



Anais da Academia Brasileira de Ciências

ISSN: 0001-3765

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Academia Brasileira de Ciências

Brasil

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Anais da Academia Brasileira de Ciências, vol. 88, núm. 1, marzo, 2016, pp. 65-74  
Academia Brasileira de Ciências  
Rio de Janeiro, Brasil

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## A new Mammutidae (Proboscidea, Mammalia) from the Late Miocene of Gansu Province, China

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*Manuscript received on April 15, 2015; accepted for publication on July 13, 2015*

### ABSTRACT

The “Yangheacun specimen”, a proboscidean specimen represented by a mandible from Miocene of China and previously described as Gomphotheriidae, is here reviewed and described as a new genus and species of Mammutidae: *Sinomammut tobieni*. This taxon is a longirostrine mastodon, lacking lower tusks, and bearing a wide last molar with oblique and non-inflated lophids, broad transverse interlophids, and yoke-like wear figures. Phylogenetic analysis of Mammutidae based on dental and mandibular features recovered *S. tobieni* as sister group of the mastodon *Mammut*. The longirostrine condition and the well-developed lower incisors seem to be primitive for Mammutidae, while the brevirostry is the derived condition, probably emerged during the middle Miocene (12-11 Mya). However, two derived conditions are recognized to the lower tusks: the absence of lower tusks (*S. tobieni*) and the occasional presence of vestigial lower tusks (*Mammut*).

**Key words:** Evolution, Longirostrine symphysis, Mammutidae, Miocene, Proboscidea.

### INTRODUCTION

The fossil record of the Proboscidea in China is abundant, however, its diversity is still being discovered, as the temporal distribution range of several genera (Tobien et al. 1986, 1988, Wang and Deng 2011, Wang et al. 2012, 2013). Recently, a very fragmentary fossil of a proboscidean with

longirostrine and a tuskless lower jaw from the Miocene of China (GIOTC 0982-9-178, the “Yangheacun specimen” of Wang et al. 2014) was recognized (but not named) as a new genus and species of the family Gomphotheriidae. Also, the authors related this unnamed new taxon to the Asian trilophodont brevirostrine gomphothere *Sinomastodon*, and proposed to include them both in the subfamily Sinomastodontinae (Wang et al. 2014).

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Two decades ago, an almost complete proboscidean mandible was discovered in a field work, the “Yanghecun specimen”. The specimen is from the Yanghecun locality, Changdao Township, Xihe County, China, probably from the Upper Miocene strata (see Wang et al. 2014 for detailed discussion). Unfortunately, most part of the specimen has been lost and only the right mandibular ramus, bearing m2 (second lower molar) and m3 (third lower molar), as well as a photo of the specimen *in situ* (Fig. 1a), were preserved. However, a detailed analysis of the “Yanghecun specimen” revealed several morphological features that preclude its recognition as a member of Gomphotheriidae. Instead, these features suggest that the “Yanghecun specimen” is probably a new taxon of Mammutidae.

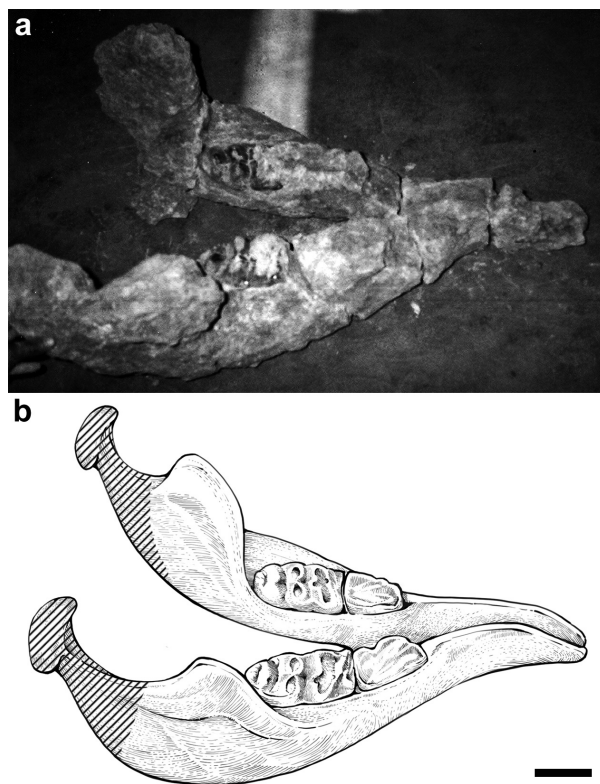
In this way, the objective of this study is to redescribe the “Yanghecun specimen”, providing a formal description and diagnosis for a new genus and species, and presenting its phylogenetic position within the Mammutidae.

The ZooBank Life Science Identifier (LSID) of this publication is: urn: lsid: zoobank.org: pub: 52076E6F-8344-4650-B7BE-A830CBED3130.

#### MATERIALS AND METHODS

Morphological comparisons were conducted for dental and mandibular specimens of Gomphotheriidae and Mammutidae housed at the collections of the American Museum of Natural History (AMNH), United States; Florida Museum of Natural History (FLMNH), United States; and Gansu Industrial Occupational Technology College (GIOTC), China.

The Mammutidae analyzed here includes all genera described and recognized in the current literature: *Zygodontodon* (Tobien 1975, Janis et al. 1998, Markov 2004, Codrea et al. 2005, Göhlich 2010), *Mammut* (Barbour 1931, Shoshani and Tassy 1996, Janis et al. 1998, Markov 2004)



**Figure 1** - The original record of “Yanghecun specimen”. Note the longirostrine symphysis fragmented in two pieces (on the right). (a) Original photo of the complete specimen, an almost complete lower jaw; (b) Reconstructed sketch of Yanghecun specimen based on original picture in (a) by Pablo Lara. The region of the condyles (hachured area) was reconstructed based on *Mammut americanum* and may not correspond anatomically to *Sinomammut*. Scale bar: 10 cm.

and *Eozygodon* (Tassy and Pickford 1983). We did not include the African taxon *Losodokodon losodokius* (Rasmussen and Gutierrez 2009) in the phylogenetic analysis, because it is known only by two upper molars (none mandibular, lower molars and/or tusks specimens), and so it is not comparable to the “Yanghecun specimen”. Furthermore, some authors suggested that the Eurasian *Mammut* is polyphyletic (see Markov 2004, Garevski et al. 2012). The taxonomy of *Mammut* is not the scope of this study. Thus, this genus is represented in our phylogenetic analysis by *Mammut americanum* (including the temporal distribution from late Miocene to late Pleistocene, from North and Central Americas, see Janis et al.

1998). The Gomphotheriidae specimens analyzed included the taxa *Gomphotherium*, *Tetralophodon*, *Sinomastodon* and *Anancus*. The molars structures studied here followed the anatomical nomenclature of Tobien (1975). The length and height of the third lower molars (m3) were used to compare Mammutidae and Gomphotheriidae specimens.

We performed a phylogenetic analysis with the help of the TNT software (Goloboff et al. 2008) using exact search (Implicit enumeration) in order to elucidate the relationships of the new taxon within the Mammutidae. All characters were unordered and equally weighted (value=1). Additionally to the new taxon here described, the ingroup is composed by all Mammutidae genera (the “Yangheacun specimen”, *Zygodont*, *Mammut* and *Eozygodon*). We are proposing a new data matrix including thirteen dental and mandibular characters (Table I). In accordance to their relationships to the Mammutidae in Gheerbrant and Tassy (2009), the selected outgroup is represented by the genera *Eritreum* and *Phiomia*.

## RESULTS AND DISCUSSIONS

Although the specimen GIOTC 0982-9-178 was originally recognized as a member of Gompho-

theriidae and more close related to the genus *Sinomastodon* (Wang et al. 2014), the presences of oblique and non-inflated lophids, broad transverse valleys between lophids, and wide m3 with yoke-like wear figures securely includes this specimen in family Mammutidae, which has the zygodont cheek dentition as one of its most important diagnostic feature (Tobien 1975).

The morphology of zygodont molars share some similarities with the bunodont molars of the Gomphotheriidae, as the subdivision of the transverse crests by a median sulcus in half lophids (lophids), which are built up by two or more small cones (the main cusp and the associated mesoconelet; see figure 3 of Tobien 1975), and the presence of a variable number of central conules and accessory conelets.

However, the central conules, or anterior and posterior crescentoids (ACr and PCr, respectively), in bunodont molars are pillar-like and markedly separated from the main cusp, while in the zygodont molars, these structures form enamel crests on posttrites (Po) and crest-like crescentoids on pretrites (Pr) (Tobien 1975, Tassy 2014). Furthermore, the wear figures in bunodont molars are usually shaped as a simple or double bounded

TABLE I

Character-taxon matrix used in the cladistic analysis of the Mammutidae, including the new taxon *Sinomammut tobieni*. Missing data (either due to non-preservation or because non-applicable) are coded as “?”. Dental, cranial and mandibular characters are: 1) Antero-posterior compression of lophs/lophids on molars: (0) absent (1) present; 2) Crest-like crescentoids on pretrites (0) absent (1) present; 3) Cheek tooth in use simultaneously (0) M1-M3 with other anterior molars (1) only M1-M3 (2) M1-M3 simultaneously in use; 4) Tritolophid of M<sub>2</sub> (0) shortened (1) enlarged; 5) Upper permanent tusks (0) shorter than lower jaw (1) longer than lower jaw; 6) Upper permanent tusks with lateral enamel band (0) absent (1) present; 7) Lower tusks shape (0) concave dorsally (1) straight; 8) Lower tusks cross section (0) flattened (1) rounded or oval; 9) Upper tusks laterally divergent (0) little divergent (1) very divergent; 10) Upper tusks (0) downcurved (1) upcurved; 11) Presence of lower tusks (1) present (2) absent; 12) Lower jaw symphysis length (0) longirostrine (1) brevirostrine; 13) Pronounced crest-like habitus on molar lophs/lophids (0) absent (1) present.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Phiomia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eritreum</i>	0	0	1	1	?	?	0	0	?	?	0	0	0
<i>Zygodont</i>	1	1	2	1	1	1	1	1	0	0	0	0	0
<i>Eozygodon</i>	1	1	2	1	1	1	0	0	0	0	0	0	0
<i>Mammut</i>	1	1	2	1	1	0	1	1	1	1	[01]	1	1
<i>Sinomammut</i>	1	1	2	1	?	?	?	?	?	?	1	0	1

trefoil (which may vary according with the number of accessory conelets, see Mothé and Avilla 2015), while wear figures in zygodont molars are more slender and diamond-shaped, due the antero-distal compression of lophids (lophids) and the crest-like shape of the crescentoids and enamel crests (simple form, more or less prominent). Thus, the wear figures in zygodont molars have spindly, unrounded and thin projections (exposed dentin; Tassy 2014).

Although the Mammutidae had a worldwide distribution, absent only in South America, Australia and Antarctica (Shoshani and Tassy 1996), it was one of the less diversified families within Elephantimorpha (Gheerbrant and Tassy 2009). Until now, the most geographically restricted genus was *Eozygodon*, which is recorded only in Africa (Tassy and Pickford 1983); the widespread genus *Zygodont* is recorded in Africa, Eurasia, North America; and *Mammut* is recorded in Eurasia, North and Central Americas (Tobien 1975). Notwithstanding, the morphological similarity with other Mammutidae taxa, the specimen GIOTC 0984-9-178 presents several unique features (these will be presented in the sequence). Thus, the specimen GIOTC 0984-9-178 is a new genus and species of Mammutidae from the Miocene of China and, despite the description of *Sinomammut tobiensis* increases the diversity of the Mammutidae, this new monospecific genus probably represents a Chinese endemic taxon.

#### SYSTEMATIC PALEONTOLOGY

PROBOSCIDEA Illiger, 1811

MAMMUTIDAE Hay, 1922

*SINOMAMMUT TOBIENI* gen. et sp. nov.

(Fig. 1, 2 and 3)

*Sinomastodon intermedius* Xie 2007, p. 169, figure 31

*Sinomastodontinae* genus et species indeterminata, Wang et al. 2014, p. 5, figure 4

ZooBank Life Science Identifier (LSID) - urn:lsid:zoobank.org:act 7B1FF891-0595-4339-8C82-7F42528931D7

**Etymology**— the genus name, *Sino*, from the latin *Sinae*, meaning Chinese, plus *mammut*, in reference to the type genus of the family Mammutidae; and, the species is named after Dr. Heinz Tobien, a great promotor of the research on Chinese Proboscidea.

**Temporal, Stratigraphic and Distributional Range**— Baodean (Chinese Neogene Land Mammal age), Late Miocene (Wang et al. 2014).

**Holotype**— GIOTC 0984-9-178, a fragmentary right lower hemimandible bearing fully worn m2 and moderately worn m3.

**Type Locality**— Yanghecun locality, Changdao Township, Xihe County (35°08'38.1"N, 105°20'29.1"E), China.

**Type Horizon**— Upper Miocene strata, situated in the center of the Xihe-Lixian Basin in the West Qingling fold belt. It is composed of brownish-red silty mudstone and mudstone, partially intercalated with conglomerates, sandy conglomerates, and coarse sandstones. The Upper Miocene is distributed in a band in a gully, unconformity overlying the Xihanshui Group (Wang et al. 2014).

**Diagnosis**— a new monospecific genus of Mammutidae from China, known from a single robust and longirostrine mandible, with straight, thin and tuskless symphysis (the symphysis region was broken and lost during collection procedures). The zygodont cheek teeth include a trilophodont m2 and a tetralophodont m3. The m3 lophids are compressed anteroposteriorly and obliquely oriented (i.e., antero-lingual to postero-labial direction); its Prs have crest-like ACr and PCr (Pr1 and Pr2 have crest-like PCr and Pr3 and Pr4 have crest-like ACr) and Po1 and Po2 have posterior zygodont crests (ZC). A small and weak posterior cingulum (PC) is present distal to the last Po; formed by six small cusps.

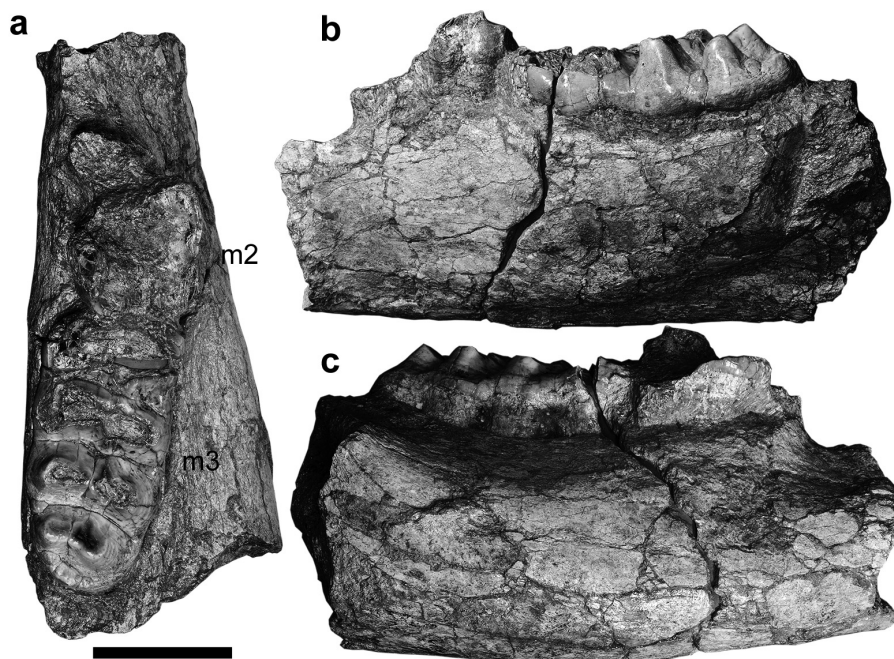
**Description of material**—the mandible has a robust body, with rounded labial portions; the longirostrine symphysis is relatively straight and thin. The original specimen presented a tuskless

lower jaw (Fig. 1a). The ascending rami are fragmented and the condyles are not preserved (Fig. 1a).

The cheek teeth include both second (m2) and third (m3) molars (Fig. 2). The m2 is trilophodont, however, its broken at the protolophids level and totally worn; no diagnostic structures are observable on its crown (Fig. 2). The m3 is wide, tetralophodont and has a small PC; the lophids are compressed antero-posteriorly and oblique (i.e., antero-internal to postero-external direction), with clearly yoke-like crests (Fig. 2 and Fig. 3d). The lingual wall is vertical, while the labial wall is more oblique towards the tip of the cusps. The right m3 lophids are worn in different levels, with exposed dentine in all of them, except for the last one (Fig. 2a). The protolophid is completely worn out and its anterior region is obliterated. The metalophid is sorely worn, but the enamel figures on Prs and Pos are still visible and the exposed dentine surfaces are medially connected. The last two lophids are slightly worn, but very well preserved; the fourth lophid has reduced width in relation to the anterior lophids.

All m3 Prs and Pos are composed by a developed primary connelet (PCo) and secondary connelet (SCo), which are smaller and weaker than the associated PCo. All right m3 Prs present developed crest-like ACr (Pr1 crest-like ACr is absent or worn out), and the first two also present crest-like PCr (Fig. 3d). The Po3 and Po4 anterior and posterior ZC are absent. The PC of right m3 is small and weak, formed by six small cusps, more developed on the Po side (Fig. 3). There is a small accessory connelet (ACo) on labial side of third interlophid area (IA). The IA is broad and well delineated (Fig. 3d). The crest-like PCr of Pr1 and Pr2 make contact with the crest-like ACr of Pr2 and Pr3, which intersect the first and second IA. The crest-like ACr of Pr4 is slightly worn and do not connect with Pr3 (Fig. 3d).

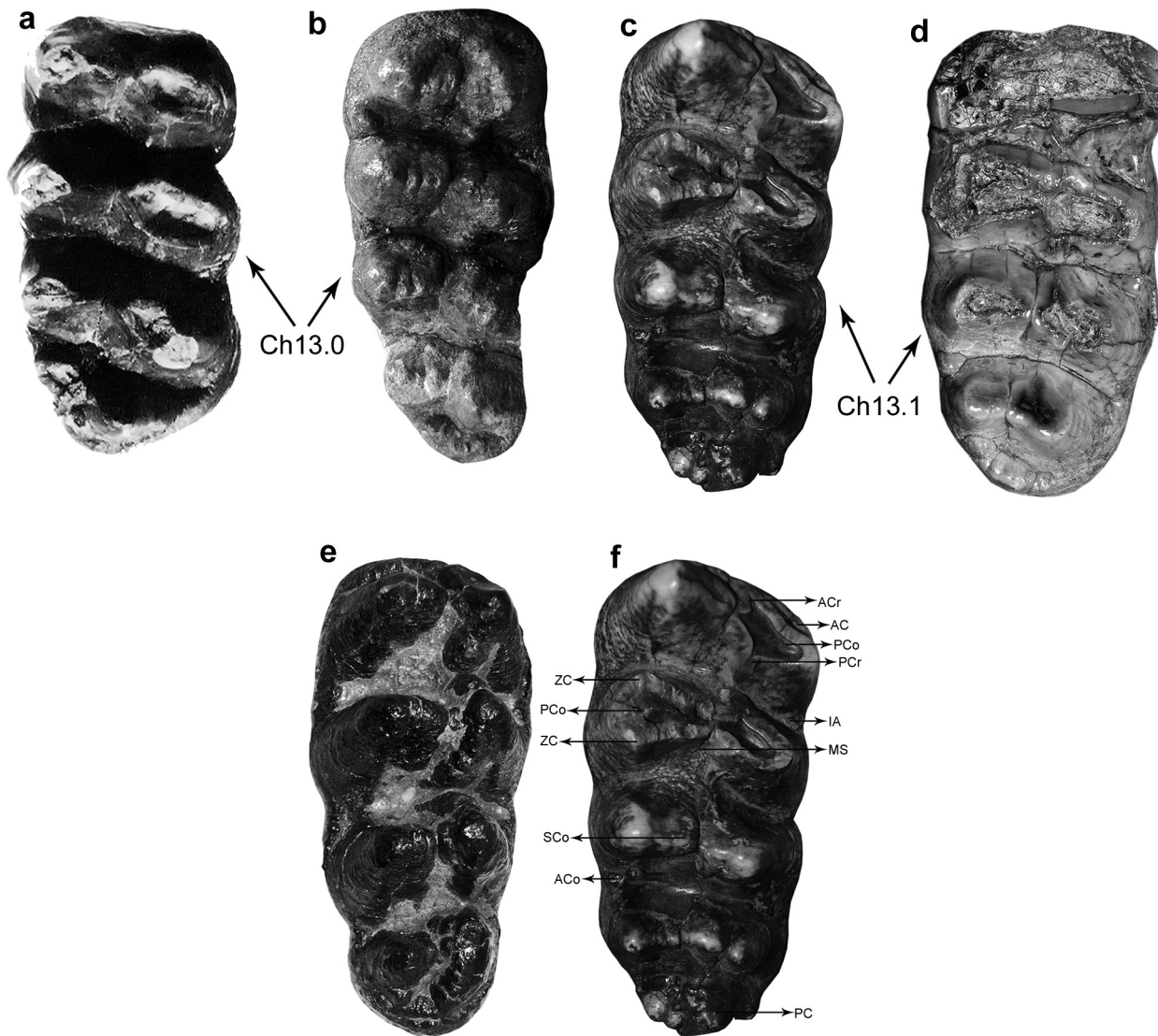
Differential diagnosis—*Sinomammot* differs from *Gomphotherium* and other Gomphotheriidae taxa by having slender and oblique lophids on m3, which is inflated and more parallel in gomphotheres (Fig. 3d and e); by having ZC on m3 Po and ACr and PCr on Pr, which are absent in



**Figure 2** - Right fragmented mandible ramus of *Sinomammot tobieni* (GIOTC 0984-9-178) with m2 and m3. (a) Occlusal view; (b) Lingual view; (c) Labial view. Scale bar: 10 cm.

Gomphotheriidae; and by having proportionally wider m3 teeth (Fig. 4). The combination of a longirostrine and tuskless lower jaw (Fig. 1) differs *Sinomammuth* from all other Mammuthidae taxa, which have longirostrine mandible with lower tusks (*Zygodontodon* and *Eozygodon*) or

brevirostrine mandible with variable presence of vestigial lower tusks (*Mammuth*; see Table II). The presence of a complete ZC only on the Po1 and Po2 differ *Sinomammuth* from *Zygodontodon*, which has developed ZC on all Pos, and from *Mammuth* and *Eozygodon*, which have vestigial crests. The poorly

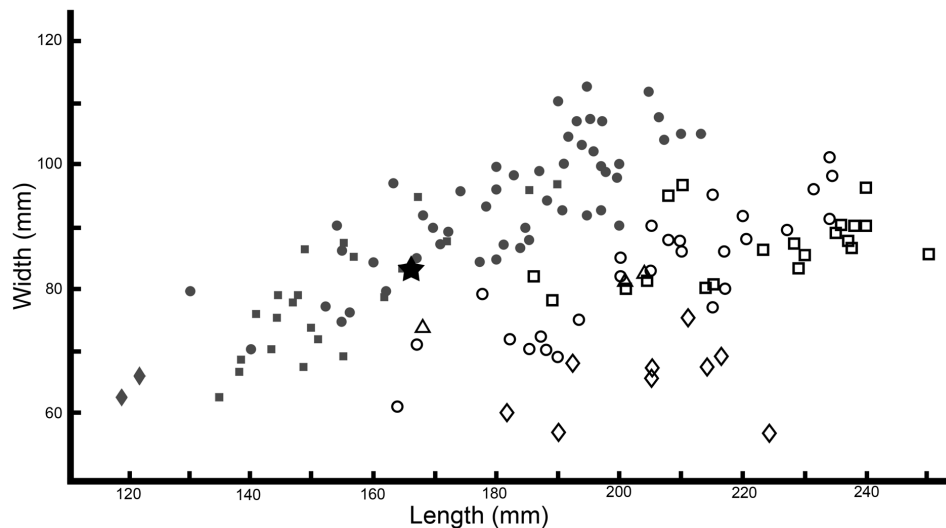


**Figure 3** - Occlusal view of third lower molars (m3) of Mammuthidae (a,b,c) and Gomphotheriidae (e) compared to m3 of *Sinomammuth tobieni* gen. et sp. nov. (d). Note the difference between the molar morphology, the shape of wear figures and the molar structures studied in this paper (abbreviations are explained on text). (a) *Eozygodon morotoensis* right m3 (from Tassy and Pickford, 1983); (b) *Zygodontodon* right m3 (AMNH 26461); (c) and (f) *Mammut americanum* left m3 (AMNH 14294); (d) *Sinomammuth tobieni* right m3 (GIOTC 0984-9-178); (e) *Gomphotherium* left m3 (AMNH 1908). Specimens (c), (e) and (f) are horizontally turned in order to facilitate anatomy recognition and comparisons. The only synapomorphy shared by *S. tobieni* and *M. americanum* - Presence of a pronounced crest-like habitus on molars - is indicated by the arrows and the abbreviation Ch13.1 (derived state, (c) and (d)) and Ch13.0 (primitive state, (a) and (b)). All specimens are out of scale.

developed and lingually oriented PC (mainly behind last Po) differentiates *Sinomammut* from other Mammutidae taxa, in which the PC is well developed and lingually oriented (mainly behind last Po, as in *Eozygodon*), poorly developed and parallel to the last Po (*Zygodontophodon*) or well developed and parallel to the last Po (*Mammuthus*).

The phylogenetic analysis performed here resulted in only one most parsimonious tree, with 15 steps, the topology as follows: (*Eozygodon* (*Zygodontophodon* (*Sinomammuthus tobieni*, *Mammuthus*)))

(see Fig. 5). A closest relationship between *Sinomammuthus tobieni* and *Mammuthus* is supported by one unambiguous synapomorphy: the emergence of the pronounced crest-like loph/lophids (character 13, state 1; see Fig. 3a to d). The clade (*Zygodontophodon* (*Sinomammuthus tobieni*, *Mammuthus*)) is supported by two synapomorphies: the straight shape (character 7, state 1) and rounded/oval cross section of the lower tusks (character 8, state 1). The lower tusks in *Eozygodon* are well developed, elongated and dorsoventrally flattened, with two strong



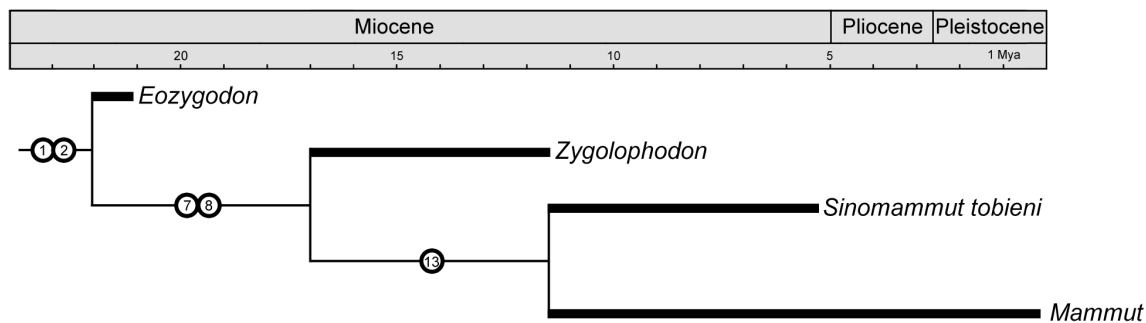
**Figure 4** - Scatter diagram of late Neogene and Pleistocene Mammutidae and Gomphotheriidae m3 width and length. Note the difference between the Mammutidae cloud (gray dots) and Gomphotheriidae (open dots). Key: *Sinomammuthus tobieni* is represented by the black star; the genus *Mammuthus* is represented by the gray circles; *Zygodontophodon* is represented by gray squares; *Eozygodon* is represented by gray diamonds; *Tetralophodon* is represented by open triangles; *Anancus* is represented by open squares; *Gomphotherium* is represented by open diamonds. Data was based on Tobien (1975), Tassy and Pickford (1983), Shoshani and Tassy (1996) and Wang et al. (2014).

**TABLE II**

*Sinomammuthus* autapomorphies compared to Mammutidae taxa. Note that the set of features of *Sinomammuthus* is unique among the Mammutidae.

<i>Sinomammuthus</i>	<i>Eozygodon</i>	<i>Zygodontophodon</i>	<i>Mammuthus</i>
Longirostrine and tuskless.	Longirostrine with lower tusks.	Longirostrine with lower tusks.	Brevirostrine with or without lower tusks.
Small distal cingulum mainly behind last Po.	Well developed distal cingulum mainly behind last Po.	Small distal cingulum behind last lophid.	Well developed distal cingulum behind last lophid.
Zygodont crests only on Po1 and Po2.	Zygodont crests absent.	Zygodont crests on all Pos.	Zygodont crests absent.





**Figure 5** - Phylogenetic hypothesis of the family Mammutidae including the new mastodon *Sinomammuthobieni*. Diagnostic characters and states are described on Table I.

concavities (at the dorsal and ventral sides; Tassy and Pickford 1983).

The calibrated phylogeny of Mammutidae (following the previously cited literature for temporal range data) allowed the recognition of the diversification of the clade *Sinomammuthobieni* plus *Mammuth* occurred during the late Early-Middle Miocene (17 to 11.6 Mya; Fig. 5). Although features related to mandibular symphysis length (brevirostrine/longirostrine condition) and to lower tusks (presence/absence) did not appear as synapomorphies, we recognize their importance to Mammutidae evolution. The longirostrine condition seems to be primitive for Mammutidae, and this condition is present in the earliest mastodon, *Eozygodon*, and also in *Zygolophodon* and *Sinomammuthobieni*. Thus, the brevirostrine condition of *Mammuth* is the derived condition, and it probably emerged during the Middle to Late Miocene (17-12 Mya, see Fig. 5).

Concerning the lower tusks, the primitive condition for the Mammutidae is well-developed incisors, which is present in *Eozygodon* (see figure 15 of Tassy and Pickford 1983: 64) and *Zygolophodon* (see figure 39 in Tobien et al. 1988: 150). However, two derived conditions are recognized in the Mammutidae: the absence of lower tusks, as recorded for *Sinomammuthobieni*; and, the occasional presence of vestigial lower tusks or its absence, as seen in *Mammuth* (Barbour 1931, Haynes 1991). The uniqueness of the longirostrine and tuskless mandible of *Sinomammuthobieni* can clearly

differ this new taxon and *Mammuth* – the latter is brevirostrine, but occasionally present small lower tusks (Barbour 1931), usually interpreted as sexual dimorphism. In fact, the loss of the lower tusks and the shortening of mandibular symphysis are evolutionary trends observed in parallel to other Proboscidea families (Shoshani and Tassy 1996), such as Gomphotheriidae and Elephantidae, from the late Miocene to Pliocene. Except for the gomphotheres *Rhynchotherium*, which kept the lower tusks during all life span (Lucas and Morgan 2008), and *Cuvieronius*, which had deciduous lower tusks at immature stage (Ferretti 2008, D. Mothé, unpublished data), all Pleistocene/Holocene proboscidean lineages (including the two extant elephants genera) are brevirostrine and dibelodont (presence of upper tusks and absence of lower tusks). These evolutionary trends in the mandible of Proboscidea are probably related to the several global climatic and environmental changes, which occurred from the late Middle Miocene on, causing modifications on feeding habits of those proboscideans (mastication mechanics, also modification in skull and molars morphology; see Maglio 1972), and probably included more abrasive vegetation, as C4 grasses, on diet (Janis 1988).

## CONCLUSIONS

A new Mammutidae monospecific genus, *Sinomammuthobieni*, is described based on a longirostrine and tuskless partial lower jaw from

the Miocene of China. This new taxon increases the diversity of the Family Mammutidae, originally composed by only four genera: *Eozygodon*, *Zygodontophodon*, *Mammut* and *Losodokodon*. The phylogeny of Mammutidae here proposed positioned *Sinomammut* as the closest taxon of the worldwide mastodon *Mammut*, and they share one synapomorphy: the presence of pronounced crest-like on loph/lophids of molars. These new mastodon also represents an important stage on the evolution of lower jaw and lower tusks in Proboscidea, since it is the unique completely tuskless longirostrine mammutid.

#### ACKNOWLEDGMENTS

The authors are grateful to all curators of the collections cited above for allowing the access to the Proboscidea specimens that supported this study; to Dr. Shiqi Wang, Dr. Taissa Rodrigues, Dr. Alexander Kellner, Dr. Marcelo Britto and Mrs. Sabrina Ferreira for improvements in content and English; to the two anonymous reviewers; Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação Carlos Chagas Filho de Amparo a Pesquisa do Estado do Rio de Janeiro (FAPERJ) granted PhD scholarship funds to the author DM (process numbers 140453/2012-01, 201081/2014-8 and E-26/100.246/2014) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) granted Post-Doctoral scholarship funds to the author LA (248772/2013-9).

#### RESUMO

O “espécime de Yanghecun”, uma mandíbula de proboscídeo do Mioceno da China e previamente descrito como Gomphotheriidae, é aqui revisado e descrito como um novo gênero e espécie de Mammutidae: *Sinomammut tobieni*. Este taxon é um mastodonte longirostrino, sem presas inferiores, e com terceiro molar largo, com lófidios oblíquos e comprimidos, interlófidios amplos e com figuras de desgaste zigodonte. A análise filogenética de Mammutidae foi baseada em características dentárias,

cranianas e mandibulares, e recuperou *S. tobieni* como grupo-irmão do mastodonte *Mammut*. A condição longirostrina e as presas inferiores bem desenvolvidas seriam primitivas para Mammutidae, enquanto a brevírostrina seria a condição derivada, provavelmente surgida durante o Mioceno médio (12-11 Ma). Entretanto, duas condições derivadas são reconhecidas para as presas inferiores de Mammutidae: a ausência destes incisivos (*S. tobieni*) e a presença ocasional de incisivos vestigiais (*Mammut*).

**Palavras-chave:** Evolução, Mammutidae, Mioceno, Proboscidea, Sífnise longirostrina.

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