
997 Western Africa might have played a major role in this history and the Tobène fauna described
998 here represents a first step in improving our evidence base in this region. The early Pliocene
999 age of this locality and some faunal similarities with localities from eastern Africa suggests
1000 there is a potential for further important discoveries at the Tobène site, notably regarding early
1001 hominid evolution.

1002

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