



New Middle Eocene proboscidean from Togo illuminates the early evolution of the elephantiform-like dental pattern

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Title: New middle Eocene proboscidean from Togo illuminates the early evolution of the elephantiform-like dental pattern.

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Abstract

Africa has played a pivotal role in the evolution of early proboscideans (elephants and their extinct relatives), yet vast temporal and geographical zones remain uncharted on the continent. A long hiatus encompassing most of the Eocene (Ypresian to the early Priabonian, around 13 Myr timespan) considerably hampers our understanding of the early evolutionary history of the group. It is notably the case with the origin of its most successful members, the Elephantiformes, i.e., all elephant-like proboscideans most closely related to modern elephants. Here we describe a proboscidean lower molar discovered in Lutetian phosphate deposits from Togo, and name a new genus and species, *Dagbatitherium tassyi*. We show that *Dagbatitherium* displays several elephantiform dental characteristics such as a three-layered Schmelzmuster, the presence of a mesoconid, transversely enlarged buccal cusps, and the individualization of a third lophid closely appressed to a minute distal cingulid. *Dagbatitherium* represents a stem Elephantiformes, pushing back the origin of the group by about ten million years, i.e., a third of its currently known evolutionary history. More importantly, *Dagbatitherium* potentially unlocks the puzzle of the origin of the unique elephantiform tooth crown organization by bridging a critical temporal and morphological gap between early bunodont incipiently bilophodont proboscidean taxa and more derived elephantiforms.

Keywords: Proboscidea, Lutetian, Togo, Elephantiformes.

Introduction

The savanna and forest elephants, *Loxodonta africana* and *L. cyclotis*, are flagship species of the African fauna and constitute some of its most iconic mammalian members. Alongside the Asian elephant, *Elephas maximus*, these two species represent the last vestige of a once-diversified order of mammals, the Proboscidea, whose evolutionary history is deeply ingrained with that of the African continent [1]. Proboscideans are part of the Afrotheria, a supercohort of mammals originating in Africa, which was recognized based on molecular data (see review in [2]). Unlike most afrotherian orders, the fossil record of proboscideans appears relatively well documented [3] and indicates that their representatives have inhabited Africa for the last 60 million years at least [4]. Intensive paleontological fieldworks on the continent unravelled a flourishing diversity of proboscidean forms in size, shape, and taxonomically, which depart significantly from the emblematic elephantine morphotype with distinctive trunk and immense projecting tusks.

Recent discoveries in eastern and North Africa, as well as in the Arabian Peninsula, have documented important proboscidean evolutionary steps at the late Paleocene-early Eocene transition [4–7] and at the late Eocene-early Oligocene transition [8–14]. Two main temporal cohorts could then be identified [3]: the early Paleogene basal taxa including eritheres, phosphatheres, daouitheres, and numidotheres, characterized by small to medium sizes and more archaic features (e.g., the inferred absence of a trunk or lesser development of incisors); and the late Paleogene taxa including barytheres, arcanotheres, moeritheres, deinotheres, and elephantiforms (palaeomastodonts and elephantimorphs), characterized by medium to large sizes and more derived cranio-dental characteristics. Such paleontological wealth partly overshadows the fact that vast temporal and geographical zones remain

uncharted in Africa, so that much uncertainty prevails with regard to the early evolutionary history of the group, especially the origin of its most successful members, the elephantiforms. The suborder Elephantiformes includes all elephant-like proboscideans that are closely related to modern elephants [15]. The tooth rows of modern elephants are characterized by brick-like molars with multiple longitudinally aligned lamellar enamel ridges. Major gaps in the fossil record have prevented any attempt to understand how this very derived dental pattern evolved from the generalised mammalian molariform teeth of the earliest proboscideans. In fact, the bunolophodont dental morphology of earliest elephantiforms startlingly contrasts with that of early proboscideans, most of them being strictly lophodont taxa [5,16,17], and the origin of the unique elephantiform crown organization represents a long-standing paleontological conundrum.

Since the most primitive elephantiforms (*Phiomia* and *Paleomastodon*) have been found in early Oligocene deposits, most notably from the Gebel el Qatrani Formation (33-30 Ma) of the Fayum [18], the transition from early proboscideans to elephantiforms was expected to occur during the end of the Eocene [19]. However, this hypothesis mainly stems from the fact that the evolutionary history of Proboscidea remains virtually unknown during most of the Eocene, with a long hiatus encompassing the end of the Ypresian to the early Priabonian (an interval of about 13 Myr; [3,20]). While relatively little paleontological work has been carried out in West Africa, this area includes two post-Ypresian localities that yielded proboscidean remains: the Malian locality of In Tafidet (middle or late Eocene; ([21] but see [22]) and the Senegalese locality of M'Bodione Dadere (middle Eocene; [20]). Recent exploration in West African Cenozoic basins revealed an untapped fossil resource [22–28]. Here we describe a proboscidean lower molar discovered in Lutetian

phosphate deposits from Togo. Based on its proportions, occlusal pattern, and enamel microstructure, this new specimen is identified as an elephantiform, representing the oldest record of this suborder. Such recognition pushes back the origin of the group by about ten million years and potentially bridges a major morphological and temporal gap between two main proboscidean evolutionary cohorts.

Results

Geological setting

The Togolese phosphate deposits are part of the Hahotoé-Kpogamé Phosphate Complex [29–31], which is exploited by the *Société Nouvelle des Phosphates du Togo* (SNPT) in the quarries of Dagbati and Kpogamé (Fig. 1A). The Hahotoé-Kpogamé Phosphate Complex consists of three members [29,31], which are from bottom to top: the phosphatic marl, the phospharenite, and the phosphatic clay (Fig. 1B). These members are essentially dominated by marls, limestones, phosphates, claystones, sands, and ferruginous sandstones. The tooth ULDG-DAG1 described here was found *in situ* in the phospharenite member of the Dagbati quarry (1°31'39.3"E/6°28'51.1"N) during a 2017 field campaign. The quarry of Dagbati covers an area of 24.43 km² and is located 2.5 km southwest of Dagbati village (Fig. 1A).

The proboscidean tooth was found in a layer at the base of the phospharenite member (Fig. 1B). This 1.5 to 2 meters thick beige coloured layer, of massive structure, presents finely smooth and discontinuous levels as well as centimetric to metric blocks of bioclastic limestones. It is composed of clay, phosphate grains, as well as numerous coprolites, elasmobranch teeth, and protocetid remains, which all characterize a rich marine environment. Johnson [31] and Johnson *et al.* [32] proposed that the phosphates of Kpogamé likely deposited in a shallow marine

environment of average salinity with moderate deposition energy. The abundance of continental minerals such as kaolinite and quartz, coupled with the presence of pollens [32], were suggestive of the proximity of the coast, which is in line with the discovery of terrestrial remains. The phospharenite layer that yielded the proboscidean tooth also contains small pockets or pellets of clay rich in foraminifers. Planktonic foraminifera collected in these clays point to Zones E7b (partim) or E8 of [33] and indicate that the phosphate deposits of the Dagbati quarry were deposited during the middle Eocene after ~46.5 and before ~44.0 Ma (SI Appendix).

Systematic palaeontology

Class MAMMALIA Linnaeus, 1758

Supercohort AFROTHERIA Stanhope et al., 1998

Superorder PAENUNGULATA Simpson, 1945

Order PROBOSCIDEA Illiger, 1811

Suborder ELEPHANTIFORMES Tassy, 1988

Family *incertae sedis*

Genus *Dagbatitherium* gen. nov.

Type species: *Dagbatitherium tassyi* sp. nov., the only known species.

Diagnosis and distribution: As for the type species, by monotypy.

Etymology: From Dagbati, the quarry where the type specimen was found, and therion, wild animal in Greek.

Dagbatitherium tassyi sp. nov.

Fig. 2 & 3

Holotype: right M/1 or M/2 (ULDG-DAG1), Department of Geology, University of Lomé, Lomé, Togo.

Diagnosis: Smallest elephantiform with brachyodont and bunolophodont molars. *Dagbatitherium* differs from all non-elephantiform proboscideans by the association of a large mesoconid, a third lophid (a tritolophid) with a large and isolated hypoconulid mesial to a minute posterior cingulid, and a three-layered Schmelzmuster with 3D enamel (3DE) on the inner zone, Hunter-Schreger bands (HSB) in the middle zone, and radial enamel (RE) in the outer zone. *Dagbatitherium* differs from *Palaeomastodon* and *Phiomia* by its small size, as well as a more brachyodont and bunodont molar pattern.

Etymology: In honour of Pascal Tassy, who erected the suborder Elephantiformes and has dedicated his life to the study of elephants and their relatives.

Type locality and age: Quarry of Dagbati, Togo (middle Lutetian, middle Eocene).

Description: The Togolese molar is brachyodont and bunolophodont; its crown is distolabially inflated. It is 37.5 mm long and 29.2 mm wide. Two pairs of main cuspids dominate the occlusal surface, the labial ones (protoconid and hypoconid) being wider and lower than the lingual ones (metaconid and entoconid). These cuspid pairs are transversally aligned and separated by a longitudinal median groove (sulcus), which is slightly lingually positioned (Fig. 2 A, B, and C). The lingual side

of the tooth is steep, while its labial side is more inclined. On the mesial side of the tooth, the enamel is deeply perforated by an interproximal facet (Fig. 2G and I). No paraconid or accessory cuspid is visible anterior to the metaconid. The preprotocristid and premetacristid are similar in length. The postmetacristid and preentocristid are present and straight. The lingual and labial cuspids join medially via crest-like internal flanks, which give the crown a rudimentary lophodont aspect. No additional median cusplets are visible on the enamel cap, but incipient cusplets are noticeable at the enamel/dentine junction (Fig. 2B) or on 3D enamel thickness distribution maps (Fig. 2C). The protolophid and hypolophid are well defined and display similar heights. There is a deep groove, deeper than the mesiodistal median groove, between the two mesial cuspids (protoconid and metaconid) and the two principal talonid cuspids (hypoconid and entoconid). The hypoflexid is deep, but the labial interlophid space is partially obstructed by a large medially displaced mesoconid, which is much lower than the main cuspids and connected to the protoconid. A short cristid obliqua joins the apex of hypoconid to the mesoconid without reaching it; it is mesiolingually oriented. The cristid obliqua is also well defined at the enamel/dentine junction (Fig. 2B). The talonid includes a third lophid (tritolophid) closely appressed to an extremely diminutive, anteroposteriorly narrow postcingulid. The tritolophid is formed by a large hypoconulid and a small postentoconulid; it is lower than the first two lophids but higher than the mesoconid. The space between the hypolophid and tritolophid is shorter than the first interlophid valley; it is defined by a markedly excavated groove, which is as deep as the longitudinal median groove but shallower than the first interlophid valley. Both the hypoconulid and postentoconulid display mesiodistally oriented internal crests (Fig. 2 A and B), so that the tritolophid is clearly distinct from the hypolophid. The tritolophid is also accompanied by an incipient

distal cingulid, which is constituted of a rectilinear association of small cuspules and corresponds to a clear distal thickening of the enamel layer (Fig. 2C and J, SI Appendix). There is no anterior, lingual or labial cingulid. Distally, an oval-shaped facet of polished wear (not visible on the 3D reconstruction) is also clearly indicative of the presence of a consecutive tooth locus. The wear pattern of the main cuspids is apical (Fig. 2C).

The Schmelzmuster, which corresponds to the spatial arrangement of the different enamel types through enamel thickness, is three-layered with 3D enamel (3DE) on the inner zone (~27% of the enamel thickness), Hunter-Schreger bands (HSB) in the middle zone (~34% of the enamel thickness), and radial enamel (RE) in the outer zone (~39% of the enamel thickness) (SI Appendix). The RE is the basic enamel type where enamel prisms are all directed away radially; HSB are a specific mode of decussation where enamel prisms decussate in transversely orientated bands; the 3DE corresponds to thick bundles of prisms that decussate in all directions [34–36].

Comparison: The Togolese molar is larger than the molars of *Eritherium*, *Phosphatherium*, *Daouitherium*, *Numidotherium*, and *Moeritherium*; and smaller than those of *Chilgatherium*, *Arcanotherium*, *Barytherium*, *Omanitherium*, *Prodeinotherium*, *Phiomia*, and *Palaeomastodon*. In *Dagbatitherium*, the preprotocristid is as developed as the premetacristid as in *Phosphatherium*, *Daouitherium*, *Numidotherium* (Fig. 3A), and *Barytherium*. The postmetacristid is present as in *Eritherium*, *Phosphatherium*, *Daouitherium*, *Numidotherium* (Fig. 3A), and *Barytherium*. The preentocristid is present and curved as in *Eritherium*, *Daouitherium*, *Numidotherium* (Fig. 3A), and *Barytherium*, while it is absent in

Arcanotherium, *Moeritherium*, *Prodeinotherium*, *Chilgatherium*, *Phiomia*, *Palaeomastodon*. The buccal cingulid is absent unlike in *Moeritherium* where it is variably present. The cristid obliqua is present as in all early proboscideans but *Phiomia* (Fig. 3C) and *Palaeomastodon*. The Togolese molar displays an individualized tritolophid like the molars of *Chilgatherium*, *Phiomia* (Fig. 3C), and *Palaeomastodon*, as well as the first molar of *Prodeinotherium*. The postentoconulid of *Dagbatitherium* is well-developed, distant from the entoconid and associated to a posterior cingulid as in *Phiomia* (Fig. 3C) and *Palaeomastodon*; it is present but reduced and close to the entoconid in *Eritherium*. In *Chilgatherium* and *Prodeinotherium*, the postentoconulid is also distant from the entoconid, but it is smaller than the hypoconulid and not associated to a distal cingulid. The hypoconulid of *Dagbatitherium* is large and well individualized as in *Moeritherium*, *Prodeinotherium*, *Phiomia* (Fig. 3C), and *Palaeomastodon*. *Dagbatitherium* displays a large mesoconid, unlike all early proboscideans, but as in *Phiomia* (Fig. 3C) and *Palaeomastodon*. The mesoconid is also variably present in *Moeritherium*. Such mesoconid corresponds to the posterior accessory conule or terminal position of the posterior crescentoid as recognized in elephantiforms and moeritheres.

The bunolophodont aspect of the *Dagbatitherium* molars also clearly contrasts with the occlusal morphology of strictly lophodont early proboscideans such as phosphatheres, daouitheres, numidotheres (Fig. 3A) and barytheres, in which molar cusps are undistinguishable from the lophids (Fig. 3A). *Dagbatitherium* also differs from *Chilgatherium* and deinotheres, which display lophodont lower molars characterized by anteriorly concave and transversely continuous crested lophids with “chisel-like” wear on their posterior faces [37]. *Dagbatitherium* and *Chilgatherium*

also display distinctive cingulid arrangements, the latter showing no distal cingulid [37].

A three-layered Schmelzmuster composed of 3DE-HSB-RE is only known in Proboscidea; it occurs in *Arcanotherium* [35] and all Elephantiformes to the exception of *Palaeomastodon*, and to a lesser extent *Phiomia* [34,36,38]. The 3DE-HSB-RE Schmelzmuster was observed in the elephantimorphs *Mammuthus*, *Gomphotherium*, *Cuvieronius*, *Anancus*, *Stegodon*, *Loxodonta*, *Mammuthus*, and *Elephas*. Recent studies [39,40] proposed that *Deinotherium* could display 3DE-HSB-RE Schmelzmuster, which clearly contrasts with previous works that recognized a single layer of 3DE for this taxon [34,38,41]. Since Białas et al. [40] do not illustrate the Schmelzmuster of *Deinotherium* in its entirety (only a small zone of ‘HSB’ is figured) and that the structure of the 3DE can vary depending on the observed tooth area [38], we consider as premature to invalidate original observations, although this point would clearly require further scrutiny. Stem elephantiforms *Phiomia* and *Palaeomastodon* differ from elephantimorphs in the absence of a distinct 3DE inner zone; they have a more primitive Schmelzmuster composed of HSB-RE similar to the condition observed in *Phosphatherium* and *Moeritherium* [35]. Interestingly, however, *Phiomia* has irregular and poorly defined HSB at places along the enamel-dentine junction, interpreted as a rudimentary type of 3DE by Pfretzschner [34] and Ferretti [36]. The mention of such incipient 3DE in the inner zone of *Palaeomastodon* by [41] is likely attributable to a confusion with *Phiomia*. Our observations (SI Appendix) confirmed that *Palaeomastodon* displays a Schmelzmuster strictly composed of HSB-RE. *Dagbatitherium* clearly differs from the lophodont *Numidotherium*, *Barytherium*, and deinotheres, which all display a single layer of 3DE.

To conclude, *Dagbatitherium* is similar to elephantiform species by a set of derived characters [15,19,35,36]: a three-layered Schmelzmuster, the presence of a mesoconid, transversely enlarged buccal cusps, and the individualization of a third lophid constituted by distinctive hypoconulid and postentoconulid, and closely appressed to an anteroposteriorly thin, nascent postcingulid (Fig. 3 B and C). The tendency to build a third lophid is reminiscent of the condition observed in early elephantiforms, with *Palaeomastodon* displaying less individualized tritolophids than *Phiomia*. As in palaeomastodont lower molars [19], a sulcus divides mesiodistally the half-lophids and the posterior part of the tooth is lingually shifted in *Dagbatitherium*. However, the Togolese molar shows no sign of differential wear between pretrite and posttrite half-lophids and does not present adaxial conelets or anterior conules, which characterize both trilophodont and tetralophodont elephantiforms.

Discussion and implications for proboscidean evolution

The Togolese molar presents an unusual combination of primitive and derived proboscidean features, which validates its attribution to a new genus. In our cladistic analysis, ULDG-DAG1 is found as the first offshoot of the elephantiforms (SI Appendix). The clade (*Dagbatitherium*–Elephantiformes) is supported by nine synapomorphies, including two non-ambiguous ones: the presence of a mesoconid on M/1-2 (115¹; RI = 1.00), and a bunolophodont molar pattern (120³; RI = 0.75). These characters are variably present in moeritheres but are absent in deinotheres, i.e., the sister clade of Elephantiformes (see below). In many respects, the bunodont incipiently bilophodont occlusal patterns of *Eritherium* molars [4,7] somewhat foreshadows the condition observed in *Dagbatitherium*. However, along with the bunolophodonty, the Togolese specimen mainly shares primitive features with

Eritherium such as the low crown and the presence of a postmetacristid, preentocristid, and cristid obliqua. It clearly departs from the latter by its larger size, its tritolophodont occlusal pattern, the presence of a mesoconid, and a more complex enamel microstructure (i.e., *Eritherium* has a basic one-layered Schmelzmuster formed by radial enamel).

Characters of enamel microstructure were proposed to be phylogenetically informative for proboscideans [35,36], even if their functional significance remains unclear [34,38]. Bertrand [38] proposed that the convergent evolution of the 3DE in lophodont taxa was functionally linked to tooth morphology and diet. In contrast, the 3DE-HSB-RE Schmelzmuster seems to mainly characterize the elephantimorphs (i.e., all elephantiforms but *Phiomia* and *Palaeomastodon*; [34,36,38]), which constitutes a diverse group of proboscideans with various ecologies. The non-elephantiform *Arcanotherium* also developed a three-layered Schmelzmuster composed of 3DE-HSB-RE [35]. However, its 3DE represents 45% of the enamel thickness, while it never exceeds 20% of the enamel thickness in elephantimorphs [35] and similarly represents ~27% in *Dagbatitherium*. This could indicate that the three-layered enamel structure of *Arcanotherium* evolved convergently with that of elephantiforms [36]. Based on enamel microstructure, *Dagbatitherium* most resembles elephantimorph taxa, but also appears more derived than *Phiomia* and *Palaeomastodon*. If *Dagbatitherium* represents a basal elephantiform, then *Palaeomastodon*, and, to a lesser extent *Phiomia*, secondarily developed a two-layered Schmelzmuster composed of HSB-RE. Although counterintuitive, similar examples of reversal have been documented in the enamel microstructure [42].

The suborder Elephantiformes comprises a diversity of elephant-like proboscideans that departs from other proboscidean species based on a number of

cranial, mandibular, and dental features [15]. We showed that *Dagbatitherium* displays several dental characteristics of Elephantiformes. Understanding the origin of the elephantiforms inevitably depends on the recognition of its sister group. Shoshani et al. [43] proposed to include all lophodont taxa (e.g., Numidotheriidae, Barytheriidae, and Deinotheriidae) in the suborder Plesielephantiformes as a sister taxon to Elephantiformes. They proposed to consider bilophodonty as a potential synapomorphy for Plesielephantiformes, but also acknowledged that the lophodonty of deinotheres might not be homologous with that of phosphatheres and numidotheres. This latter view was confirmed by phylogenetic and comparative analyses that clearly refuted the possibility of grouping all strict lophodont primitive proboscideans into a single suborder [9,44]). The (*Dagbatitherium*, elephantiforms) clade shares a number of dental characteristics with *Moeritherium* (see SI Appendix), showing that moerithere molars anticipate the morphology of palaeomastodonts in many respects. However, a sister-group relationship between elephantiforms and deinotheres is so far widely supported by several shared derived cranial, and postcranial characters [9,15,44] (45 synapomorphies, including 27 non-ambiguous ones; SI Appendix). Despite this, both groups display very distinctive bunolophodont and lophodont dental patterns (Fig. 3), which prevent any straightforward reconstruction of a putative shared ancestral dental morphotype.

Dagbatitherium undoubtedly displays dental characteristics previously used to unite Elephantiformes [45], such as intermediate molar tritolophy, M/1-2 presence of a hypoconulid and postentoconulid (related to tritolophy), M/1-2 with no accessory conule in the 2nd interlophid, and transverse expansion of molar crowns. However, Tassy [45,46] also explicitly united elephantiforms based on a number of cranial features, including orbital retraction above M1, absence of paroccipital processes, and

presence of a nasal fossa, as well as elongation of the mandibular symphysis, anteroposterior extension of the diastema between the lower tusks and cheek teeth, and presence of evergrowing tusks. Although such a trait combination is unlikely to be found in the earliest representatives of the group, documenting more dental and cranial features of *Dagbatitherium* will be vital to ascertain its phylogenetic position among elephantiforms.

A close relationship between *Dagbatitherium* and elephantiforms would extend the ancestral roots of elephantiforms by at least ten million years, instead of the idea of a rather fast transition from lophodont ancestors at the end of the Eocene. It would also imply a considerable gap in the fossil record for both elephantiforms and deinotheres (Fig. 3). The recent description of *Saloumia* [20], a middle Lutetian proboscidean from Senegal, is in line with this assumption. With its pronounced bunodonty and putative affinities with *Moeritherium* or basal elephantiforms, *Saloumia* could potentially push the origin of the (*Moeritherium*, (Elephantiformes, Deinotheriidae)) clade well back into the middle Eocene [20]. The resulting ghost lineages could then be partially filled by the description of the new Togolese taxon. Alternatively, *Dagbatitherium* could be considered as close to the elephantiforms/deinotheres dichotomy, suggesting a derivation of the deinotheres lophodonty from a more bunolophodont dental pattern. This phylogenetic hypothesis would find support in the cusp and crown organization of the early Oligocene *Chilgatherium* [37], which is often considered as the most primitive deinotheres (Fig. 3), although its phylogenetic position is still debated [13,14]. However, this hypothesis would also imply an unlikely sequence of evolutionary steps along the branch leading to deinotheres, such as the combined loss of the mesoconid, 3DE-HSB-RE Schmelzmuster, and tritoloph(id)s of second and third molars. A close

relationship between *Dagbatitherium* and elephantiforms is thus preferred here and supported by our cladistics analysis.

Considering the diversity of early Eocene lophodont taxa (Fig. 3), true lophodontology was viewed as the primitive dental pattern for proboscideans [9,15,16,43,44], from which the bunolophodontology of *Moeritherium* and Elephantiformes would derive (reversal). Following this evolutionary scenario, proboscideans would constitute the only mammalian group that evolved bunodont dental morphologies from an ancestral lophodont state. The discovery of late Paleocene and Ypresian proboscidean taxa with bunodont incipiently bilophodont posterior jugal teeth, respectively *Eritherium* [4] and *Khamsaconus* [7], enabled a new view of this unpredicted scenario, although lophodontology still remained pervasive among the two main Paleogene cohorts (Fig. 3). The successive descriptions of *Saloumia* [20] and *Dagbatitherium* unravel major gaps in our understanding of the early evolutionary history of proboscideans, notably by generating considerable ghost lineages. Its age and morphology make *Dagbatitherium* a good candidate to bridge a critical temporal and morphological gap between early bunodont incipiently bilophodont taxa (*Eritherium* and *Khamsaconus*) and elephantiforms. As such, this discovery raises the possibility that a major dichotomy in early proboscidean evolution has been overlooked, between a clade that embraces bunolophodont taxa (*Moeritherium* and elephantiforms) and a clade that unites early lophodont taxa (*Phosphatherium*, *Daouitherium*, *Barytherium*, and *Numidotherium*). Based on few dental characters, this hypothesis appears highly tentative and would need to be further tested with additional material from the middle Eocene, which remains a poorly documented interval for terrestrial clades in Africa. The unexpected discovery of a proboscidean tooth makes the Togolese phosphate deposits even more valuable to

fill this major stratigraphic gap and demonstrates the great potential for new exciting discoveries in this undersampled part of the continent.

Material and Methods

3D reconstruction of the tooth - The specimen was imaged using high-resolution microtomography (μ CT) at the MRI platform of the *Institut des Sciences de l'Evolution de Montpellier* (ISE-M). Image segmentation of the tooth was performed on the μ CT images with Avizo.Lite 2019.4 (Visualization Sciences Group) software. The 3D virtual restoration and enamel thickness distribution maps were performed with MorphoDig software (v. 1.5.3; [47]). The virtually restored 3D model is deposited in MorphoMuseum [48].

Enamel microstructure - Enamel microstructures of *Dagbatitherium* and *Palaeomastodon* were studied combining light and SEM microscopies, following the protocol detailed in Tabuce et al. [49]. Observations are based on a vertical section on the mesial flank of the metaconid for *Dagbatitherium* and on the labial flank of the protocone for *Palaeomastodon*.

Phylogenetic analysis - A matrix of 202 characters and 18 taxa has been assembled to assess the phylogenetic position of the new Togolese species (SI Appendix). The core of this matrix is based on [9], with the addition of the recently described *Eritherium azzouzor* [4,7], *Omanitherium dhofarensis* [10], and the elephantiform *Eritreum melakeghebrekristosi* [50]. In order to take into account our morphological observations, and to highlight the anatomical diversity of the proboscidean lower molars, we have been led to modify five phylogenetic characters from [9] and add two

characters modified from [4] as well as several new characters (SI Appendix). The parsimony analysis was performed with the software PAUP* 4.0a169 [51] through a Branch Swapping heuristic search using the Tree Bisection Reconnection method (TBR; [52]) with 10,000 replications, random taxa addition, 100 trees held by replication and Accelerated Transformation optimization (ACCTRAN; [53,54]). Branch support has been quantified with Bremer support values [55].

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Figure legends

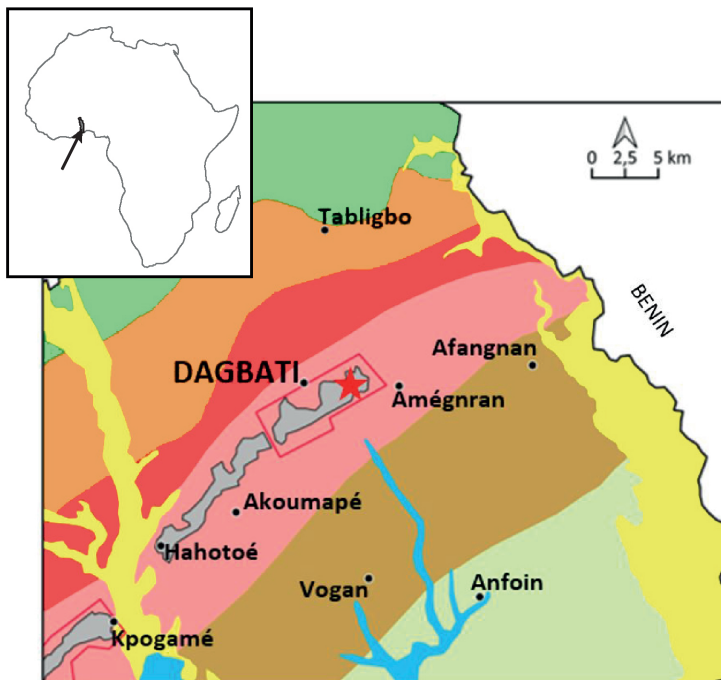
Figure 1 – (A) Map showing the geographic location and geologic setting of the Dagbati quarry. *Colour code*: dark green, Mesozoic; orange, Paleocene; red, Ypresian; pink, late Ypresian to Lutetian; brown, Bartonian; light green, Oligo-Miocene; yellow, Quaternary; grey, phosphate quarry. (B) Composite section described in this study and lithostratigraphy (see SI Appendix for detailed legends); the red star indicates the position of ULDG-DAG1 in the section. (C) Photo showing the fossil ULDG-DAG1 *in situ* in the phosphate deposits at the base of the section.

Figure 2 – 3D reconstructions of the molar ULDG-DAG1. The enamel is in grey, the dentine in yellow. A, B, and C, occlusal views; D and E, buccal views; F, lingual view; G and I, mesial views; H and J, distal views. C, I, and J; 3D enamel thickness distribution maps with spectral colors. The thickest enamel is represented in red, the thinnest enamel is represented in dark blue. Color scale: 0-1.85 mm. *Abbreviations*: dc, distal cingulum; end, entoconid; hyl, hypoconulid; hyd, hypoconid; if, interproximal facet; med, metaconid; msd, mesoconid; p. end, postentoconulid; p. med, postmetacristid; prd, protoconid; pr. end, pretentocristid. The dashed line indicates the crista obliqua. Scale bar represents 1cm.

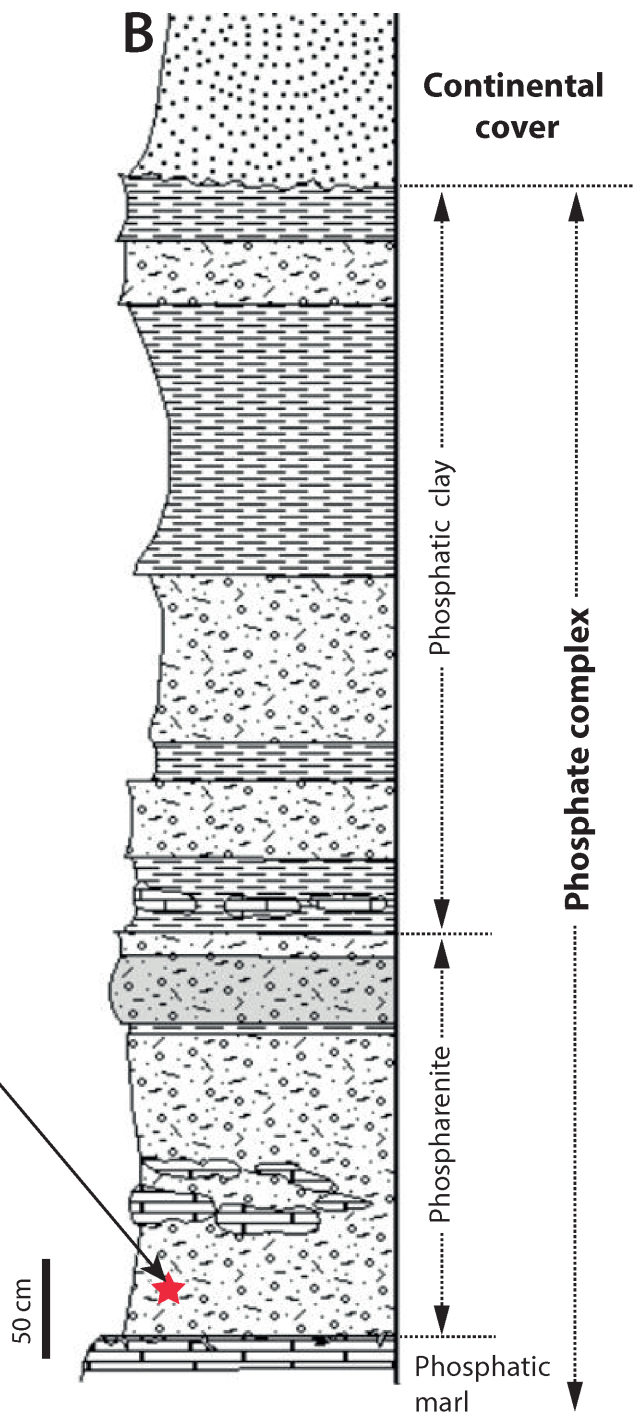
Figure 3 – Upper part, molar comparisons between a typical lophodont Eocene non-elephantiform (A, *Numidotherium*, UOK34), *Dagbatitherium* (B, ULDG-DAG1), and a bunolophodont primitive elephantiform (C, *Phiomia*, BMNH Coll C.W.A 1906,

image inverted). Same legend as Fig. 2. Number in italics represent character states, which are indicated here in the form: *Character^{state}*. Lower part, phylogenetic position of *Dagbatitherium tassyi* n. gen. n. sp. based on the topology of the strict consensus tree (see SI Appendix), which is here transposed onto a chronostratigraphical context (Neogene not to scale). Heuristic searches yielded 4 equally most parsimonious trees of 390 steps each (consistency index = 0.6387; retention index = 0.6966). The phylogenetic position of *Saloumia* follows [20], that of *Chilgatherium* follows [37]. The gray zone shows a long hiatus in their fossil record encompassing most of the Eocene. When known, the dental and enamel types are presented for each taxon. The number of lophids in each schematic lower dental pattern expresses differences between bilophodont, trilophodont (*Dagbatitherium*, *Chilgatherium*, *Phiomia*, and *Palaeomastodon*), and multi-lophodont (extant elephants) taxa. Differences in the development of bunodonty is expressed in the cuspid size. *Abbreviations*: D, ancestral node of Deinotheres; E, ancestral node of Elephantiformes.

A



B



C

