New mammutid proboscidean teeth from the Middle Miocene of tropical and southern Africa

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Received 4 April 2006. Accepted 2 February 2007

The genus *Zygolophodon* is widespread but rare in Middle Miocene deposits of Eurasia, and until recently it was not reliably reported from sub-Saharan Africa. Most previous records of the genus in the latter continent are based on specimens of another proboscidean *Eozygodon morotoensis.* In 1985 a tooth from Tunisia was attributed to *Zygolophodon* and in 2002 four teeth from Egypt were attributed to the same genus, while in 2005 a fragment of lower third molar was found at Daberas Mine, Orange River, Namibia, and two upper molars were found in the Ngorora Formation, Tugen Hills, Kenya. The purpose of this note is to describe and interpret the Ngorora molars. Two newly discovered specimens of *Eozygodon morotoensis* from Uganda complete the paper.

Keywords: *Zygolophodon, Eozygodon*, Proboscidea, Mammutidae, Kenya, Namibia, Middle Miocene, biogeography.

INTRODUCTION

The rare but geographically widely distributed Middle Miocene proboscidean *Zygolophodon* (Fig. 1) has had a chequered taxonomic history, partly on account of the paucity of its remains but mainly because its cheek dentition superficially resembles those of bunodont gomphotheres (Tobien 1975; Tassy 1985). There are, however, several characters which distinguish the teeth of these two groups, although in advanced wear stages it can be difficult to attribute teeth correctly.

Zygolophodon was previously reported from tropical African deposits (Madden 1980) based on a fragment of an upper premolar from Moruorot, Kenya, dated to *c.* 16.2 Ma. However, Pickford & Tassy (1980) and Tassy & Pickford (1983) reclassified the specimen as *Eozygodon morotoensis,* which has flattened lower tusks, thinner enamel in the cheek teeth, and more antero-posteriorly compressed cusps than in *Zygolophodon,* among other characters. However, with the discovery and naming of *Zygolophodon aegyptensis,* the affinities of the Moruorot

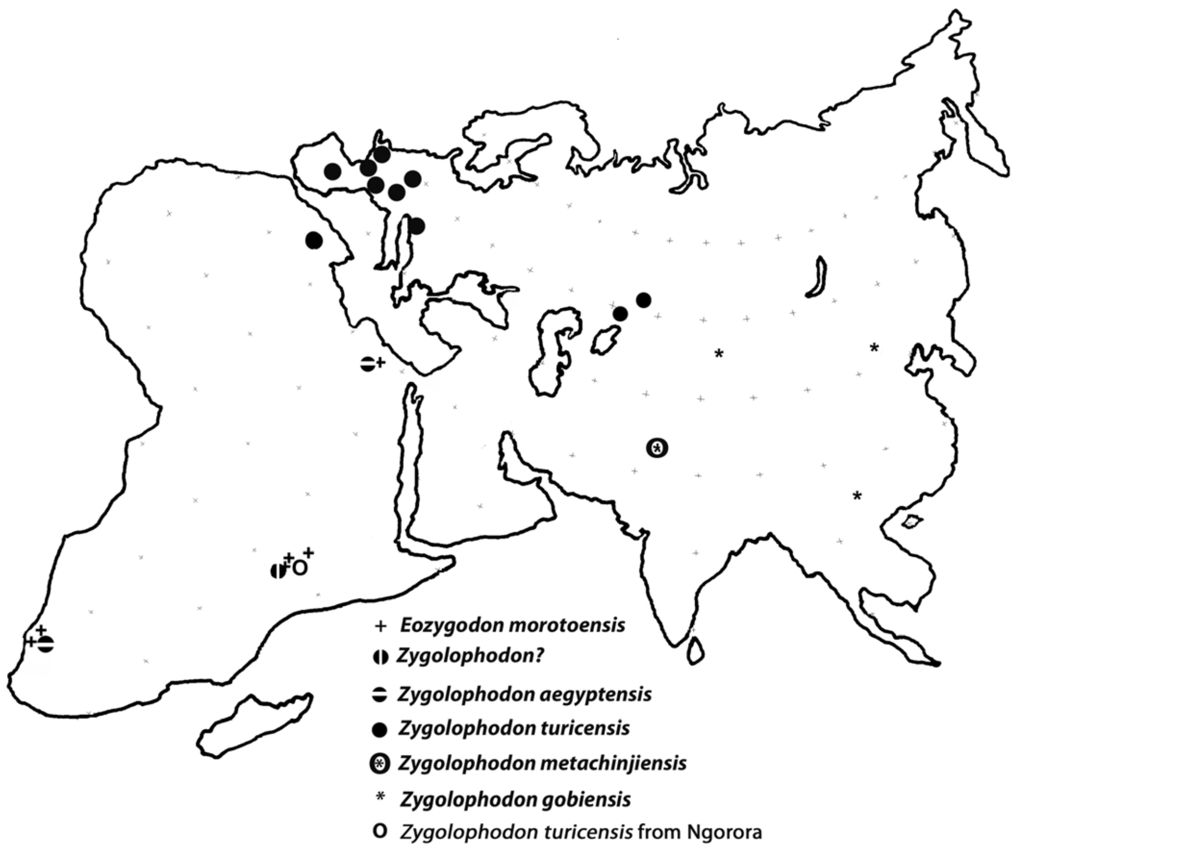

Figure 1. Old World distribution of *Zygolophodon* species and *Eozygodon.* The Kenyan material is closest in size to *Z. gobiensis* from Tung Gur, China, but is morphologically similar to *Z. turicensis* from Europe. The Rusinga (Kenya) records require confirmation.

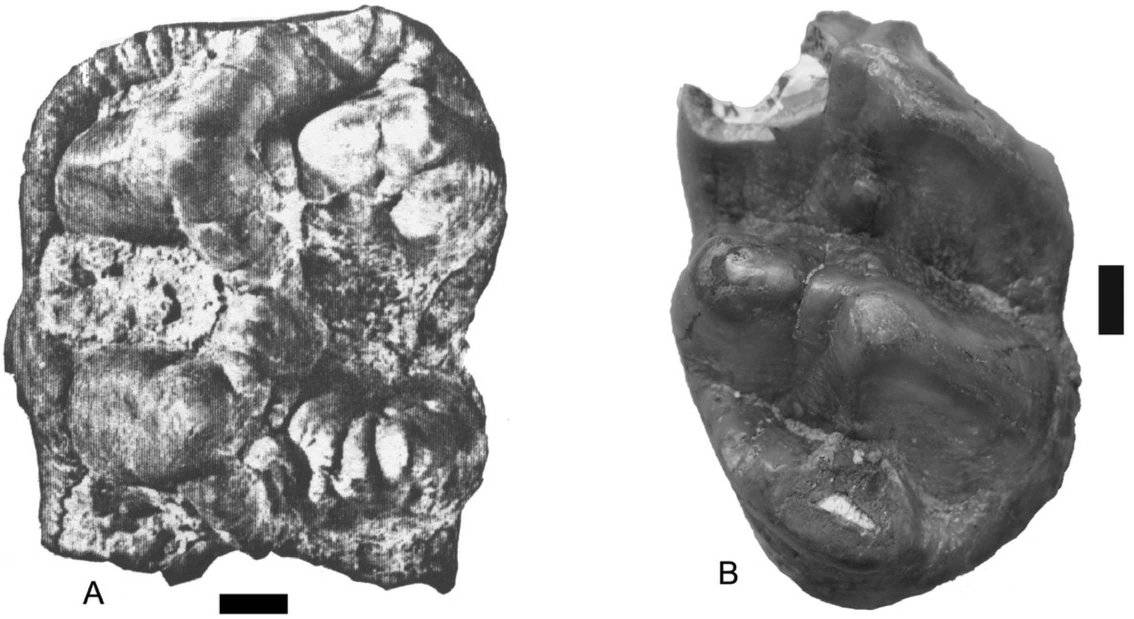

Figure 2. *Zygolophodon* from Tunisia and Namibia. **A**, *Zygolophodon turicensis* from Jebel Cherichera, Tunisia (photograph reproduced from Tassy, 1985); **B**, *Zygolophodon* cf. *aegyptensis* from Daberas, Namibia. Scale bars = 10 mm.

specimen requires reassessment. Two specimens from the Maghreb have been tentatively attributed to *Zygolophodon,* a deciduous tooth from the Late Miocene of Menacer, Algeria (Thomas & Petter 1986), which is possibly a specimen of *Zygolophodon borsoni,* and an incomplete upper molar from the Middle Miocene of Jebel Cherichera, Tunisia, found more than a century ago (Errington de la Croix 1887) and attributed to *Zygolophodon turicensis* by Tassy (1985, pp. 509–510, fig. 213). The specimen possesses a well-developed lingual cingulum (Fig. 2A). Sanders & Miller (2002) described the species *Zygolophodon aegyptensis* on the basis of four teeth from Wadi Moghara, Egypt and Pickford (2003) mentioned the possible presence of *Eozygodon morotoensis* at the same site on the basis of a mandible with lower third molar roots that indicate a crown size considerably shorter than any of the teeth of *Zygolophodon aegyptensis.*

Several teeth from Rusinga Island, Kenya, originally identified as *Trilophodon angustidens kisumuensis* by MacInnes (1942) were attributed to *Zygolophodon* by Van Couvering & Van Couvering (1976) and tentatively to *Archaeobelodon* by Tassy (1986). The two upper second molars in the sample possess antero-posteriorly compressed lophs, zygodont crests and a median sulcus, all features that occur in mammutids, but they appear to lack the lingual cingulum that is usually present in these proboscideans. The third molars from Rusinga show some resemblances to those of *Z. aegyptensis* from Wadi Moghara, Egypt, described by Sanders & Miller (2002). The status of these specimens requires re-examination.

The Daberas, Namibia, specimen is the rear half of a lower third molar (Pickford, in press) with compressed and oblique lophids typical of mammutids. It is quite small, (breadth of penultimate lophid is 59 mm) being the same order of magnitude as the holotype of *Z. aegyptensis* (breadth of first lophid 55.8 mm (Sanders & Miller 2002)) but differs from it by having somewhat straighter posterior lophids which are not as anteriorly convex as those of the Egyptian specimen. It differs from the two well-preserved specimens of *Eozygodon morotoensis* from East Africa (Pickford & Tassy 1980; Tassy & Pickford 1983) by its more oblique lophids, the stronger development of the anterior and posterior ridges (acr and pcr) and the strongly sloping buccal margin of the pretrite cuspids. Its enamel is also about 33% thicker (4 mm compared to 3 mm for *Eozygodon morotoensis*) (Fig. 2B).

The fossils which are the main focus of this paper are from Grildain, near Bartabwa, in Member A of the Ngorora Formation, Tugen Hills, Kenya, a late Middle Miocene deposit (*c.* 13 Ma) (Fig. 1). The fossils were found by Mr Kiptalam Cheboi during the Kenya Palaeontology Expedition. The aim of this note is to describe and interpret these teeth and to discuss their biochronological and biogeographic implications. Newly recovered specimens of *Eozygodon morotoensis* are included in the analysis.

SYSTEMATIC DESCRIPTIONS

Order Proboscidea Illiger, 1811
Family Mammutidae Hay, 1922
Genus *Zygolophodon* Vacek, 1877

Species *Zygolophodon turicensis* (Schinz, 1824), Figs 1–3

Material. Bar 158'05, left and right M2/s.

Locality. Grildain, near Bartabwa, Tugen Hills, Kenya.

Age. Member A, Ngorora Formation, *c.* 13 Ma.

Description. Bar 158'05 comprises left and right second upper molars in medium wear (Fig. 3, Tables 1 & 2). The crowns are trilophodont, with antero-posteriorly compressed lophs, the pretrite half being separated from the posttrite half by a clear median sulcus. The pretrite cusps are trifoliate, with prominent anterior (acr) and posterior (pcr) ridges (anterior and posterior accessory conules) leading towards the median sulcus (Tobien 1996) but not crossing it. The posttrite cusps are almost rectangular in occlusal outline with rounded corners, and the buccal

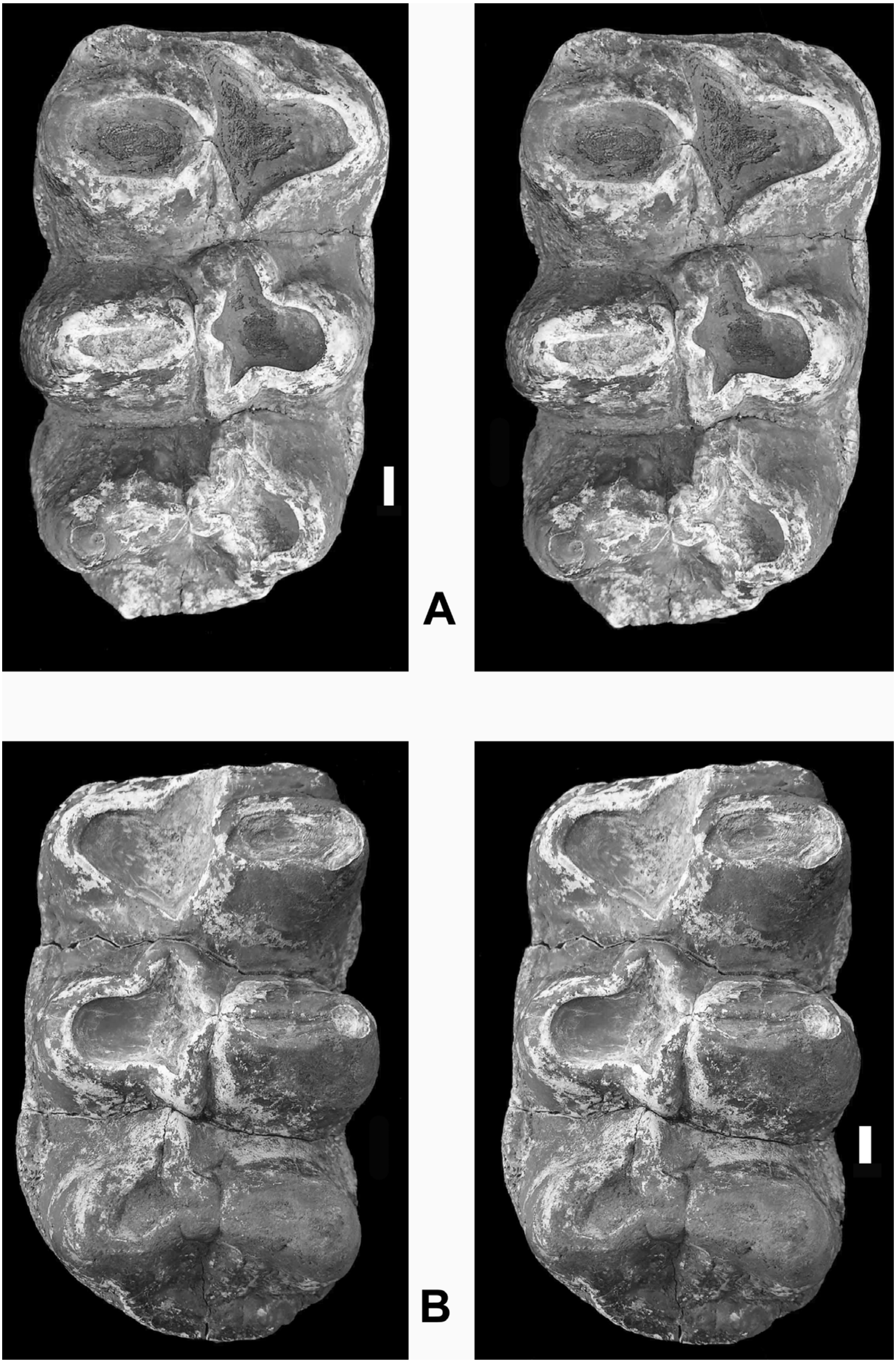

Figure 3. Stereo pairs of Bar 158'05, upper second molars of *Zygolophodon turicensis* (Schinz, 1833) from Grildain, Ngorora Formation, Member A, Tugen Hills, Kenya. Scale bars = 10 mm.

Table 1. Measurements (in mm) of Bar 158′05, upper second molars attributed to *Zygolophodon turicensis.*

Tooth	Length	Breadth 1st loph	Breadth 2nd loph	Breadth 3rd loph
Right M2/	134.5	79.6	81.3	77.3
Left M2/	133.3	80.5	82.8	80.0

wall is almost vertical. The posttrite cusps possess zygodont crests (zc) which have been somewhat reduced in stature by wear, but which are nevertheless perfectly clear, particularly in the left upper molar. The interloph valleys are broad, especially in the posttrite half. The lingual cingulum is continuous from mesial to distal but is not as prominent opposite the lophs as between them. The anterior cingulum stretches the full breadth of the tooth, but the posterior one is not as broad, extending across only about two-thirds of the breadth. Finally, the enamel is appreciably thicker in these specimens than it is in *Eozygodon morotoensis* (Pickford & Tassy 1980) (Fig. 4).

Discussion. The morphology of the Ngorora upper molars is compatible more with the genus *Zygolophodon* than with *Eozygodon.* Molar dimensions and thickness of the enamel differentiate the two genera, as does the degree of compression of the lophs. The Ngorora teeth are large for *Zygolophodon,* plotting out at the top end of the range of variation close to material from Tung Gur, China, the type locality of *Zygolophodon gobiensis* Osborn & Granger (1932) and somewhat larger than most of the European teeth attributed to *Zygolophodon turicensis.* The specimen from Jebel Cherichera, Tunisia (1886-15 MNHN) attributed to *Zygolophodon turicensis* is appreciably smaller (breadth first loph 66.9 mm, second loph 68.6 mm) (Tassy, 1985) (Fig. 2A) than the Tugen specimens (breadth first loph of the two specimens, 81.3 and 82.3 mm) (Fig. 3). In view of the vast distance between the Tugen Hills and the Gobi Desert, and the fact that the Kenyan sample is restricted, the Ngorora teeth are attributed to *Zygolophodon turicensis.*

Genus *Eozygodon* Tassy & Pickford, 1983

Species *Eozygodon morotoensis* (Pickford & Tassy, 1980), Figs 1 & 4

Material. Mor II 18′01, left M2/, Mor II 19′05, right M2/.

Locality. Moroto II, northeast Uganda.

Age. Base of the Middle Miocene (although some authors (Gebo *et al.* 1997) have estimated a basal Early Miocene age in excess of 20 Ma).

Description. The left upper second molar Mor II 18′01 is an almost complete though damaged specimen in medium wear. The tooth has broken into sections which have drifted apart in the sediment, but have retained their positions relative to one another. There are three lophs and a beaded distal shelf-like cingulum. The thin enamel (3 mm on the pretrite cusp of the second loph), perfectly formed lophs with a central sulcus and a continuous beaded lingual cingulum are all features that are typical of *Eozygodon morotoensis,* the type locality of which is Moroto I (Pickford & Tassy 1980; Tassy & Pickford 1983). Taking into account the displacement of the various pieces, the crown measures *c.* 89 mm long by *c.* 60 wide at the second loph (Table 2).

Mor II 19′05 is an unworn but damaged right M2/ (Fig. 4, Table 2). The lophs are extremely antero-posteriorly compressed with sharp transversely oriented apices. The

Table 2. Metric comparison of upper second molars, Bar 158′05, *Zygolophodon turicensis* from Grildain, Ngorora Formation, Member A (*c.* 13 Ma), Tugen Hills, Kenya (original data) with M2/s of European *Zygolophodon* species (data from Göhlich, 1998), *Eozygodon morotoensis* (data from Pickford & Tassy 1980, and original data), possible *Zygolophodon* from Rusinga (data from MacInnes 1942) and material from Wadi Moghara (data from Sanders & Miller 2002).

Specimen	Locality	Taxon	Length	Breadth
Din 687	Esselborn	*Z. turicensis*	103	73
Din 868	Esselborn	*Z. turicensis*	115	72
Din 724	Esselborn	*Z. turicensis*	114	79
A/V 0039	Elgg	*Z. turicensis*	92	63
1996 I 28a	Montréjeau	*Z. turicensis*	82	59
LVPVH	Rajégats	*Z. turicensis*	126	80
Si 13	Simorre	*Z. turicensis*	113	68
SML 356	Malartic	*Z. turicensis*	107	69
SML 501d	Malartic	*Z. turicensis*	111	79
SML 501c	Malartic	*Z. turicensis*	110	79
Mor I′61 rt	Moroto I	*E. morotoensis*	89.3	62.4
Mor I′61 lt	Moroto I	*E. morotoensis*	89.2	62
ME 7545	Meswa Bridge	*E. morotoensis*	83	63.8
Mor II 18′01	Moroto II	*E. morotoensis*	89	60
Mor II 19′05	Moroto II	*E. morotoensis*	81.5	66.5
AM 02 1994	Auchas	*E. morotoensis*	86.8	62.4
AM 02 1994	Auchas	*E. morotoensis*	84.6	62.3
Bar 158′05 rt	Ngorora A	*Z. turicensis*	134.5	81.3
Bar 158′05 lt	Ngorora A	*Z. turicensis*	133.3	82.8
2202–4	Tung Gur	*Z. gobiensis*	130	88
2202–5	Tung Gur	*Z. gobiensis*	128	88
DPC 5932	Moghara	*Z. aegyptensis*	112.5	68
M 15323	Rusinga	*Zygolophodon?*	105	64
M 15324	Rusinga	*Zygolophodon?*	104	60

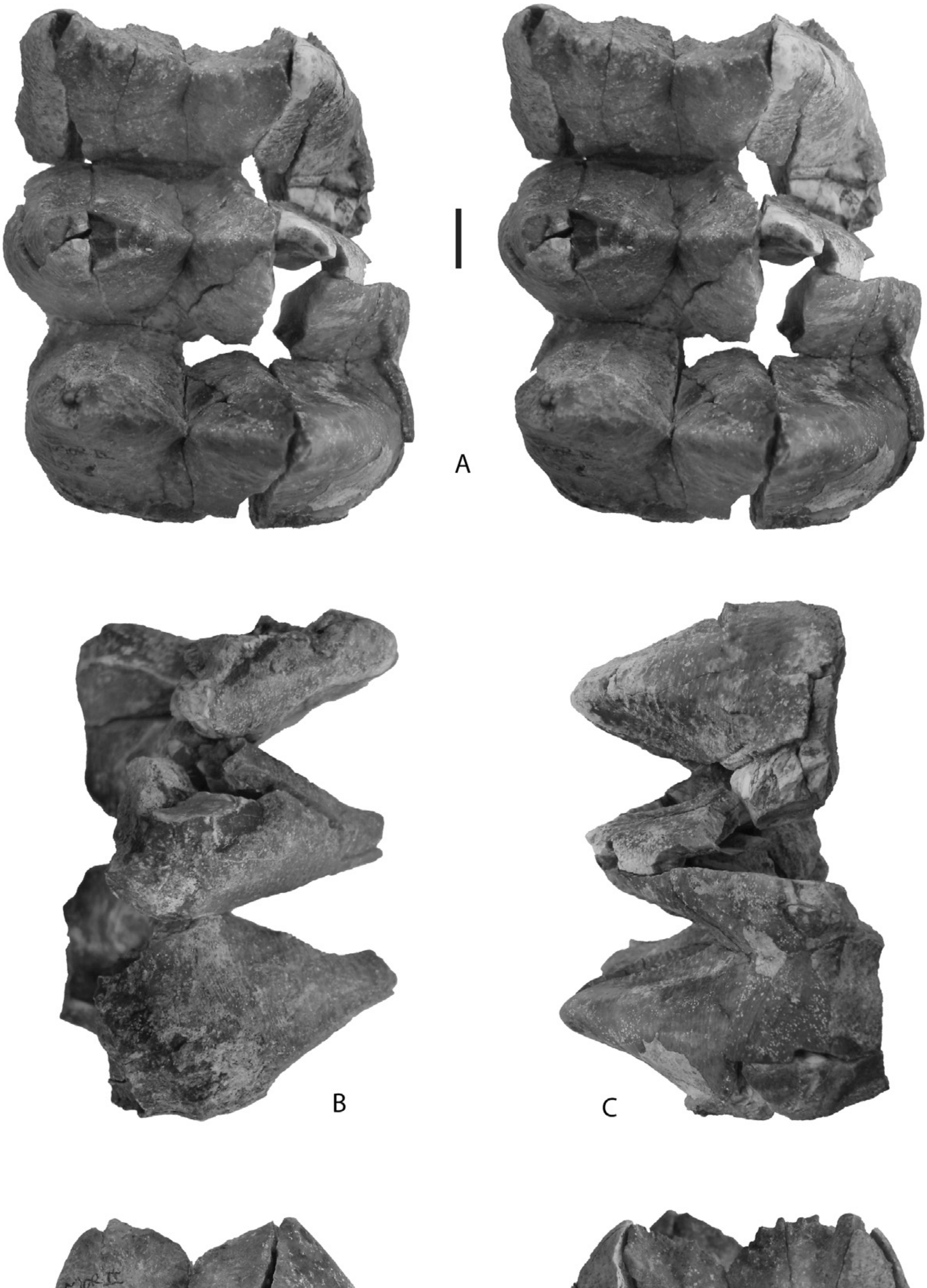

Figure 4. Mor II 19'05, right M2/, *Eozygodon morotoensis,* from Moroto II, northeast Uganda. Scale bar = 10 mm.

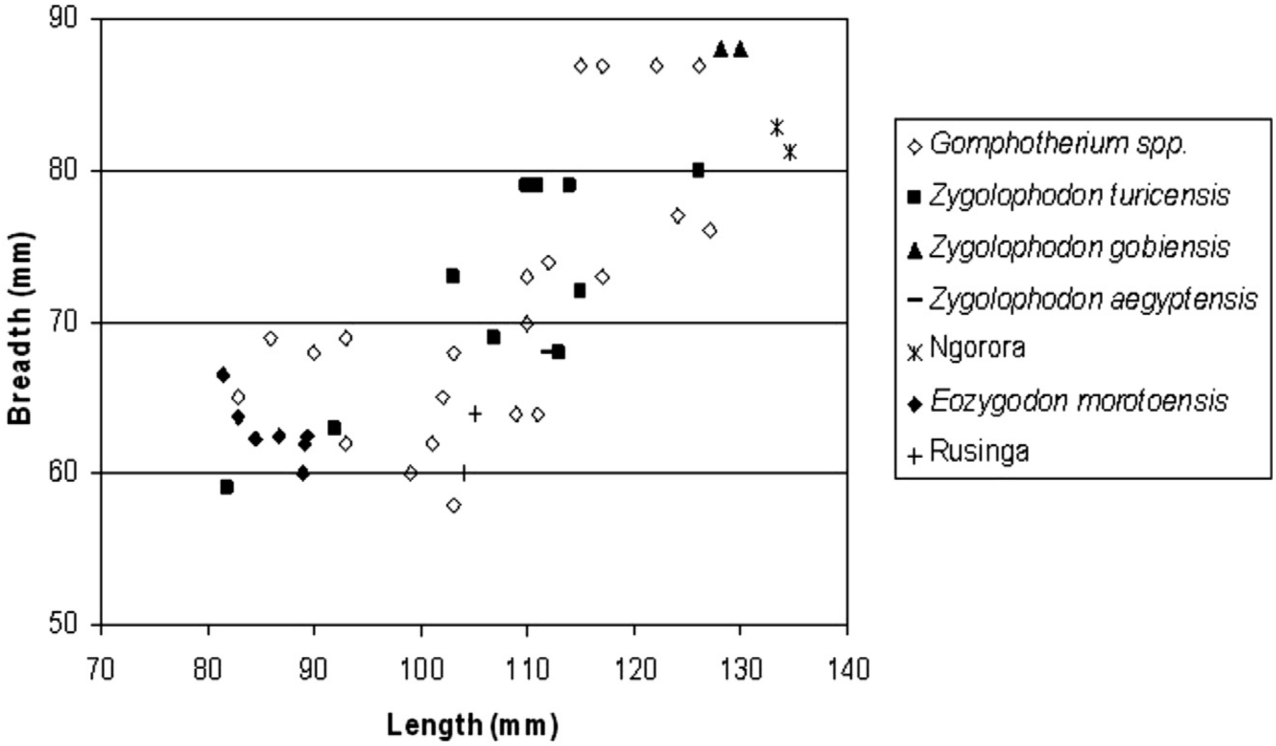

Figure 5. Bivariate plot (in mm) of M2/s of gomphotheres (open symbols) and mammutids (closed symbols). The almost complete overlap in dimensions reveals that mammutid teeth are not particularly wide when compared to those of gomphotheres, as previously claimed (Tobien 1975). It is the third molars which are shorter than expected, not wider than expected.

profile of the cutting edges of the lophs descends from the apex of the cusps toward the median sulcus (Fig. 4D,E). The central sulcus is deep, and the anterior (acr) and posterior (pcr) ridges of the pretrite cusps are weakly expressed, so that the transverse valleys are not blocked (Fig. 4B,C). The zygodont crests are weakly developed, and the buccal walls of the posttrite cusps are more vertical than the pretrite ones. There is a prominent lingual cingulum on the third loph, but it has broken off in the other two cusps. In this unworn specimen it is possible to see that the half lophs are subdivided at the apex into about 12 or 13 beads, presumably small cones, but the sulci between the beads quickly fade cervically, so that even with slight wear, all signs of the beads disappear and the lophs take on a rectangular outline with rounded corners.

Discussion. These two upper molars from Moroto II are extremely similar to the type material from Moroto I. They represent a new locality record for the species *Eozygodon morotoensis.*

GENERAL DISCUSSION

There has been a great amount of uncertainty about the systematic status and material content of the genus *Zygolophodon,* summarized but not completely resolved by Osborn (1936). Historically, many fossils have been erroneously attributed to *Zygolophodon* and some genuine mammutid specimens have been misidentifed as gomphotheres. Tobien (1975, 1996) clarified the situation by showing that there were only a few species which were quite variable in details of morphology and size, but which showed constancy in certain morphological characters in the molars such as the presence of zygodont crests, a median sulcus, almost vertical posttrite cusp walls, and presence of lingual cingulum, among other features.

Some authors have tended to create new taxa on the basis of minor variants within these few species. In Europe, Tobien (1975, 1996) recognized two species, *Zygolophodon turicensis* and *Mammut borsoni.* In mid-latitude Asia he recognized *Zygolophodon gobiensis* (Dubrovo 1970; Osborn & Granger 1932) and *Mammut borsoni* (Borissiak 1936), and in India *Zygolophodon metachinjiensis* (Tassy 1983) (Fig. 1). In North America there are several taxa of mammutids, some of which Tobien (1975 1996) considered to be very close to *Zygolophodon* (e.g. *Miomastodon merriami*), but others distinct *Pliomastodon matthewi* and *Mammut americanum.* In Africa, the only mammutid known to Tobien was *Eozygodon morotoensis* (Pickford & Tassy 1980; Tassy & Pickford 1983).

Tobien (1975, 1996) concluded that the molars of mammutids tended to be wider than those of gomphotheres, but this is only apparent in the third molars. Upper second molars of gomphotheres and mammutids overlap almost completely in dimensions (Fig. 5), which reveals that in fact mammutid molars are not markedly broader than those of gomphotheres, but that their third molars are shorter, the talon/id complex being less pronounced than those of gomphotheres.

A bivariate plot of the upper second molars of mammutids reveals that the Ngorora specimens fall at the upper end of the range of metric variation of the species belonging to *Zygolophodon,* in particular they are close in dimensions to teeth of *Z. gobiensis* from Tung Gur, Mongolia. The latter site is late Middle Miocene, often being considered equivalent in age to MN 7/8 of the European biozonation. This is close to the age of the

Ngorora specimens, *c.* 13 Ma. Basal Middle Miocene specimens are generally smaller, and the smallest of all are the teeth of *Eozygodon morotoensis* which range in age from 22–16.5 Ma. It is likely that as in many proboscidean lineages, the mammutids increased in size through the Middle Miocene, but the quantity of specimens is rather too low for them to be used as a biochronological tool. Tobien postulated a long chronological range for the species *Z. turicensis*, from MN4 to MN 12–13 (Göhlich, 1999).

Prior to the discovery of the Tugen mammutid teeth, the only confidently identified African material attributed to *Zygolophodon*, was from Tunisia (Tassy 1985) and Egypt (Sanders & Miller 2002). The Kenyan and Namibian specimens thus represent major range extensions of the palaeodistribution of the genus *Zygolophodon*.

CONCLUSIONS

Newly recovered teeth from basal Middle Miocene deposits at Moroto II, Uganda, fall comfortably within the range of metric and morphological variation of *Eozygodon morotoensis* (Pickford, & Tassy 1980).

A partial lower third molar from Daberas Mine, Orange River Valley, Namibia, has thicker enamel than *Eozygodon morotoensis* and it has better developed anterior and posterior pretrrite ridges, indicating that it belongs to *Zygolophodon*, possibly the species *Z. aegyptensis* recently described from Wadi Moghara, Egypt (Sanders & Miller 2002). This find suggests a basal Middle Miocene age for the deposits at Daberas from which the tooth came, possibly quite early in the period on account of the diminutive dimensions of the specimen.

Two mammutid upper molars from Grildain, Ngorora Formation (*c.* 13 Ma), Tugen Hills, Kenya, are close in size to specimens of *Zygolophodon gobiensis* from Tung Gur, Mongolia (Osborn & Granger 1932) but are more similar in morphology to specimens of *Zygolophodon turicensis* from Europe. They are interpreted to represent a large individual of the latter species.

The discovery of these teeth in tropical and southern Africa indicates that mammutids were not only extremely widespread in Eurasia and the New World, but were equally widespread in Africa. The known geochronological range of mammutids in Africa spans the period 22.5 to 13 Ma.

I am anxious to thank K. Cheboi, who found the specimens described here. The Kenya Palaeontology Expedition is a collaborative project affiliated with the Community Museums of Kenya (Director, E. Gitonga) with research authorization from the Ministry of Education, Science and Technology. The expedition is supported by the Ministry of Foreign Affairs, the CNRS, the Muséum National d'Histoire Naturelle, and the Collège de France. Thanks to members of the Kenya Palaeontology Expedition, in particular B. Senut and the villagers of Bartabwa, Tugen Hills.

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