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

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Running Header: A mid-Eocene proboscidean from Senegal

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

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

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Introduction

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

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

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

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

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

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

Geological setting

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

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

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

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

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

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

Material and methods

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

Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Proboscidea Illiger, 1811

Family *incertae sedis*

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.

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

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

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

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

Systematic attribution and discussion

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

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

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

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

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

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

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

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

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

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

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Accessibility of supplemental data

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

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Figure captions

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

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

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

AGE	FORMATION
Quaternary	
Pliocene	
Middle to late Miocene	SALOUM FORMATION
Bartonian	TAIBA FORMATION
Lutetian	LAM LAM FORMATION
Late Ypresian	THIES FORMATION
Early Ypresian

1

4 mm

3

2

mesial flank of
the metacone

ectostyle

paracone

parastyle

paraconule

protocone

hypocone

2 mm

entostyle