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

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ABSTRACT

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

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

1. Introduction

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

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

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

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

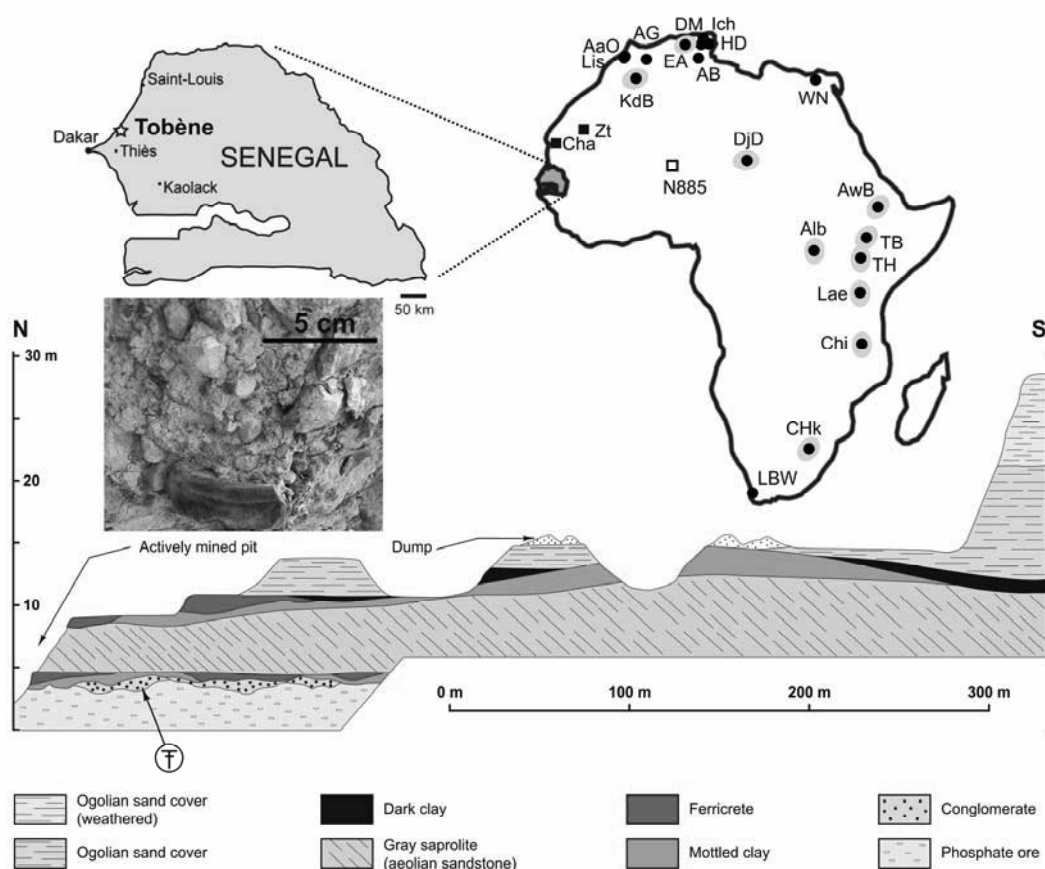


Fig. 1 [one and half column]. Location of the Tobène locality (Taïba Ndiaye Quarry), Senegal, with schematic cross-section of the southern part of the Tobène pit as exposed and investigated in November 2013 (15°02'15"N 16°48'40"W). The photography shows a tooth remain of *Deinotherium* SN-Tob-12-03 in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

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

2. Material and Methods

2.1. Geological context

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

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

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

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

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

2.2. Fossil materials

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

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

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

3. Systematic paleontology

3.1. Description of cf. Osteolaemus

Class Reptilia Laurenti, 1768

Order Crocodylia Gmelin, 1789

Family Crocodylidae Cuvier, 1807

cf. Osteolaemus

3.1.1. Studied material

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

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

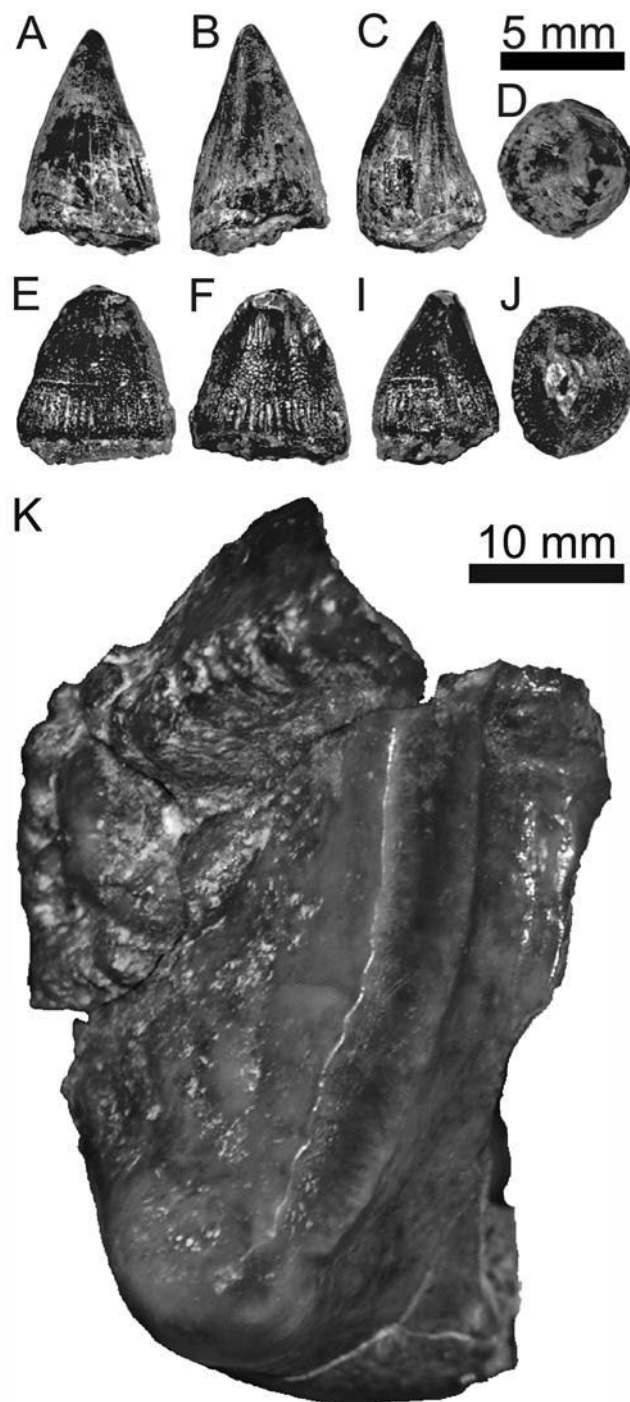
206 the extant genus, encompassing Gambia and Senegal (Eaton, 2010), it would not be surprising

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.

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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*.

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217 3.2. *Description of Deinotherium bozasi*

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219 Class Mammalia Linnaeus, 1758

220 Order Proboscidea Illiger, 1811

221 Family Deinotheriidae Bonaparte, 1845

222 Genus *Deinotherium* Kaup, 1829

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224 *Deinotherium bozasi* Arambourg, 1934

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226 3.2.1. Studied material

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

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230 3.2.2. Description

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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

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

3.3. Description of Nyanzachoerus cf. jaegeri

Class Mammalia Linnaeus, 1758

Order Cetartiodactyla Montgelard, Douzery and Catzeflis, 1997

Family Suidae Gray, 1821

Subfamily Tetraconodontinae Lydekker, 1876

Genus *Nyanzachoerus* Leakey, 1956

Nyanzachoerus cf. jaegeri

3.3.1. Studied material

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

3.3.2. Description

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

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

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

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

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

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Class Mammalia Linnaeus, 1758
Order Cetartiodactyla Montgelard, Douzery and Catzeflis, 1997
Suborder Ruminantia Scopoli, 1777
Family Giraffidae Gray, 1821

cf. *Giraffa* sp. indet.

3.4.1. Studied material

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

3.4.2. Description

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

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

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

3.5. Description of cf. *Simatherium demissum*

Class Mammalia Linnaeus, 1758

Order Cetartiodactyla Montgelard, Douzery and Catzeflis, 1997

Suborder Ruminantia Scopoli, 1777

Family Bovidae Gray, 1821

Subfamily Bovinae Gray, 1821

Tribe Bovini Gray, 1821

cf. *Simatherium demissum*

3.5.1. Studied material

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

3.5.2. Description

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

The M/1 is largely broken and extremely worn; only the lingual wall remains visible. The mesowear is sharp and not blunt (Fig. 3J) as in derived Bovini. No cement is visible on the

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

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

Diagnoses of early African Bovini are mainly based on skull and horn morphologies. Differences in the lower teeth of *Simatherium* and *Ugandax* are unclear, but dental variation is 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

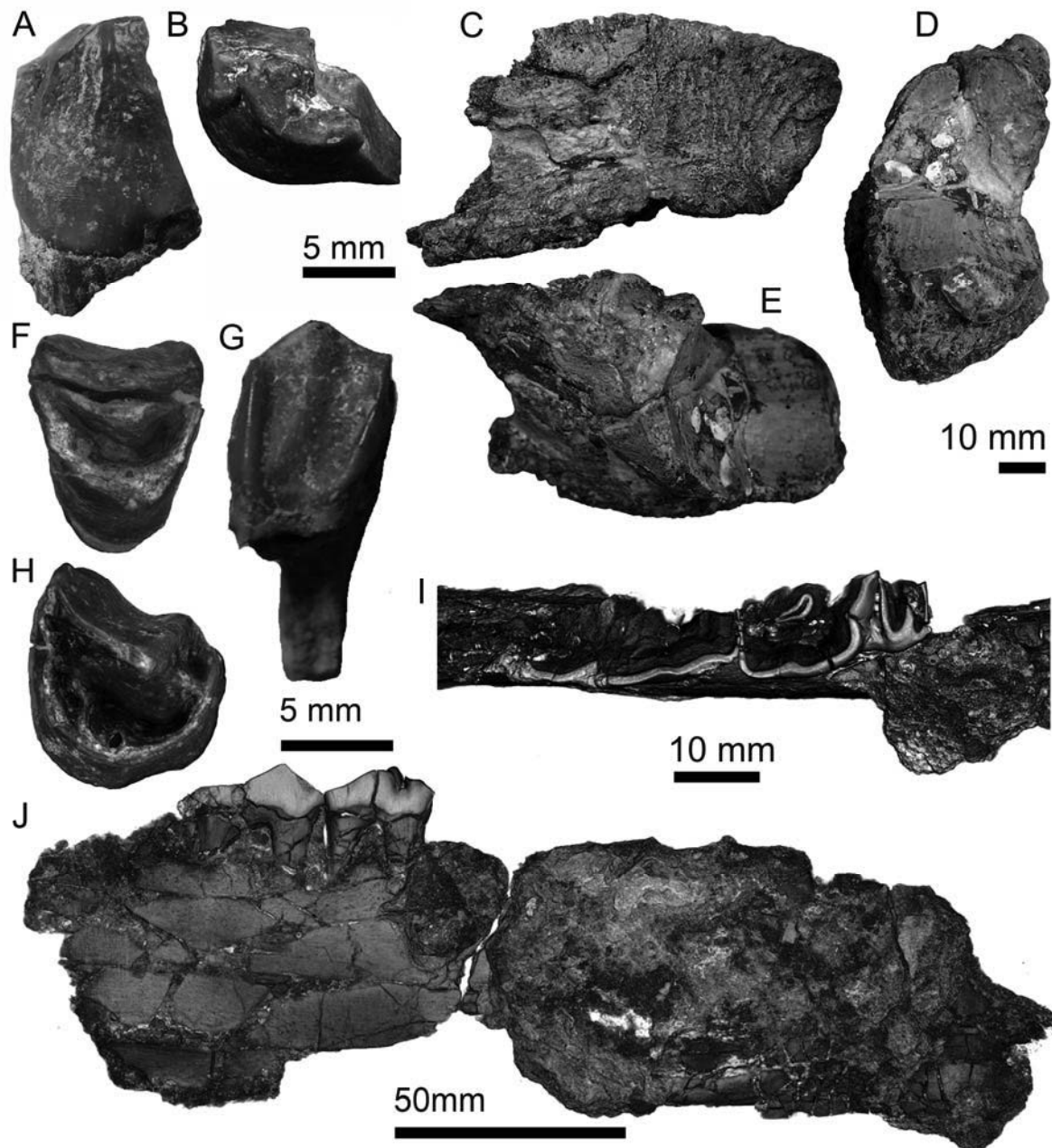


Fig. 3. [double column] Remains of Artiodactyla from Tobène. A-B: Disto-labial fragment of left P4/ (SN-Tob-13-27) of *Nyanzachoerus* cf. *jaegeri* in labial (A) and occlusal (B) views. C-E: a complete ungual phalanx of cf. *Giraffa* (SN-Tob-12-01) in plantar (C), proximal (D) and dorsal (E) views. F-G: Upper right P4/ of a cf. Caprinae (SN-Tob-12-09) in occlusal (F) and labial (G) views. H: Upper right P3/ (SN-Tob-15-19) of Antilopini indet. in occlusal view. I-J: 3D reconstruction of left mandible with fragmentary and worn P/4-M/1 of cf. *Simatherium 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

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

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

3.7. Description of Caprinae indet.

Class Mammalia Linnaeus, 1758

Order Cetartiodactyla Montgelard, Douzery and Catzeflis, 1997

Suborder Ruminantia Scopoli, 1777

Subfamily Caprinae Gray, 1821

Caprinae indet.

3.7.1. Studied material

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

3.7.2. Description

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

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

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

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

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

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

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

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

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

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

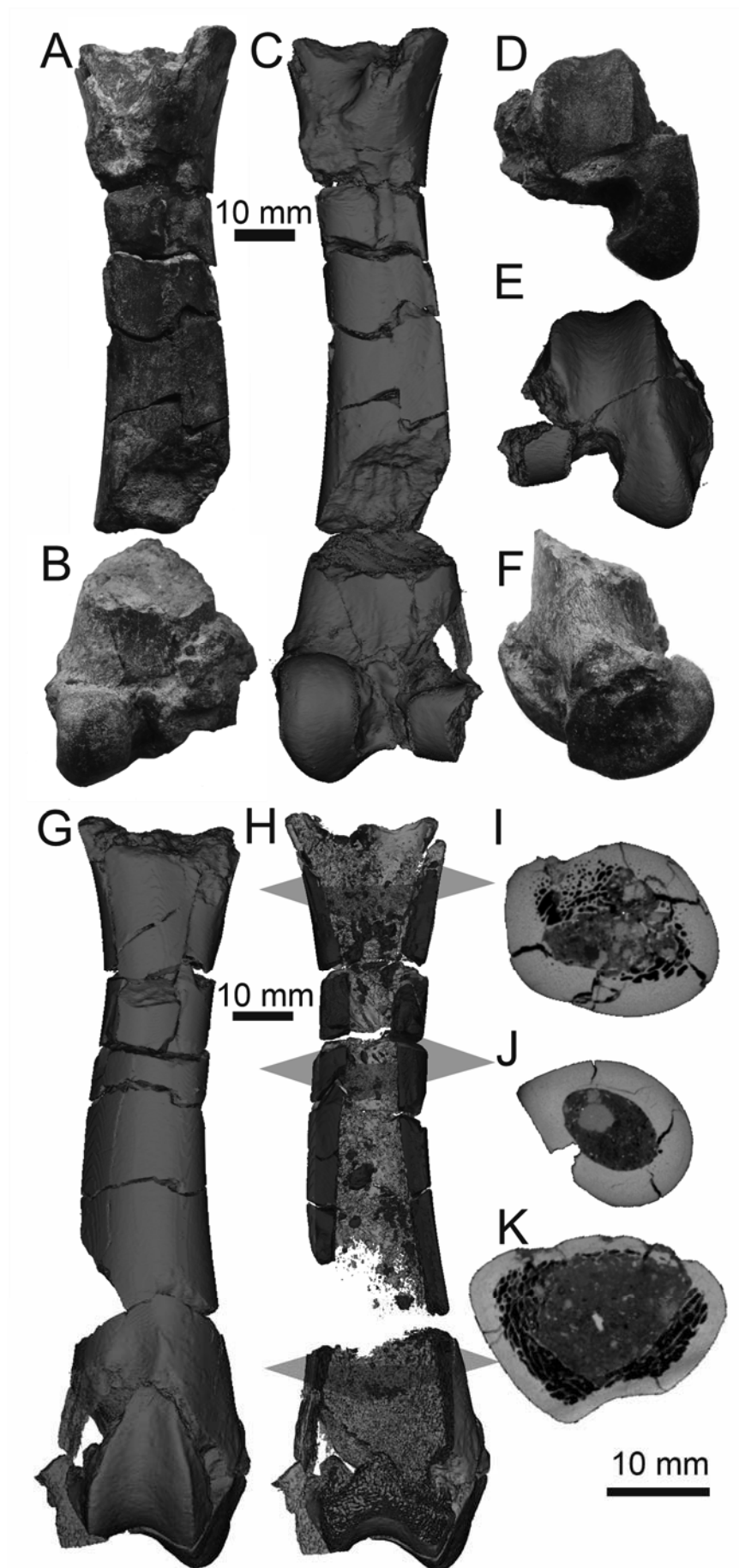


Fig. 4. [one and half column] Incomplete right femur of a Lutrinae indet. from Tobène (SN-Tob-12-02) and its 3D model reconstruction. Caudal (A and B), distal (D) and medial (F) views of the fossil; caudal (C), distal (E), cranial (G) views of the 3D model reconstruction. Coronal section along the proximo-distal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

3.9. Description of *Mustelidae* cf. *Mellivorinae*

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Mustellidae Fisher, 1817

Mustelidae cf. *Mellivorinae*

3.9.1. Studied material

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

3.9.2. Description

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

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

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

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

3.10. Description cf. *Genetta* sp.

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

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

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

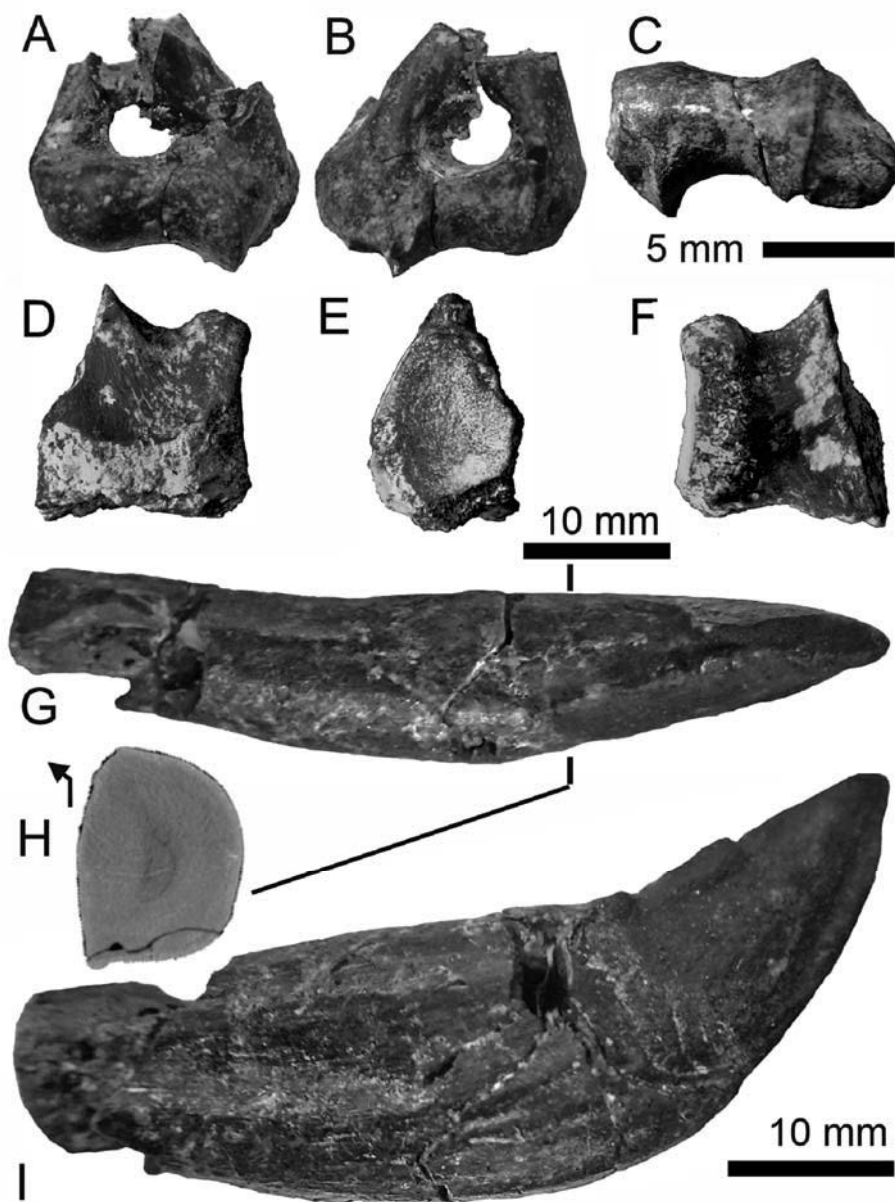


Fig. 5. [one and half column] Remains of Carnivora from Tobène. A-C: Distal epiphysis of a right humerus of cf. *Genetta* sp. (SN-Tob-12-08) in cranial (A), caudal (B) and distal (C) views. D-F: Proximal extremity of a right scapula of a *Mustelidae* cf. *Mellivorinae* (SN-Tob-15-18) in lateral (D),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

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

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

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

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

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

4. Discussion

4.1. Age of the fossiliferous conglomerate

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

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

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>

Table 1. Faunal list of Tobène.

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

Three specimens from Tobène seem to present affinities with typical forms of early 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

indeterminate Bovini is present in the early Pliocene of Lissasfa in Morocco (Geraads et al., 2010), but likely belongs to *Ugandax*. The systematic of early Bovini needs to be clarified and the mandibular remains from Tobène are too fragmentary to propose a clear specific or even generic attribution. Such early Bovini with large and low-crowned teeth have only been discovered in early Pliocene localities (“early *Simatherium*” Fig. 6, Table 2), which suggests 4 Ma as a minimum age for Tobène.

Our results indicate, all species identified in the Tobène conglomerate (Table 1) are younger than the beginning of the Pliocene (5.3 Ma) and older than 3.4 Ma i.e., onset of the last regional weathering episode in Sahel (Fig. 6; Beauvais et al., 2008). The comparison of the Tobène fauna with most African Late Neogene localities indicates an early Pliocene age for the Tobène fossiliferous conglomerate, which we tentatively propose were formed during the Kerian AFLMA most likely between 4.4 and 4 Ma, based on the three taxa discussed above (Fig. 6).

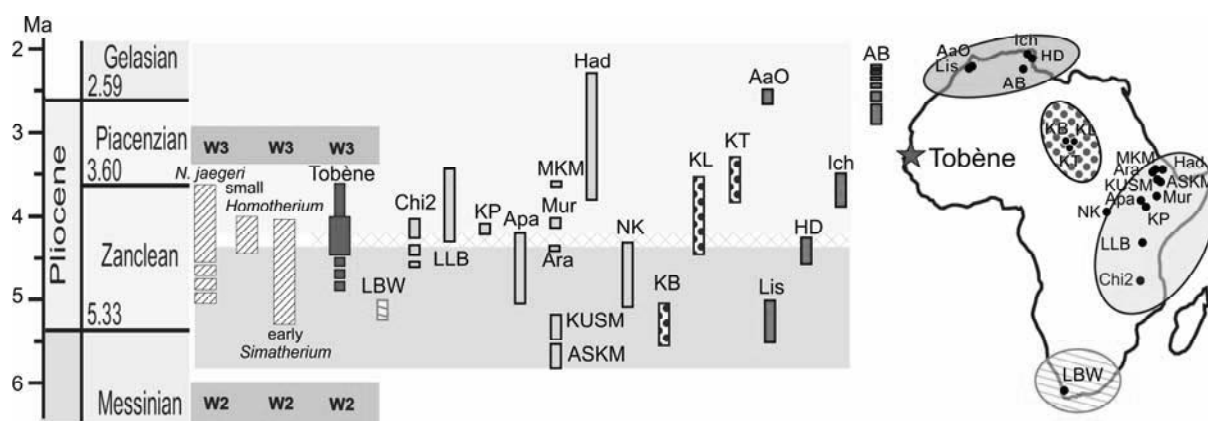


Fig. 6. [double column] Chronological distribution of the Tobène fauna compared to selected Pliocene localities in Africa and chronological extension of some pertinent mammal remains found in Tobène. AB Aïn Brimba, Tunisia (Arambourg 1979); Apa: lower Apak member of the Nachukui Formation, Lothagam, Kenya (McDougall and Feibel, 2003); Ara: Ara-VP-1, Aramis, Middle Awash Ethiopia (White et al., 2009); ASKM and KUSM: Asa Koma Member

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

4.2. Paleobiogeography and paleoenvironment

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

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

This inventory shows that *i*) large mammalian faunas from the Neogene of Africa are best and mostly known from eastern Africa and that *ii*) western Africa remains a paleontological wasteland for Neogene continental faunas. Considering Pliocene times, western Africa is 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	X	X		X		X	X		X	X	X	X		
(<i>Simatherium</i>)														
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>Homotherium</i>				X			X	X						X
(small)														

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

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

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

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

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

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

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

5. Conclusions

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