

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

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**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) have yielded scarce *Moeritherium*-like dental remains. Here, we study one of these remains from Senegal and name a new genus and species, *Saloumia gorodiskii*. This taxon, confidently mid-Lutetian in age, evokes *Moeritherium* and elephantiforms with its wrinkled enamel, lack of centrocrista, and strong lingual cingulum. However, due to its pronounced bunodonty, which departs from the bunolophodonty of both *Moeritherium* and elephantiforms, we cannot exclude the possibility 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, known only from the late Eocene (*Moeritherium* and *Barytherium*) and early Oligocene (*Moeritherium*, *Phiomia*, and *Palaemastodon*) of the Fayum, Egypt (e.g., Andrews, 1906; Osborn, 1936). After more than 50 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; Jaeger et al., 2012; Seiffert 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 *Numidoherium*, 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 (palaemastodonts 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 documented only from Moroccan deposits, while other Paleogene species are known from a few African (e.g., Algeria, Egypt, Libya, Ethiopia, and Kenya) and Arabian (Saudi Arabia and Oman) sites. Most important, 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., Pickford et al., 2008; Adaci et al., 2016). Proboscideans are also absent from the only two unambiguous middle Eocene continental mammalian sites in Africa, the faunas of Aznag in Morocco (Tabuce et al., 2005) and Mahenge in Tanzania (Kaiser et al., 2006). By 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). Gorodiski and Lavocat (1953) described ?*Moeritherium* sp., also from middle Eocene sediments, on the basis of the Senegalese molar here studied. Since its initial description, this molar has never been figured; Domning et al. (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.

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 except an indeterminable minute mammalian tooth fragment. Considering the difficulties in discovering 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

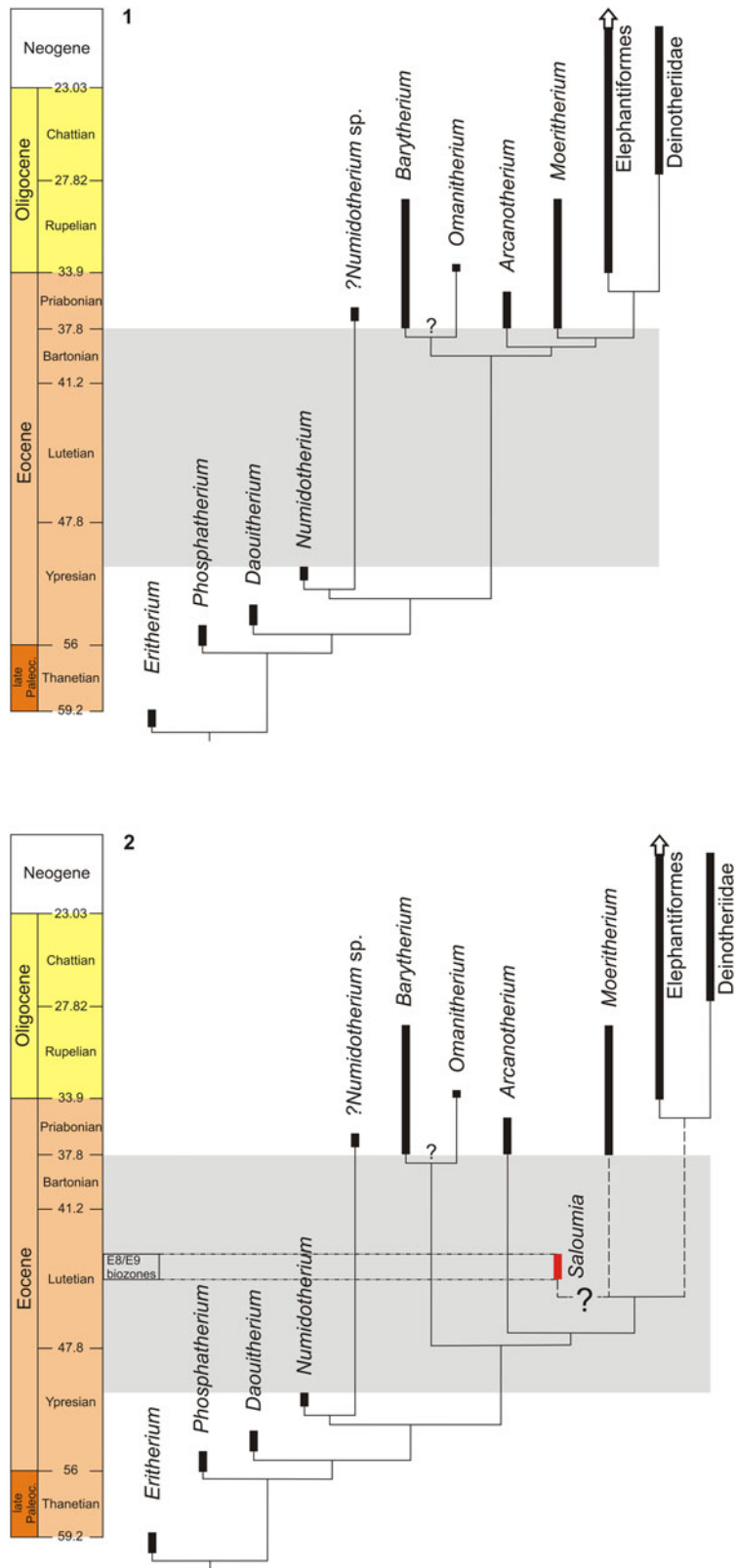
M’Bodione Dadere village is located north of the town of Kaolack in the Sine-Saloum region of the central-western part of Senegal (Fig. 2). In this flat area, outcrops are absent due to an important coverage of Quaternary to Recent sands (10–20 m), which unconformably overlie Paleogene to Pliocene levels. Access to a detailed stratigraphy and to Paleogene deposits is only possible thanks to drill cores and water-well cuttings. Fortunately, 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

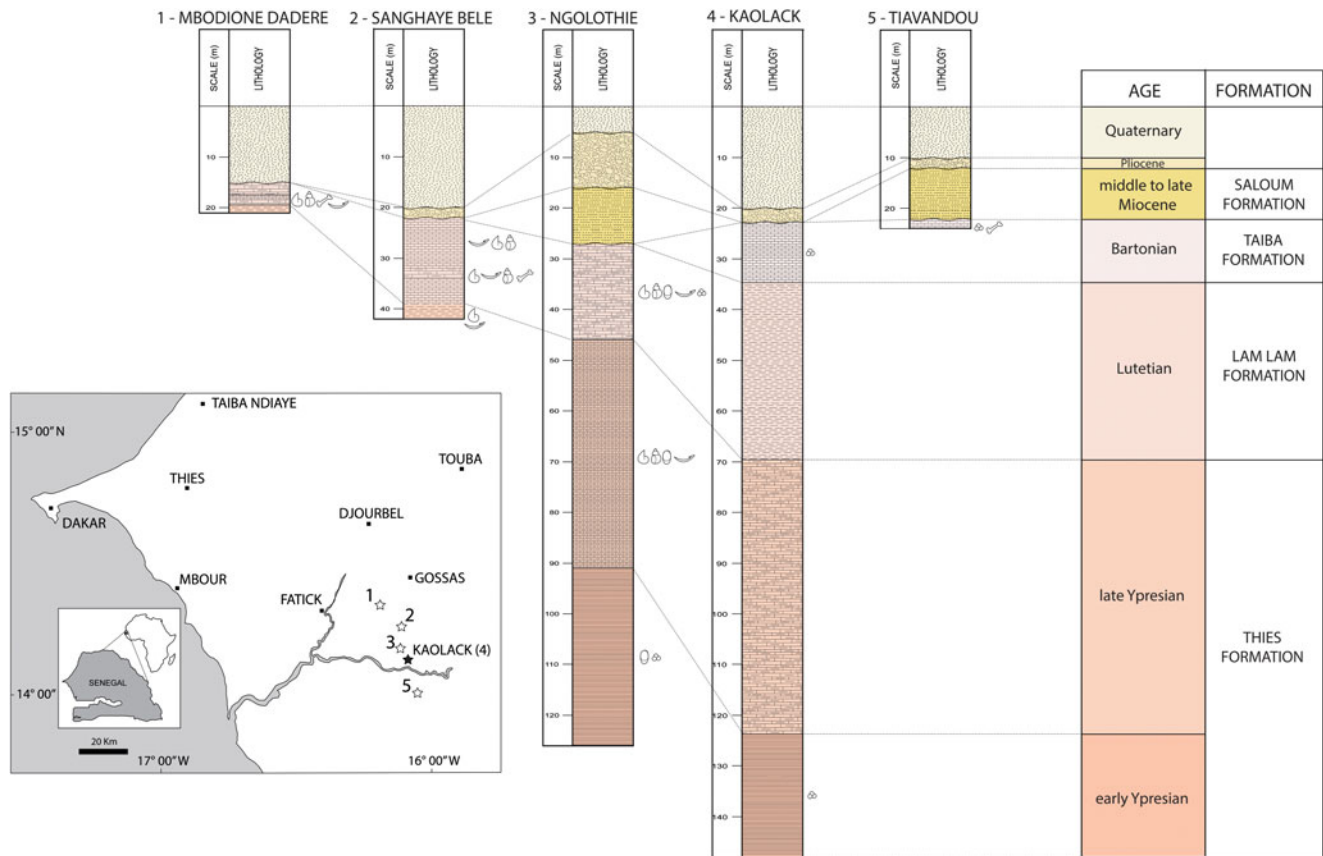
(late Lutetian to early Bartonian; Roger et al., 2009a; Sarr, 2013) yielded several teeth, 18 vertebrae, and rib fragments of an archeocete identified as ‘*Zeuglodon*’ cf. *Z. osiris* by C. Arambourg (Elouard, 1966). More recently, in a revision of the African fossil record of archeocetes, Gingerich (2010) suggested that these remains were too large to be attributed to *Saghacetus osiris* (Dames, 1894) (the new name for *Zeuglodon osiris*), the size being more similar to *Dorudon atrox* (Andrews, 1906), 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 part 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 of 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 24 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 m 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 macroselideans by size and gross morphology (R. Tabuce, personal observation).

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 mollusks, among them the lamellibranch *Ostrea meunieri*, Douvillé, 1920, 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* Finlay, 1939, *Cassigerinelloita amekiensis* Stolk, 1965, and *Pseudohastigerina micra* (Cole, 1927), 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* Nuttall, 1930; Flicoteaux, 1975; Roger et al., 2009a), whereas the top of the formation (Lam Lam marls) yielded a rich planktonic foraminifera association (*Truncorotaloides*



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

*rohri* Brönnimann and Bermudéz [1953], *Acarinina topilensis* [Cushman, 1925], *Globigerapsis* sp., *G. index*, *Acarinina collactea* [Finlay, 1939], *Pseudoglobigerinella bolivariana* [Petters, 1954], *Acarinina pentacamerata* [Subbotina, 1947], 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, ca. 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 computed tomography (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 three-dimensional (3D) rendering were performed using manual segmentation with Avizo 7.1 (VSG). A 3D reconstruction of MNHN.F.MCA 1 was deposited in MorphoMuseum (<https://doi.org/10.18563/journal.m3.104>). 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

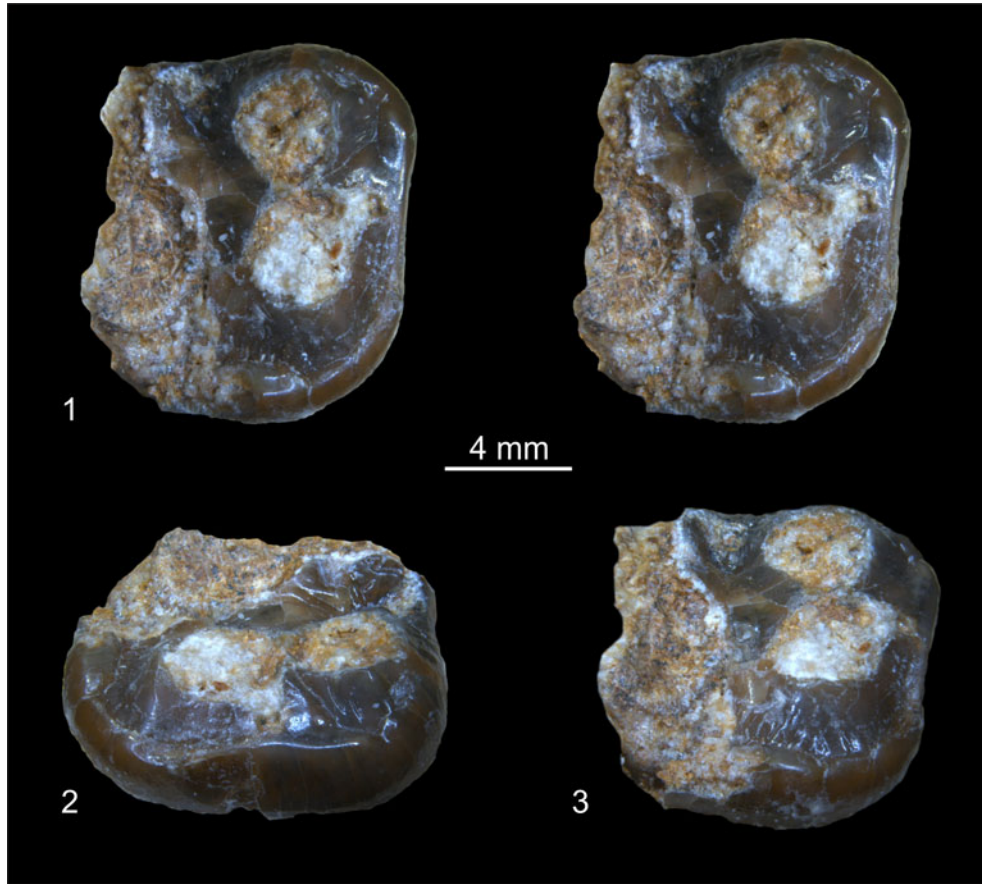
*Type species.*—*Saloumia gorodiskii* n. gen. n. sp., only species.

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

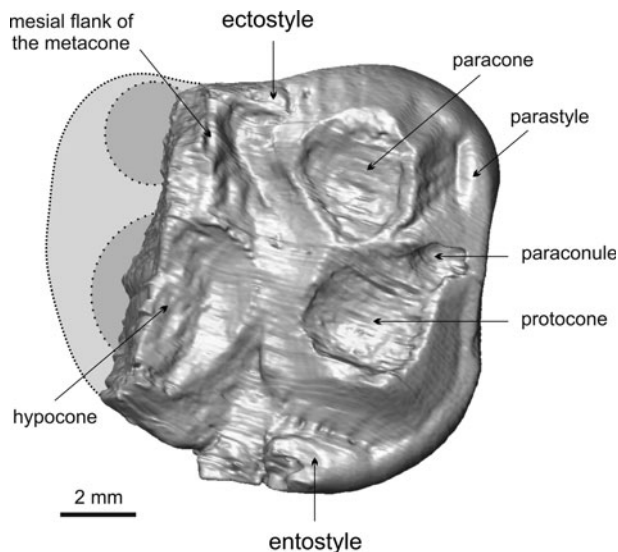
*Etymology.*—From the coastal river Saloum, which flows south of the village of M’Bodione Dadere.

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

*Saloumia gorodiskii* new species  
 Figs. 3, 4



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



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

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

**Diagnosis.**—*Saloumia gorodiskii* differs from *Eritherium* and *Phosphatherium* by larger size, wrinkled enamel, strong

lingual cingulum, and no centrocrista; its morphology also differs from *Phosphatherium* by a pronounced bunodonty. *Saloumia gorodiskii* differs from *Moeritherium* ssp., *Phiomia*, and *Palaeomastodon* by smaller size, more bunodont and not bunolophodont dental pattern, relatively lower crown, and more labial positions of the protocone and hypocone.

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

**Description.**—MNHN.F.MCA 1 is a low-crowned and incompletely preserved upper molar, missing its distal part (length > 10.7 mm; width = 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 is 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 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 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, p. 316). During the 1950s, Paleogene proboscideans were documented only 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* Andrews, 1904, 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* Delmer et al., 2006, 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 (W. Sanders, personal communication, 2019; see also Seiffert et al., 2008; Seiffert, 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 half as large as *Moeritherium trigodon* and *M. lyonsi* and differs from these two species by having a relatively lower crown and a more labial position of both the protocone and hypocone and by the occurrence of a labial cingulum. We note, however, that *M. ‘gracile’* Andrews, 1902, which is a synonym of *M. lyonsi* Andrews, 1901 (see Sanders et al., 2010; W. Sanders, personal communication, 2019), has a labial cingulum, according to Delmer et al. (2006). Finally, as mentioned by Gorodiski and Lavocat (1953), the bunodonty of *Saloumia* differs markedly 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). By contrast, *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 *Numidoherium* (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 the possibility 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, p. 286). *Khamsaconus* was never included in a phylogenetic analysis with both *Eritherium* and *Phosphatherium*, but Gheerbrant et al. (2012) favored a close phylogenetic relationship among these three genera. *Saloumia* shares with *Eritherium* only 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 important, *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 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 *Palaomastodon*. 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 example present in AMNH 13449 (*Palaomastodon beadnelli* Andrews, 1901; see Osborn, 1936, p. 144) and NHMUK M8851 (*Phiomia serridens* Andrews and Beadnell, 1902; see Tassy 1982, p. 234). *Palaomastodon* and *Phiomia* differ from *Saloumia* by a larger size, the lack of connection between the paracone 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 *Palaomastodon*, 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 important, 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 generate considerable ghost lineages within proboscidean phylogeny (Fig. 1.2). 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>.

## References

- Adaci, M., Bensalah, M., Tabuce, R., Mebrouk, F., Marivaux, L., Otero, O., Zaoui, D., Benyoucef, M., and Mahboubi, M., 2016, L’Eocène continental du complexe de Gour Lazib (Sahara nord-occidental, Algérie): Mémoire du Service Géologique de l’Algérie, v. 19, p. 63–89.
- Adnet, S., Cappetta, H., and Tabuce, R., 2010, A new Eocene vertebrate fauna (selachians and mammals) from southwestern Morocco: Preliminary report. Age and palaeobiogeographical implications: Geological Magazine, v. 147, p. 860–870.
- Al-Kindi, M., Pickford, M., Al-Sinani, Y., Al-Ismaïli, I., Hartman, A., and Heward, A., 2017, Large mammals from the Rupelian of Oman—Recent finds: Fossil Imprint, v. 73, p. 300–321.
- Andrews, C.W., 1901, Über das Vorkommen von Proboscidiern in untertertiären Ablagerungen Aegyptens: Tagesblatt des V Internationalen Zoologischen-Kongresses, Berlin, v. 6, p. 4–5.
- Andrews, C.W., 1902, Preliminary note on some recently discovered extinct vertebrates from Egypt (Part III): Geological Magazine, Decade IV, New Series, v. 9, p. 291–295.
- Andrews, C.W., 1904, Further notes on the mammals of the Eocene of Egypt (Part I): Geological Magazine, Decade V, New Series, v. 1, p. 109–115.
- Andrews, C.W., 1906, A descriptive catalogue of the Tertiary Vertebrata of the Fayûm, Egypt: London, British Museum, 324 p.
- Andrews, C.W., and Beadnell, H.J.L., 1902, A Preliminary Note on Some New Mammals from the Upper Eocene of Egypt: Cairo, National Printing Department, p. 1–9.
- Arambourg, C., Kikoine, J., and Lavocat, R., 1951, Découverte du genre *Moeritherium* Andrews dans le tertiaire continental du Soudan: Comptes Rendus de l’Académie des Sciences, Paris, v. 233, p. 68–70.
- Brönnimann, P., and Bermúdez, P.J., 1953, *Truncorotaloides*, a new foraminiferal genus from the Eocene of Trinidad, B.W.I.: Journal of Paleontology, v. 27, p. 817–820.
- Cole, W.S., 1927, A foraminiferal fauna from the Guayabal formation in Mexico: Bulletin of American Paleontology, v. 14, no. 51, p. 1–47.
- Cooper, L.N., Seiffert, E.R., Clementz, M., Madar, S.I., Bajpai, S., Hussain, S.T., and Thewissen, J.G.M., 2014, Anthracobunids from the middle Eocene of India and Pakistan are stem perissodactyls: PLoS ONE, v. 9, p. e109232.

- Court, N. 1994, The periotic of *Moeritherium* (Mammalia, Proboscidea): Homology or homoplasy in the ear region of Tethytheria McKenna, 1975?: *Zoological Journal of the Linnean Society*, v. 112, p. 13–28.
- Cushman, J.A., 1925, New foraminifera from the upper Eocene of Mexico: Contributions from the Cushman Laboratory for Foraminiferal Research, v. 1, p. 4–9.
- Dames, W.B., 1894, Über Zeuglodonten aus Aegypten und die Beziehungen der Archaeoceten zu den übrigen Cetaceen: Geologische und Paläontologische Abhandlungen, Jena, v. 5, p. 189–222.
- Delmer, C., 2009, New data on the Paleogene proboscidean *Numidotherium savagei*: Reassessment of its generic attribution and interpretations of the homologies of the lower incisors in the proboscideans: *Acta Palaeontologica Polonica*, v. 54, p. 561–580.
- Delmer, C., Mahboubi, M., Tabuce, R., and Tassy, P., 2006, A new species of *Moeritherium* (Proboscidea, Mammalia) from the Eocene of Algeria: New perspectives on the ancestral morphotype of the genus: *Palaentology*, v. 49, p. 421–434.
- Domning, D.P., Ray, C.E., and McKenna, M.C., 1986, Two new Oligocene desmostylians and a discussion of tethytherian systematics: *Smithsonian Contributions to Paleobiology*, v. 59, p. 1–56.
- Douvillé, H., 1920, L'Éocène au Soudan et au Sénégal: *Bulletin du Comité d'Études historiques et scientifiques de l'Afrique occidentale française*, v. 2, p. 113–171.
- Elouard, P., 1966, Découverte d'un archéocète dans les environs de Kaolack: *Notes Africaines*, v. 109, p. 8–10.
- Ferretti, M.P., and Debruyne, R., 2011, Anatomy and phylogenetic value of the mandibular and coronoid canals and their associated foramina in proboscideans (Mammalia): *Zoological Journal of the Linnean Society*, v. 161, p. 391–413.
- Finlay, H. J., 1939, New Zealand Foraminifera: Key species in stratigraphy: *Transactions of the Royal Society of New Zealand*, v. 68, p. 89–128.
- Flicoteaux, R., 1974, Biozonation des formations paléogènes de la retombée orientale du dôme de Ndias (Sénégal occidental), Vth African Colloquium on Micropalaentology, Addis-Abeba, Ethiopia, 1972: Madrid, Enadimsa, p. 349–362.
- Flicoteaux, R., 1975, Sur l'attribution à l'Eocène moyen des couches calcaires et argilo-phosphatées de Pallo (Plateau de Thiès, Sénégal occidental): *Bulletin de la Société Géologique de France*, v. 17, p. 430–434.
- Gevin, P., Mongereau, N., and Truc, G., 1975, La Hammada du Dra (Sahara Algerien, Frontière Algero-Marocaine). Etat des connaissances actuelles: Documents du Laboratoire de Géologie, Faculté des Sciences, Lyon, p. 305–319.
- Gheerbrant, E., 2009, Paleocene emergence of elephant relatives and the rapid radiation of African ungulates: *Proceedings of the National Academy of Sciences USA*, v. 106, p. 10717–10721.
- Gheerbrant, E., and Tassy, P., 2009, L'origine et l'évolution des éléphants: *Comptes Rendus Palevol*, v. 8, p. 281–294.
- Gheerbrant, E., Sudre, J., Cappetta, H., and Bignot, G., 1998a, *Phosphatherium escuillei* du Thanétien du Bassin des Ouled Abdoun (Maroc), plus ancien proboscideen (Mammalia) d'Afrique: *Géobios*, v. 30, p. 247–269.
- Gheerbrant, E., Sudre, J., Sen, S., Abrial, C., Marandat, B., Sigé, B., and Vianey-liaud, M., 1998b, Nouvelles données sur les mammifères du Thanétien et de l'Yprésien du Bassin d'Ouarzazate (Maroc) et leur contexte stratigraphique: *Palaeovertibrata*, v. 27, p. 155–202.
- Gheerbrant, E., Sudre, J., Tassy, P., Amaghaz, M., Bouya, B., and Iarochene, M., 2005, Nouvelles données sur *Phosphatherium escuillei* de l'Eocène inférieur du Maroc, apports à la phylogénie des Proboscidea et des ongulés lophodontes: *Géodiversitas*, v. 27, p. 239–333.
- Gheerbrant, E., Bouya, B., and Amaghaz, M., 2012, Dental and cranial anatomy of *Eritherium azzouzorium* from the Paleocene of Morocco, earliest known proboscidean mammal: *Palaentographica Abteilung A*, v. 297, p. 151–183.
- Gingerich, P.D., 2010, Cetacea, in Werdelin, L., and Sanders, W.J., eds., *Cenozoic Mammals of Africa*: Berkeley, University of California Press, p. 873–899.
- Gorodiski, A., and Lavocat, R., 1953, Première découverte de mammifères dans le tertiaire continental (Lutétien) du Sénégal: *Comptes Rendus Sommaires de la Société Géologique de France*, v. 15, p. 314–316.
- Illiger, C.D., 1811, *Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis*: Berlin, C. Salfeld, 302 p.
- Jaeger, J.-J., et al., 2010, New rodent assemblages from the Eocene Dur At-Talah escarpment (Sahara of central Libya): Systematic, biochronological, and palaeobiogeographical implications: *Zoological Journal of the Linnean Society*, v. 160, p. 195–213.
- Jaeger, J.-J., et al., 2012, Dur at Talah vertebrate locality revisited: New data on its stratigraphy, age, sedimentology and mammalian fossils, in Salem, M.J., Elbakai, M.T., and Abuturuma, Y., eds., *Geology of Southern Libya*, Volume 1: Malta, Gutenberg Press, p. 241–258.
- Kaiser, T.M., Ansoerge, J., Arratia, G., Bullwinkel, V., Gunnell, G.F., Herendeen, P.S., Jacobs, B., Mingram, J., Msuya, C., and Musolf, A., 2006, The maar lake of Mahenge (Tanzania); unique evidence of Eocene terrestrial environments in sub-Saharan Africa: *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften*, v. 157, p. 411–431.
- Lavocat, R., 1955, *Titres et travaux scientifiques: Romorantin*, Imprimerie Centrale, 95 p.
- Linnaeus, C., 1758, *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis*. Volume 1: Regnum animale (tenth edition): Stockholm, Laurentii Salvii, 824 p.
- Nuttall, W.L.F., 1930, Eocene foraminifera from Mexico: *Journal of Paleontology*, v. 4, p. 271–293.
- O'Leary, M.A., Roberts, E.R., Bouare, M., Sissoko, F., and Tapanila, L., 2006, Malian Paenungulata (Mammalia: Placentalia): New African afrotheres from the early Eocene: *Journal of Vertebrate Paleontology*, v. 26, p. 981–988.
- O'Leary, M.A., Sarr, R., Malou, R., Sow, E.H., Lepre, C., and Hill, R.V., 2012, A new fossil amiid from the Eocene of Senegal and the persistence of extinct marine amiids after the Cretaceous–Paleogene boundary: *Copeia*, v. 4, p. 603–608.
- Osborn, H.F., 1936, Proboscidea. A monograph of the discovery, evolution, migration and distinction of the mastodonts and elephants of the world: Volume 1. *Moeritherioidea, Deinotherioidea, Mastodontoidea*: New York, American Museum Press, 802 p.
- Petters, S.W., 1954, Tertiary and Upper Cretaceous Foraminifera from Colombia, South America: Contributions from the Cushman Foundation for Foraminiferal Research, v. 5, p. 37–41.
- Pickford, M., 2015, Large ungulates from the basal Oligocene of Oman: 2 – Proboscidea: *Spanish Journal of Palaentology*, v. 30, p. 209–222.
- Pickford, M., Senut, B., Morales, J., Mein, P., and Sanchez, I.M., 2008, Mammalia from the Lutetian of Namibia: *Memoir of the Geological Survey of Namibia*, v. 20, p. 465–514.
- Roger, J., Banton, O., Barusseau, J.P., Castaigne, P., Comte, J.-C., Duvail, C., Nehlig, P., Noël, B.J., Serrano, O., and Travi, Y., 2009a, Notice explicative de la cartographie multicouches à 1/500 000 et 1/20 000 de la zone d'activité du Cap-Vert: Ministère des Mines, de l'Industrie et des PME, Direction des Mines et de la Géologie, Dakar, p. 120.
- Roger, J., Barusseau, J.P., Duvail, C., Nehlig, P., Noël, B.J., and Serrano, O., 2009b, Notice explicative des cartes géologiques à 1/500 000 du bassin sédimentaire sénégalais: Ministère des Mines, de l'Industrie et des PME, Direction des Mines et de la Géologie, Dakar, p. 48.
- Sanders, W.J., Gheerbrant, E., Harris, J.M., Saegusa, H., and Delmer, C., 2010, Proboscidea, in Werdelin, L., and Sanders, W.J., eds., *Cenozoic Mammals of Africa*: Berkeley, University of California Press, p. 161–251.
- Sarr, R., 2013, Ostracodes nouveaux du Paléogène du Sine-Saloum (Sénégal, Afrique de l'Ouest): *Biostratigraphie, paléoenvironnement: Revue de Paléobiologie*, v. 32, p. 569–588.
- Seiffert, E.R., 2007, A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence: *BMC Evolutionary Biology*, v. 7, no. 224, p. 1–13.
- Seiffert, E.R., 2010, Chronology of Paleogene mammal localities, in Werdelin, L., and Sanders, W.J., eds., *Cenozoic Mammals of Africa*: Berkeley, University of California Press, p. 19–26.
- Seiffert, E.R., Bown, T.M., Clyde, W.C., and Simons, E.L., 2008, *Geology, paleoenvironment, and age of Birket Qarun Locality 2 (BQ-2), Fayum Depression, Egypt*, in Fleagle, J.G., and Gilbert, C.C., eds., *Elwyn Simons: A search for origins*: New York, Springer, p. 71–86.
- Seiffert, E.R., Nasir, S., Al-Harthy, A., Groenke, J.R., Kraatz, B.P., Stevens, N.J., and Al-Sayigh, A.R., 2012, Diversity in the later Paleogene proboscidean radiation: A small barytheriid from the Oligocene of Dhofar Governorate, Sultanate of Oman: *Naturwissenschaften*, v. 99, p. 133–141.
- Stolk, J., 1965, Contribution à l'étude des corrélations microfauniques du Tertiaire inférieur de la Nigéria méridionale: *Mémoire du Bureau de Recherches Géologiques et Minières*, v. 32, p. 247–267.
- Subbotina, N.N., 1947, Danian and Paleogene Foraminifera of the northern Caucasus: *Trudy Vsesoyuznogo Neftyanogo Nauchno-Isledovatel'skogo Geologo-Razvedochnogo Instituta (VNIGRI), Microfauna of the oil fields of the USSR*, v. 1947, p. 39–160.
- Sudre, J., 1979, Nouveaux mammifères éocènes du Sahara Occidental: *Palaeovertibrata*, v. 9, no. 3, p. 83–115.
- Tabuce, R., Adnet, S., Cappetta, H., Noubhani, A., and Quillevéré, F., 2005, Aznag (bassin d'Ouarzazate, Maroc), nouvelle localité à séliens et mammifères de l'Eocène d'Afrique: *Bulletin de la Société Géologique de France*, v. 176, p. 381–400.
- Tassy, P., 1982, Les principales dichotomies dans l'histoire des Proboscidea (Mammalia): une approche phylogénétique: *Geobios*, v. 6, p. 225–245.



Tessier, F., 1952, Contribution à la stratigraphie et à la paléontologie de la partie ouest du Sénégal (Crétacé et Tertiaire): Bulletin de la Direction des Mines de l'Afrique Occidentale Française, Dakar, v. 14, p. 570.

Vandenberghe, N., Hilgen, F.J., and Speijer, R.P., 2012, The Paleogene Period, in Gradstein, F.M., Ogg, J.G., Schmitz, M.D., and Ogg, G.M., eds., The Geological Time Scale 2012: Oxford, Elsevier Science, p. 855–921.

Werdelin, L., and Sanders, W.J., 2010, Cenozoic Mammals of Africa: Berkeley, University of California Press, 986 p.

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