

Remarks on the cranium of *Eozygodon morotoensis* (Proboscidea, Mammalia) from the early Miocene of Africa, and the question of the monophyly of Elephantimorpha

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Abstract

Anatomical characters of the cranium of *Eozygodon morotoensis* from Auchas (early Miocene of Namibia) discovered by Pickford in 2003 are discussed. The characters of the hypothetical ancestral morphotype of the Mammutidae are checked in relation to the discovery in Africa of elephantiforms and mammutids in the late Oligocene and early Miocene, such as *Phiomia major* from Chilga, aff. *Phiomia* from Lokone, and *Losodokodon losodokius* from Losodok. The question of the monophyly or diphyly of the Elephantimorpha is raised once more; the hypothesis of monophyly is supported by a cladistic analysis mainly based on the cranial characters displayed by *Eozygodon morotoensis*. The paraphyly of Mammutidae is a result that implies further investigation.

Keywords

Cranial osteology, phylogenetics, *Eozygodon*, Mammutidae, Elephantimorpha, Proboscidea.

1. INTRODUCTION

The remarkable discovery of proboscideans in the early Miocene of Auchas (Namibia) by Pickford (2003), especially cranial remains of the mammutid *Eozygodon morotoensis* (Pickford & Tassy, 1980) allows for a re-examination of the cranial anatomy of the species, and induces new approaches on the debated questions of the basal dichotomies of Elephantiformes and of the monophyly of Elephantimorpha. On this topic, Pickford (2003) recalled the diphyletic hypothesis of Elephantiformes made first by Matsumoto (1924) followed by Tobien (1971, 1976, 1978) and Madden (1980): the zygalophodont (mammutids) and bunolophodont (gomphotheres) proboscideans of the Miocene evolved from the Paleogene genera *Palaeomastodon* and *Phiomia* respectively. Later this hypothesis was transformed, with *Phiomia* considered to be the stem of amebelodonts (shovel-tuskers) only among bunolophodonts (Borissiak, 1929; Osborn, 1936; Coppens *et al.*, 1978).

In contrast, Matsumoto (1927) himself later proposed a monophyletic origin for mastodons (mammutids), gomphotheres and elephants, the implied node being subsequent to the branching of both *Palaeomastodon* and *Phiomia*. Cladistic analyses further supported this hypothesis (Tassy, 1982, 1988, 1990a, 1996a) [an altered

variant of the hypothesis is the origination of the whole group from *Palaeomastodon* (Domning *et al.*, 1986)]. Among Elephantiformes, that is the clade including all proboscideans closer to elephants than to deinotheres, the Elephantimorpha (Shoshani *et al.*, 1998; Shoshani & Tassy, 2005) is composed of mastodons, gomphotheres and elephants. The first dichotomy of Elephantimorpha is: (Mammutidae, Elephantida), the taxon Elephantida being composed of gomphotheres *sensu lato*, stegodonts and elephants. A consensus has been reached on the monophyly of Elephantimorpha (= Elephantoides), as can be seen, for instance, in the classification of Proboscidea adopted by Sanders *et al.* (2010). Yet McKenna & Bell's (1997) classification of Mammalia had already raised a doubt, no Elephantiformes being recognized and no taxon comprising both Mammutoides and Elephantoides being retained or named.

In any case, the description of a late Oligocene fauna in Ethiopia with the association of paleomastodonts and gomphotheres (Sanders *et al.*, 2004), of an elephantiform somewhat "intermediate" between *Phiomia* and Elephantimorpha in the late Oligocene of Eritrea (Shoshani *et al.*, 2006), on the one hand; and, on the other, of primitive mammutids in the late Oligocene of Kenya (Rasmussen & Gutierrez, 2009) and in the early Miocene of Namibia (Pickford, 2003) brings new data which are

explored here. In particular more anatomical features of the cranium of *E. morotoensis* are described in the context of testing the respective putative synapomorphies of Elephantimorpha, Elephantida, and Mammutidae.

2. MATERIAL AND METHODS

The cranium AM 02 from Auchas is housed at the Geological Survey Museum of Namibia (Windhoek, Namibia). A cast (M 6014 MNHN) was made at the Muséum national d'Histoire naturelle (Paris) when the original specimen was stored for preparation and study (Fig. 1). Fortunately, the cranium is preserved three dimensionally and damaged parts can be reconstructed. During fossilization, the right side has been slightly compressed antero-medially, especially the basicranium; the zygomatic process of the frontal is crushed and the zygomatic process of the squamosal partially missing.



Fig. 1: *Eozygodon morotoensis*, Auchas, Namibia. Palate of cranium AM02 - Geological Survey Museum of Namibia, Windhoek, Namibia (original) during preparation at the Muséum national d'Histoire naturelle (MNHN) in Paris in 1998, and before the making of the cast M 6014 housed in MNHN. The right P4 is still *in situ*. Photograph by P. Tassy. Scale is given by the lens cap (diameter = 57 mm).

On the left side, the processus zygomaticus of the maxilla is pushed dorsally in the orbit. The jugal is missing on both sides. The dorsal border of the nasal fossa is damaged and the processus nasalis is broken; on the best preserved side (left) the bone is thin so that not much of the nasal is missing. Photographs of the original specimen are to be found in Pickford (2003, pls 2-3). In this article the drawings of the cranium (orientated in the alveolar plane, except the view of the basicranium) take into consideration the restoration (mainly based on symmetry) of the damaged and deformed parts (Figs 2-3). For comparative purpose, a cast housed at the MNHN of a cranium of the same size which belongs to *Mammut americanum* (Kerr, 1792) (original: MCZ 11107) from Hacketstown, New Jersey [first described by Warren (1855) and Osborn (1936)] is used. This perfect cranium belonged to an immature individual; it was sectioned by Warren (1855) in the sagittal plane to allow for a detailed description of the internal structure.

The phylogenetic analysis is an unweighted parsimony run with the Willi Hennig edition of TNT v.1.1 (Goloboff *et al.*, 2008), exact algorithm (implicit enumeration) with collapsing branches with no possible support ("rule 3": max length = 0). A posteriori weighting is run with TNT v.1.1 and also with Hennig86 (Farris, 1988) for old-fashioned options such as successive weighting which is different from the implied weighting of TNT.

Abbreviations: AM, Auchas Museum, Namibia; KNM, National Museum of Kenya; MCZ, Museum of Comparative Zoology, Harvard; MNHN, Muséum national d'Histoire naturelle, Paris.

3. CRANIAL CHARACTERS OF *EOZYGODON MOROTOENSIS*

The species *Eozygodon morotoensis* was originally described as *Zygodon morotoensis* by Pickford & Tassy (1980) from a dentition discovered by Bishop (1967) at Moroto, Uganda. More dental and postcranial material found at Meswa Bridge, Kenya, was allocated to this species, under the binom *E. morotoensis* (Tassy & Pickford, 1983). Both localities are early Miocene, Moroto being more recent than Meswa (Tassy, 1990b; Pickford & Senut, 2003; Sanders *et al.*, 2010) or equivalent in age, more than 20 Ma (Gebo *et al.*, 1997; Harrison & Andrews, 2009).

More recently, the early Miocene locality of Auchas (Namibia) yielded two crania (one is edentulous) described by Pickford (2003) so that the cranial features of *E. morotoensis* are no longer hypothetical. Pickford (2003) and Sanders *et al.* (2010) have already emphasized on the main characteristics: cranium high, basicranium flexed and shortened, rostral region narrow, occipital plate tilted forward, palate deep. The specimen AM 02 is indeed remarkable and is the basis of further considerations herein.

Dental age and dental displacement: This specimen AM 02 belongs to a young adult: M3 is just erupted and only slightly worn on the anterior side of the first loph (Fig. 1). Its dental age is XVII according to Tassy (1996c). This dental scale, based on trilophodont gomphotheres, applies partly here: in *Gomphotherium angustidens* (Cuvier, 1817), P4 is lost when M3 is erupted.

On the left side of the cranium from Auchas, P4 and M1 are missing and alveoli are in resorption, but on the right side P4 and M1 are retained (although P4 was already in the resorptive stage and fell from the socket during preparation); M1 is entirely worn (Fig. 1). Such dissymmetry in the wear on right and left dental arches is common in proboscideans. As a matter of fact, the P4 was described as a left one by Pickford (2003, pl. 2, fig. 3) because it was oddly-orientated: contrary to molars, in premolars the posterior half is more worn than the anterior half owing to the contact with the first lophid of m1 (moreover the shape and orientation of the lophs are clearly those of a right P4).

When M3 is entirely erupted, the retention of P4 (even if it occurs irregularly) is probably a plesiomorphous stage of the horizontal tooth displacement of *E. morotoensis* compared to gomphotheres.

Size and proportions: Among proboscideans with a continuous growth, such as elephants, the proportions of the cranium vary much during postnatal growth. Compared to adults, the palate and the face of juveniles are less enlarged (Eales, 1926; Van der Merwe *et al.*, 1995). The auditory bullae occupy much of the basicranium in the newborn while they are coiled in adults where the postglenoid and posttympanic regions of the squamosal and the paroccipital process of the exoccipital are much enlarged. It is the same in *M. americanum* (Osborn, 1936, figs 131-132).

The size of the adult cranium of *E. morotoensis* (measurements of AM 02 in Pickford, 2003: tabl. 3) is the same as that of a juvenile *M. americanum*. Sanders *et al.* (2010) consider that diminutive features (small teeth) do not alter the body size. Yet, speaking about the size of the skull, the cranium AM 02 belongs to a young adult (M3 erupted), c.24-26 years in African equivalent age [analogy with *M. americanum* equivalences established by Saunders (1977)]. It is comparable in dimension not to that of an adult *M. americanum* but to a juvenile (c.10 years) such as the one from Hacketstown (Warren, 1855; Osborn, 1936) with I2 in the socket, and dP4-M1 erupted. The proportions of both are different although superficially similar. In the adult cranium AM 02 of *E. morotoensis* the palatal and facial regions (Fig. 2A-C) are less elongated than in the adult *M. americanum*, proportions somewhat reminiscent of juvenile elephants and *M. americanum* (Osborn, 1936). Yet, in a young *M. americanum* the relatively reduced facial area compared to the cerebral area is a juvenile feature destined to change during postnatal ontogeny. The relatively short

face of adult *E. morotoensis* is due partly to the small size of the tusks (the right I2 is partially preserved on AM 02), comparable to those described at Meswa (Tassy & Pickford, 1983), a plesiomorphous trait inherited from Paleogene elephantiforms. The same conclusion can be drawn from the narrowness of the rostral trough of the premaxillae (*fossa incisiva*; not *fossa incisiva* or *foramen palatinum maxillae*) of *E. morotoensis*. In *E. morotoensis* the premaxillae are only slightly enlarged at the tip, and the tusks only slightly divergent (Fig. 2B-C, Fig. 3A). In *M. americanum* the flaring of premaxillae and maxillae is present, even in juveniles where the area of the rostral trough is short and the tusks not yet erupted or fully developed.

In this respect the primitive rostral trough of *E. morotoensis* is closer to that of gomphotheres with small or moderate tusks than to *M. americanum*.

Palate: The opening of the choanae is large, limited laterally by a high alisphenoid (Figs 2A-B, 3C). In lateral view (Fig. 2A), behind the alisphenoid is nearly at right angle to the palate. The pterygoid crest of the alisphenoid is much thickened in its palatine part (*hamulus pterygoideus*). Behind the M3, the maxilla (maxillary tuberosity of *processus alveolaris maxillae*) and the *processus pyramidalis* of the palatine bone are not enlarged, because of either the recent eruption of the molar or the primitive stage of horizontal displacement. The other skull of *Eozygodon morotoensis* found at Auchas is an edentulous skull where only the roots can be seen. In this second cranium (Pickford, 2003: pl. 5, figs 3-4) the palatine and the maxillary tuberosity are enlarged behind the last molar, probably due to the individual age of this specimen (older than dental age XVII). It can be concluded that in *E. morotoensis* the remodelling of the bone around M3 is still active.

As Pickford (2003) noticed, the palate is very deep between the molars, much more than in *M. americanum* and Elephantida in general. This is perhaps a specific trait of *E. morotoensis*. In connection with this morphology, on the lateral side, the alveolar part of the maxilla (*processus alveolaris maxillae*) is high above the molars, between the *margo alveolaris* and the *processus zygomaticus maxillae*.

As already stated, the maxilla and premaxilla are not enlarged so that the ventral area of the maxillae (*processus palatinus*) and the dorsal *fossa incisiva* of the premaxillae are narrow (Figs 2B, 3A). The *crista interalveolaris* is only slightly directed laterally (Fig. 2B), unlike *M. americanum* either juvenile or adult. In lateral view (left side) the curved premaxilla espouses precisely the shape of the tusk (Fig. 2A), the ventral concavity of which being much marked, as for the individual from Meswa Bridge (Tassy & Pickford 1983).

Orbital region and temporal fossa: The shape of the orbit in *E. morotoensis* is reminiscent of that of

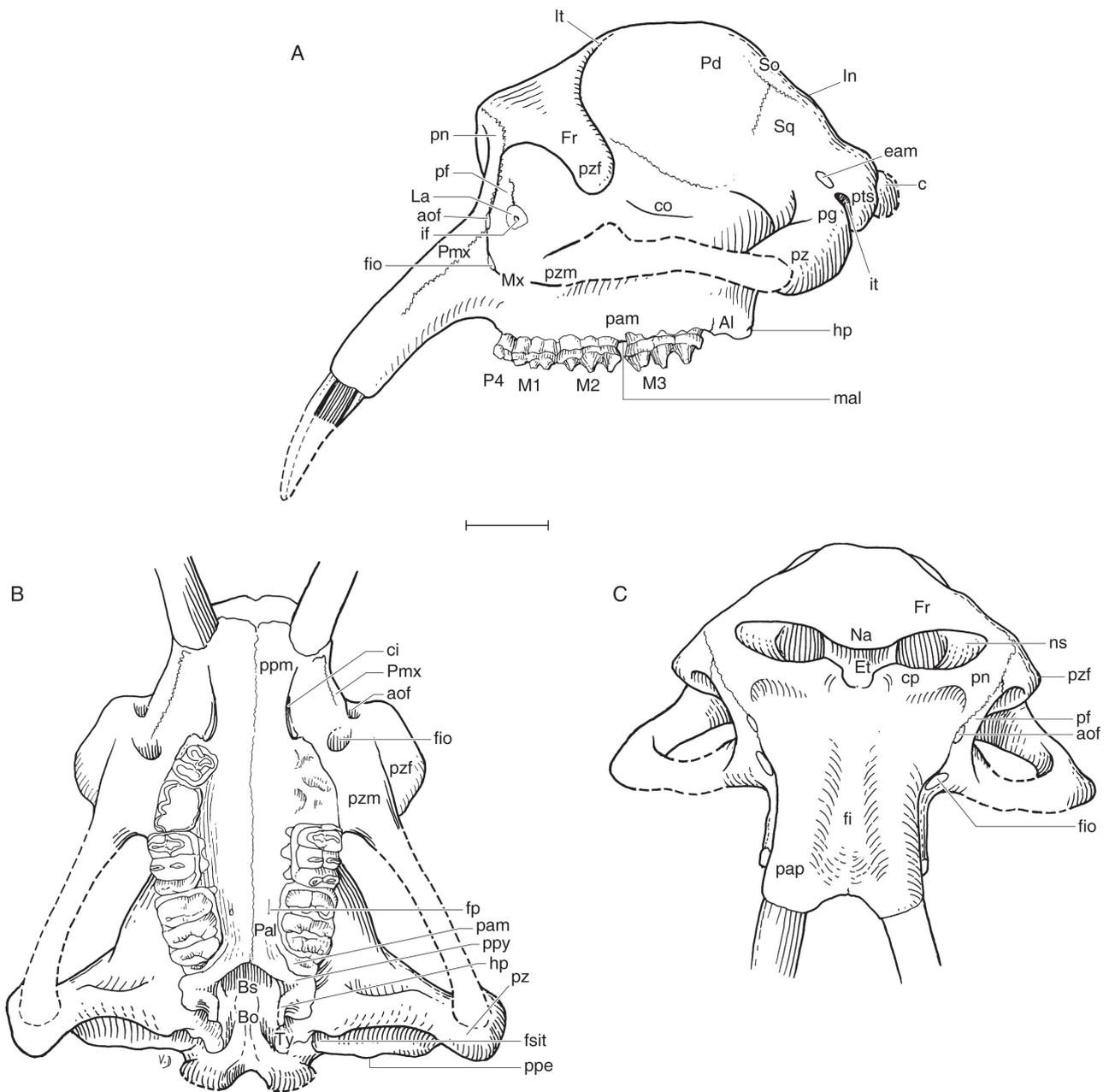


Fig. 2A-C: Reconstructed cranium of *Eozygodon morotoensis*, Auchas, Namibia, Early Miocene. A, lateral view; B, occlusal view; C, cranial view. Scale = 100 mm. Abbreviations: Al, alisphenoid; aof, ante-orbital foramen; Bo, basioccipital; Bs, basisphenoid; c, condyle; ci, *crista interalveolaris*; co, *crista orbitotemporalis*; cp, *corpus* of the premaxilla; eam, external auditory meatus; Et, ethmoid; fi, *fossa incisiva* (premaxilla); fio, *foramen infraorbitalis*; fp, *foramen palatinum major*; Fr, frontal; hp, *hamulus pterygoideus*; fsit, *foramen stylomastoideus* and fossa for insertion of the tympano-hyal; it, *incisura tympanica*; La, lacrimal; lf, lacrimal foramen; Lt, *linea temporalis*; ma, *margo alveolaris maxillae*; M1, M2, M3, first, second and third molars; Mx, maxilla; Na, nasal (*processus nasalis*); ns, nasal step of the premaxilla; P4, fourth premolar; Pa, parietal; Pal, palatine; pam, *processus alveolaris maxillae*; pap, *processus alveolaris* of the premaxilla; pf, *processus frontalis* of the maxilla; pg, postglenoid part of the squamosal; Pmx, premaxilla; pn, *processus nasalis* of the premaxilla; ppe, paroccipital process of the exoccipital; ppm, *processus palatinus* of the maxilla; ppy *processus pyramidalis* of the palatine; pts, poststypanic part of the squamosal; pz, *processus zygomaticus* of the squamosal; pzf, *processus zygomaticus* of the frontal; pzm, *processus zygomaticus* of the maxilla; So, supraoccipital; Sq, squamosal; Ty, tympanic.

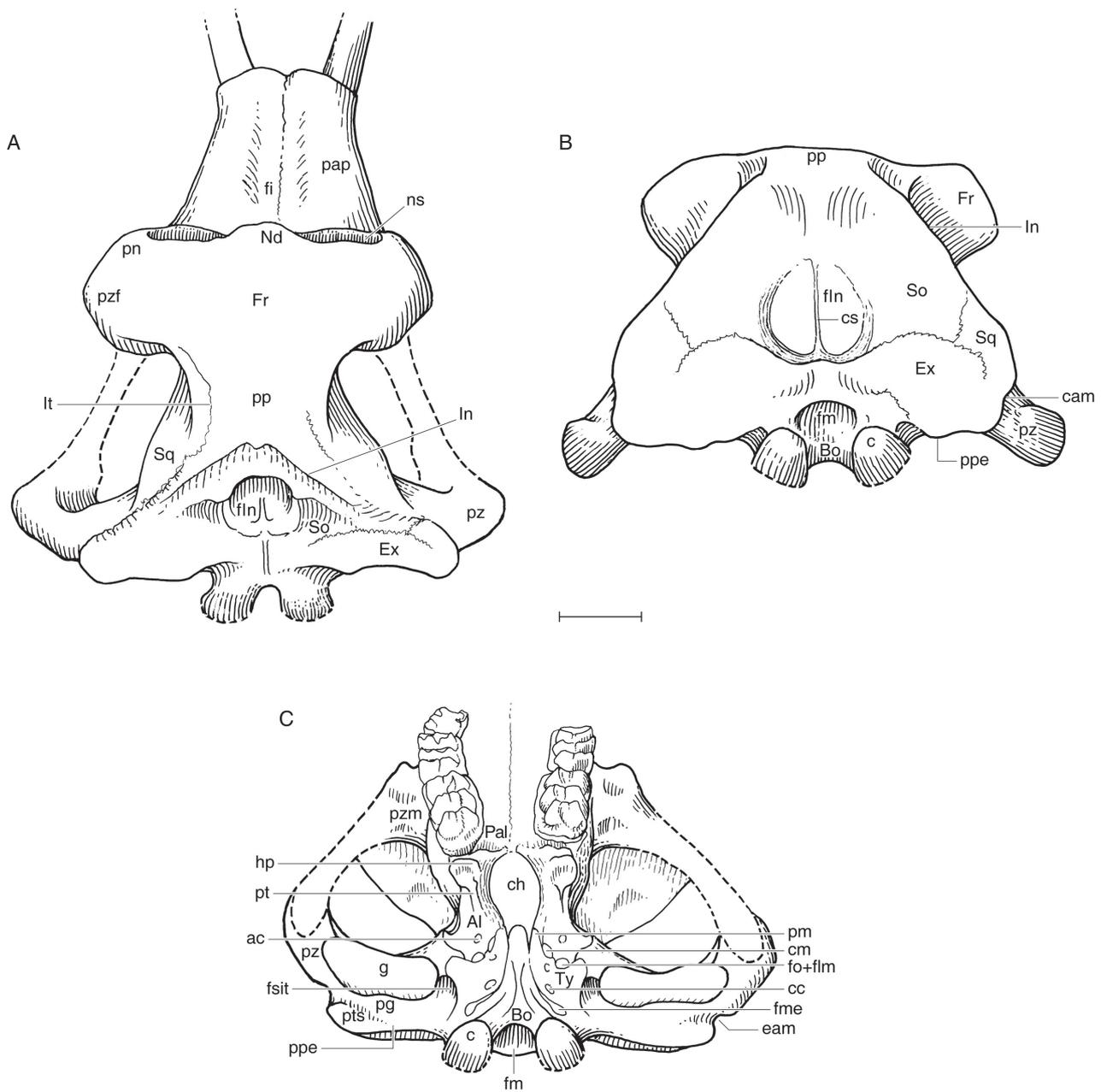


Fig. 3A-C: Reconstructed cranium of *Eozygodon morotoensis*, Auchas, Namibia, Early Miocene. A, dorsal view; B, occipital view; C, basicranium. Scale = 100 mm. Abbreviations: same as Fig. 2 and ac, alisphenoid canal (posterior opening); cc, *canalis caroticus*; ch, choanae; cm, *canalis musculotubarius*; cs, *crista sagittalis externa*; Ex, exoccipital; fm, *foramen magnum*; fln, *fossa for ligamentum nuchae*; fme, *foramen metoticum*; fo+flm, fused *foramen ovale* and *foramen lacerum medium*; g, *glenoid fossa (fossa mandibularis)*; pm, *processus muscularis* of the tympanic; pp, *planum parietale*; pt, *processus pterygoideus* of the alisphenoid.

M. americanum. It is high and narrow giving to the orbit a somewhat rectangular contour (Fig. 2A). It is even more rectangular than in the American mastodon. This difference is due to the straight anterior rim made by the *processus frontalis* of the maxilla which is very robust but not swollen. The *processus zygomaticus* of the frontal is inflated and so is the anterior part of the *crista orbitotemporalis*. In dorsal view (Fig. 3A) the lateral

protrusion of the processus is pronounced and sharp. The orbit contains a lacrimal bone with a lacrimal foramen, a primitive character which persists in *M. americanum* (Tassy, 1995: fig. 9). In the adult of *M. americanum* the limits of the lacrimal bone are barely visible (fused early with the frontal) unlike *E. morotoensis* where the bone is clearly delimited on the well-preserved right side. The ventral part of the orbit is composed of the maxilla

through a very robust *processus zygomaticus maxillae*. On both sides the jugal is not preserved. Yet, the flat surface of the insertion of the jugal on the squamosal is wide but does not seem to extend beyond the posterior border of the glenoid fossa.

Anterior to the orbit, the shape of the *processus frontalis* of the maxilla and of the *processus nasalis* of the premaxilla is peculiar. Both bones are not swollen as they are in *M. americanum* and Elephantida. On the contrary, they form a gutter which extends from a large *foramen infraorbitale* up to a smaller upper ante-orbital foramen (Fig. 2A, C). The presence of two ante-orbital foramina is a symplesiomorphy among members of Elephantiformes (Tassy, 1995, fig. 15B); the gutter-like *processus frontalis* of the maxilla is specific to *E. morotoensis*.

The temporal fossa is short (Figs 2A, 3A). This is due to the short longitudinal extension of the parietal and means that the cerebral part is not extended. Compared to gomphotheres and elephants, this is a primitive trait which persists in *M. americanum*. What is peculiar to *E. morotoensis* is that the fossa (although short) is high, as in *M. americanum*, and even relatively higher compared to the length of the cranium (owing to the short face of *E. morotoensis* already mentioned). The suture between squamosal and parietal is only partly visible on the left side. The temporal line (*linea temporalis*) is only slightly marked so that the limit between the fossa and the fronto-parietal roof is smooth. On dorsal view (Fig. 3A), the lateral suture between the frontal and the parietal is not seen. Nevertheless the *planum parietale* is relatively large. The temporal lines do not join.

The two openings of the alisphenoid canal can be located but due to the fossilization and preservation, the other foramina situated at the hind part of the *crista orbitotemporalis* cannot be observed.

The elevation of the cranium of *E. morotoensis* with a high temporal fossa has been emphasized by Pickford (2003). This means that mammutids developed a high cranium with a short temporal fossa, a unique combination compared to the wide temporal fossa of elephants and gomphotheres.

Nasal area: The nasal fossa is well preserved (Fig. 2A, C; Fig. 3A). It is moderately retracted (above M1) compared to *M. americanum* (above M2). It is separated from the rostral trough (*fossa incisiva*) of the premaxillae by a prominent thickened ridge, the *corpus* of the premaxilla [called “posterodorsal process of premaxilla” by Tassy (1994, 1995), and “*corpus* of the incisive bone” by Van der Merwe *et al.* (1995)] largely opened in the middle where the ethmoid cartilage inserts. This ridge is rather straight and its thickening is not due to the deepening of the *fossa incisiva* which is less hollowed than in either *M. americanum* or elephants.

The most remarkable features of the nasal fossa are its transversal extension and the shape of the *processus nasalis* of the premaxilla. In dorsal view, the aperture

extends laterally beyond a line that can be drawn from the ante-orbital foramen (it can be seen on the completely preserved left side with no deformation). This situation never occurs in *M. americanum*. In this species the width of the nasal fossa is known to be extremely variable (Osborn, 1936: figs 131-132; Tassy, 1994: fig. 4). However even in the individuals with a wide external aperture the width is inferior to that of *E. morotoensis*. Probably in connection with this extension, the medial surface of the *processus nasalis* of the premaxilla is enlarged. It makes a step-like internal border (Fig. 2C). This trait is absent in *M. americanum* (even in specimens with a large nasal fossa) and is reminiscent of the derived structure seen in elephants and some gomphotheres (Tassy, 1994: fig. 4). The plesiomorphous condition shared by *Phiomia* and primitive gomphotheres was considered as the persistence of an elephantiform trait in Mammutidae (Tassy, 1994: fig. 4; 1995). Yet, this conclusion must be modified. The derived morphology of *E. morotoensis* necessarily implies a homoplasy for this character.

Occipital region: In posterior view (Fig. 3B) the occipital has a peculiar triangular contour somewhat reminiscent of that of *Phiomia serridens* Andrews & Beadnell, 1902. This shape is due to the extraordinary enlargement of the squamosal and the relatively weak lateral extension of the supraoccipital. In that respect, *E. morotoensis* is very different from either *M. americanum* or Elephantida. For example, in early and middle Miocene taxa such as the amebelodontid *Archaeobelodon* aff. *filholi* from Mwit (Kenya) and the European gomphothere *Gomphotherium angustidens*, the contour of the occipital is rounder owing to the development of the supraoccipital (Tassy, 1986: pl. 3; Tassy, 2013: fig. 17) although the cranium is less elevated than in elephants. The fossa for the insertion of the *ligamentum nuchae* is large with a thin *crista sagittalis externa*.

The condyles are broken but their basis and the foramen magnum are preserved. In lateral view (Fig. 2A) they are on the same level as the lacrimal bone in the orbit. This is surprisingly high for an early Miocene proboscidean as stressed by Pickford (2003). Yet, it is less high than in elephants or gomphotheres such as *Anancus* where the condyles are in the same plane as the *p. zygomaticus* of the frontal. The reason is that in *E. morotoensis* the basioccipital is not flexed despite the great elevation of the alisphenoid wing. However, the condyles are located higher than in *M. americanum* where they are aligned with the *processus zygomaticus* of the maxilla (Osborn, 1936: figs 131-132).

Basicranium: The most striking feature of the basicranium (Fig. 3C) is the lateral extension of the zygomatic part of the squamosal and the enlarged glenoid fossa (*fossa mandibularis*). Although the width taken at the external border of the glenoid fossae is comparable

to that of a young *M. americanum* (dP4 in function and M1 erupted), the zygomatic arches are much extended. On the *processus zygomaticus* of the squamosal, the area of insertion of the jugal is enormous, thicker than in *M. americanum* and Elephantida. In contrast, the posttympanic part of the squamosal is longitudinally compressed, and the contiguous paroccipital process of the exoccipital is especially thin, in the shape of a crest: these proportions are retained in *M. americanum*, and differ in Elephantida where the exoccipital is bulging.

The auditory bulla is not extended laterally so that the glenoid fossa borders laterally the large fossa for the tympano-hyal. This fossa also contains the *f. stylomastoideum*, but its limits are not visible on the specimen. The fossa is so large so that one cannot entirely exclude the presence of a *canalis temporalis* such as occurs in *Moeritherium* and *Phiomia* (Tassy, 1981) – a structure lost in *M. americanum* and all other known elephantimorphs. Yet, if this canal exists its contour is not seen owing to preservational factors.

Anterior to the bulla, a large antero-posteriorly extended foramen corresponds to the *f. ovale* + the *f. lacerum medium*. Medial to this double foramen, the anterior crest of the bulla (*processus muscularis*) bears a distinctive elongated foramen for the Eustachian tube (*canalis musculotubarius*). On the medial surface of the bulla, the carotid foramen (*canalis caroticus*) is clearly separated from the basioccipital. Posterior to the tympanic bulla, a large slit filled with matrix corresponds to the *foramen metoticum* (including *canalis hypoglossi*), but there is no trace of a distinct condyloid foramen.

In conclusion, the proportions of the auditory bulla are reminiscent of that of the Paleogene genus *Phiomia* (Andrews, 1906: pl. 12; Tassy, 1981: pl. 6) and (to a lesser extent) of gomphotheres such as *Gomphotherium angustidens* (Tassy, 1995: fig. 5). The lateral extension of the tympanic bulla seen in elephants and (to a lesser extent) in *M. americanum* must have evolved independently.

As emphasized by Pickford (2003), the basicranium is high compared to the alveolar plane (Fig. 2A). This angulation is mainly due to the height of the alisphenoid wing. The rest of the basicranium is not inclined in the same plane as the alisphenoid but forms an acute angle with it. This morphology is seen in *M. americanum* (Osborn, 1936) and is different from that of elephants and gomphotheres of the tetralophodont grade characterized by an elevated basicranium such as *Anancus*. From this viewpoint, the cranial mammutid morphology is already present in early Miocene species such as *E. morotoensis*. In early and middle Miocene gomphotheres such as *G. angustidens* (Tassy, 2013: fig. 13), the alisphenoid and the basicranium are lower and in line with respect to the alveolar plane, a primitive condition.

Dentition: The dentition of the cranium from Auchas (Figs 1, 2A-B) is identical to these of the two individuals

described at Moroto and at Meswa Bridge (Pickford & Tassy, 1980; Tassy & Pickford, 1983; Pickford, 2003). The three dentitions differ only in minute details that can be interpreted as individual variation or even as stages of wear (e.g. the crenulated thin pretrite crests are only seen on germs or fresh teeth, and are rapidly removed by wear, giving to such teeth a somewhat more lophodont appearance).

The youngest specimen in individual age is the holotype from Moroto (m3 is a germ), the oldest is the specimen from Meswa Bridge (the third loph of M3 shows wear facets). No difference can be seen between these individuals, in the strength of the cingulum or the zygodont crests. Auchas and Meswa differ in respect to the enlargement of distocrista and postcingulum of M3. At Auchas the distocrista is a thinly serrated crest on the pretrite posterior side of the third loph; the crest joins a unique bulbous posttrite cingular cusp. At Meswa the distocrista is bulbous and continuous with the posttrite cingular cusps, making the posterior side of the molar more like an incipient 4th loph. The important variation in the development of the last loph and postcingulum on M3s of Neogene elephantimorphs has long been known, including late mammutids such as *M. americanum* described by Cuvier (1821). As a consequence, no evolutionary significance can be safely attributed to the different shapes of the postcingulum area of the M3s from Auchas and Meswa.

The upper tusks from Auchas and Meswa are similar, with a strong ventral curve. They bear a lateral enamel band. The transverse section is rounder at Auchas with less marked dorsal and ventral sulcus. The presence of these two sulci (an unusual character for upper tusks of Neogene proboscideans) is perhaps a specific trait of *E. morotoensis*.

4. BRIEF SUMMARY ON MIOCENE AND LATER TAXA

While the osteology of *M. americanum*, the last species of the mammutid lineage, is well documented, that of the commonest Miocene Eurasian *Zygodontopsalis turicensis* (Schinz, 1824) is still a mystery. A possible synonym is *Mastodon atavus* Borissiak, 1936 from the Miocene of Kazakhstan (see Tobien, 1973; Tassy, 1990b); in that case the mandible (longirostrine) and most of the skeleton are known but not the cranium (Borissiak, 1936). One skull of *Z. turicensis* from the middle Miocene of Villefranche d'Astarac, France, with long face and long mandibular symphysis (Pontier, 1926) appears to be largely reconstructed (Duranthon *et al.*, 1995; Heizmann *et al.*, 1996), especially the upper rostral trough (*fossa incisiva*) and the symphysis of the mandible. A contemporaneous isolated mandible from Freising (Germany) allocated to *Z. turicensis* with a moderately extended symphysis (Osborn, 1936) was destroyed during World War II.

Zygodolophodon aegyptensis Sanders & Miller, 2002, an early Miocene African species is known from four molars only (Sanders & Miller, 2002) while the hypodigm of the late Oligocene *Losodokodon losodokius* Rasmussen & Gutierrez, 2009 includes six teeth (Rasmussen & Gutierrez, 2009). The late Miocene mammutids named *Mammut* cf. *borsoni* (Hays, 1834) or *Mammut obliquelophus* Mucha, 1980 (see Markov, 2008) are close to the much transformed Pliocene species *M. borsoni*, and this taxon gives no more clue than *M. americanum* to the elucidation of the morphology of the ancestral morphotype of mammutids.

5. LATE OLIGOCENE DISCOVERIES

Chilga: The late Oligocene fauna of Chilga, Ethiopia (Kappellmann *et al.*, 2003; Sanders *et al.*, 2004) has an association of taxa known both in the Fayum and in Neogene sites. The four species described at Chilga [*Phiomia major*, aff. *Palaeomastodon* sp. (two species) and cf. *Gomphotherium* sp.] are represented by numerous teeth but unfortunately no skull or partial skull (Sanders *et al.*, 2004). Yet the occurrence of cf. *Gomphotherium* sp. (four teeth: P4, p4, m2, m3) implies that the differentiation of gomphotheres [that is Elephantida in Shoshani *et al.*'s (1998) cladistic classification] had occurred as early as the late Oligocene.

Dogali: The bunolophodont *Eritreum melakeghebrekristosi* Shoshani *et al.*, 2006 described from the late Oligocene Formation of Dogali, Eritrea, circa 26.8 Mya, is somewhat intermediate between *Phiomia* and *Gomphotherium* (Shoshani *et al.*, 2006). The species is based on only one specimen, a partial mandible with right and left m2, left m3. Its size fits with that of the largest *Phiomia* (Shoshani *et al.*, 2006: fig. 4). The pretrite trefoils are as well developed as in gomphotheres. The small m3 is closer to gomphotheres with an incipient 4th lophid, more derived than in any known m3 of *Phiomia* (derived) and even slightly more developed than the 4th lophid of cf. *Gomphotherium* sp. from Chilga (Shoshani *et al.*, 2006: fig. 3; Sanders *et al.*, 2004: fig. 16B). The striking character of *Eritreum melakeghebrekristosi* is the alleged horizontal tooth displacement (Shoshani *et al.*, 2006), a synapomorphy of Elephantimorpha. This developmental character is a conjecture based on the state of wear of m2 together with non erupted m3, and unfilled alveoli of m1. Although this conclusion is likely, the loci of p3-p4s – a crucial trait – are not preserved on the mandible from Dogali.

Losodok and Lokone: The mammutid *Losodokodon losodokius* Rasmussen & Gutierrez, 2009 is recognized in the late Oligocene of Kenya, at Losodok (Rasmussen & Gutierrez, 2009). This is the oldest known mammutid so far. This species demonstrates that the differentiation

of mammutids had already occurred at early as the late Oligocene.

The hypodigm of *L. losodokius* consists of only six molars and premolars and demonstrates how difficult it is to interpret isolated teeth. Two complete fourth premolars are described by Rasmussen & Gutierrez (2009: fig. 11) as one upper and one lower. From the illustration, I interpret both teeth as upper premolars. One, only slightly worn on the second loph (KNM-LS 18214; Rasmussen & Gutierrez, 2009: fig. 11C) is left and the other, just a little more worn (KNM-LS 18212; Rasmussen & Gutierrez, 2009: fig. 11D), is right. Three characters seen on both premolars support this view: 1) premolars from Losodok are nearly quadrangular as are P4s; p4s of all known elephantiforms (that is *Palaeomastodon*, *Phiomia*, cf. *Gomphotherium* sp. from Chilga, and Neogene taxa) are relatively narrow compared to P4, and the anterior lophid is not enlarged; 2) on P4 the pretrite halflophs are anteriorly displaced compared to the posttrite ones, so that KNM-LS 18212 is a right P4 and KNM-LS 18414 a left P4; 3) as noted above for the P4 of *E. morotoensis*, on upper premolars, contrary to molars, the hind part is always worn first, owing to the occlusion with the anterior lophid of m1 (which erupts earlier than the premolars), and this is the case for the premolars from Losodok.

This emendation is a detail but as an upper premolar KNM-LS 18212 matches perfectly with the right P4 of the holotype of *E. morotoensis* (Pickford & Tassy, 1980: fig. 4-2a). This means stasis in the evolution of the P4 between *L. losodokius* and *E. morotoensis*.

The molars of *L. losodokius* compare closely with *E. morotoensis*. Only a few differences can be found. At Losodok, as shown by Rasmussen & Gutierrez (2009: fig. 10) the hind part of the M3 is narrower than in *E. morotoensis*, a somewhat more derived character. The M2 of *L. losodokius* also has a narrow third loph with a sagittally inflated postcingulum, in contrast to the square morphology of *E. morotoensis* at Moroto, Meswa and Auchas. Unfortunately Rasmussen & Gutierrez (2009: fig. 10) compare this molar with KNM ME 18 of *E. morotoensis* from Meswa, which is a m2 and not a M2, as described by Tassy & Pickford (1983: figs 4, 7). In fact KNM ME 18 occludes with the M2 KNM ME 16 (same individual), and on this M2 the third loph does not taper posteriorly.

In any case, from the viewpoint of the crown morphology, the molars of both species show the same interlophs with weak or absent pretrite trefoils.

The size of the P4 and M2 fits with that of *E. morotoensis* (Rasmussen & Gutierrez, 2009: tabl. 6; Pickford & Tassy, 1980: tabl. 1). The P4 is the same as that of the holotype of the middle Miocene *Zygodolophodon turicensis* (Pickford & Tassy, 1980: tabl. 1). The M3 of *L. losodokius* (length = 92.26 mm according to Rasmussen & Gutierrez, 2009) is smaller than the M3 of *E. morotoensis* (109.3–114.5 mm according to Tassy & Pickford (1983: table 2) and Pickford (2003: table 2). This diminutive size could

Table 1: Description of the seventeen characters (numbered 0-16) and character-states, used for the parsimony analysis (see also data matrix Table 2).

- 0= antero-posterior compression of lophids absent (0), present (1)
 1= posttrite zygodont crests absent (0), present (1)
 2= horizontal tooth displacement absent (0), present (1)
 3= pretrite central conules weak (0), large (1)
 4= trilophodonty with postcingulum on M3 and tetralophodonty with postcingulum on m3 absent (0), present (1)
 5= on lower molars antero-lingual cingulum of first lophid present (0), reduced (1), fused with lingual cuspid (2)
 6= external nasal aperture retracted above premolars or limit P4/M1 (0), above M1 (1), above M2 (2)
 7= cranial vault low (0), high (1)
 8= vertical extension of the alisphenoid wing (=“high basicranium”) absent (0), present (1)
 9= rostrum of the premaxilla narrow (0), enlarged (1)
 10= cerebral development of squamosal and supraoccipital absent (0), present (1)
 11= lacrimal foramen present (0), absent (1)
 12= insertion for the mesethmoid cartilage long (0), short (1)
 13= at the basis of the nasal fossa, corpus of the premaxilla low (0), high (1)
 14= in the nasal fossa, processus nasalis of premaxilla straight (0), enlarged with a step-like shape (1)
 15= lateral development of the zygomatic process of the squamosal strong (0), reduced (1)
 16= lateral extension of the auditory bulla absent (0), present (1)

be interpreted as a primitive character, but the shape of the hind part with a narrow third loph seems more derived than in *E. morotoensis*. Perhaps the shape of the hind part of both M2 and m3 of *L. losodokius* is a specific character.

At Lokone, in the same region (Lake Turkana, Northern Kenya), from a comparable horizon (late Oligocene), Ducrocq *et al.* (2010) describe a m2 of “aff. *Phiomia*”. This m2 displays a reduced antero-lingual cingulum at the base of the first lophid, as in Neogene mammutids and gophotheres.

6. PHYLOGENETIC IMPLICATIONS

Understanding the phylogenetic impact of *E. morotoensis* and newly found Oligocene elephantiforms is equivalent to testing the alternative hypotheses: diphyletic or monophyletic origin of Elephantimorpha. Particularly, several synapomorphies among the thirteen labelled as “unambiguous” for Elephantioidea (here Elephantimorpha) by Tassy (1996a: tabl. 6-1) can be checked through a parsimony analysis (Tables 1, 2; Figs 4-6).

The cranial characters observed in *E. morotoensis* partly alter what was previously thought about the traits of the respective ancestral morphotypes of Elephantimorpha, Elephantida and Mammutidae. The zygolophodont tooth pattern is shared by *E. morotoensis*, *L. losodokius* and other mammutids such as *M. americanum*. Yet, this tooth pattern has in common with *Palaeomastodon beadnelli* only the weak development of central conules [character 3(0) of Tables 1, 2], a plesiomorphous state among elephantiforms and not a zygolophodont derived trait. Hence, the clade (*Palaeomastodon*, Mammutidae) is not supported.

Table 2: Data matrix of the Elephantiformes. See list of characters in Table 1.

hypothetical ancestor	0000000000000000
<i>Palaeomastodon beadnelli</i>	00000000000000?0?
<i>Phiomia serridens</i>	00000100000000000
<i>Phiomia major</i>	00?000???????????
Aff. <i>Phiomia</i>	00?0?2???????????
<i>Eritreum melakeghebrekristosi</i>	001112???????????
<i>Mammut americanum</i>	11101221111011011
<i>Losodokodon losodokius</i>	11?01???????????
<i>Eozygodon morotoensis</i>	11101211100011100
Elephantida	00111221011111111

Methodological questions

This analysis emphasizes the impact of the anatomical traits observed in *E. morotoensis*. It is based on seventeen mostly preserved characters (eleven cranial) applied to ten terminal taxa. Although the few characters observed on the new late Oligocene African taxa do not bring much information, but instead emphasize the lack of observable characters, they are introduced here since this paper focuses on their phylogenetic meaning. Yet the analysis is limited to only a few taxa and characters. As such it aims to bring more precise information in respect to the problem (monophyly, or not, of Elephantimorpha), than an analysis of the members of the entire order Proboscidea, which would include a massive proportion of unknown data with problematic optimizations. In contrast, current phylogenetic practices support the addition of numerous taxa and characters, in fact as many as possible. The result of such a choice is rather an uninformative exercise based on the optimizations of “?”. The use of gigantic matrices is a trend which can be criticized on several grounds (Simões *et al.*, 2017). The choice of a minute analysis of pertinent characters

associated with one identified phylogenetic question is here felt to be entirely justified. Less is more. In relation to molecular practices currently forcefully advised for morphological analyses (Puttick *et al.*, 2017), the size of the matrix (17 characters x 10 terminal taxa) – among other reasons – precludes also any Bayesian analysis.

The trees are rooted with a hypothetical ancestor that bears character states coded from a comparison with non-elephantiform proboscideans (*Phosphatherium*, *Barytherium*, *Moeritherium*, *Prodeinotherium*) with known cranial features mainly described and/or coded by Harris, 1973; Tassy, 1981; Huttunen, 2004; Gheerbrant *et al.*, 2005; Delmer, 2009.

The terminal taxon Elephantida (that is, the clade made of gomphotheres and elephants) is not problematic and has not recently been questioned. Hence, the character states of Elephantida (Tabl. 1) are a combination of characters observed in various taxa: the stem species *Gomphotherium annectens*, and other members of *Gomphotherium* “*annectens* group” and of *Gomphotherium* “*angustidens* group” for characters unknown in *G. annectens* (Tassy, 1994, 1996b, 2013; Gasparik & Markov, 2009; Göhlich, 2010).

The analysis does not rule out the monophyly of Elephantimorpha. The node Elephantimorpha (Fig. 4) is a polytomy largely due to the numerous unknown characters listed in aff. *Phiomia* from Lokone and

L. losodokius from Losodok. The genus *Phiomia* is polyphyletic but none of its three terminal taxa is closer to Elephantida. The variation of the reduction of the anterolingual cingulum on lower molars (character 5) explains this pattern. The most derived condition [character 5(2)] is present in aff. *Phiomia* (Ducrocq *et al.*, 2010) but not in *Phiomia major* (Sanders *et al.*, 2004). *Phiomia serridens* (type species of the genus, including *P. wintoni*) appears to be closer to Elephantimorpha on the basis of the intermediate state 5(1) of this character. Implied weighting run with TNT does not change the number of equally parsimonious trees (sixteen). The same result is reached by the successive weighting run with Hennig86. As a consequence, the pattern of the consensus tree remains the same (Fig. 4).

An analysis restricted to taxa which contain at least one third of the characters, that is, six terminal taxa (*Palaeomastodon beadnelli*, *Phiomia serridens*, *Eritreum melekeghebrekristosi*, *Mammuth americanum*, *Eozygodon morotoensis*, and Elephantida) yields only one tree, with the same pattern (Fig. 5). The explanation is simple: the tree is basically structured by synapomorphies devoid of ambiguous optimization, and the noise is not important: taxa with missing data such as *Phiomia major*, aff. *Phiomia* and *L. losodokius* only reduce resolution and create ambiguity in optimizations, but little contradiction.

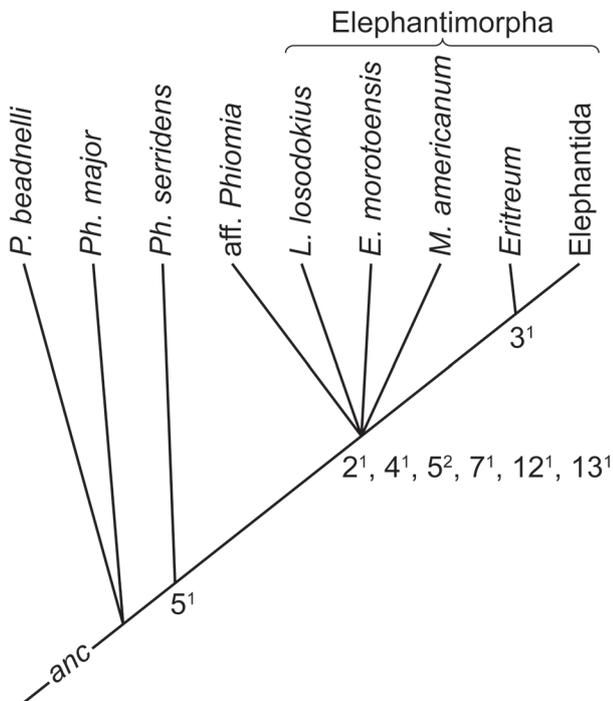


Fig. 4: Elephantiformes: strict consensus tree of the 16 equally parsimonious trees of 23 steps (ci = 82, ri = 86) based on 10 taxa and 17 characters (see Table 2). Listed apomorphies are non ambiguous and non homoplastic (ri = 1). (Parsimony analysis with exact algorithm ie of TNT, multistate characters additive).

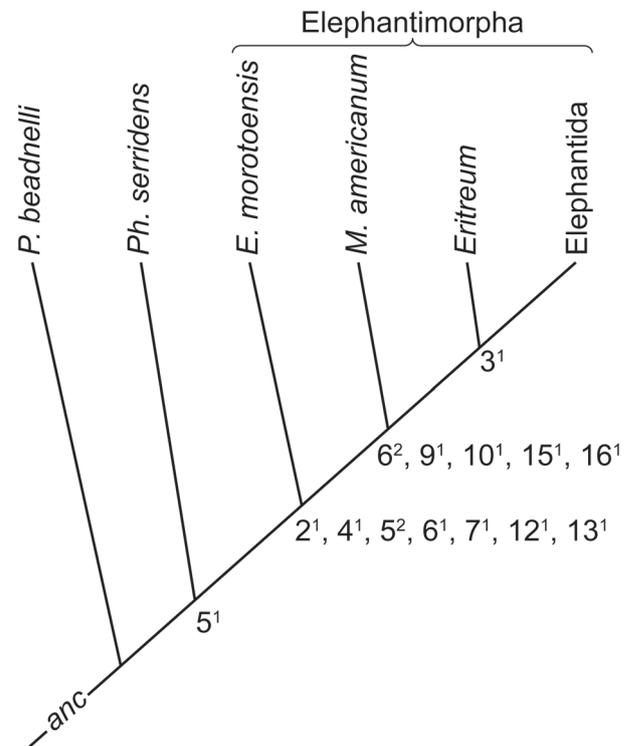


Fig. 5: Elephantiformes: tree based on 7 taxa and 17 characters (only one parsimonious tree, 23 steps, ci = 82, ri = 84). Listed apomorphies are unambiguous and non homoplastic (ri = 1). (Parsimony analysis with exact algorithm ie of TNT, multistate characters additive).

Analysis of the result

The clade Elephantimorpha: The Elephantimorpha (Fig. 4) is supported by six characters. Two are dental, the trilophodonty of M3 and tetralophodonty of m3 [4(1)] ($ri = 1$), and the entire reduction of the antero-lingual cingulum of lower molars [5(2)] ($ri = 1$). This latter character was previously supposed to diagnose unambiguously the Elephantimorpha (Tassy, 1994). Here it is an additive multistate, with state 5(1) being a trait of the clade (Elephantimorpha, *Phiomia serridens*) because some rare molars of *Phiomia serridens* already show the derived elephantimorph condition according to Ducrocq *et al.* (2010). In this study, this polymorphic state of *P. serridens* is understood as an intermediate state, and it is the only character that supports sister group relationships between *P. serridens* and Elephantimorpha. This node collapses when the character is coded non additive.

Among the other characters one is the horizontal tooth displacement [2(1)] ($ri = 1$), the others are cranial characters: high cranial vault 7(1)] ($ri = 1$), short mesethmoid cartilage in the nasal fossa [12(1)] ($ri = 1$), high corpus of the premaxilla at the base of the nasal fossa [13(1)] ($ri = 1$).

In the nasal fossa, the enlargement of the *processus nasalis* of the premaxilla [14(1)] ($ri = 0$) is homoplastic, with either convergence in *M. americanum* and (Elephantida, *Eritrea*), or an elephantimorph synapomorphy with reversal in *E. morotoensis*.

In the restricted analysis (Fig. 5) a seventh unambiguous synapomorphy of *Eozygodon morotoensis* and other elephantimorphs is the retracted nasal fossa above M1 [6(1); $ri = 1$]. In contrast, the two derived states 5(1)(2) ($ri = 0.66$) are ambiguously optimized on the polytomy.

The clade (Elephantida, *Eritreum*): The late Oligocene species *Eritreum melakeghebrekristosi* is the sister group of Elephantida [on both analyses (Figs 4,5)] based on one dental character, the enlargement of pretrite central conules [3(1)] ($ri = 1$).

Problematic Mammutidae: A remarkable result is the paraphyly of Mammutidae (Figs 4, 5). Among the 16 trees summarized by the consensus tree (Fig. 4), none includes a clade consisting of (*Eozygodon*, *Losodokius*, *Mammut*). It recalls the unweighted parsimony analysis of Proboscidea (39 terminals) by Shoshani (1996).

Here, the zygolophodonty (two dental characters) is not sufficient to recognize Mammutidae as a clade. If the characters that diagnose zygolophodonty (0 and 1) are given an a priori weight of 3, the Mammutidae becomes monophyletic, sister group of (Elephantida, *Eritrea*). This would content most students in proboscidean systematics. Yet, such a weighting should not be used to force the monophyly of Mammutidae, but should be based on some rationale. For instance, one may score separately each postcanine tooth, but both zygolophodont traits, compression of the loph(ids) and zygodont posttrite

crests, appear simultaneously on the different teeth, with no gradient. It is likely that this morphological pattern is a trait of the dentition. It has long been known (Butler, 1956; Jernvall & Thesleff, 2000) that molar traits, especially related to development, frequently apply to the whole dentition, and not separately to each molar and/or premolar. Hence the same morphology is here described once for the whole series of premolars and molars.

The paraphyly of Mammutidae is explained by the discrepancy of the cranial characters of *E. morotoensis* when compared to both *M. americanum* and Elephantida – characters that are unknown in *Eritreum*, the sister group of Elephantida.

M. americanum share with Elephantida (Fig. 4) the retraction of the nasal fossa above M2 [6(2)], an enlarged premaxilla [9(1)], an enlarged squamosal and supraoccipital in the cerebral area [10(1)], a reduced zygomatic part of the squamosal [15(1)], a lateral extension of the auditory bulla, even if it is moderate compared to elephants [16(1)]. The primitive state of all these characters is retained by *E. morotoensis*. Relatively to these five characters ($ri = 1$) the two zygolophodont characters [0(1) and 1(1)] are fully homoplastic ($ri = 0$), either a trait of Elephantimorpha with a reversion in (Elephantida, *Eritrea*), or a convergence in *E. morotoensis* and *M. americanum* (Fig. 6A-B).

When all taxa are analysed, Elephantimorpha becomes a polytomy (Fig. 4). In that case, not only the two zygolophodont characters but all conflicting characters (0, 1, 6, 9, 10, 15, 16) are homoplastic and ambiguous, optimized as state 0 or state 1 for Elephantimorpha.

More data are needed to elucidate the Mammutidae enigma. More generally, much of the evolution of the cranium of elephantiforms can be considered a priori as strongly affected by homoplasy, but the same can apply for dental traits. Do bunolophodont features derive from a zygolophodont ancestral morphotype, or is only the reverse plausible? Based on the present state of knowledge, both are equally likely. This question evokes that of other Palaeogene Proboscidea when bunodont and lophodont taxa coexist, such as *Erethium*, *Phosphatherium*, *Moeritherium*, *Arcanatherium* and *Omanitherium* (Gheerbrant *et al.*, 2005; Gheerbrant, 2009; Delmer, 2009; Seifert *et al.*, 2012). From this viewpoint, *Moeritherium* is peculiar and informative: it exemplifies the problem since it includes lophodont and bunodont species (Delmer *et al.*, 2006).

7. CONCLUSION

The cranium of *Eozygodon morotoensis* displays a peculiar mosaic of characters. Among Elephantiformes, the individuality of *E. morotoensis* compared not only to *Mammut americanum* but also to *Phiomia serridens* and to Elephantida is the main innovation resulted from study of the cranium from Auchas (Namibia).

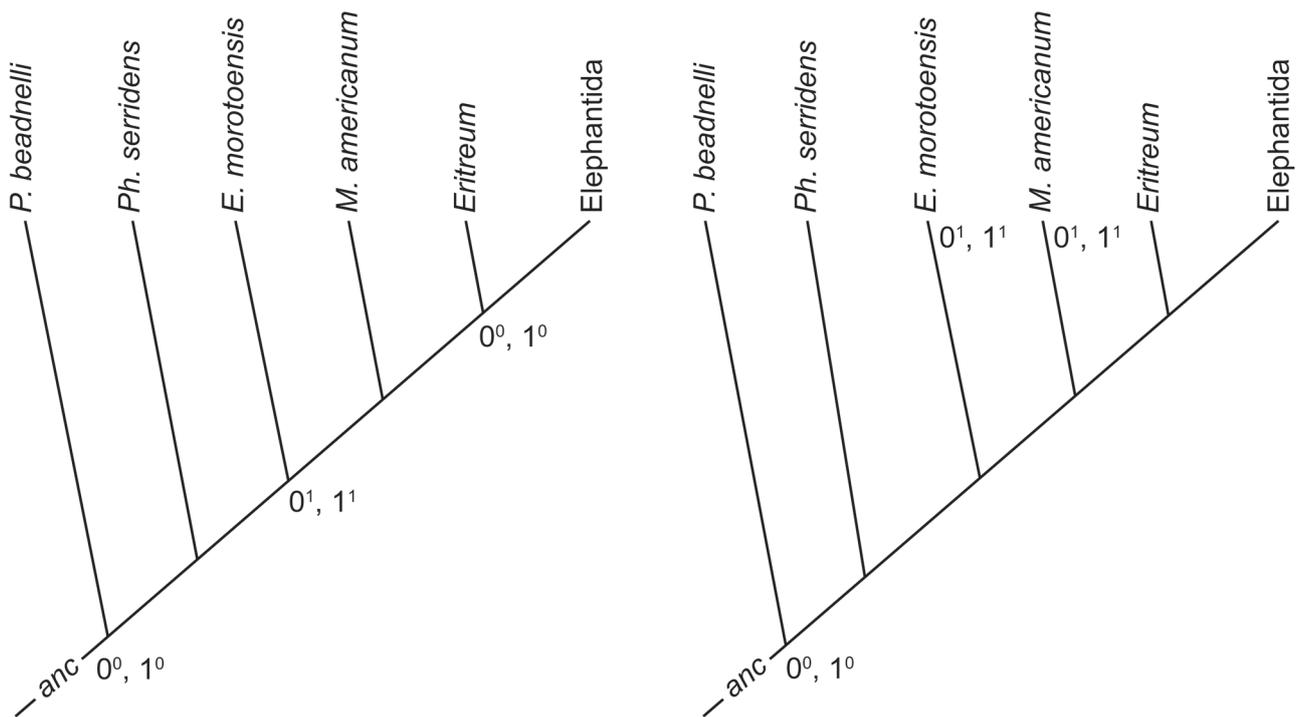


Fig. 6: Ambiguous optimizations (four steps) of the zygolophodont characters (0, 1 – see Tables 1-2) on the tree based on 7 taxa and 17 characters (Fig. 4). 6A, zygolophodonty as a derived condition for Elephantimorpha and reversal to a bunodont condition in (*Eritreum*, Elephantida); 6B, zygolophodonty as a convergence between *Eozygodon* and *Mammut*.

Although the monophyly of Elephantimorpha cannot be ruled out on the basis of the anatomy of *E. morotoensis* and from the few dental characters described in late Oligocene elephantiforms, several putative synapomorphies of Elephantimorpha previously proposed should be abandoned. They concern the reduced zygomatic part of the squamosal, the auditory bulla, the retraction of the nasal fossa above M2, the cerebral development of squamosal and exoccipital (which implies a homoplasy for the inflated temporal fossa), and the enlargement of the premaxilla.

Other characters seen on the Auchas specimen were not included in the parsimony analysis because of uncertainty. They merit future re-examination. For instance, one is the loss of the *canalis temporalis* system, a probable synapomorphy of Elephantimorpha. However, one cannot be a hundred per cent sure about the presence or absence of the canal in *E. morotoensis*. The same conclusion can be drawn about the independence or (more likely) the confluence of the *foramen ovale* and *foramen lacerum medium* in *E. morotoensis* and, as a consequence, in the ancestral morphotype of Elephantimorpha.

Nevertheless, the hypothesis of a diphyletic origin of elephantimorphs with a sister group relationships between *Palaeomastodon* and Mammutidae (no known synapomorphy so far) is unwarranted. The paraphyly of Mammutidae is a rather unexpected result although it was surmised by Shoshani (1996). Yet when known

and described, the crania of the mammutid species *Zygodon turicensis*, *Z. atavus*, and *Z. aegyptensis*, may allow reassessment of mammutid monophyly. The knowledge of more cranial characters of the Fayûm species *Palaeomastodon beadnelli*, of *Eritreum melakeghebrekristosi*, *Losodokodon losodokus*, and of other Oligocene taxa is still needed. Moreover, from what has been learned from the studies of the last twelve years, it is very likely that new discoveries from late Oligocene and early Miocene localities will add to better understanding of proboscidean palaeobiodiversity in this crucial epoch, perhaps associated to surprising results. Who could have imagined that *E. morotoensis* would have had flattened lower tusks (Tassy & Pickford, 1983) and a nearly vertical basicranium (Pickford, 2003)?

ACKNOWLEDGEMENTS

Firstly I wish to thank Martine Faure who has asked me to participate in this volume in honour of the late Claude Guérin. Sevet Sen's editorial skill was appreciated. Informations on the discovery of the cranium from Auchas, Namibia, were given by M. Pickford (formerly College de France, Paris). The cast M 6014 was made by Ph. Richir (Muséum national d'Histoire naturelle, Paris). Historical information on the fate of the juvenile skull and casts of *Mammut americanum* from Hacketstown, New

Jersey, was gathered through the goodwill of C. Norris and S. Bell (American Museum of Natural History, New York) and of W. C. Amaral and the late F. A. Jenkins Jr. (Museum of Comparative Zoology, Harvard). I thank M.-A. Angel (UMR 7207, MNHN, Paris) for her help in bibliographic research. Thanks go to Fabrice Fack for his phylogenetic insight. I am much grateful to J.J. Hooker (NHM, London) for a thorough language check of my broken English manuscript. Last but not least, the artistic contribution by Dominique Visset, as ever, and by A. Lethiers (UMR 7207, University P. & M. Curie, Paris) was crucial. I am grateful to Ursula Göhlich and one anonymous reviewer who helped to improve this article.

REFERENCES

- Andrews C. W. 1906. *A descriptive catalogue of the Tertiary Vertebrata of the Fayûm, Egypt*. British Museum of Natural History, London, xxxvii+324 pp.
- Bishop W.W. 1967. The later Tertiary in East Africa – Volcanics, sediments and faunal inventory. In: Bishop W.W. & Clark J.D. (Eds), *Background to Evolution in Africa*. The University of Chicago Press, Chicago: 31-56.
- Borissiak A. 1929. On a new direction in the adaptive radiation of Mastodonts. *Paleobiologica*, 2: 19-33.
- Borissiak A. 1936. *Mastodon atavus* n. sp., der primitivste Vertreter der Gruppe *M. angustidens*. *Travaux de l'Institut paléozoologique de l'Académie des Sciences de l'URSS*, 5: 172-234.
- Butler P.M. 1956. The ontogeny of molar pattern. *Biological Reviews*, 31: 30-69.
- Coppens Y., Maglio V.J., Madden C.T. & Beden M. 1978. Proboscidea. In: Maglio V.J. & Cooke H.B.S. (Eds), *Evolution of African mammals*. Harvard University Press, Cambridge: 336-367.
- Cuvier G. 1821. Sur le Grand mastodonte, improprement nommé Mammouth par les Anglais et les habitans des Etats-Unis. In: Cuvier G., *Recherches sur les ossemens fossiles. Nouvelle édition, t.1*. Dufour et D'Ocagne, Paris: 206-249.
- Delmer C. 2009. Reassessment of the generic attribution of *Numidotherium savagei* and the homologies of lower incisors in proboscideans. *Acta Palaeontologica Polonica*, 54: 561-580.
- Delmer C., Mahboubi M., Tabuce R. & Tassy P. 2006. A new species of *Moeritherium* (Proboscidea, Mammalia) from the Eocene of Algeria: new perspectives on the ancestral morphotype of the genus. *Palaeontology*, 49: 421-434.
- Domning D.P., Ray C. & McKenna M.C. 1986. Two new Oligocene desmostylians and a discussion of tethytherian systematics. *Smithsonian Contributions to Paleobiology*, 59: 1-56.
- Ducrocq S., Boisserie J.-R., Tiercelin J.-J., Delmer C., Garcia G., Kyalo M.F., Leakey M. G., Marivaux L., Otero O., Peigné S., Tassy P. & Lihoreau F. 2010. New Oligocene vertebrate localities from Northern Kenya (Turkana Basin). *Journal of Vertebrate Paleontology*, 30: 293-299.
- Duranthon F., Heizmann E. P. J. & Tassy P. 1995. *Safari Miocène*. Catalogue de l'exposition, Muséum d'Histoire Naturelle, Toulouse, 40 pp.
- Eales N.B. 1926. The anatomy of the head of a foetal African Elephant, *Elephas africanus* (*Loxodonta africana*). *Transactions of the Royal Society of Edinburgh*, 54: 491-551.
- Farris J. S. 1988. *Hennig86, ver. 1.5. Program and Documentation, Distributed by the Author*. Port Jefferson Station, New York.
- Gasparik M. & Markov G. N. 2009. *Gomphotherium 'annectens group'* (Proboscidea) in Hungary. *Fragmenta Palaeontologica Hungarica*, 27: 73-79.
- Gebo D.L., MacLatchy L., Kityo R., Deino A., Kingston J. & Pilbeam D. 1997. A hominoid genus from the early Miocene of Uganda. *Science*, 276: 401-404.
- Gheerbrant E. 2009. Paleocene emergence of elephant relatives and the rapid radiation of African ungulates. *Proceedings of the National Academy of Sciences of the United States*, 106: 10717-10721.
- Gheerbrant E., Sudre J., Tassy P., Amaghaz M., Bouya B. & Iarochène M. 2005. Nouvelles données sur *Phosphatherium escuilliei* (Mammalia, Proboscidea) de l'Eocène inférieur du Maroc, apports à la phylogénie des Proboscidea et des ongulés lophodontes. *Geodiversitas*, 27: 229-333.
- Göhlich U. B. 2010. The Proboscidea (Mammalia) from the Miocene of Sandelzhausen (southern Germany). *Paläontologische Zeitschrift*, 84: 163-204.
- Goloboff P.A., Farris J.S. & Nixon K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, 24: 774-786.
- Harris J.M. 1973. *Prodeinotherium* from Gebel Zelten, Libya. *Bulletin of the British Museum (Natural History) Geology*, 23: 283-348.
- Harrison T. & Andrews P. 2009. The anatomy and systematic position of the early Miocene proconsulid from Meswa Bridge, Kenya. *Journal of Human Evolution*, 56: 479-496.
- Heizmann E. P. J., Duranthon F. & Tassy P. 1996. Miozäne Großsäugetiere. *Stuttgarter Beiträge zur Naturkunde, Serie C*, 39: 1-60.
- Huttunen K. 2004. On a *Prodeinotherium bavaricum* (Proboscidea, Mammalia) skeleton from Franzensbad, Czech Republic. *Annalen des Naturhistorischen Museums in Wien*, 105A: 333-361.
- Jernvall J. & Thesleff I. 2000. Reiterative signalling and patterning during mammalian tooth morphogenesis. *Mechanisms of Development*, 92: 12-29.
- Kappelman J., Rasmussen D.T., Sanders W.J., Feseha M., Bown T., Copeland P., Crabaugh J., Fleagle J., Glantz M., Gordon A., Jacobs B., Maga M., Muldoon K., Pan A., Pyne L., Richmond B., Ryan T., Seiffert E., Sen S., Todd L., Wiemann M.C. & Winkler A. 2003. Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia. *Nature*, 426: 549-552.
- Madden C.T. 1980. *Zygodon* from subsaharan Africa, with observations on the systematics of palaeomastodontid Proboscideans. *Journal of Paleontology*, 54: 57-64.
- Markov G.N. 2008. The Turolian proboscideans (Mammalia) of Europe: preliminary observations. *Historia naturalis bulgarica*, 16: 139-150.
- Matsumoto H. 1924. A revision of *Palaeomastodon* dividing it into two genera, and with a description of two new species. *Bulletin of the American Museum of Natural History*, 50: 1-58.
- Matsumoto H. 1927. On two new mastodonts and an archetypal stegodont of Japan. *The Science Reports of the Tôhoku Imperial University, Sendai, Geology* (2), 10: 1-11.

- McKenna M.C. & Bell S.K. 1997. *Classification of mammals above the species level*. Columbia University Press, New York, xii+ 631 pp.
- Osborn H. F. 1936. *Proboscidea. Volume 1 Moeritherioidea, Deinotherioidea, Mastodontoidea*. The American Museum Press, New York, xl + 802 pp.
- Pickford M. 2003. New Proboscidea from the Miocene strata in the lower Orange River valley, Namibia. *Memoir Geological Survey Namibia*, 19: 207-256.
- Pickford M. & Senut B. 2003. Miocene palaeobiology of the Orange River Valley, Namibia. *Memoir Geological Survey Namibia*, 19: 1-22.
- Pickford M. & Tassy P. 1980. A new species of *Zygodon* (Mammalia, Proboscidea) from the Miocene hominoid localities of Meswa Bridge and Moroto (East Africa). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 1980-4: 235-251.
- Pontier G. 1926. Contribution à l'étude du *Mastodon turicensis* Schinz. *Annales de la Société Géologique du Nord*, 51: 149-164.
- Puttick M.N., O'Reilly J.E., Tanner A.R., Fleming J.F., Clark J., Holloway L., Lozano-Fernandez J., Parry L.A., Tarver J.E., Pisani D. & Donoghue P.C. J. 2017. Uncertain-tree: discriminating among competing approaches to the phylogenetic analysis of phenotype data. *Proceedings of the Royal Society B Biological Sciences* 284 DOI: 10.1098/rspb.2016.2290.
- Rasmussen D. T. & Gutierrez M. 2009. A mammalian fauna from the late Oligocene of Northwestern Kenya. *Palaeontographica Abteilung A*, 288: 1-52.
- Sanders W. J. & Miller E.R. 2002. New proboscideans from the early Miocene of Wadi Mohara, Egypt. *Journal of Vertebrate Paleontology*, 22: 388-404.
- Sanders W. J., Kappelman J. & Rasmussen D. T. 2004. New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia. *Acta Palaeontologica Polonica*, 49: 365-392.
- Sanders W. J., Gheerbrant E., Harris J. M., Saegusa H. & Delmer C. 2010. Proboscidea. In: Werdelin L. & Sanders W.J. (Eds), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, Los Angeles, London: 161-251.
- Saunders J. J. 1977. Late Pleistocene Vertebrates of the Western Ozark Highland, Missouri. *Illinois State Museum Reports of Investigation*, 33: 1-118.
- Seifert E.R., Nasir S., Al-Harthy A., Groenke J. R., Kraatz B.P., Steven N.J. & 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*, 99: 133-141.
- Shoshani J. 1996. Para- or monophyly of the gomphotheres and their position within Proboscidea. In: Shoshani J. & Tassy P. (Eds), *The Proboscidea. Evolution and palaeoecology of elephants and their relatives*. Oxford University Press, Oxford, New York, Toronto: 149-177.
- Shoshani J. & Tassy P. 2005. Advances in proboscidean taxonomy & classification, anatomy & physiology, and ecology & behavior. *Quaternary International*, 126-128: 5-20.
- Shoshani J., Golenberg E.M. & Yang H. 1998. Elephantidae phylogeny: morphological versus molecular results. *Acta Theriologica Supplement*, 5: 89-122.
- Shoshani J., Walter R.C., Abraha M., Brehe S., Tassy P., Sanders W.J., Marchant G.H., Libsekal Y., Ghirmai T. & Zinner D. 2006. A proboscidean from the late Oligocene of Eritrea, a "missing link" between early Elephantiformes and Elephantimorpha, and biogeographic implications. *Proceedings of the National Academy of Sciences of the United States*, 103: 17296-17301.
- Simões T.R., Caldwell M.W., Palci A. & Nydam R.L. 2017. Giant-taxon-character matrices: quality of character constructions remain critical regardless of size. *Cladistics* 33: 198-219.
- Tassy P. 1981. Le crâne de *Moeritherium* (Proboscidea, Mammalia) de l'Eocène de Dor el Talha (Libye) et le problème de la classification phylogénétique du genre dans les Tethytheria McKenna, 1975. *Bulletin du Muséum national d'Histoire naturelle 4^e Série Section C*, 3: 87-147.
- Tassy P. 1982. Les principales dichotomies dans l'histoire des Proboscidea (Mammalia) : une approche phylogénétique. *Geobios Mémoire Spécial*, 6: 225-254.
- Tassy P. 1986. *Nouveaux Elephantoidea (Mammalia) dans le Miocène du Kenya; essai de réévaluation systématique*. Cahiers de Paléontologie - Travaux de paléontologie est-africaine. Editions du C.N.R.S., Paris, 135 pp.
- Tassy P. 1988. The classification of Proboscidea: how many cladistic classifications? *Cladistics*, 4: 43-57.
- Tassy P. 1990a. Phylogénie et classification des Proboscidea (Mammalia): historique et actualité. *Annales de Paléontologie*, 76: 159-224.
- Tassy P. 1990b. The "Proboscidean Datum Event": how many proboscideans and how many events? In: Lindsay E.H., Fahlsbusch V. & Mein P. (Eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 237-252.
- Tassy P. 1994. Gaps, parsimony, and early Miocene elephantoids (Mammalia), with a reevaluation of *Gomphotherium annexens* (Matsumoto, 1925). *Zoological Journal of the Linnean Society*, 112: 101-117.
- Tassy P. 1995. Origin and differentiation of the Elephantiformes (Mammalia, Proboscidea). *Verhandlungen des Naturwissenschaftlichen Vereins Hamburg* 34 (1994): 73-94.
- Tassy P. 1996a. Who is who among the Proboscidea? In: Shoshani J. & Tassy P. (Eds), *The Proboscidea. Evolution and palaeoecology of elephants and their relatives*. Oxford University Press, Oxford, New York, Toronto: 39-48.
- Tassy P. 1996b. The earliest gomphotheres. In: Shoshani J. & Tassy P. (Eds), *The Proboscidea. Evolution and palaeoecology of elephants and their relatives*. Oxford University Press, Oxford, New York, Toronto: 89-91.
- Tassy P. 1996c. Growth and sexual dimorphism among Miocene elephantoids: the example of *Gomphotherium angustidens*. In: Shoshani J. & Tassy P. (Eds), *The Proboscidea. Evolution and palaeoecology of elephants and their relatives*. Oxford University Press, Oxford, New York, Toronto: 92-100.
- Tassy P. 2013. L'anatomie cranio-mandibulaire de *Gomphotherium angustidens* (CUVIER, 1817) (Proboscidea, Mammalia): données issues du gisement d'En Péjouan (Miocène moyen du Gers, France). *Geodiversitas*, 35: 377-445.
- Tassy P. & Pickford M. 1983. Un nouveau mastodonte zygodononte (Proboscidea, Mammalia) dans le Miocène inférieur d'Afrique orientale: systématique et paléoenvironnement. *Geobios*, 16: 53-77.
- Tobien H. 1971. *Moeritherium, Palaeomastodon, Phiomia* aus dem Paläogen Nordafrikas und die Abstammung der

- Mastodonten (Proboscidea, Mammalia). *Mitteilungen aus dem Geologischen Institut der Technischen Universität Hannover*, 10: 141-163.
- Tobien H. 1973. On the evolution of mastodonts (Proboscidea, Mammalia). Part 1: The bunodont trilophodont groups. *Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden*, 101: 202-276.
- Tobien H. 1976. Zur paläontologischen Geschichte der Mastodonten (Proboscidea, Mammalia). *Mainzer Geowissenschaften Mitteilungen*, 5: 143-225.
- Tobien H. 1978. The structure of the mastodont molar (Proboscidea, Mammalia) Part 3: The Oligocene mastodont genera *Palaeomastodon*, *Phiomia* and the Eo/Oligocene Paenungulate *Moeritherium*. *Mainzer Geowissenschaften Mitteilungen*, 6: 177-208.
- Van der Merwe N.J., Bezuidenhout A.J. & Seegers C.D. 1995. The skull and mandible of the African elephant (*Loxodonta africana*). *Onderstepoort Journal of Veterinary Research*, 62: 245-260.
- Warren J.C. 1855. *Description of a skeleton of the Mastodon giganteus of North America*. John Wilson & Son, Boston, 260 pp.

