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1 **Filling a gap in the proboscidean fossil record: a new genus from**
2 **the Lutetian of Senegal**

3
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17
18 **Running Header:** A mid-Eocene proboscidean from Senegal

19
20 **Abstract.**— A long hiatus encompassing most of the Eocene (end of the Ypresian to the early
21 Priabonian) breaks up the proboscidean evolutionary history, which is otherwise documented
22 by a rich fossil record. Only two post Ypresian localities from West Africa (Mali and Senegal)
23 yielded scarce *Moeritherium*-like dental remains. Here, we study one of these remains from
24 Senegal and name a new genus, *Saloumia*. This taxon, confidently mid-Lutetian in age, evokes
25 *Moeritherium* and elephantiforms in view of its wrinkled enamel, the lack of centrocrista, and

26 its strong lingual cingulum. However, due to its pronounced bunodonty, which departs from
27 the bunolophodonty of both *Moeritherium* and elephantiforms, we cannot exclude that *Saloumia*
28 documents an early experiment in dental diversity among Paleocene-Eocene proboscideans,
29 without direct relationships with later proboscideans.

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31 UUID: <http://www.zoobank.org/0B6B83F8-817D-498C-A672-8FFA8F81A978>

32

33 **Introduction**

34

35 Although the Afro-Arabian landmass has played a pivotal role in the evolutionary history of
36 early placental mammals (Werdelin and Sanders, 2010), the sub-Saharan Paleogene fossil
37 record remains very scarce, particularly in West Africa, where relatively little paleontological
38 work has been carried out. However, the potential to discover Eocene placentals was
39 demonstrated over half a century ago when a fragmentary proboscidean molar was described
40 from the middle Eocene (Lutetian) of M'Bodione Dadere, Senegal by Gorodiski and Lavocat
41 (1953). These authors compared this molar with those of *Moeritherium*, a genus from the late
42 Eocene-early Oligocene period. Interestingly, they correctly noticed that the M'Bodione
43 Dadere proboscidean was significantly smaller than all known *Moeritherium* species. Despite
44 this substantial morphological difference, Gorodiski and Lavocat (1953) were reluctant to
45 establish a new taxon based on this fragmentary molar, judging that Paleogene proboscideans
46 were too poorly known to substantiate the definition of a new taxon. At the time, early
47 proboscidean evolution was documented by just four genera, only known from the late Eocene
48 (*Moeritherium* and *Barytherium*) and early Oligocene (*Moeritherium*, *Phiomia* and
49 *Palaeomastodon*) of the Fayum, Egypt (e.g., Andrews, 1906; Osborn, 1936). After more than
50 fifty years of field research, the fossil record of stem proboscideans is now much better known

51 (Gheerbrant and Tassy, 2009; Sanders et al., 2010). Considerable progress has been made in
52 several other parts of Africa (Morocco, Algeria, Libya, Kenya, and Ethiopia) and the Arabian
53 Peninsula (Oman and Saudi Arabia), notably at the late Paleocene-early Eocene transition
54 (Gheerbrant et al., 1998a, 2005, 2012; Gheerbrant, 2009) and, to a lesser degree, at the late
55 Eocene-early Oligocene transition (Delmer et al., 2006; Delmer, 2009; Adnet et al., 2010;
56 Seiffert et al., 2012; Jaeger et al., 2012; Pickford 2015; Al-Kindi et al., 2017).

57 Despite these fundamental advances, some unresolved problems persist. Among them,
58 the origin and phylogenetic position of the genus *Moeritherium* remain uncertain. Two
59 phylogenetic scenarios have been recently proposed for the relationships of *Moeritherium*
60 within Proboscidea. First, according to Seiffert et al. (2012), *Moeritherium* could have a basal
61 position in the phylogeny, near *Daouitherium* and *Numidotherium*, two stem proboscideans
62 from the Ypresian of Morocco and Algeria, respectively. Second, *Moeritherium* has a more
63 elevated position in the phylogeny, being considered as the sister-group of the clade
64 Deinotheriidae-Elephantiformes (Seiffert, 2007; Delmer, 2009; Gheerbrant and Tassy, 2009;
65 Ferretti and Debruyne, 2011; Cooper et al., 2014). In any case, these contradictory scenarios
66 illuminate longstanding uncertainties regarding the transition from early proboscideans to
67 elephantiforms (palaeomastodonts and elephantoids). Particularly, the homology between the
68 lower incisors of early proboscideans and the ever-growing lower tusks of elephantiforms is
69 still debated (Delmer, 2009; Jaeger et al., 2012; Al-Kindi et al., 2017).

70 Current data suggest that the transition from early proboscideans to elephantiforms
71 occurred during the end of the Eocene (Priabonian) (Fig. 1a), but a simple examination of the
72 Paleogene proboscidean fossil record reveals geographical and temporal sampling biases in our
73 understanding of the evolutionary history of proboscideans. Earliest proboscideans are only
74 documented from Moroccan deposits, while other Paleogene species are known from few
75 African (e.g., Algeria, Egypt, Libya, Ethiopia, and Kenya) and Arabian sites (Saudi Arabia and

76 Oman). Most importantly, this history is largely truncated by a hiatus encompassing the end of
77 the Ypresian to the early Priabonian, so that the proboscidean fossil record is virtually unknown
78 during most of the Eocene (Sanders et al., 2010) (Fig. 1a). It is noteworthy that the group is
79 absent from the rich faunas from Gour Lazib (late early or early middle Eocene, Algeria),
80 Chambi (late early or early middle Eocene, Tunisia) and Namibia (?Lutetian-Bartonian) (e.g.,
81 Adaci et al., 2016; Pickford et al., 2008). Proboscideans are also absent from the only two
82 unambiguous middle Eocene continental mammalian sites in Africa, i.e. the faunas of Aznag in
83 Morocco (Tabuce et al., 2005) and Mahenge in Tanzania (Kaiser et al., 2006). In contrast, the
84 only two ?mid-Eocene localities that yielded proboscidean remains were from West Africa.
85 Arambourg et al. (1951) described *Moeritherium* sp. from two isolated molars discovered from
86 marine sediments near In Tafidet, Mali (middle or late Eocene) (see Gheerbrant et al., 1998a
87 fig.6c; Delmer et al., 2006; O’Leary et al., 2006). Also from middle Eocene marine sediments,
88 Gorodiski and Lavocat (1953) described ?*Moeritherium* sp. based on the Senegalese molar here
89 studied. Since its initial description, this molar has never been figured; Domning (1986),
90 Gheerbrant et al. (1998a), and Delmer et al. (2006) briefly discussed its morphology and
91 concluded that it was too small to belong to a *Moeritherium* species.

92 In order to better document this peculiar Eocene proboscidean, we organized systematic
93 prospecting for fossil vertebrates at and around M’Bodione Dadere in 2010 and 2011. Although
94 we discovered a rich marine fauna represented by numerous sharks and rays, no additional
95 mammalian specimens have been discovered to the exception of an indeterminable minute
96 mammalian tooth fragment. Considering the difficulties to discover new specimens of
97 proboscideans in the rare Eocene Senegalese outcrops, we reassess the *Moeritherium*-like molar
98 from M’Bodione Dadere. Both its provenance (West Africa) and age (Lutetian) make this tooth
99 a pivotal asset to better understand the early history of proboscideans, as it fills an important
100 gap in their paleogeographic and chronological fossil record.

101

102 **Geological setting**

103

104 M'Bodione Dadere village is located north of the town of Kaolack in Sine-Saloum region,
105 central-western part of Senegal (Fig. 2). In this flat area, outcrops are absent due to an important
106 coverage of Quaternary to Recent sands (10-20 meters), which unconformably overly
107 Paleogene to Pliocene levels. Access to a detailed stratigraphy and to Paleogene deposits is only
108 possible thanks to drill cores and water-well cuttings. Fortunately, sediments excavated from
109 levels attributed to two Lutetian-Bartonian shallow marine formations yielded vertebrate
110 fossils.

111 From the water-well of Tiavandou, South to Kaolack (Fig. 2), nummulitic limestone
112 attributed to the Taïba Formation (late Lutetian to early Bartonian) (Roger et al., 2009a; Sarr,
113 2013) yielded several teeth, 18 vertebrae, and rib fragments of an archeocete identified as
114 '*Zeuglodon*' cf. *osiris* by C. Arambourg (Elouard, 1966). More recently, in a revision of the
115 African fossil record of archeocetes, Gingerich (2010) suggested that these remains were too
116 large to be attributed to *Saghacetus osiris* (the new name for *Zeuglodon osiris*), its size being
117 more similar to *Dorudon atrox*, another archeocete well known from the early Priabonian of
118 the Fayum. Unfortunately, after unfruitful research in the collections of the University of Dakar,
119 the specimens seem to have been lost.

120 In the northern of the Sine-Saloum region, other water-well cuttings attributed to the
121 middle Eocene Lam Lam Formation yielded vertebrate remains. The most recent example is
122 the discovery of an actinopterygian maxilla attributed to an amiid (O'Leary et al., 2012) in
123 Tewrou Poram, North to the town of Gossas (Fig. 2). The earliest discovery of vertebrates in
124 the Lam Lam Formation corresponds to that of the M'Bodione Dadere proboscidean. On the
125 24th of August 1952, Alexandre Gorodiski was in charge of geological mapping in the area of

126 Thiès (on behalf of the Federal Direction of Mines and Geology of French West Africa) when
127 he discovered the proboscidean molar from cuttings of the 20 meters deep well of M'Bodione
128 Dadere; the molar was described by R. Lavocat (Gorodiski and Lavocat, 1953; see also Lavocat,
129 1955). By chance, A. Gorodiski also collected samples of the coquina limestone from the well
130 cuttings. This revealed two new fragments of mammal teeth showing 'condylarth' affinities
131 (Gevin et al., 1975; Sudre, 1979); these indeterminable specimens, housed in the collections of
132 the University of Montpellier, also evoke herodotiine macroscelideans by size and gross
133 morphology (RT, pers. obs.).

134 In order to reconstruct the geological context of the M'Bodione Dadere proboscidean,
135 we compared the stratigraphic sequence established by Gorodiski and Lavocat (1953) with
136 nearby logs from drill cores (Gossas, Ngolothie, and Kaolack; Fig. 2) and with our direct
137 observations of recent water-well cuttings located at Sanghaye Bele village (11 km southeast
138 of M'Bodione Dadere) (Fig. 2). At M'Bodione Dadere and Sanghaye Bele, the fossiliferous
139 deposits attributed to the Lam Lam Formation correspond to those of a coquina limestone and
140 a yellow to white clayey limestone alternating with marls; at M'Bodione Dadere these deposits
141 are capped by phosphate nodules. The invertebrate fauna is composed of echinoids and
142 molluscs, among them the lamellibranch *Ostrea meunieri* which is known from the 'Lutetian'
143 of Senegal (Tessier, 1952; see Roger et al., 2009b p.16). Well samples from M'Bodione Dadere
144 and Sanghaye Bele did not provide any characteristic microfauna, but equivalent levels from
145 the Ngolothie borehole near Kaolack (Fig. 2) yielded the planktonic foraminifera
146 *Globigerinatheka* gr. *index*, *Cassigerinelloita amekiensis*, and *Pseudohastigerina micra*, which
147 characterize E8 to E11 biozones (middle Lutetian to early Bartonian) (Sarr, 2013). North of the
148 Senegalese basin, the base of the Lam-Lam Formation (Pallo limestone and phosphate clays) is
149 E8 in age (middle Lutetian) (presence of *Hantkenina aragonensis*) (Flicoteaux, 1975; Roger et
150 al., 2009a), whereas the top of the formation (Lam-Lam marls) yielded a rich planktonic

151 foraminifera association (*Truncorotaloides rohri*, *T. topilensis*, *Globigerapsis* sp., *G. index*,
152 *Globorotalia collactea*, *G. bolivariana*, *G. pentacamerata*, and *Hantkenina* spp.), which
153 indicates E9 biozone (middle Lutetian) (Flicoteaux, 1974; Roger et al., 2009b). These regional
154 correlations indicate a secure middle Lutetian age (E8-E9 biozones, ~44 Ma, Vandenberghe et
155 al., 2012) for the M'Bodione Dadere proboscidean.

156

157 **Material and methods**

158

159 *Repositories and institutional abbreviations.*—the holotype MNHN.F.MCA 1 and unique
160 specimen of *Saloumia gorodiskii* is housed in the collections of the Museum National d'Histoire
161 Naturelle, Paris (MNHN). A CT scan of MNHN.F.MCA 1 was acquired at the Montpellier Rio
162 Imaging (MRI) micro-CT imaging station Skyscan 1076 (Montpellier, France). Image
163 segmentation and 3D rendering were performed using manual segmentation with Avizo 7.1
164 (VSG). A 3D reconstruction of MNHN.F.MCA 1 was deposited in MorphoMuseum
165 (<http://morphomuseum.com/>; xx-xx). Other institutional abbreviations: AMNH (American
166 Museum of Natural History, New York, USA) and NHMUK (Natural History Museum,
167 Department of Palaeontology, London, UK).

168

169 **Systematic paleontology**

170

171 Class Mammalia Linnaeus, 1758

172 Order Proboscidea Illiger, 1811

173 Family *incertae sedis*

174

175 Genus *Saloumia* new genus

176

177 *Type species.*—*Saloumia gorodiskii* n. gen. n. sp., only species.

178

179 *Diagnosis.*—As for the type species, by monotypy.

180

181 *Etymology.*—From the coastal river Saloum which flows south of the village of M'Bodione

182 Dadere.

183

184 *Remarks.*—The specimen described here is identified as a proboscidean based on its relative
185 large size, quadrituberculy, wrinkled enamel, small parastyle, well-developed lingual cingulum,
186 blunt paraconule mesiolabially located to the protocone, and the lack of a centrocrista. The
187 particular combination of these dental characters is unknown in other African “ungulates” from
188 the Paleogene (hyraxes, embrithopods, sirenians, and “condylarths”).

189

190 *Saloumia gorodiskii* new species

191 Figs. 3,4

192

193 *Holotype.*—MNHN.F.MCA 1, right upper molar, which rests on indurated coquina limestone.

194

195 *Diagnosis.*—*Saloumia gorodiskii* differs from *Eritherium* and *Phosphatherium* by larger size,
196 wrinkled enamel, strong lingual cingulum, and no centrocrista; its morphology also differs from
197 *Phosphatherium* by a pronounced bunodonty. *Saloumia gorodiskii* differs from *Moeritherium*
198 ssp., *Phiomia* and *Palaeomastodon* by smaller size, more bunodont and not bunolophodont
199 dental pattern, relative lower crown, and with the protocone and hypocone in more labial
200 positions.

201

202 *Occurrence*.—M^oBodione Dadere (14° 20.706'N, 16° 11.151'W), Lam-Lam Formation, middle
203 Lutetian, planktonic foraminiferal biozones E8-E9, ~44 Ma.

204

205 *Description*.—MNHN.F.MCA 1 is a low-crowned and incompletely preserved upper molar,
206 missing its distal part (L > 10.7 mm; W = 12.3 mm) (Figs. 3-4). The apexes of the four principal
207 cusps (paracone, metacone, protocone, and hypocone) were broken away (“scalped”), possibly
208 before fossilization; there are no significant wear on these cusps. Only the mesial flanks of the
209 metacone and hypocone are preserved. The hypocone is relatively centrally positioned and as
210 large as the protocone and was certainly wider than the metacone. The paracone and protocone
211 are fully bunodont and connected at their base but without a high loph connecting them.
212 However, this loph, if it was incipiently developed, may have been erased as the apexes of
213 protocone and paracone were broken away. A large paraconule, whose apex is also broken
214 away, is underlined by dental wear facets; it is closely appressed to the mesiolabial flank of the
215 protocone; the paraconule also connects to the mesial cingulum. There is no trace of a
216 metaconule. The shallow valley between the paracone and metacone is deeper and larger than
217 that between the protocone and hypocone. The transverse valley is thus poorly defined. The
218 cingulum is continuous from the labial border of the paracone to the lingual face of the teeth; it
219 is particularly very well-developed, forming an entostyle located lingual to the transverse
220 valley. The cingulum is also inflated labially to the transverse valley, forming an ectostyle. The
221 enamel is wrinkled, especially on the paracone and lingually to the protocone.

222

223 *Etymology*.—The species is named after the geologist Alexandre Gorodiski who discovered the
224 fossiliferous locality and the holotype.

225

226 *Remarks.*— The thick enamel, the lack of a well-defined ectoflexus, and the parastyle, which
227 is not enlarged and not mesially projected but strongly appressed to the paracone, precludes that
228 MNHN.F.MCA 1 is a deciduous premolar. Likewise, the probability that MNHN.F.MCA 1
229 corresponds to a fully molariform premolar is also excluded because the molarization of
230 premolars in proboscideans is documented only during the mid-early Oligocene (in the
231 elephantiforms *Phiomia* and *Palaeomastodon*).

232

233 **Systematic attribution and discussion**

234

235 Gorodiski and Lavocat (1953) attributed MNHN.F.MCA 1 to ?*Moeritherium* sp. in view of its
236 quadritubercular dental pattern and the morphology of its cingulum. However, they insisted that
237 ‘it would not be prudent to exclude the possibility that this specimen may belong to another
238 [new] primitive bunodont genus, especially because main cusps appear to have been more
239 obviously bunodont than those of known *Moeritherium* species’ (Gorodiski and Lavocat,
240 1953:316). During the 1950’s, Paleogene proboscideans were only documented by
241 *Moeritherium*, *Barytherium*, *Phiomia*, and *Palaeomastodon*. The genus *Moeritherium* was then
242 considered as ancestral among proboscideans. Today, the phylogenetic position of
243 *Moeritherium* remains debated. Such an uncertainty is surprising considering that dental,
244 cranial, and postcranial anatomy of *Moeritherium* has been well-known for more than a century.
245 The genus is particularly well documented in the Fayum where it is known by two species. The
246 consensus view consists in attributing all specimens from the Gebel el Qatrani Formation (early
247 Oligocene) to *Moeritherium trigodon*, and those from the Qasr el Sagha Formation (late
248 Eocene) to *M. lyonsi* (Sanders et al., 2010; but see Delmer et al., 2006).

249 These two Fayumian moeritheres are characterized by a bunolophodont dental pattern.
250 The oldest attested *Moeritherium* species, *M. chehbeurameuri*, corresponds to a smaller and
251 more lophodont taxon; it was described from the Priabonian of Bir El Ater, Algeria (Delmer et
252 al., 2006). This species was also listed from the ?late Eocene locality of Dur At-Talah, Libya
253 (Jaeger et al., 2010, 2012) and from the late Eocene locality of Birket Qarun-2, Fayum (Sanders,
254 pers. comm. to RT, 2019; see also Seiffert, 2008, 2010).

255 *Saloumia* evokes all these *Moeritherium* species by three derived characters: wrinkled
256 enamel, the lack of centrocrista, and the well-developed lingual cingulum that was considered
257 as a diagnostic feature of the genus (Figs. 3-4). As a result, these three dental characters could
258 support a sister-group relationship between *Saloumia* and *Moeritherium*. However, the
259 association of a convolute and a distocrista (see Delmer et al., 2006) distally to the hypocone,
260 which is also a diagnostic character of the upper molars of *Moeritherium*, cannot be described
261 in *Saloumia* due to the poor preservation of the holotype. *Saloumia* also evokes the Fayumian
262 *Moeritherium* species by quadrituberculy, small parastyle, blunt paraconule mesiolabially
263 located to the protocone, and blunt crest joining the protocone to the parastyle via the
264 paraconule. However, these traits are primitive among proboscideans and thus do not support a
265 close relationship between *Saloumia* and Fayumian *Moeritherium* species. Moreover, *Saloumia*
266 is twice smaller than *Moeritherium trigodon* and *M. lyonsi*, and also differs from these two
267 species by a relative lower crown, a more labial position of both the protocone and hypocone,
268 and by the occurrence of a labial cingulum. We note however that *M. "gracile"*, which is
269 synonym of *M. lyonsi* (see Sanders et al. 2010; Sanders, pers. comm. to RT, 2019) has however
270 a labial cingulum according to Delmer et al. (2006). Finally, as mentioned by Gorodiski and
271 Lavocat (1953), the bunodonty of *Saloumia* markedly differs from the bunolophodonty of all
272 the Fayumian moeritheres.

273 The bunolophodonty that characterizes the Fayumian *Moeritherium* species was long
274 viewed as primitive for Proboscidea. As such, *Moeritherium* has long been recognized as close
275 to the origin of the order (see also Seiffert et al., 2012). In contrast, nowadays *Moeritherium* is
276 often interpreted as a highly specialized genus (Court 1994), more closely related to the
277 deinotheriid-elephantiform clade than to the older genera *Phosphatherium*, *Daouitherium*, and
278 *Numidotherium* (e.g. Delmer, 2009; Gheerbrant and Tassy, 2009; Sanders et al., 2010; Ferretti
279 and Debruyne, 2011; Cooper et al., 2014). The true lophodonty of earliest Eocene genera was
280 then considered as the primitive dental pattern of proboscideans (Gheerbrant et al., 2005).
281 Following this hypothesis, the bunolophodonty of the Fayumian *Moeritherium* would derive
282 from a true lophodonty. This result was strengthened by the description of the Priabonian
283 lophodont *M. chehbeurameuri*.

284 Nevertheless, in our opinion, the question of the primitive dental pattern of moeritheriids
285 is not resolved yet (see also Seiffert et al. 2012). Indeed, *Moeritherium* sp. from the middle/late
286 Eocene of In Tafidet, Mali (Arambourg et al., 1951) is clearly more bunodont than its
287 penecontemporaneous *M. chehbeurameuri* (Supplemental Data). As a result, we cannot exclude
288 that *Moeritherium* derives from a bunodont incipiently bilophodont lineage morphologically
289 close to *Saloumia*. Interestingly, the Malian *Moeritherium* also shares with *Saloumia* a minute
290 ectostyle on the labial cingulum. This trait is primitive when compared to *M. chehbeurameuri*.
291 The species from In Tafidet appears also primitive by comparison with *M. chehbeurameuri* and
292 *Saloumia* by the occurrence of both a postparacrista and premetacrista (Supplemental Data);
293 these crests constitute the centrocrista when associated with the ectostyle (this style is then
294 named mesostyle, e.g., Gheerbrant et al., 2012). Accordingly, the primitive dental morphology
295 of *Moeritherium* is yet uncertain. Interestingly, a bunodont incipiently bilophodont origin for
296 this genus recently received significant support from the discovery of *Eritherium*, a late
297 Paleocene proboscidean characterized by bunodont incipiently bilophodont molars

298 (Gheerbrant, 2009). Furthermore, *Khamsaconus*, another early Ypresian proboscidean from
299 Morocco, displays the same bunodont incipiently bilophodont pattern. This dental pattern is
300 today viewed as primitive for proboscideans (Gheerbrant et al., 2012).

301 Direct comparisons with the holotype of *Khamsaconus*, a very small DP4 and unique
302 specimen, is however impossible. Note that the fragmentary bunodont-bunolophodont lower
303 molar attributed to *Khamsaconus* by Gheerbrant et al. (1998b) is now attributed to a basal
304 hyracoid (see Gheerbrant et al., 2005:286). *Khamsaconus* (the DP4) was never included in a
305 phylogenetic analysis with both *Eritherium* and *Phosphatherium*, but Gheerbrant et al. (2012)
306 favored a close phylogenetic relationship between these three genera. *Saloumia* only shares
307 with *Eritherium* primitive features: quadrituberculy, low crown, reduced parastyle (compared
308 with *Phosphatherium*), blunt crest joining the protocone to the parastyle, and labial position
309 and larger size of the protocone and hypocone relative to the paracone and metacone
310 respectively. Most importantly, *Saloumia* differs from *Eritherium* and *Phosphatherium* by four
311 derived characters: larger size, wrinkled enamel, lack of a continuous centrocrista, and strong
312 lingual cingulum. *Saloumia* further differs from *Eritherium* by a more pronounced bunodonty.

313 *Phosphatherium* and other Eocene genera (*Daouitherium*, *Barytherium*, and
314 *Arcanotherium*) clearly depart from *Saloumia* by their true lophodonty. Among them, the
315 undetermined species *Daouitherium* sp., known by a unique lower molar (Gheerbrant et al.,
316 2005 p.285), is however of similar size. Although larger and fully lophodont, *Arcanotherium*
317 evokes *Saloumia* by its moderately wrinkled enamel and the development of its lingual
318 cingulum. Such derived characters are also present in the bunolophodont *Phiomia* and
319 *Palaeomastodon*. These basal elephantiforms also share with *Saloumia* the lack of centrocrista,
320 a strong lingual cingulum, and a variable occurrence of an ectostyle. The latter character is for
321 instance present in AMNH 13449 (*Palaeomastodon beadnelli*; see Osborn 1936:144) and
322 NHMUK M8851 (*Phiomia serridens*; see Tassy 1982:234). *Palaeomastodon* and *Phiomia*

323 differ however from *Saloumia* by a larger size, the lack of connection between the paraconule
324 and the parastyle, a more lingual position of both the protocone and hypocone, and four main
325 cusps of similar size. Finally, the tritolph (the third loph, distal to the metaloph), which is
326 diagnostic of *Phiomia* and *Palaeomastodon*, cannot be checked in *Saloumia* due to the poor
327 preservation of the specimen.

328 To conclude, although poorly known, *Saloumia* appears sufficiently distinct from other
329 early proboscideans to be considered a valid genus. *Saloumia* shares with stem early Paleogene
330 proboscideans (*Eritherium* and *Phosphatherium*) only primitive features. Most importantly,
331 three derived characters observed in *Saloumia* (wrinkled enamel, lack of centrocrista, and
332 strong lingual cingulum) could indicate a possible affinity with either *Moeritherium* or basal
333 elephantiforms. If correct, this hypothesis would push back the origin of the (*Moeritherium*-
334 (Elephantiformes-Deinotheriidae)) clade well into the middle Eocene and generates
335 considerable ghost lineages within proboscidean phylogeny (Fig. 1b). However, this hypothesis
336 remains highly speculative given our current level of knowledge on *Saloumia*. Its very
337 pronounced bunodonty is well-distinct from the bunolophodonty of *Moeritherium* and basal
338 elephantiforms, so that *Saloumia* could also document an early experiment in dental diversity
339 among Paleocene-Eocene proboscideans, with no direct relationships with later Paleogene
340 proboscideans.

341

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343

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351

352 **Accessibility of supplemental data**

353

354 Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.51c59zw4c>

355

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500

501

502 Figure captions

503

504 **Figure 1:** Phylogeny of Paleogene proboscideans based on the cladistics analysis proposed by
505 Delmer (2009), Gheerbrant and Tassy (2009), Gheerbrant (2012), and Seiffert et al. (2012);
506 grey zone shows the important gap in their fossil record. The question mark indicates that
507 *Omanitherium* could be closer to *Arcanotherium* and *Numidotherium* than to *Barytherium* as
508 proposed by Pickford (2015) and Al Kindi et al. (2017) (1); possible phylogenetic relationships
509 of *Saloumia gorodiskii* n. gen. n. sp. from the mid-Lutetian of Senegal (2). Following this
510 scenario, *Saloumia* could represent a suprageneric taxa close to the clade including
511 *Moeritherium* and Elephantiformes.

512

513 **Figure 2:** Geographic position, stratigraphic position, and regional correlations of M'Bodione
514 Dadere site that yielded the holotype of *Saloumia gorodiskii* n. gen. n. sp.

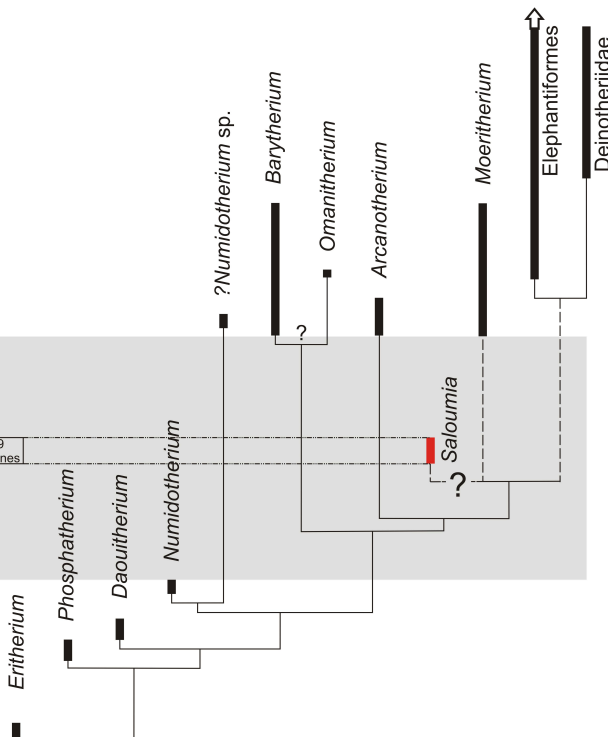
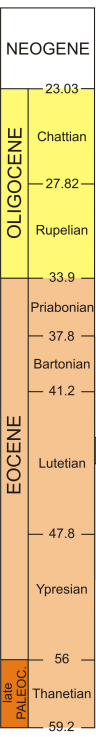
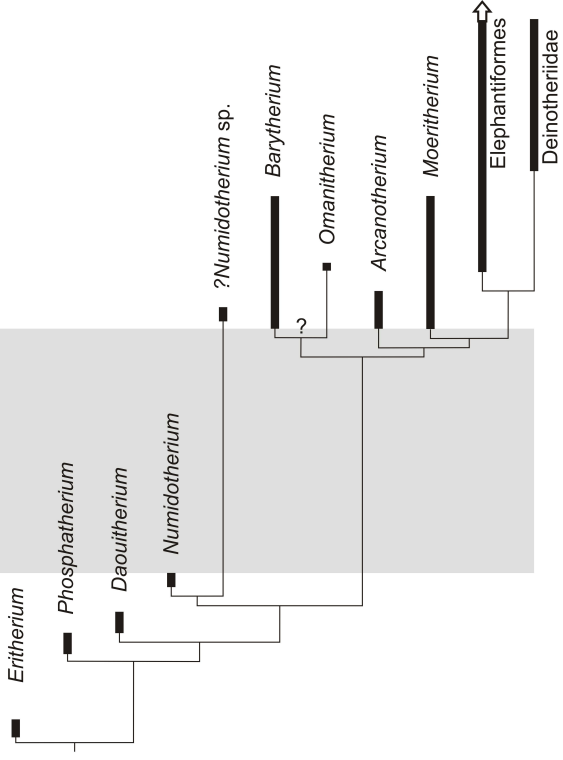
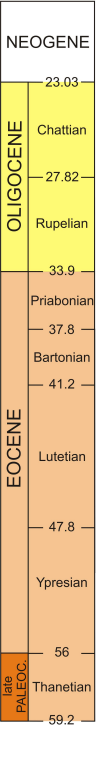
515

516 **Figure 3:** *Saloumia gorodiskii* n. gen. n. sp., MNHN.F.MCA 1, right upper molar, in occlusal
517 (stereo pair) (1), oblique mesial (2), and oblique lingual (3) views.

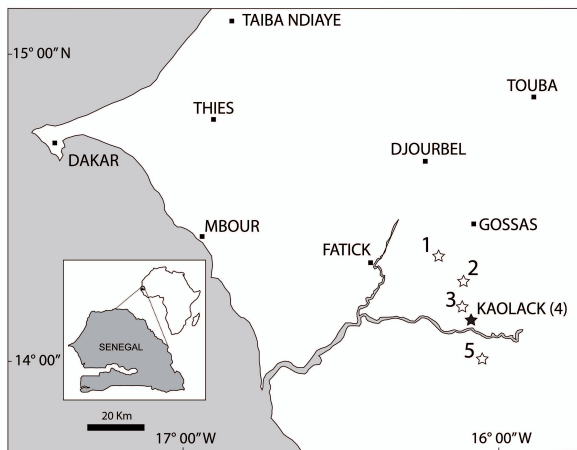
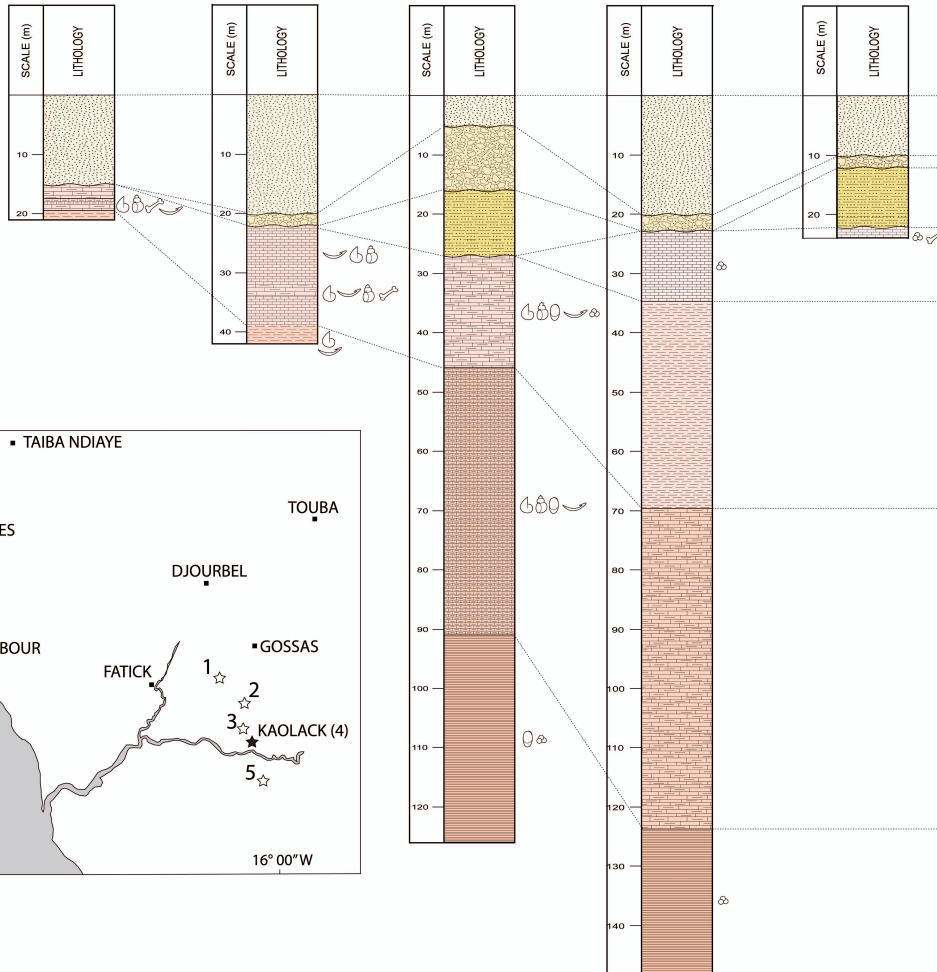
518

519 **Figure 4:** *Saloumia gorodiskii* n. gen. n. sp., MNHN.F.MCA 1, right upper molar, in occlusal
520 view (3D rendering from X-ray microtomography).

521



1 - MBODIONE DADERE 2 - SANGHAYE BELE 3 - NGOLOTHIE 4 - KAOLACK 5 - TIAVANDOU



1



4 mm

2



3



mesial flank of
the metacone

ectostyle

paracone

parastyle

paraconule

protocone

hypocone

2 mm

entostyle

