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New zygolophodonts from Miocene of China and their taxonomy postprint

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Abstract

The zygodont proboscideans from the Miocene strata of China are widely distributed. However, the materials are scarce, and their classification has experienced a longtime controversy, from the chaotic state of multiple Zygolophodon species to the only one species, Zygolophodon gobiensis. The combined species Z. gobiensis comprises both the gracile type with a high degree of zygodonty and the robust type that is between the typical bunodont and zygodont morphology. Recently, as the robust type has been re-allocated to another genus Miomastodon and new fossil remains were discovered, it is necessary to further evaluate and classify the zygodont proboscideans from the Miocene of China. In the present paper, we restudied the previously published zygodont specimens of the gracile type, as well as several unpublished Mammutidae specimens. The former including Z. nemonguensis, Z. gromovae, Z. jiningensis, Z. chinjiensis and two specimens of Gomphotherium xiaolongtanensis, represents Zygolophodon in the original sense in China. In these specimens, the tip of the loph(ids) are sharp. The anterior and posterior pretrite central conules are absent or very weak, and the anterior and posterior crescentoids are sharp and slender. The posttrite mesoconelets are well subdivided and the zygodont crests are developed. In buccal view, the loph(id)s are “ -shaped” and the interloph(id) s are “V-shaped”. Their molar morphology resembles that of Z. turicensis, and hereby, they were identified as Zygolophodon cf. Z. turicensis. Several unpublished specimens from Hezheng, Gansu, Tunggur, Nei Mongol, Tongxin, Ningxia and Junggar, Xinjiang exhibit a lower degree of zygodonty, corresponding to the “robust type of Zygolophodon” in which the molar morphology is between the typical bunodonts and zygodonts. The pretrite crescentoids are thicker than Zygolophodon cf. Z. turicensis, and the pretrite central conules usually present on the first and second interloph(id)s. According to the stratigraphic age and characteristics, two species, Miomastodon gobiensis and Mio. tongxinensis were identified. The anterior and posterior pretrite crescentoids of Mio. tongxinensis are weaker and the pretrite central conules are larger than Mio.gobiensis. Geographical distribution indicates that Miomastodon is the predominant member of zygodophodonts in the Early and Middle Miocene in northern China. The discovery of new materials and the reclassification of zygodophodonts provide further evidence for dispersal of Mammutidae from Eurasia to North America and the evolutionary relationships among the species of the family Mammutidae in China.

Full Text

Preamble

New zygolophodonts from Miocene of China and their taxonomy

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Abstract

Zygolophodont proboscideans from the Miocene strata of China are widely distributed but represented by scarce materials, and their classification has long been controversial, evolving from a chaotic state with multiple Zygolophodon species to recognition of only one species, Zygolophodon gobiensis. The combined species Z. gobiensis comprises both the gracile type with a high degree of zygodonty and the robust type that exhibits morphology intermediate between typical bunodont and zygodont forms. Recently, as the robust type has been reallocated to another genus, Miomastodon, and new fossil remains have been discovered, it has become necessary to further evaluate and classify the zygodont proboscideans from the Miocene of China. In this paper, we restudied previously published zygodont specimens of the gracile type, as well as several unpublished Mammutidae specimens. The former, including Z. nemonguensis, Z. gromovae, Z. jiningensis, Z. chinjiensis, and two specimens of Gomphotherium xiaolongtanensis, represents Zygolophodon in the original sense in China. In these specimens, the tips of the loph(ids) are sharp, the anterior and posterior pretrite central conules are absent or very weak, and the anterior and posterior crescentoids are sharp and slender. The posttrite mesoconelets are well subdivided and the zygodont crests are developed. In buccal view, the loph(id)s are “ -shaped” and the interloph(id)s are “V-shaped.” Their molar morphology resembles that of Z. turicensis, and they are hereby identified as Zygolophodon cf. Z. turicensis. Several unpublished specimens from Hezheng, Gansu, Tunggur, Nei Mongol, Tongxin, Ningxia, and Junggar, Xinjiang exhibit a lower degree of zygodonty, corresponding to the “robust type of Zygolophodon” in which molar morphology is intermediate between typical bunodonts and zygodonts. The pretrite crescentoids are thicker than in Zygolophodon cf. Z. turicensis, and the pretrite central conules are usually present on the first and second interloph(id)s. Based on stratigraphic age and characteristics, two species, Miomastodon gobiensis and Mio. tongxinensis, were identified. The anterior and posterior pretrite crescentoids of Mio. tongxinensis are weaker, and the pretrite central conules are larger than in Mio. gobiensis. Geographical distribution indicates that Miomastodon is the predominant member of zygolophodonts in the Early and Middle Miocene in northern China. The discovery of new materials and the reclassification of zygolophodonts provide further evidence for the dispersal of Mammutidae from Eurasia to North America and the evolutionary relationships among Mammutidae species in China.

Key words: China, Miocene, Mammutidae, Zygolophodon, Miomastodon

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1 Introduction

Mammutidae is one of the two main branches of Elephantiformes, equivalent to the zygodont mastodonts. This group has a wide geographical distribution, having been discovered on all continents except Antarctica, Oceania, and South America, and temporally ranging from the Late Oligocene to the end of the Pleistocene. According to current research, Mammutidae contains six genera: Losodokodon Rasmussen & Gutierrez, 2009; Eozygodon Tassy & Pickford, 1983; Zygolophodon Vacek, 1877; Miomastodon Osborn, 1922; Mammut Blumenbach, 1799; and Sinomammut Mothé et al., 2016 (Shoshani and Tassy, 2005; Rasmussen and Gutierrez, 2009; Mothé et al., 2016; Wang et al., 2020). In China, although five of the six genera (all except Losodokodon) have been reported, fossil mammutids are scarce, except in the Yushe Basin, Shanxi Province, where Mammut borsoni is rich and well-preserved from the Late Miocene to Pliocene.

Zygolophodon is another genus frequently reported in China, with an age earlier than that of Mammut. Materials have been mainly discovered from Miocene localities in northern China, such as Tunggur, Junggar, Tongxin, and Linxia, as well as scattered materials from southern China. Because most remains are isolated cheek teeth with ambiguous provenance, classification has remained controversial. Tobien et al. (1988) attributed all remains to one species, Z. gobiensis. However, the tooth morphotypes of Z. gobiensis sensu Tobien et al. (1988) include not only the typical zygodont type but also some intermediate forms between gomphotheres and mammutids.

In recent years, benefiting from the discovery of new materials and the development of biostratigraphy, a re-study of Zygolophodon from China has become imperative. Wang et al. (2020) attributed the untypical zygodonts (intermediate morphotype between zygodonts and bunodonts) to Miomastodon, while the typical zygodonts should be retained in the genus Zygolophodon (close to Z. turicensis). In this article, we further discuss new materials of Zygolophodon and Miomastodon from the Miocene of China.

Materials and methods

The new materials reported herein include an incomplete mandible (1986-NMG-DM) from the Damiao locality, Nei Mongol (Inner Mongolia), housed in the Inner Mongolia Museum; a complete right m3 (IVPP V26615) collected by Chen Guan-Fang from the Tunggur Formation in Nei Mongol, housed in IVPP; three specimens housed in HMV, including a broken mandible (HMV1808) from the Hujialiang Formation at Laogou locality, Gansu, a right M3 (HMV1938), and a right M2 (HMV1939) from the Linxia Basin (precise locality unknown); a right M3 (IVPP V26803) from Tongxin, Ningxia, probably from Dingjiaergou, Zhangenbao Formation; and an incomplete right M3 (IVPP V30715) discovered by Wang Shi-Qi from the Halamagai Formation of the Junggar Basin, Xinjiang. The above specimens were attributed to Miomastodon.

A left m3 (IVPP V26802) presented by Daiyuan Primary School of Luonan County, Shaanxi Province, is currently stored in IVPP (precise locality unknown) and was attributed to Zygolophodon. Furthermore, previously published zygodont materials that can be attributed to Zygolophodon and Miomastodon from China were also reevaluated.

The terminology of occlusal structures of zygodont cheek teeth follows Wang et al. (2020), and the terminology of mandibular anatomical structure follows Tassy (2013). Measurements of mandibles and cheek teeth follow Tassy (2013, 2014) and were obtained using callipers.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; GPM, Gansu Provincial Museum, Lanzhou, China; HMV, Hezheng Paleozoological Museum, Hezheng, Gansu, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NMB, Naturhistorisches Museum Basel, Basel, Switzerland; PIN, Paleontological Institute, Moscow, Russia; THP, Tianjin Natural History Museum, Tianjin, China.

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2 Systematic paleontology

Order Proboscidea Illiger, 1811
Family Mammutidae Hay, 1922
Genus Zygolophodon Vacek, 1877
Type species: Zygolophodon turicensis (Schinz, 1824)

Diagnosis: The tooth loph(id)s are anteroposteriorly compressed with a sharp cutting edge in fresh molars. The lophs of upper cheek teeth are perpendicular to the median sulcus, and the lophids of lower cheek teeth are oblique to the median sulcus. The anterior and posterior pretrite central conules are absent or very weak. In fresh molars, the anterior and posterior pretrite crescentoids display fine serrated knobs and exhibit thin crests after slight wear. The pretrite mesoconelets are also subdivided and crest-like. The posttrite half loph(id)s display a high degree of subdivision, and the zygodont crests are developed. The interloph(id)s are open, not obstructed by the crescentoids. The anterior and posterior pretrite crescentoids almost reach the bottom of the interloph(id)s. In lateral view, the loph(id)s are “ -shaped,” and the interloph(id)s are deep “V-shaped.”

Referred species: Zygolophodon aegyptensis (Sanders and Miller, 2002); Z. atavus (Borissiak, 1936).

Zygolophodon cf. Z. turicensis (Schinz, 1824) (Fig. 1 [Figure 1: see original paper]; Table 1)

Synonymy:
Zygolophodon (Turicus) nemonguensis Chow and Chang, 1961, p. 249–250, pl. 2, 3, figs. 4, 4a
Zygolophodon gromovae Dubrovo, 1970, p. 136–138, figs. 1, 2
Zygolophodon jiningensis Chow and Chang, 1974, p. 35–36, pl. 15, figs. 1, 1a
Zygolophodon chinjiensis (Osborn, 1929) Chow et al., 1978, p. 71–72, pl. 8, figs. 1, 2
Gomphotherium xiaolongtanensis Chow and Chang, 1974, p. 24, pl. 5, fig. 2 [Figure 2: see original paper]
Zygolophodon gobiensis (Osborn and Granger, 1932) Tobien et al., 1988, p. 149, 151, 153, 154, figs. 40, 42, 45, 46; Chen, 2021, p. 20–22, fig. 9 [Figure 9: see original paper]
?Zygolophodon metachinjiensis (Osborn, 1929) Chen, 2021, p. 25–26, fig. 13 [Figure 13: see original paper]

Referred materials: IVPP V2487 (Fig. 1A–B), left M3, from Ulanqab, Nei Mongol (precise locality unknown); PIN 2202-4 and PIN 2202-5, left and right maxilla from the same individual with M2–M3, PIN 2202-6, left M3, from Middle Miocene of Tunggur region, Sonid Left Banner, Nei Mongol (Dubrovo, 1970);

IVPP RV74003 (Fig. 1C–D), left M3, from Jining, Ulanqab, Nei Mongol (precise locality unknown); IVPP V4688.1 (Fig. 1E–F), complete left M3, from the Late Miocene Xiaolongtan Formation, Xiaolongtan coal mine, Kaiyuan, Yunnan; IVPP V4688.2 (Fig. 1G), posterior half of a right M3; IVPP V4685.7 (Fig. 1H) and V4685.8 (Fig. 1I), fragments of a left and a right M1, from the Late Miocene Xiaolongtan Formation, Yuxi coal mine, Yuxi, Yunnan; IVPP V5156 (Fig. 1J), fragmentary right M3 with the two anterior lophs, from Middle Miocene of Erlanggang, Fangxian, Hubei; IVPP V26802 (Fig. 1K–L), incomplete left m3, retaining the first three lophids, granted by the Daiyuan Primary School of Luonan County, Shaanxi Province (precise locality unknown).

Description:
M1 (IVPP V4685.7, Fig. 1H; V4685.8, Fig. 1I): The two specimens are deeply worn. The anterior and posterior pretrite crescentoids are developed, and the anterior and posterior pretrite central conules are absent. The distal end of the first posterior pretrite crescentoid is inflated, homologous to the posterior pretrite central conule. The posttrite half lophs are anteroposteriorly compressed and show an approximately oval enamel ring due to deep wear. The anterior and posterior zygodont crests are developed. The interlophs are relatively narrow. Cingula are developed on the anterior and posterior margins of the tooth and on the opening of interlophs on the pretrite side.

M3 (IVPP V2487, Fig. 1A–B; RV74003, Fig. 1C–D; V4688.1, Fig. 1E–F; V4688.2, Fig. 1G; V5156, Fig. 1J): The M3 is tetralophodont, and the second loph is the widest. The pretrite main cusps are high and sharp. The anterior and posterior pretrite crescentoids and mesoconelets are crest-like, and the anterior and posterior pretrite central conules are absent. The posttrite main cusps are large, and the mesoconelets are subdivided. The zygodont crests are developed and thin crest-like. The second posterior pretrite crescentoids originate from the mesoconelets rather than from the main cusps. The interlophs are open. Cingula develop on the entire tooth crown margin except for the labial side. In lateral view, the lophs are “Λ-shaped,” the anterior and posterior pretrite crescentoids reach the bottom of the interlophs, and the interlophs are “V-shaped.”

m3 (IVPP V26802, Fig. 2K–L): The lophids are oblique to the longitudinal axis. The pretrite main cusps are high and sharp. The anterior and posterior pretrite crescentoids and mesoconelets are crest-like. The posttrites are anteroposteriorly compressed, main cusps are high and sharp, and mesoconelets are subdivided. The zygodont crests are developed. The second anterior and posterior pretrite crescentoids originate from the mesoconelets. The second and third posttrites have weak anterior crescentoids. The interlophids are open, and cementum is absent. Cingulids are developed on the anterior margin of the tooth. In lateral view, the lophids are “ -shaped.” The first interlophid shows a deep “V-shaped” sleeved by a shallow “V-shaped,” and the second interlophid is deep “V-shaped.”

Genus Miomastodon Osborn, 1922
Type species: Miomastodon merriami (Osborn, 1921)

Referred species: Mio. tongxinensis Chen, 1978; Mio. gobiensis (Osborn & Granger, 1932); Mio. metachinjiensis (Osborn, 1929).
Diagnosis: See Wang et al. (2020).

Miomastodon gobiensis (Osborn & Granger, 1932) (Figs. 2, 3A—G; Tables 1, 2)

Type specimen: AMNH 26461, a right hemimandible from the Tunggur Formation, Tamuqin Fauna, late Middle Miocene, ~MN7/8 (Osborn and Granger, 1932; Wang et al., 2020).

Referred material: HMV1939 (Fig. 3A [Figure 3: see original paper]), right M2 (precise locality unknown); HMV1938 (Fig. 3B), right M3 (precise locality unknown); IVPP V26803 (Fig. 3C), right M3, probably from the Dingjiaergou locality, Zhangenbao Formation; 1986-NMG-DM (Fig. 2A–C, 4D), incomplete mandible, Damiao locality, Tunggur Formation; HMV1808 (Fig. 2D–E, 4G), broken mandible with left and right m3, Laogou locality; IVPP V26615 (Fig. 3E–F), right m3, locality 86027, Tunggur Formation.

Description:
M2 (HMV1939, Fig. 3A): The first two pretrite half lophs show trifoliate patterns due to wear. The anterior and posterior pretrite crescentoids are strong. The first posterior pretrite and the second anterior pretrite central conules are present. The posttrite half lophs are anteroposteriorly compressed. The posttrite main cusps and the mesoconelets are indistinguishable, and the mesoconelets are subdivided and crest-like. The interlophs are open, and a large amount of cementum is developed. Cingula are developed on the anteroposterior and lingual sides of the crown.

M3 (HMV1938, Fig. 3B; IVPP V26803, Fig. 3C): The M3 is tetralophodont, but the fourth loph is less developed. The first two pretrite half lophs show trifoliate patterns due to wear, and the anterior and posterior crescentoids are strong. The distal end of the second anterior pretrite crescentoid is inflated like a central conule. The third anterior pretrite central conule is developed, and the posterior one is absent. The posttrite half lophs are anteroposteriorly compressed and show oval enamel rings under wear. The posterior zygodont crests are developed. The posterior two lophs are chevroned. The interlophs are open, and cementum is developed. The cingula are weakly developed at the anterior and posterior margins of the crown.

Mandible (1986-NMG-DM, Fig. 2A–C): The mandible lacks the left and right rami. The mandibular tusks are broken from the opening of the incisive alveoli. The m2 is deeply worn, with the anterior root highly excavated from the alveolus. The m3 is moderately worn. In dorsal view (Fig. 2A), the two corpora are moderately diverged at an angle of ~30°. The posterior end of the corpus is moderately widened relative to the anterior end, and the mandible is considerably constricted at the symphyseal part. The symphysis is relatively narrow and moderately elongated. The distal part of the symphysis is widened, stronger than that of the type specimen (AMNH 26461). The symphyseal trough is deep and bordered by thick interalveolar crests. The caudal end of the symphysis is in line with the rostral end of the tooth row. The distal end of the symphysis exhibits an anteriorly oriented apex.

In lateral view (Fig. 2B), the mandibular corpus is relatively high, with a thicker rostral end. The symphysis is anteriorly protruded with a downward deflection, which is stronger than that of the type specimen (AMNH 26461). There are three mental foramina: the caudalmost one is small, at the level of the anterior end of the tooth row; a second, larger one is ~92 mm rostral to the first one, showing a rostrally elongated groove; and a third one is the rostralmost mental foramen, located somewhat ventral of the symphysis (~113 mm rostroventral to the second one).

In rostral view (Fig. 2C), the symphyseal trough dips down rostrally, showing a smooth and deep trough. The cross-section of the mandibular tusks is oval, with the dorsoventral diameter larger than the mediolateral diameter, which we call the “erected oval cross-section.”

HMV1808 (Fig. 2D–E): The mandible lacks the left and right rami, and the rostral end of the symphysis has been damaged. The left and right m2 alveoli were healing. The m3 is deeply worn, indicating that it belongs to an old individual. In dorsal view, the corpora are anteriorly narrowed, the symphyseal trough is relatively wide, and the two interalveolar crests are parallel. The posterior edge of the symphysis is in a straight line with the front edge of the m2 alveolus. In rostral view, the two tusk alveolar sockets are deep, close to each other, and the cross-sections are round.

m2 (1986-NMG-DM, Fig. 2A): The m2 is deeply worn. The lophids are gradually wider from anterior to posterior. The pretrite half lophids are trifoliate, with a posterior lobe larger than the anterior one. The ectoflexid is U-shaped, and the entoflexid possesses parallel borders. No accessory cusps rise from the posterior cingulid.

m3 (1986-NMG-DM, Fig. 3D; IVPP V26615, Fig. 3E–F; HMV1808, Fig. 3G): The m3 is tetralophodont with a thick enamel layer. The lophids are oblique to the longitudinal axis, and the first three lophids are equal in width. The pretrite and posttrite main cuspids are relatively high and large. The first pretrite and posttrite mesoconelets are subdivided and crest-like, but other pretrite and posttrite mesoconelets are less subdivided. The first anterior and posterior pretrite crescentoids are developed, with papillary anterior and posterior pretrite central conules at the distal ends. The distal ends of the second anterior and posterior pretrite crescentoids are inflated, homologous to the central conules. Zygodont crests are developed. Cingulids are developed at the anterior and posterior margins of the crown. In lateral view, the lophids are “ -shaped,” but the tips are blunter than in Z. turicensis. The interlophids are stuffed up by the accessories (central conules and crescentoids), showing a deep “V-shaped” sleeved by a shallow “V-shaped” pattern.

Miomastodon tongxinensis Chen, 1978 (Fig. 3H; Table 1)

Type specimen: IVPP V5584 (Chen, 1978: pl. II, fig. 2), a deeply worn right m3 from the Zhangenbao Formation, Tongxin, Ningxia, late Early or early Middle Miocene.

Referred material: IVPP V30715, an incomplete right M3, from the east cliff of the Dingshanyanchi Terrace, Junggar Basin, Xinjiang.

Description: IVPP V30715 (Fig. 3H): The first loph is wider than the second. The first pretrite half loph possesses a moderately developed mesoconelet. It has three aligned anterior central conules that link to the anterior cingulum. It also has a thick posterior crescentoid and a prominent posterior central conule. The second pretrite half loph possesses a slightly anteriorly displaced mesoconelet. The anterior and posterior crescentoids are weak, and the anterior and posterior pretrite central conules are equally developed. A posterior pretrite intermediate crescentoid is also present, as in some specimens of Mammutidae. The posttrite half lophs are anteroposteriorly compressed. The first posttrite comprises three conelets: the outmost one represents the original main cusp, and the inner two are subdivided mesoconelets. A weak anterior zygodont crest and a relatively strong posterior zygodont crest are present. Another two weak, crest-like posterior central conules are aligned with the posterior zygodont crest. The second posttrite half loph is similar to the first one. The zygodont crests and posterior central conules are weaker than those of the first posttrite but additionally possess a crest-like anterior posttrite central conule. The cingula are strong. In lateral view, the interloph shows a deep "V-shaped" sleeved by a shallow "V-shaped" pattern.

3 Comparison and discussion

Many species under the genus Zygolophodon have been established in China. Osborn and Granger (1932) reported a right hemimandible from Tunggur, Nei Mongol, and identified it as Serridentinus gobiensis. The genus Serridentinus should belong to a bunodont type and has been synonymized with Gomphotherium. Tobien (1972) considered that the tooth morphology is closer to zygodont mastodonts. Tassy (1985) identified another mandibular fragment with m3 in the AMNH collections from Tunggur as Z. gobiensis. Chow and Chang (1961) reported an M3 from the Miocene of Nei Mongol and erected the species Zyglophodon (Turicus) nemonguensis. Dubrovo (1970) reported a left and a right upper maxilla belonging to the same individual and a left M3, all from the Middle Miocene of Tunggur, Nei Mongol, and erected the species Z. gromovae. Chow and Chang (1974) reported a left M3 from the Miocene of Jining, Nei Mongol, and erected the species Zygolophodon (Turicus) jiningensis. Chow et al. (1978) reported three specimens from the Late Miocene of the Xiaolongtan Formation, Yunnan, and identified them as Z. chinjiensis. Yan (1979) reported a fragment of m3 from the Middle Miocene of Fangxian, Hubei Province, and identified it as Z. nemonguensis. Tobien et al. (1988) synonymized all Chinese zygodont proboscideans with one species, Z. gobiensis. Besides the materials listed above, they also included Mio. tongxinensis from Tongxin, Ningxia, published by Chen (1978), and two specimens of Gomphotherium xiaolongtanensis from Xiaolongtan, Kaiyuan, Yunnan, published by Chow et al. (1978). The type specimen was assigned as the mandible (AMNH 26461) of Z. gobiensis. Chen (2021) believed that there is more than one species of Zygolophodon in China, and some materials may not belong to Z. gobiensis, such as Mio. tongxinensis. However, she still insisted on grouping them into one genus and did not compare the materials discovered in recent years.

It has long been recognized that two tooth morphotypes are present in mastodont proboscideans: the bunodont and zygodont types, representing the two major branches of elephantimorphs, Gomphotheriidae and Mammutidae. Morphology of zygodonty occurred at a very early stage of elephantimorphs, i.e., the Early Oligocene, represented by Palaeomastodon (Matsumoto, 1924; Tobien, 1978; Madden, 1980; Sanders et al., 2004). The Late Oligocene Losodokodon was an entirely zygodont elephantimorph (Rasmussen and Gutierrez, 2009). However, intermediate tooth morphology forms coexisted continuously with typical bunodonts and zygodonts during the Late Neogene, which has created difficulties in the taxonomy of related taxa. For example, in Europe, G. subtapiroideum obfuscates the boundary between G. angustidens and Z. turicensis (Schlesinger, 1917; Lehmann, 1950; Mazo, 1996; Göhlich, 1999; Radović and Bradić-Milinović, 2018); in Asia, Serridentinus gobiensis and S. metachinjiensis were transferred to Zygolophodon (Tassy, 1985; Tobien, 1996).

According to Tassy (1985), Z. turicensis in Europe contains both robust (intermediate morphology) and gracile (typical zygodont) types, and he mentioned that the molars of AMNH 26461, the type hemimandible of Serridentinus gobiensis, represent the robust type. Tobien et al. (1988) also pointed out that AMNH 26461 corresponds to the robust types and Z. gromovae corresponds to gracile types. Recently, Wang et al. (2020) further attributed these Asian robust types to Miomastodon. Tobien et al. (1988) mentioned that the gracile zygodont specimens from China are smaller than Z. turicensis from Europe and sometimes lack pretrite mesoconelets. However, these differences do not seem sufficient to establish a new species, and the size of the upper M3 (IVPP V2487, Z. (Turicus) nemonguensis) from Nei Mongol is rather large. The type specimen of Z. turicensis (Fig. 1M—N) is an m2 from the Middle Miocene near Zurich, Switzerland. The lophids are sharp, the anterior and posterior crescentoids are thin, the central conules are absent, and the interlophids are open and “V-shaped” in lateral view. Compared with the type specimen, the above-mentioned Chinese gracile type materials exhibit the same degree of zygodonty, corresponding to the European gracile type Z. turicensis described by Tassy (1985). Therefore, Chinese gracile type zygodonts are here attributed to Zygolophodon and identified as Zygolophodon cf. Z. turicensis.

The earliest known Zygolophodon is Z. aegyptensis from the Early Miocene, about 18.0–17.0 Ma ago, in Moghara, Egypt (Sanders and Miller, 2002). Compared with Z. aegyptensis, Zygolophodon cf. Z. turicensis is larger, has a better-developed fourth loph, the third loph of M3 is not convex in the median sulcus, and shows a higher degree of zygodonty. Another species of Zygolophodon is Z. atavus from the Early Miocene Jilančik beds of Kazakhstan, Central Asia (Borissiak, 1936). The mandibular symphysis is longer than in Z. turicensis (Březina, 2014; Sanders and Miller, 2002). The two mandibular tusks are relatively developed and close to each other, and the cross-section has a larger mediolateral than dorsoventral diameter. The dimensions of the m3 and the width-length ratio of the first two lophids fall within the ranges of Zygolophodon (Wang et al., 2020). Due to its early age (Early Miocene), Z. atavus may represent a more primitive feature of Zygolophodon. Apparently, Zygolophodon cf. Z. turicensis from China is more progressive in morphology and later in age.

The incomplete mandible (1986-NMG-DM) recovered from the late Middle Miocene of the Damiao locality, Nei Mongol, shows intermediate tooth morphology between Gomphotheriidae and Mammutidae, belonging to the robust zygodont types. The pretrite crescentoids are thick, and the central conules are present. The posttrite half lophids are anteroposteriorly compressed, and the interlophids are open. In addition, the mandibular symphysis is relatively narrow and moderately elongated, and the cross-section of the mandibular tusk is erected oval. These characters are in accordance with the diagnosis of Mio. gobiensis. It differs slightly from the type hemimandible (AMNH 26461) in the more ventral bend of the symphysis and the more lateral expansion in the distal symphysis. These differences are treated as intraspecific variations here.

The mandible (HMV1808) was excavated from the same locality as the Mio. gobiensis cranium (GPM ZR001141) (Li Y et al., 2021). Like the type specimen of Mio. gobiensis (AMNH 26461), the hemimandibles of HMV1808 also taper rostrally, and the symphyseal trough is smooth. Observing from the alveoli of the mandibular tusks, the left and right mandibular tusks are also rod-shaped and close to each other. Although the m3 is deeply worn, the lophids are weakly anteroposteriorly compressed, the anterior and posterior crescentoids are strong, and the anterior and posterior pretrite central conules are present. According to these morphological characteristics, it is reasonable to classify HMV1808 as Mio. gobiensis.

On the two deeply worn upper molars (HMV1938, M3; HMV1939, M2), the lophs are less sharp, the anterior and posterior crescentoids are strong and distally inflated, indicating that the anterior and posterior pretrite central conules are developed, and the posttrite half lophs are less subdivided compared to typical zygodonts. The third loph of M3 is chevroned. These two molars are very similar to M2 and M3 on the cranium of Mio. gobiensis (GPM ZR001141) and are hereby attributed to the same species.

On the complete right m3 (IVPP V26615) from Nei Mongol, the lophids are slightly anteroposteriorly compressed and blunt in lateral view, the anterior and posterior pretrite central conules are developed, the posttrite half lophids are moderately subdivided, and the interlophids show patterns of a deep "V" sleeved by a shallow "V" in lateral view. These features meet the diagnosis of Mio. gobiensis.

Although the right M3 (IVPP V26803) from Tongxin is deeply worn, the retained features show that the lophs are slightly anteroposteriorly compressed, the anterior and posterior crescentoids are strong, the posttrites are moderately subdivided, and the zygodont crests are weak. Therefore, it is reasonable to classify it as Miomastodon. This specimen was discovered from Dingjiaergou, Zhangenbao Formation in the Tongxin region, Ningxia, but its stratigraphic position is higher than IVPP V5584, the type specimen of Mio. tongxinensis. Compared with V5585, the same individual as V5584, the fourth loph of V26803 is more developed, the second anterior and posterior pretrite crescentoids are thicker, and the second posterior pretrite central conule is more obvious and larger. Therefore, we attribute the Dingjiaergou specimen to Mio. gobiensis.

The incomplete right M3 (IVPP V30715) was broken from the second interloph; however, the first two lophs are complete. Chen (1988) reported two jaws with M2–M3 from Botamoyin of the Halamagai Formation, establishing a new species, "junggarensis," and doubtfully attributed it to Zygolophodon. Chen (2021) further attributed them to Zygolophodon and identified them as Z.? zunggarensis. However, these specimens cannot currently be found, and the attribution of "zunggarensis" remains problematic. Wang et al. (2020) temporarily attributed them to Miomastodon sp. and mentioned that they might be close to Mio. tongxinensis. Specimen V30715 was recovered from the same horizon as the hypodigm of Z.? zunggarensis in 2021, and the absolute age is about 16 Ma (Ye et al., 2012), close to Mio. tongxinensis from the Tongxin region. On the second loph of V30715 and V8583 (Chen, 1988:270—273, pl. IV, fig. 3), the anterior and posterior pretrite crescentoids are weaker, but the pretrite central conules are obvious and rather large, similar to V5585 (Mio. tongxinensis, Chen, 1978: pl. II, fig. 1). Therefore, we refer V30715 to Mio. tongxinensis.

We further compared the tooth dimensions of some zygodont proboscideans from China (Fig. 4 [Figure 4: see original paper]). The M3 (RV74003, Z. jiningensis) from the Miocene (?) of Jining is the smallest and probably one of the earliest representatives of Chinese Zygolophodon. The type M3 of Z. (Turicus) nemonguensis is the largest Zygolophodon currently found in China. In terms of species, the M3 of Mio. tongxinensis is smaller than other zygodont proboscideans, and Mio. gobiensis has a similar width-length proportion to Zygolophodon cf. Z. turicensis. However, all Miocene zygodonts from China are smaller than Mammut borsoni in China.

4 Geographical distribution of zygolophodonts in China

Zygolophodon has been discovered in Tunggur and Jining of Nei Mongol, Luonan of Shaanxi, Fangxian of Hubei, and Yuxi and Xiaolongtan of Yunnan in China. Z. gromovae was discovered from the Middle Miocene of Tunggur, Nei Mongol. Z. (Turicus) nemonguensis and Z. gromovae obviously belong to typical gracile type zygodonts (Dubrovo, 1970, 1974; Duangkrayom et al., 2017). The left m3 from Luonan County, Shaanxi Province, although only retaining the front three lophids, also belongs to typical gracile type zygodonts. Another material identified as Z. (Turicus) nemonguensis is the fragmentary M3 (IVPP V5156) from Fangxian, Hubei. According to the features of the preserved part, it is slightly more primitive than the type specimen of Z. (Turicus) nemonguensis and has a precise location. According to Deng et al. (2019), the Fangxian locality belongs to the Tunggurian, Middle Miocene. Therefore, we speculate here that the age of the type specimen may be the same as the Fangxian material or slightly later. Other materials classified as Zygolophodon cf. Z. turicensis are from the Xiaolongtan Formation in Yunnan, including Z. chinjiensis and two specimens of "Gomphotherium xiaolongtanensis." In previous studies, such as Deng et al. (2019) and Li et al. (2015), the age of the Xiaolongtan Formation was assigned to the Middle Miocene. However, according to the latest research by Li C et al. (2021), the Xiaolongtan Formation may belong to the early Late Miocene. Therefore, Zygolophodon cf. Z. turicensis in China might range from the late Early or early Middle Miocene (possibly from Jining) to the end of the Middle Miocene in northern China and further extend to southern China in the early Late Miocene. Duangkrayom et al. (2017) reported the first record of Zygolophodon from the Late Miocene in Tha Chang, Thailand, Southeast Asia, indicating that Zygolophodon did not enter lower latitudes until the Late Miocene. The Zygolophodon specimens from Tha Chang might represent a dispersal link between South and East Asia during the Middle and Late Miocene, a view further supported by the Zygolophodon cf. Z. turicensis specimens from China.

Miomastodon has been discovered in Tongxin of Ningxia, the Junggar Basin of Xinjiang, the Linxia Basin of Gansu, and the Tunggur region of Nei Mongol (Wang et al., 2020; Li Y et al., 2021). Both Miomastodon and Zygolophodon are found in the Middle Miocene of northern China, whereas Zygolophodon is rare and sporadically distributed, although it appeared in southern China during the early Late Miocene. In China, Miomastodon was the predominant member of Mammutidae during the Early and Middle Miocene and is only found in northern China. The ancestral species is Mio. tongxinensis, which possibly spanned approximately 17–14 Ma in the late Early to early Middle Miocene of Tongxin (Li et al., 2023) and the Junggar Basin. The derived species, Mio. gobiensis, is distributed in the late Middle Miocene of the Linxia and Tunggur basins.

The type locality of Mio. merriami is Virgin Valley, McGee, Humboldt Co., Nevada, North America, early Barstovian (15.18–15.84 Ma) (Osborn, 1921;

Koenigswald et al., 2021). However, the age of Gomphotherium spreading from Eurasia to America is ~16 Ma (Qiu, 2003), indicating that at least in the early Middle Miocene, Mammutidae, represented by Miomastodon, from Eurasia had entered North America along with Gomphotherium.

A cladistic analysis was carried out to clarify the phylogenetic positions of Mammutidae from China (Fig. 5 [Figure 5: see original paper]). Since materials of Eozygodon sp. and Zygolophodon cf. Z. turicensis are scarce, we added two species, Eozygodon morotoensis and Z. turicensis. On this basis, we propose evolutionary relationships and geohistoric distribution of Mammutidae species in China (Fig. 6 [Figure 6: see original paper]). According to Fig. 6 and Zhang and Wang (2021), Miomastodon shows a higher degree of zygodonty than Eozygodon. In China, Zygolophodon might have derived from Eozygodon and further given rise to Mammut.

5 Conclusions

In this paper, we comprehensively studied old and new specimens of Zygolophodon and Miomastodon. The specimens attributed to Zygolophodon show a high degree of zygodonty that is strongly comparable with the type species, Z. turicensis, from the Middle and Late Miocene of Europe, whereas other specimens from the Early and Middle Miocene of northern China show a relatively low degree of zygodonty and can be attributed to Miomastodon. Two species, Mio. gobiensis and Mio. tongxinensis, were identified. In the Early and Middle Miocene, Miomastodon was the predominant member of Mammutidae in northern China, and at least in the early Middle Miocene, Miomastodon entered North America. Zygolophodon evolved from Eozygodon and further evolved into Mammut in China.

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Supplementary file: Can be found on the website of Vertebrata PalAsiatica (http://www.vertpala.ac.cn/EN/2096-9899/home.shtml) in Online First.

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