Attributing "Gomphotherium shensiense" to Platybelodon tongxinensis, and a New Species of Platybelodon from the Late Middle Miocene (Postprint)

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Full Text

Preamble

Attributing "Gomphotherium shensiense" to *Platybelodon tongxinensis*, and a New Species of *Platybelodon* from the Latest Middle Miocene

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Abstract

Platybelodon is the predominant proboscidean of northern China' s Middle Miocene. However, the cranial and cheek tooth morphologies are not clearly diagnosed, and the differential diagnoses between *Platybelodon* and *Gomphotherium* have not been comprehensively examined. Here we restudied the cranium previously identified as *Gomphotherium shensiense.* The upper tusks lack an enamel band, the rostrum is long and narrow, the facial part is rostrally positioned, and a large "prenasal slope" is present. These characters are distinct from those of any species of *Gomphotherium* but fit well with some primitive species of *Platybelodon*, i.e., *P. tongxinensis* and *P. danovi.* The molars are also close to the type specimen of *P. tongxinensis* in the tetralophodont M3 with mesiodistally wide interlophs, curved outline, and a tendency toward cementodonty. In this article, we synonymize *Gomphotherium shensiense* with *P. tongxinensis.*

Moreover, we recognize a new species, *Platybelodon tetralophus*, from the *P. grangeri* material collected by the AMNH expedition in the Tunggur region. *Platybelodon tetralophus* differs from *P. grangeri* and other species in the tetralophodont M2 and m2, representing the most derived species within *Platybelodon.* It has only occurred in the uppermost horizon of the Tunggur Formation, i.e., the Tamuqin Fauna (Platybelodon Quarry and Wolf Camp Quarry of AMNH). This work represents a comprehensive revision of the genus *Platybelodon.*

Key words: *Platybelodon*, *Gomphotherium*, biostratigraphy, biochronology

Trilophodont longirostrine gomphotheres were previously attributed to one genus, *Gomphotherium* (= *Trilophodon*, *Tetrabelodon*) (Falconer, 1857; Cope, 1884). However, recent studies indicate that gomphotheres can be subdivided into three family-level groups: the Choerolophodontidae, Amebelodontidae, and Gomphotheriidae (Gheerbrant and Tassy, 2009). They differ from one another mainly in the morphology of the mandibular symphysis and mandibular tusks, which indicates that adaptive radiations account for food-procurement behaviors among gomphotheres. However, the differences in cranium and cheek teeth among families are subtle and somewhat difficult to address. Therefore, one should be careful when basing identification on single crania and isolated teeth.

Chang and Zhai (1978) established *Gomphotherium shensiense* from Tianhegou, Lintong, Shaanxi Province, which was once considered a basic type of *Gomphotherium* in China (Tobien et al., 1986). Recently, we investigated and surveyed large samples of gomphothere specimens from all localities in northern China. It is clearly shown that *Gomphotherium* was never an important component in any Early-Middle Miocene sites. Notably, *Platybelodon* gradually became the dominant taxon after ~14.5 Ma (i.e., during most of the Middle Miocene). Therefore, species of *Gomphotherium* previously established based on cranium and mandible should be further studied. In the present article, we amend *G. shensiense* and attribute it to *Platybelodon* based on cranial and dental morphology. We further establish a new species, *Platybelodon tetralophus*, from the uppermost horizon of the Tunggur Formation.

1.1 Materials and Terminology

The material described in the present work is housed in the AMNH and IVPP. Comparative material is housed in the AMNH, IVPP, HMV, and MNHN. Other specimens were illustrated in previous publications (Schlesinger, 1917; Borissiak, 1929; Barbour, 1931; Osborn and Granger, 1931, 1932; Belyaeva and Gabunia, 1960; Gabunia, 1973; Gaziry, 1976; Chang and Zhai, 1978; Chen, 1978; Tassy, 1986, 2013, 2014; Tobien et al., 1986; Ye and Jia, 1986; Guan, 1991; Wang and Qiu, 2002; Göhlich, 2010; Wang et al., 2013, 2015b). The terminology of the occlusal structure of gomphotheriid cheek teeth and cranium follows Tassy (2013: figs. 13, 14; 2014: fig. 2 [Figure 2: see original paper]).

1.2 Measurements and Specimen Illustrations

Cheek teeth measurements follow Tassy (2014: fig. 3 [Figure 3: see original paper]). Measurements were preferentially obtained using calipers (in mm). If not available, photos and 3D digital models were also used. The illustrations of mandibles and molars in the present article are captured snapshots of 3D digital models generated by a handheld Artec Spider 3-dimensional scanner.

1.3 Institutional Abbreviations

AMNH, American Museum of Natural History, New York, USA; HMV, Hezheng Paleozoological Museum, Hezheng, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; KNM, National Museum of Kenya, Nairobi, Kenya; MNHN, Muséum National d' Histoire Naturelle, Paris, France.

2 Systematic Paleontology

Order Proboscidea Illiger, 1811
Family Amebelodontidae Barbour, 1927
Genus *Platybelodon* Borissiak, 1928

Diagnosis: Amebelodontid of moderate to large size. Neurocranium low or slightly arched; basicranium not elevated and not redressed; orbit posteriorly positioned (orbital rostral end not beyond the mesial end of the last cheek tooth in function); perinasal fossa large; prenasal slope (an area rostral to the nostril aperture, surrounded by the nasal processes of premaxillae) large; incisive alveoli long and narrow with a slit-like incisive fossa, lacking subnasal fossae; upper tusks slightly ventrally bent, lacking enamel bands; mandibular symphysis greatly elongated, strongly widened in rostral part, with a deep symphyseal trough; lower tusks wide and flattened, possibly having dentinal rods; cheek teeth with wide interlophs/interlophids, showing tendencies of developing posttrite trefoils, pseudoanancoidy, and cementodonty; M3/m3 tending to be narrow and curved.

Type species: *Platybelodon danovi* Borissiak, 1928.

Referred species: *Platybelodon grangeri* (Osborn, 1929); *P. tongxinensis* (Chen, 1978); *P. dangheensis* Wang and Qiu, 2002; *P. barnumbrowni* (Barbour, 1931); *P. tetralophus* sp. nov. (see below).

Platybelodon tongxinensis (Chen, 1978)

Gomphotherium tongxinense Chen, 1978: pl. 1, figs. 1, 2
Gomphotherium shensiense Chang and Zhai, 1978: pl. 21, fig. 2
Platybelodon tongxinensis (Chen, 1978) Ye and Jia, 1986: pls. 1, 2
Platybelodon danovi Borissiak, 1928: Guan, 1991: p. 10, footnote
Gomphotherium cf. *subtapiroideum* (Schlesinger, 1917) Wang et al., 2015b: figs. 5, 6a—c

Type specimen: IVPP V 5572, paired m3 and M3, belonging to a single individual.

Type locality and horizon: Collected from Gujiazhuangzi, Tongxin (Chen, 1978), recovered from the Zhangenbao Formation, possibly from Shataigou locality (cycle C?) (Ye and Jia, 1986). Age: late Early-early Middle Miocene (Wang, 2021).

Diagnosis: Differs from *P. grangeri* in the tetralophodont M3 and tetrapantalophodont m3, in the larger nasal bones, in the less developed prenasal slope, in the shorter incisive alveoli, and in lacking a transverse ledge at the proximal end of the mandibular symphysis. Differs from *P. barnumbrowni* in the longer mandibular symphysis. Differs from *P. danovi* in its larger size. Differences between *P. tongxinensis* and *P. dangheensis* are unclear, possibly in the shorter mandibular symphysis in adults of the latter; *P. dangheensis* and *P. tongxinensis* may be synonyms.

Studied material: IVPP V 3084, a nearly complete cranium with deeply worn M2 and moderately worn M3.

Locality and horizon of the present material: Tianhegou, Lintong, Shaanxi Province, from the Lengshuigou Formation (Chang and Zhai, 1978). The age was estimated to be middle Early Miocene.

Description: The cranium is obliquely crushed from the left-dorsal to right-ventral direction. The zygomatic arch of both sides, most parts of the upper tusks, and the rostral end of the incisive alveoli were broken.

The cranium (Fig. 1A [Figure 1: see original paper]—E) is rostrocaudally elongated and low. In dorsal view (Fig. 1A), the neurocranium is relatively short compared with the alveolar region. The nuchal crest is slightly rostrally concave in the middle. The two temporal lines strongly converge in the middle; however, the distance between them is still relatively large, and the dorsal plate of the neurocranium is trapezoid with a larger rostral edge. The nasal is relatively large and shaped like an equilateral triangle. The dorsolateral edges of the nostril aperture extend rostrolaterally, resulting in a pair of perinasal fossae that are rostrocaudally narrow and extend laterally and slightly rostrally. The insertion for the ethmoidal cartilage is relatively small. Rostrally to each perinasal fossa, there is a large broad region surrounded by the nasal processes of the premaxillae, termed the prenasal slope. The presence of a large prenasal slope is a distinct feature for *Platybelodon* and *Aphanobelodon* (Wang et al., 2017).

The dorsal infraorbital foramen is located at the rostral end of the prenasal slope, far from the nostril aperture. The rostrum (incisive alveoli) is long and narrow and tapers rostrally, with the two alveoli close together leaving a narrow incisive fossa. Many fine grooves run obliquely along the medial side of the incisive alveolus, indicating strong attachment for the nasalis lateralis.

In ventral view (Fig. 1B), the specimen is not well preserved, especially around the tympanic regions. The occipital condyle is long and triangular. The two condyles are not strongly diverged, exhibiting a narrow foramen magnum. The basioccipital and basisphenoid bones are narrow and possess a median crest. The left tympanic bulla (better preserved than the right) is relatively small. The glenoid fossa, although incomplete, is relatively large. A deep groove for the secondary external acoustic meatus extends along the caudal edge of the glenoid fossa. The choanae are embedded in a block of rock. The palate between the two cheek tooth rows is narrow, and the zygomatic process of the maxilla is triangular. The rostrum is long and narrow.

In lateral view (Fig. 1C, D), the nasal bone is located at the top of the cranium and is slightly dorsally oriented. The occipital surface is almost perpendicular to the long axis of the cranium. The occipital condyle is ventrally rather than caudally oriented. The temporal fossa is large. The orbit is round with a strong postorbital process. The nostril aperture is caudal to the postorbital process. The dorsal and ventral infraorbital foramina are rostral to the zygomatic process of the maxilla and are very close to each other. The facial part is relatively dorsoventrally low but rostrally positioned, with the rostral end of the orbit at the level of the middle M3. The rostrum is long and horizontally stretched.

In caudal view (Fig. 1E), the occipital surface is low and fan-shaped. The occipital condyles are triangular with a wide intercondyloid notch between them. The ligamentum nuchae fossa is rounded and separated medially by a vertical, thin crest. The occipital surface is obliquely deformed due to external pressure.

The upper tusks (Fig. 1A–D) are mostly broken with only proximal remains remaining. The cross-section is round and the enamel band is absent.

Figure 1: *Platybelodon tongxinensis*, IVPP V 3084, cranium, from Tianhegou, Lintong, Shaanxi, the Lengshuigou Formation, in dorsal (A), ventral (B), left lateral (C), right lateral (D), and caudal (E) views; as well as the right (F) and left (G) M2–M3 tooth rows in occlusal view.

The deeply worn M2 (Fig. 1F, G) is trilophodont with a moderately developed posterior cingulum. The M3 (Fig. 1F, G) has four complete lophs. It is highly bunodont. The contour of the teeth is slightly curved with a convex buccal side, especially in the left one. The interlophs are relatively mesiodistally wide. Cingula are developed along the mesial and lingual margins, and cementum was developed in the interlophs.

In the first loph of the right M3 (Fig. 1F), the pretrite half loph is trifoliated. The anterior central conule is large and bulbous. The mesoconelet is small. Three thick, crest-like posterior central conules are present, and the lingual-most one should be regarded as the normal posterior central conule or the crescentoid. The posttrite half loph is transversely elongated with two grooves on the posterior enamel wall. A small posterior posttrite central conule is present. In the second loph, the pretrite main conelet is irregularly subdivided. The anterior pretrite central conule is also large and bulbous, the mesoconelet is also small, and the posttrite central conule is small or even absent. The posttrite half loph is subdivided into four conelets, and a small posterior posttrite central conule is present. The distal two lophs are relatively simple. Both pretrite half lophs have a large and subdivided anterior central conule. The third posttrite half loph has a clear mesoconelet.

In the left M3 (Fig. 1G), the first pretrite trefoil is broken. The second pretrite main conelet is undivided, and a posterior pretrite central conule is present. The second posttrite half loph is subdivided into three conules, and the third pretrite half loph has a mesoconelet. The other characters are identical to the right one.

Platybelodon tetralophus sp. nov. (Fig. 2A—D)

Platybelodon grangeri (Osborn, 1929) Osborn and Granger, 1932: figs. 2–7
Platybelodon grangeri (Osborn, 1929) Wang et al., 2013: fig. 12 [Figure 12: see original paper]

Type specimen: AMNH 26574, left hemimandible bearing moderately worn m2 and not fully erupted m3.

Type locality and horizon: Tunggur, uppermost layer of the Tunggur Formation. Age: latest middle Miocene (~12—11.5 Ma) (Qiu et al., 2013).

Referred specimens: All *Platybelodon* specimens from the Platybelodon Quarry and Wolf Camp Quarry in AMNH.

Etymology: Referring to the four-lophed/lophided M2/m2 that is unique in *Platybelodon*.

Diagnosis: Differs from other species of *Platybelodon* in the almost complete tetralophodont m2 and nearly complete tetralophodont M3; in the stronger pseudoanancoidy and narrowness of the last molar; and in the secondary incomplete pretrite trefoil. The mandibular symphysis is intermediate between the long form of *P. tongxinensis* and *P. grangeri* and the short form of *P. barnumbrowni*.

Figure 2: Cheek teeth of *Platybelodon* and *Gomphotherium* in occlusal view. A–D. *Platybelodon tetralophus* sp. nov., from the Platybelodon Quarry, Tamqin Fauna of the Tunggur region: A. AMNH 26574, left m2, the holotype; B. AMNH 26479, left M2; C. AMNH 26473, mirrored right M3; D. AMNH 26475, left m3; E. *P. tongxinensis*, IVPP V 3084, right M3 (holotype of *Gomphotherium shensiense*), from Tianhegou, Lintong; F. *P. tongxinensis*, IVPP V 5572, right M3, the holotype, from Shataigou, Tongxin; G. *P. danovi*, right M3, the holotype, from Kuban region, Caucasus, after Borissiak, 1929; H. *P. grangeri*, HMV 1788, right M3, from Hujialiang, Linxia; I. *Gomphotherium angustiden*, MNHN.F.SEP 266, right M3, from En Péjouan, after Tassy, 2014; J. *G. connexum*, IVPP V 8572, right M3, from the Halamagai Fauna, Ulungur region.

3.1 *Platybelodon tongxinensis*

The cranium of IVPP V 3084 is "Platybelodon-type"rather than "Gomphotherium-type." The most useful diagnostic feature is the upper tusk that lacks enamel bands. Among trilophodont longirostrine proboscideans, besides members of Choerolophodontidae, *Platybelodon* is the only genus that possesses enamelless upper tusks, which further differ from those of choerolophodontids in the ventral bend (though this feature is unclear in V 3084 due to breakage). In *Gomphotherium* and other amebelodontids, the enamel band is pronounced (Fig. 3).

Figure 3: Various crania of trilophodont gomphotheres, not to scale. A–E. Dorsal view, the white transparent areas indicating the incisive fossa (if) and prenasal slope (ps); F–J. Lateral view, the vertical dash lines indicating the rostral end of the orbit. A, G. *Archaeobelodon aff. filholi*, KNM MI 7532, from Mwiti, Kenya, after Tassy, 1986; B. *Gomphotherium productum*, AMNH 10582, from Clarendon, Texas; C, J. *G. tassyi*, IVPP V 22780, from Erdaoqu, Zhongning, Ningxia (upper Zhangenbao Formation); D, I. *G. angustidens*, MNHN.F.SEP 186, from En Péjouan, after Tassy, 2013; E, F. *Platybelodon grangeri*, HMV 0939 (E) and 0940 (F), from Hujialiang, Linxia; H. *P. danovi*, the holotype,

from Kuban region, Caucasus, after Borissiak, 1929.

In V 3084, the rostrum is long and narrow with a slit-like incisive fossa, and its distal end is narrow (Fig. 1A). This morphology is also unique in *Platybelodon* (except for *Aphanobelodon*, which lacks upper tusks) (Fig. 3E), while in other taxa, including *Gomphotherium* (Fig. 3B—D), especially in the Choerolophodontidae, the rostrum is shorter and wider with stronger upper tusks.

In V 3084, a large "prenasal slope" —a term for this feature introduced in this article—is present. The prenasal slope is relatively small in *Gomphotherium* species, such as in *G. angustidens*, *G. tassyi*, and *G. productum*, resulting in a short distance between the dorsal infraorbital foramen and the nostril aperture (Fig. 3B—D). In a typical amebelodontid cranium, *Archaeobelodon aff. filholi* from Mwiti, Kenya, the prenasal slope is also smaller (Tassy, 1986) (Fig. 3A) than that of V 3084 and other species of *Platybelodon*.

Another important feature is the rostrally positioned facial part in V 3084, which was also seen in the *Platybelodon* sample (Fig. 3F, H). The rostral end of the orbit is at the level of the middle M3. In *Gomphotherium* species (*G. angustidens*, *G. tassyi*, and *G. productum*) (Fig. 3I, J), even in the most primitive species *G. annectens* (Tassy, 1994), the orbital rostral end reaches at least the level of the M2/M3 boundary. A rostrally positioned facial part seems to be a common feature in amebelodontids (Sanders et al., 2010), e.g., in *Archaeobelodon aff. filholi* and *Protanancus brevirostris* (Tassy, 1986; Wang et al., 2015a) (Fig. 3G). In derived species of choerolophodontids, the facial part is also rostrally positioned. This feature appears to be convergent with amebelodontids, caused by the caudal shift of the orbit.

Based on the above synapomorphies, it is quite certain that the cranium V 3084 belongs to *Platybelodon*. In the derived species *P. grangeri*, the rostrum is even longer and narrower, and the prenasal slope is even larger, but the nasal bones are weaker (Fig. 3E, F). In V 3084, these features (if present) are closer to the states in the type cranium of *P. danovi* (Borissiak, 1929) (Fig. 3H). Therefore, V 3084 represents a relatively ancestral species of *Platybelodon*.

The upper M3 also shows several synapomorphies of *Platybelodon*. The contour of V 3084' s M3s, especially that of the left one, is slightly curved. While this feature is more or less present in *Platybelodon* samples (i.e., in *P. danovi* and *P. grangeri*) (Fig. 2G, H), it is lacking in any other genus, especially in *Gomphotherium*. The interlophs of V 3084 are relatively wide (mesiodistally) as in other species of *Platybelodon* (Fig. 2A–H). In most species of *Gomphotherium*, the interlophs are crowded (Tassy, 2014) (Fig. 2I, J). In *G. tassyi* and *G. subtapiroideum*, the interlophids are also wide, but the cheek teeth show more zygodont features than those of *Platybelodon*. The initial cementodonty in V 3084 is also a synapomorphy of *Platybelodon* (Fig. 2A–H) (Wang et al., 2013).

The M3 of V 3084 differs from *Platybelodon grangeri* in the smaller number of lophs, in the less developed posttrite central conules and cementodonty, and in lacking pseudoanancoidy. The morphology is closer to the type specimens of

P. tongxinensis and *P. danovi* (Fig. 2E–H). The width-length ratio is slightly larger than in other species of *Platybelodon*, but the length and width still fall within the ranges of *P. tongxinensis* (Fig. 4 [Figure 4: see original paper]). V 3084 even differs from the type specimens of *P. tongxinensis* and *P. danovi* in the less well-developed second pretrite trefoil. Furthermore, the lack of a second posterior pretrite central conule (a primitive condition in gomphotheres) is also unique to *Platybelodon*. Therefore, the Tianhegou specimen might be even more ancestral than any known species of *Platybelodon*, and the age of the Tianhegou locality is potentially relatively early, possibly ~18–17 Ma.

Chen (1978) established *Gomphotherium tongxinense* based on m3s/M3s from the Zhangenbao Formation, Tongxin. She mentioned the unique features of this species among *Gomphotherium*, especially the mesiodistally wide interlophs, weak cementodonty, and weak cingula/cingulids. These differential features are exactly the synapomorphies of *Platybelodon*. She also mentioned that the teeth of "G. tongxinense" are very close to *G. shensiense*, except for the smaller fourth loph and absence of the second posterior pretrite central conule in the latter (Chen, 1978). As we have discussed, these can be regarded as more ancestral features in V 3084 than those of *Platybelodon tongxinensis*, or merely interspecific variations. The two names were published in 1978 (Chang and Zhai, 1978; Chen, 1978), but *G. tongxinense* was published in April, earlier than *G. shensiense* which was published in December. Ye and Jia (1986) attributed *G. tongxinense* to *Platybelodon* because they found that teeth of "G. tongxinense" were accompanied by flattened lower tusks with dentinal rods in the Shataigou locality. Guan (1991) further synonymized *P. tongxinensis* with the type species *P. danovi*, which was followed by Wang et al. (2013). Actually, the cranial, mandibular, and molar morphologies are very similar between *P. tongxinensis* and *P. danovi*. However, *P. danovi* is smaller in size than *P. tongxinensis* (Fig. 4). Here we temporarily regard *P. tongxinensis* as a valid species.

Chang and Zhai (1978) reported *Gomphotherium shensiense* based on the only specimen V 3084. They stated that *G. shensiense* is large in size, but the molar morphology is rather simple. Tobien et al. (1986) amended Chinese mastodonts. They invalidated a dozen *Gomphotherium* species but retained "G. shensiense" as valid because of the ventrally bending incisors without an enamel band and the slight cementodonty. However, this differential diagnosis exactly points to *Platybelodon*. Wang et al. (2015b) revised Chinese *Gomphotherium* and attributed "Gomphotherium shensiense" to "Gomphotherium cf. subtapiroideum." This attribution is incorrect. Although the molar of V 3084 shows mesiodistally wide interlophs like *G. subtapiroideum*, and the multi-crests of the first posterior pretrite central conule are somewhat comparable with the type specimen of *G. subtapiroideum*, the molar morphology is highly bunodont, the cingula are weak, and cementum is present, which is not seen in the less-bunodont molars of *G. subtapiroideum* (Schlesinger, 1917; Göhlich, 2010). The complicated first posterior pretrite central conule is actually a basic mode common in gomphotheres and mammutids. In most cases, these additional structures are small, but in the *G. subtapiroideum* type specimen and in V 3084 these elements become pronounced. However, in *G. subtapiroideum* these additional structures are crest-like (zygodont), while in V 3084 they are bunodont. Ultimately, we synonymize *Gomphotherium shensiense* with *Platybelodon tongxinensis*.

Another primitive species is *Platybelodon dangheensis*, which is only represented by an immature mandible (Wang and Qiu, 2002). The mandible is short and wide; however, we should not overestimate the importance of this feature in the type specimen of *P. dangheensis* because the mandible is juvenile. Mandibular morphology is highly variable depending on age and sex. The age of *P. dangheensis* was previously estimated to be ~20 Ma (Wang and Qiu, 2002). This age is too early for *Platybelodon*. The tectonic influence of the Danghe region is formidable, making interpretation of paleomagnetic data difficult. However, the accompanied taxa, i.e., *Turcocerus*, *Amphimoschus* (Li et al., 2020, 2021), are all no earlier than ~18 Ma from elsewhere in Eurasia (Gentry et al., 1999). We postulate that *P. dangheensis* might be a junior synonym of *P. tongxinensis*, although further verification should be carried out.

Mandibles of adult *P. tongxinensis* have been published from Tongxin (Guan, 1991) and Linxia (Wang et al., 2003) basins, which have a rather long symphysis. Ye et al. (1989) and Wang and Qiu (2002) thought that the symphysis of *P. tongxinensis* is longer than that of *P. grangeri*. However, Wang et al. (2003) considered that the relatively longer or shorter symphysis represents individual variation (especially for sexual dimorphism) rather than an evolutionary trend. Here we further clarify this problem. In typical individuals of *P. grangeri*, for example, the type mandible from Tairum Nur of Tunggur and specimens from Hujialiang Locality of the Linxia Basin (see Wang et al., 2003), the symphysis is as long as that of *P. tongxinensis*. However, in mandibles from the Tamuqin Fauna of Tunggur (e.g., Platybelodon Quarry and Wolf Camp Quarry), the symphysis exhibits a tendency to be shorter. In the present article, we have attributed the specimens from the Tamuqin Fauna to a new species, *P. tetralophus* (see below). In the latest species of *Platybelodon*, *P. barnumbrowni* from the Clarendonian of North America, the symphysis became very short (Barbour, 1931).

3.2 *Platybelodon tetralophus*

The *Platybelodon* specimens from the Platybelodon Quarry and Wolf Camp Quarry, previously attributed to *P. grangeri*, are remarkable for the tetralophodont M2 and m2 (Fig. 2A, B). The M3 is a complete pentalophodont and the m3 is hexalophodont, and therefore are very narrow (Fig. 2C, D). However, the pretrite trefoils are weakened as the posterior central conules of the M3 and m3 almost vanish, which was seen in the not fully mature teeth (Fig. 2C, D). The posttrite half lophids also become simple, as the mesoconelets of the m3 also vanished. The pseudoanancoidy is prominent. However, the M1/m1 and DP4/dp4 are trilophodont.

Platybelodon tetralophus only occurs in the uppermost layer of the Tunggur

Formation, i.e., the Tamuqin Fauna, dated to 12—11.5 Ma (Qiu et al., 2013). In the lower horizons, the Moergen and Tairum Nur faunas, *Platybelodon* was only represented by *P. grangeri* with trilophodont M2 and m2, and the type specimen of *P. grangeri* was from the Tairum Nur Fauna (Osborn and Granger, 1931). Therefore, *Platybelodon* appears to have experienced rapid evolution near the end of the Middle Miocene. It should be noted that this morphological modification in *Platybelodon* is not unique. The tetralophodont M2 and m2 (not in Dp4 and dp4) reappeared independently in the *Amebelodon*-*Torynobelodon* clade (Lambert, 1990), and the strong anancoidy accompanied by simplification of trefoil patterns further reappeared independently in *Anancus* (Konidaris and Roussiakis, 2018), both at later ages.

3.3 Geography and Biochronology

In Figure 5 [Figure 5: see original paper], we show the biochronologic ranges of known species of *Platybelodon*, as well as their geographic distributions.

Platybelodon tongxinensis from the Tianhegou locality is the most primitive cranium known so far. However, the cranium is the only specimen from the Tianhegou locality, and no dating work was carried out, so we estimate it at ~18—17 Ma. The type specimen of *P. tongxinensis* is from the Shataigou locality, possibly ~16—15 Ma (cycle C?) (Wang, 2021). *Platybelodon tongxinensis* from the Shinanu Fauna was also estimated at ~17—15 Ma (unpublished data). Another species, *P. dangheensis*, possibly synonymous with *P. tongxinensis*, occurs in the Xishuigou Fauna, Danghe region, and Halamagai Fauna, Ulungur region. It might range from ~17.5—14.5 Ma (Sun et al., 2010).

Outside China, *P. danovi* was also reported from Kuban, Russia; Belomechetskaya, Georgia; Arapli, Turkey; and the Varna area, Bulgaria (Belyaeva and Gabunia, 1960; Gabunia, 1973; Gaziry, 1976; Markov, 2008). The age of Belomechetskaya is Badenian of the central Paratethys based on Qiu and Qiu (1990), and the age is about 15 Ma (Hilgen et al., 2012). Some other publications also estimated *P. danovi* from East Europe and West Asia to be MN6 (Göhlich, 1999; Pickford et al., 2000), possibly slightly later than that of *P. tongxinensis* from China (Fig. 5). The problem might stem from age determination or faunal correlation, which should be further addressed. In Loperot of Kenya, *Platybelodon* sp. is dated to ~17 Ma (Sanders et al., 2010). We temporarily refer to these *Platybelodon* species as the "*Platybelodon danovi* group," representing a primitive stage of *Platybelodon* evolution.

The primitive morphotype of *Platybelodon grangeri* might appear at Kekemaideng Fauna, Ulungur region; Hujialiang, Linxia; and Tairum Nur Fauna, Tunggur region, estimating ~14.5 Ma (Ye et al., 2012; Qiu et al., 2013). The occurrence of *P. grangeri* is of great importance in Chinese Neogene chronology—*P. grangeri* is possibly the best biostratigraphic marker for the Tunggurian Stage.

The derived morphotype of *Platybelodon grangeri* was reported from Laogou, Linxia; Zhongning, Ningxia; Yingbeihou, Lintong, Shaanxi (Lengshuigou Formation); as well as from the Moergen Fauna, Tunggur region (Chang and Zhai, 1978; Chen, 1978). The latest appearance of the species is ~12 Ma.

Platybelodon tetralophus is only known from the Tamuqin Fauna, Tunggur region, dating to 12—11.5 Ma and was probably extinct by the end of the Middle Miocene (Qiu et al., 2013). It is the last species of *Platybelodon* in Eurasia. However, in the Late Clarendonian, *Platybelodon barnumbrowni* from the Snake River, Nebraska, is the only known species of *Platybelodon* in North America (Barbour, 1931; Lambert and Shoshani, 1998).

4 Conclusion Remarks

The cranium previously attributed to *Gomphotherium shensiense* is not a *Gomphotherium* but a primitive *Platybelodon*, which we synonymize with *P. tongxinensis*. The specimens of *Platybelodon* from the uppermost horizon of the Tunggur Formation (i.e., Platybelodon Quarry and Wolf Camp Quarry) should be attributed to a new species, *Platybelodon tetralophus* sp. nov., characterized by tetralophodont M2/m2. Species of *Platybelodon* show strong biochronologic significance, and *Platybelodon grangeri* is a good candidate for a biostratigraphic marker for the Chinese Tunggurian.

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Note: Figure translations are in progress. See original paper for figures.