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# Morphological and ecological diversity of Amebelodontidae (Proboscidea, Mammalia) revealed by a Miocene fossil accumulation of an upper-tuskless proboscidean

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Amebelodontidae is the most taxonomically and morphologically diverse group of proboscideans. However, relative to the morphological variation of the mandible and mandibular tusks, ecological and phylogenetic differentiations within Amebelodontidae have been largely debated. Here we evaluate a middle Miocene fossil accumulation of a new amebelodontid, *Aphanobelodon zhaoi* gen. et sp. nov. This species lacks upper tusks, which is unique in elephantiforms. The mandible and mandibular tusk morphologies of *A. zhaoi* are similar to those of the genus *Platybelodon*, which is the typical representative of one of the two main amebelodontid branches (the other branch is represented by *Amebelodon*). We suggest that *Amebelodon* potentially used its mandible and mandibular tusks to dig for food in relatively hard substrates; whereas *Platybelodon* is more specialized and possibly used its mandibular tusks for cutting soft vegetation. *Aphanobelodon zhaoi* morphology indicates that it is an offshoot of the platybelodont clade within Amebelodontidae, because it has primitive undifferentiated states of the mandible and mandibular tusks. Cladistic analysis indicates that *Aphanobelodon*, *Platybelodon* and *Torynobelodon* comprise a monophyletic group within Amebelodontidae. This study enhances our knowledge regarding proboscidean evolutionary history in terms of morphology, taxonomy and biology.

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**Keywords:** Amebelodontidae; functional morphology; evolution; proboscidean

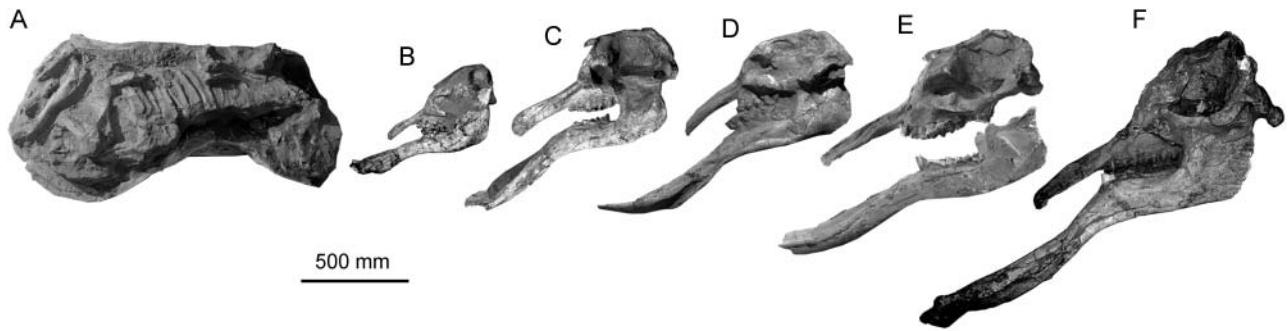
## Introduction

The family Amebelodontidae is a group of peculiar proboscideans that possess an extremely elongated mandibular symphysis and flattened mandibular tusks (Barbour 1927; Borissiak 1929; Osborn 1936). It is also the most diverse proboscidean family, and nine genera have been established (Gheerbrant & Tassy 2009; Sanders *et al.* 2010). Amebelodontids vary in mandibular symphysis and mandibular tusk morphology, and also in the inner structure of the mandibular tusks (i.e. dentinal tubulars in *Platybelodon* and *Torynobelodon*, compared with concentric laminations in other genera) (S.-Q. Wang *et al.* 2015). It has been debated why amebelodontids developed various types of mandibular symphysis and mandibular tusks, how these extinct proboscideans used their shovel-like mandible and tusks, and whether they show distinct ecological positions (Barbour 1927; Borissiak 1929; Osborn 1936; Lambert 1992; Semprebon *et al.* 2011; S.-Q. Wang *et al.* 2015). Furthermore, amebelodontid phylogeny has

also been debated, because strong parallel evolution appears to be present (Shoshani 1996; Prado & Alberdi 2008; S.-Q. Wang *et al.* 2015).

Here, we report on a fossil accumulation of a new proboscidean taxon. This accumulation (Fig. 1, Supplemental Fig. S1), containing a single species, includes an adult male, two adult females, four subadults and three juveniles (Supplemental Table S1). Most of the individuals are completely preserved and all of the bones are articulated (Fig. 1, Supplemental Fig. S2). Thus, this material provides complete osteological and anatomical information for the new taxon, and also provides insights into various aspects of biology, such as sexual dimorphism, ontogeny and dietary preference. Although most of these skeletons have not been prepared except for a female skull (HMV1880), this material provides sufficient information for anatomical and taxonomic evaluation of the taxon. Here, our description and discussion are mainly based on the one prepared skull. Analysis of the entire skeleton will be performed in the future.

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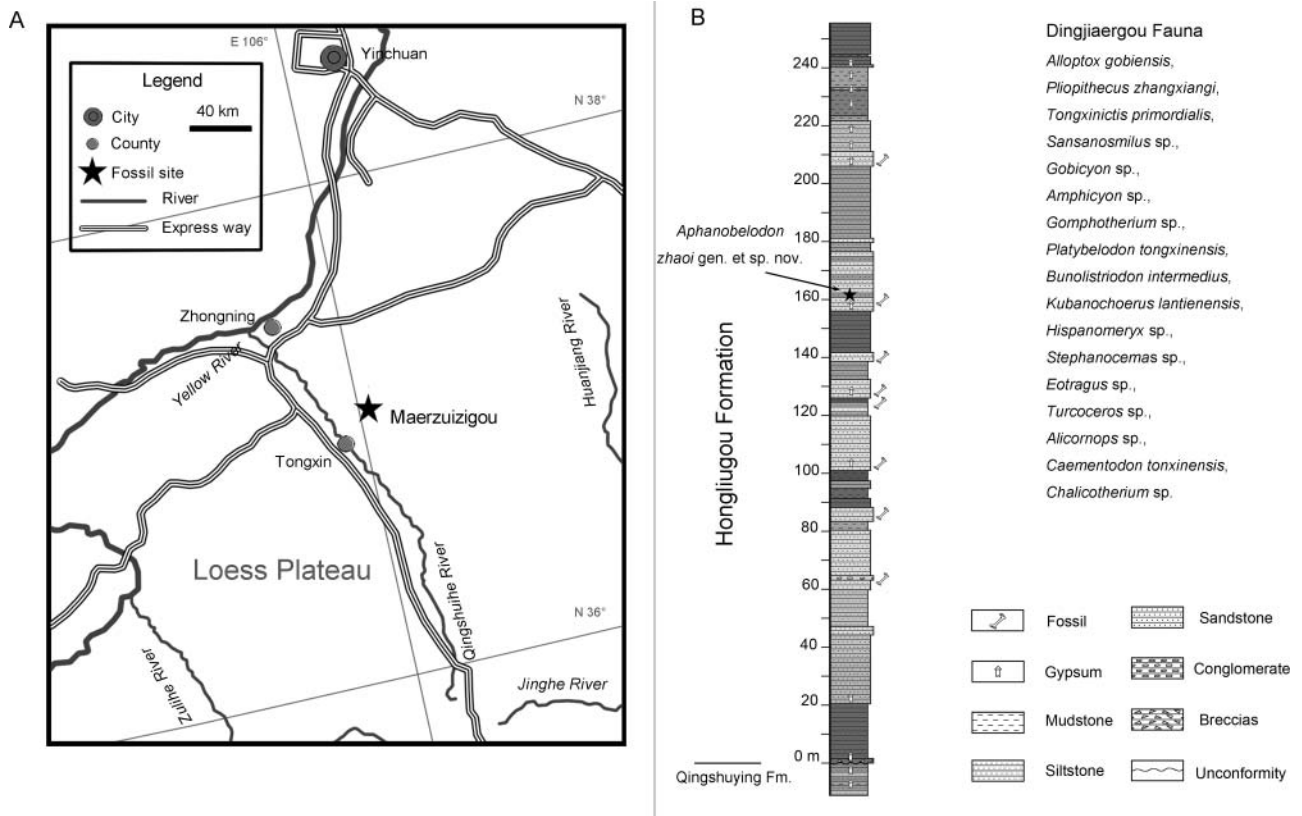
**Figure 1.** Selected individuals from the fossil accumulation of *Aphanobelodon zhaoi* gen. et sp. nov. showing the age-sex structure and burial state, all in lateral view. **A**, skeleton of HMV1916, baby; **B**, skull of HMV1912, juvenile; **C**, skull of HMV1918, subadult ?male; **D**, skull of HMV1920, subadult ?female; **E**, cranium and mandible of HMV1880, adult female, the holotype (horizontally reversed); **F**, skull of HMV1919, adult male.

### Abbreviations

Institutional abbreviation: **HMV**, Hezheng Paleozoological Museum, Hezheng, China. Other abbreviations: **CI**, consistency index; **MN**, European Mammal Neogene-Zone; **MPT**, most parsimonious tree; **RI**, retention index.

### Geological setting

The material of the new taxon was discovered in the Zhan-genbao Formation exposed in Maerzuizigou quarry, northern China (Fig. 2A). Sediments of the Zhan-genbao Formation are dominated by sandstones and siltstones



**Figure 2.** Geographical and geological information on the study material. **A**, location of the Maerzuizigou quarry **B**, the Jinggou section of the Miocene Zhan-genbao Formation (for a detailed description, see Supplemental data). The star in panel **B** indicates the horizon (No. 19) of the Maerzuizigou quarry that yielded *Aphanobelodon zhaoi* gen. et sp. nov. The faunal list is revised from Guan (1988) and Qiu *et al.* (1999).



**Figure 3.** Habitat reconstruction of *Aphanobelodon zhaoi* gen. et sp. nov. of the Dingjiaergou Fauna during the early middle Miocene, by Yu Chen (the artist has granted permission to use the illustration).

punctuated by mudstones (Fig. 2B). The fossil accumulation was discovered in horizon 19 of the Zhangenbao Formation. Detailed description of the sedimentology is given in the Supplemental data (after S.-Q. Wang *et al.* 2016b). The lithofacies of the Zhangenbao Formation comprise blocky or tabular organic-rich sandstones and siltstones, which potentially indicates marshy floodplain or lake-margin wetland deposits (Allen & Collinson 1986). Only one species, *Aphanobelodon zhaoi* gen. et sp. nov., has been identified from this fossil accumulation. In the adjacent area (Tongxin), more than 10 quarries yielding 27 mammalian taxa have been reported (Guan 1988; Qiu *et al.* 1999; S.-Q. Wang & Ye 2015; S.-Q. Wang *et al.* 2015) (Fig. 3). These taxa constitute the Dingjiaergou fauna that is correlated with MN6 (Qiu *et al.* 1999). Three proboscidean taxa have been discovered previously in this fauna: *Platybelodon tongxinensis*, *Protanancus tobieni* and *Gomphotherium* sp. (Ye & Jia 1986; Guan 1988; S.-Q. Wang *et al.* 2015).

## Material and methods

### Material

All of the material of *Aphanobelodon zhaoi* gen. et sp. nov. is housed in the HMV (Supplemental Table S1). The

comparative taxa included *Phiomia serridens*, *Serbelodon barbourensis*, *Archaeobelodon filholi*, *Protanancus tobieni*, *Pr. chinjiensis*, *Amebelodon fricki*, *Platybelodon danovi*, *Pl. tongxinensis*, *Pl. grangeri*, *Torynobelodon dangheensis* and *Torynobelodon barnumbrowni*; these species cover all shovel-tusker morphotypes (Matsumoto 1922, 1924; Barbour 1927, 1932; Borissiak 1929; Osborn & Granger 1932; Frick 1933; Osborn 1936; Tobien 1973; Tassy 1983, 1984; Ye & Jia 1986; Guan 1988, 1991, 1996; Ye *et al.* 1989; S.-Q. Wang *et al.* 2013, 2015; S.-Q. Wang & Ye 2015). It should be noted that '*Pl. grangeri*' from the Moergen Fauna of Tunggur, China, shows a higher evolutionary grade than the *Pl. grangeri* type specimen from the Tairum Nor Fauna (S.-Q. Wang *et al.* 2013). The '*Pl. grangeri*' from the Moergen fauna possesses a complete fourth lophid in m2 and displays a stronger (and relatively shorter) mandibular symphysis; therefore, in the present paper, we refer to it as tetralophodont *Platybelodon* (a new species). Moreover, *Pl. tongxinensis* from the Tongxin area, China, has often been assigned as *Pl. danovi* in recent publications (Ye & Jia 1986; Guan 1988, 1991, 1996; Qiu *et al.* 1999; S.-Q. Wang *et al.* 2013), and *Torynobelodon dangheensis* was considered a *Platybelodon* species by B.-Y. Wang & Qiu (2002).

### Measurements and terminology

Cranial and mandibular measurements follow Tassy (2013). All measurements were taken using calipers. The terminology of occlusal structures of gomphotheriid cheek teeth follows Tassy (2014), and the terminology of the cranium and mandible follows Tassy (2013) and Ferretti (2010). Rock colour description follows the Munsell colour chart (Landa & Fairchild 2005), and the grain size subdivision is based on the Wentworth grain size chart (Krumbein & Aberdeen 1937).

### Microwear study

The feeding preference of the new taxon was determined by microwear analyses, with the main procedures based on those described in Calandra *et al.* (2010). Shearing facet casts of the second loph of the M3 in HMV1919, HMV1880 and HMV1921 were made, and digital microphotographs were taken. In each 0.4 mm × 0.4 mm digital microphotograph, the scratches and pits were quantified, and results were compared to extant proboscidean and ungulate microwear databases to determine the dietary categories of browser versus grazer (Solounias & Semprebon 2002). The cast-making protocol was based on that of Solounias & Moelleken (1992). The microwear data of *Platybelodon grangeri* and extant elephants is from Semprebon *et al.* (2016, fig. 3B).

### Cladistic analysis

A cladistic analysis was performed to investigate the possible phylogenetic interrelationships of our new taxon and shovel-tusked elephantiforms. The data matrix contains 38 unordered characters and 18 taxa, in which *Deinotherium* was the outgroup (see Supplemental appendices S1 and S2). In particular, characters 0, 6–11, 14, 23, 29, 30, 31, 32, 35 and 37 were included, because they represent known morphological variations among gomphotherid taxa. The remaining characters were chosen based on their previously suggested importance in gomphotheriid and elephantid phylogenetics (Shoshani 1996; Tassy 1996; Prado & Alberdi 2008). Cladograms were obtained from a parsimony analysis carried out using the TNT 1.1 program (Goloboff *et al.* 2003). The reported results were based on MPTs and a strict consensus rule tree. Node support was calculated by a bootstrap analysis (1000 replicates). Data for the examined taxa were obtained from previous publications (Andrews 1906; Matsumoto 1924; Barbour 1927, 1929; Borissiak 1929; Osborn & Granger 1932; Frick 1933; Mottl 1969; Tobien 1973; Tassy 1983, 1986; Lambert 1990; Guan 1991; B.-Y. Wang & Qiu 2002; S.-Q. Wang *et al.* 2013, 2015; Konidaris *et al.* 2014).

### Body mass estimation

We estimated the body masses of individuals of *Aphanobelodon zhaoi* based on their humerus lengths (when the humeral length of the individual could be measured). The equation is a linear regression function with the formula  $\log_{10}(\text{mass in kg}) = -4.145 + 2.635(\log_{10}X)$ , where  $X$  (in mm) is the length of the humerus (Christiansen 2004). The body mass data of extant elephants were taken from Nowak (1999), and other estimates of body masses of fossil elephantiforms were from Christiansen (2004) using the same method.

### Systematic palaeontology

Order **Proboscidea** Illiger, 1811

Family **Amebelodontidae** Barbour, 1927

Genus ***Aphanobelodon*** gen. nov.

**Type species.** *Aphanobelodon zhaoi* sp. nov.

**Etymology.** *Aphano-*, invisible, indicating lack of upper tusks; *belodon*, front tooth, a masculine root typical of longirostrine elephantiforms.

**Diagnosis.** Upper permanent tusks always absent in every ontogenetic age and both sexes. Rostrum slender, elongated. Mandible extremely elongated and expanded in the distal part; lower tusks flattened as in *Platybelodon*, however with internal concentric lamination; Dp4, M1, and M2 bunodont and trilophodont; molars with incipient secondary trefoils, incipient pseudo-anancoidy, strong choerodonty and heavy cementodonty.

***Aphanobelodon zhaoi*** sp. nov.

(Figs 4, 5)

**Etymology.** Dedicated to Mr Rong Zhao who discovered and excavated the material.

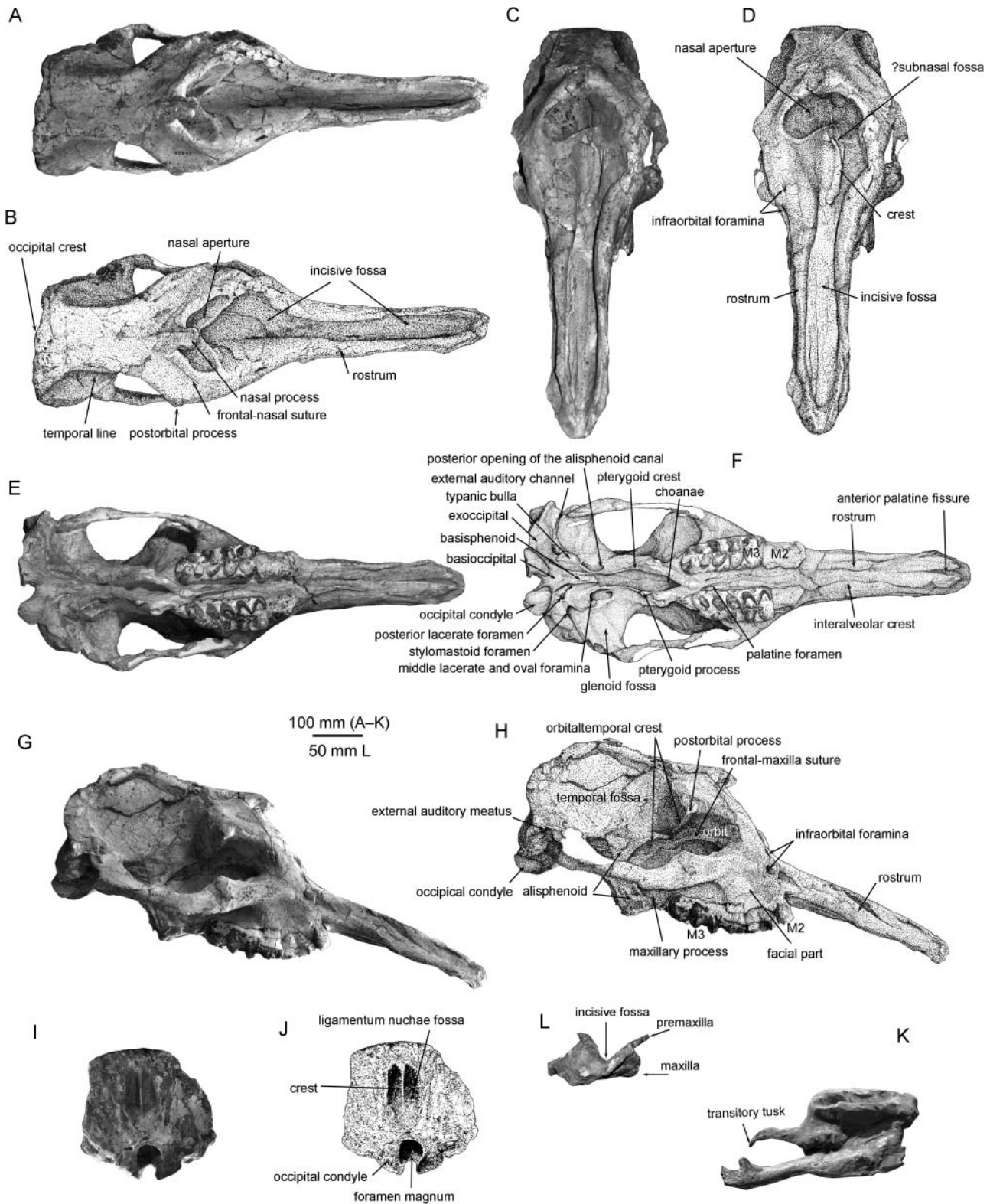
**Diagnosis.** As for the genus.

**Type locality and horizon.** Maerzuizigou quarry (37°05'21.8"N, 106°00'58.4"E, Fig. 2A), horizon 19 of the Zhangenbao Formation (previously named the Hongliugou Formation, but renamed because of synonymy) (Fig. 2B), middle Miocene, MN6 (Qiu *et al.* 1999; S.-Q. Wang & Ye 2015; S.-Q. Wang *et al.* 2015, 2016b).

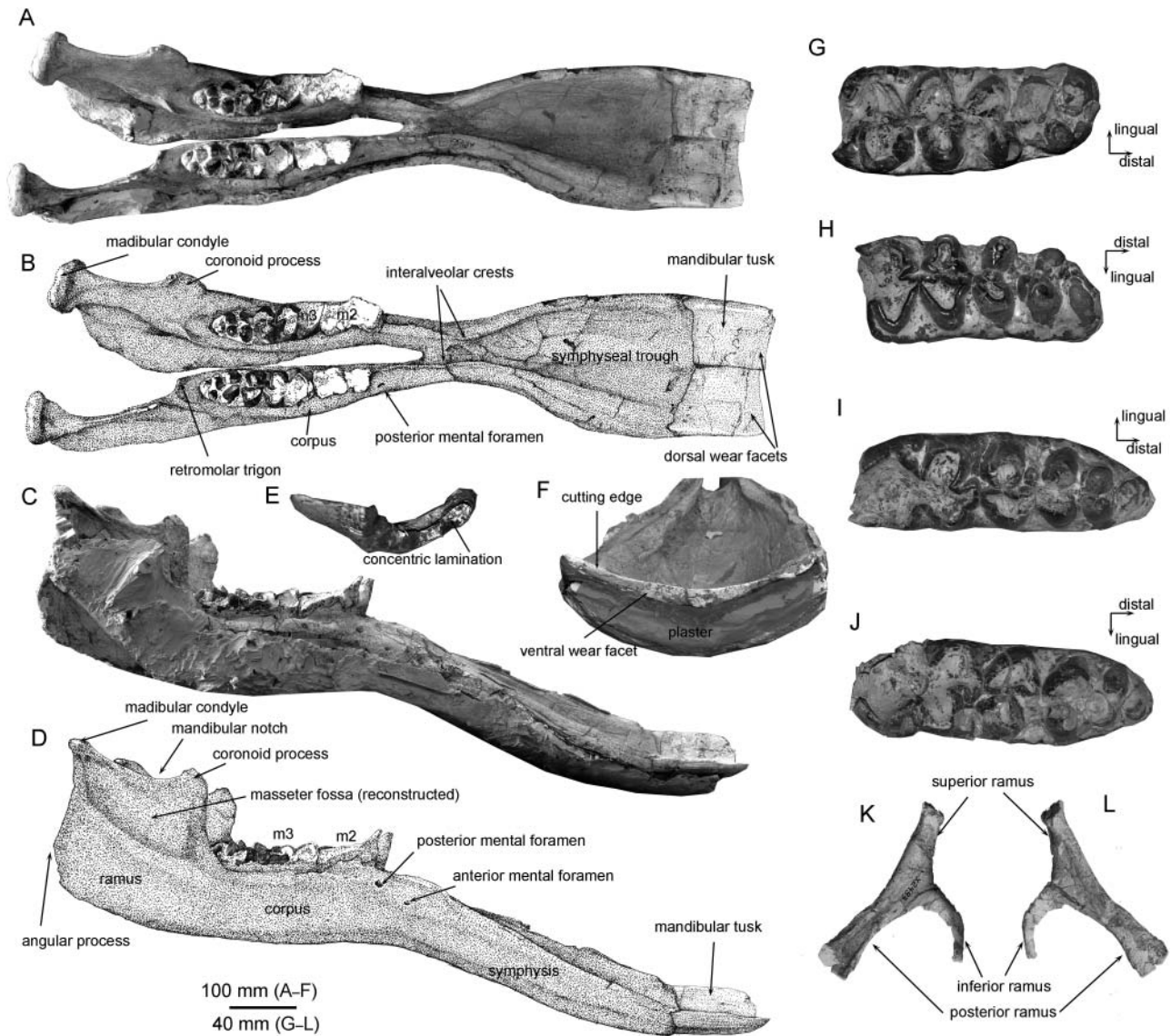
**Occurrence.** Early middle Miocene, MN6, East Asia.

**Holotype.** HMV1880: a complete cranium with associated mandible and partial skeleton, adult female, dental age XX (Tassy 2013).

**Paratypes.** See Supplemental Table S1; all of the material is from the same locality and horizon as the holotype.



**Figure 4.** Crania of *Aphanobelodon zhaoi* gen. et sp. nov. (all parts show HMV1880, the type specimen, except K, which shows HMV1916, a juvenile). **A**, dorsal view; **B**, sketch and annotations of **A**; **C**, anterodorsal view; **D**, sketch and annotations of **C**; **E**, ventral view; **F**, sketch and annotations of **E**; **G**, lateral view; **H**, sketch and annotations of **G**; **I**, posterior view; **J**, sketch and annotations of **I**; **K**, skull of HMV1916, showing the small transitory upper tusk; **L**, apical view of the tip of the premaxillae showing the closed incisive alveolar sockets.



**Figure 5.** Mandibles, cheek teeth and stylohyoid of *Aphanobelodon zhaoi* gen. et sp. nov. (all parts show HMV1880, the type specimen, except E, which shows HMV1918, a subadult). **A**, mandible, in dorsal view; **B**, sketch and annotations of **A**; **C**, mandible, in lateral view (lateral side is covered by plaster); **D**, sketch and annotations of **C** (the masseter fossa is reconstructed); **E**, HMV1918, apical view of the lower tusks, showing the concentric lamination in the cross section of the left lower tusk; **F**, apical view of the lower tusks, showing the sharp cutting edge of the lower tusks; **G**, right M3, in occlusal view; **H**, left M3, in occlusal view; **I**, left m3, in occlusal view; **J**, right m3, in occlusal view; **K**, left stylohyoid, in lateral view; **L**, left stylohyoid, in medial view.

## Description

**Cranium.** See Figure 4, Supplemental Table S2. In dorsal view (Fig. 4A, B), the cranium is anteroposteriorly elongated and laterally compressed with little lateral expansion of zygomatic arches. The occipital crest is almost straight, not anteriorly concave. The two temporal lines converge from the posterolateral flanges of the two temporal fossae, run parallel along the lateral edges of the nearly rectangular braincase, and diverge before they reach the postorbital processes. The sutures of the anterior

edge of the frontal bones are visible, and the frontal is in contact with the nasal, premaxillary and maxilla bones from medial to lateral. The nasal bone extends laterally along the superior rim of the nasal aperture, and possesses a strongly protruded nasal process. The contour of the nasal aperture forms two anterolaterally expanded lateral wings, and the superior rim of the nasal aperture reaches the level of the two postorbital processes. The two premaxillae anterior to the nasal aperture are very broad at first, enclosing a large incisive fossa. Then, the two premaxillae steeply taper and prominently protrude, forming

a slender rostrum. The incisive fossa also tapers and runs through the entire length of the rostrum.

In anterodorsal view (Fig. 4C, D), the nasal aperture is fabaceous. Although the opening is broad, no clear step-like perinasal fossae (Tassy 1994, 2014) are visible. In the type specimen, although deformed by vertical pressure, there is a crest in the middle line of the base part of the incisive fossa (Ferretti 2010). This crest may be bifurcated at the ventral border of the nasal aperture, enclosing a small subnasal fossa. To our knowledge, this crest is not observed in other elephantiforms. The infraorbital foramina are duplicated – there is a large, subcircular ventral opening and a small, slit-like dorsal one. In the long and narrow rostrum, the distal part of the incisive fossa is relatively wide, and is bordered by two crest-like bony walls. These two walls are homologous to the incisive sockets of the other elephantiforms. From the apical view of the rostrum (Fig. 4L), the incisive fossa is deep and V-shaped, and the bones (premaxillae at dorsal part and maxillae at ventral part) are very thin. No openings for tusks are developed.

In ventral view (Fig. 4E, F), the occipital condyle is sub-triangular. The two condyles are divergent, forming a sharp intercondyloid notch. The basioccipital tapers anteriorly and is fused with the basisphenoid by a tough basal tuberosity. The tympanic bulla is not laterally expanded; is irregular shaped with a prominent anteromedial angle; and is surrounded by foramina: a posterior, triangular posterior lacerate foramen (*foramen metoticum*), and a lateral, large and rounded stylomastoid foramen. The middle lacerate foramen and oval foramen (*foramen ovale*) are confluent and located beneath the anterior margin of the bulla. A rounded posterior opening of the alisphenoid canal is anterior to the anterior edge of the bulla and links the confluent opening of the middle lacerate and oval foramina by a shallow groove. The glenoid fossa is large, with an anterior slop that is inclined dorsally. The exoccipital is strong, anterolaterally elongated. Between the glenoid fossa and the exoccipital, there is a broad and shallow groove for the external auditory channel. The choanae are narrow with a sharp apex on the anterior rim. Lateral to the choanae, a strong pterygoid process is laterally hooked, and the pterygoid crest extends posteriorly to the tympanic bulla. The palate is deformed by transverse pressure. The palatine foramen is slit-like. The zygomatic process of the maxilla is not strong. Two interalveolar crests extend anteriorly along the narrow rostrum, and slightly converge in the middle. The anterior palatine fissure is weak.

In lateral view (Fig. 4G, H), the braincase is low. However, in the presumed male specimen HMV1919, the braincase is relatively raised (Fig. 1F). The temporal fossa is anteroposteriorly expanded. The basicranium is almost not erected, the occipital condyle does not posteroventrally protrude, and a notch for the external auditory

meatus is posterior to the zygomatic arch. The orbitotemporal crest extends posteroventrally to reach the anterior edge of the alisphenoid. A large fissure is located beneath the anterior margin of the alisphenoid, in which the optic foramen, the anterior lacerate foramen (*foramen orbitale*) and the round foramen (*foramen rotundum*) are present. The anterior edge of the alisphenoid turns anteroinferiorly to the pterygoid process and wraps up the posterior end of the maxillary process. The orbit is relatively small and the anterior rim is located at the level of the anterior part of the M3, and the postorbital process is just at the level of the posterior end of the tooth row. In the orbit, the transverse suture between the frontal and the maxilla clearly runs from the anterior rim to the anterior margin of the orbitotemporal crest. The facial part of the maxilla is anteriorly elongated, and that ventral to the zygomatic process is low. The infraorbital foramina are just anterior to the zygomatic process of the maxilla, and they are relatively distant from the anterior rim of the orbit. The rostrum is slim and slightly downwardly inclined.

In posterior view (Fig. 4I, J), the occipital surface is subcircular. The foramen magnum is also subcircular and surrounded by two fabaceous occipital condyles. The ligamentum nuchae fossa is dorsoventrally oval and divided into two parts by a thin crest in the middle.

**Mandible.** See Figure 5A–D, Supplemental Table S3. In dorsal view (Fig. 5A, B), the left hemimandible is slightly deformed by the transverse pressure, and the right one is not deformed. The mandibular condyle forms a transversely cylindrical bar. The corpus is narrow and tapers anteriorly. The retromolar trigone is prominent. The posterior border of the symphysis is distant from the anterior end of the tooth row. The symphysis is elongated and trough-shaped. The basal part of the symphysis is narrow and steeply widens distally. No transverse ledge is present at the narrowest part of the symphysis. The two interalveolar crests run along the lateral margins of the deep symphyseal trough. The anterior edge of the symphysis is only slightly anteriorly convex. This is intermediate between *Platybelodon*, in which this edge is almost straight, and *Amebelodon*, in which this edge forms an anteriorly oriented apex.

In lateral view (Fig. 5C, D), in order to protect the specimen, plaster has not been removed; therefore, the masseter fossa in Figure 5D is reconstructed. The ramus of the mandible is long and low. The coronoid process is blunt, and the mandibular condyle is small. The mandibular notch is shallow. The angular process is slightly protruded, and is at the level of the occlusal surface. The anterior and posterior ramal borders are perpendicular to the occlusal surface and less posteriorly inclined. The corpus is relatively high. The posterior mental foramen is relatively big, and is positioned at the level of the anterior



end of the tooth row. The anterior mental foramen is small. The symphysis is moderately ventrally deflected.

**Teeth.** See Figures 1, 4 and 5. The upper tusks are absent in all specimens except the newborn HMV1917, in which the left tusk is tiny, ventrally bent and covered by enamel (Fig. 4K). It is identified as a transitory upper tusk. All the rostria of all crania are slender with a relatively wide incisive fossa that cannot support tusks (Figs 1, 3). The sockets for upper tusks are closed (Fig. 4L). Thus, upper tusks were evidently not developed in this taxon, rather than shed or not exposed to the alveoli. This feature is unique not only in Amebelodontidae but also in Elephantiformes (tuskless males have also been reported in some populations of *Elephas maximus*, but it is not a stable character in *Elephas maximus*; see Kurt *et al.* 1995).

The lower tusk (Fig. 5A–F) is broad and flattened, as in *Platybelodon*. No tubular structures but concentric lamination is present on the cross section, as observed from the anterior breakage of the lower tusk in HMV1918 (Fig. 5E). The exposed length is much smaller than the length of the symphysis. The lower tusk is slightly dorsally curved in lateral view. In basal view, the left tusk is slightly left-handedly twisted, and mirrors the right one. In dorsal view, the two tusks are slightly convergent with both nearly orthogonal anteromedial and anterolateral angles. The anterior edge of the tusk is slightly concave. In apical view, the tusk is very thin, forming a sharp cutting edge (Fig. 5F). The wear facet is present on both dorsal and ventral sides of the tusk. The dorsal facet is long, and the ventral one short (both in the distal-apical direction) (Fig. 5A–D, F). Measurements of HMV1880 (left/right, in mm): lateral exposed length, 146/150; medial exposed length, 111/100; maximal width (at alveolus), 114/111; height, 24/25; length of the wear facet on the dorsal surface, 65.5/64.5.

Both M2 and m2 are worn to the roots without any remains of enamel. Both are rectangular and presumably have three loph(id)s.

The M3 (Fig. 5G, H) is anteroposteriorly rectangular and composed of five lophs. Chevroning and pseudo-anancoidy are present on the second to fourth lophs, and the last loph is much incipient. Pretrite trefoils are present on the first two lophs with symmetrical anterior and posterior central conules. The third and fourth pretrite half-lophs only have a mesoconelet and an anterior central conule. Posttrite half-lophs are relatively simple. The first three posttrite half-lophs have incipient posterior posttrite central conules, and the second loph also has a small anterior posttrite central conule. The third posttrite half-loph is subdivided into three main cusps. Cementum is very heavy, and small conules are developed in the interlophs, thus showing strong cementodontology and choerodontology. Cingula are present on the anterior, lingual and posterior margins of the tooth. Measurements (left/right, in mm):

length, 155/163; width at loph 1, 67/71.5; loph 2, 65.5/66; loph 3, 61.5/63.5; loph 4, 59/57; height at the posttrite side of loph 3, 48/51.5.

The m3 (Fig. 5I, J) is anteroposteriorly oval and composed of five lophs plus a strong posterior cingulid. The first two lophs are deeply worn. The third pretrite half-lophid is trifoliate, and the posterior central conule is also present on the third posttrite half lophid. The fourth and fifth pretrite and posttrite half-lophids are rather simple, and only have a main cuspid with somewhat subdivision on its summit. Cementum is very heavy (cementodontology), and small conules are developed in the interlophids (choerodontology), similar to those in the M3. Cingulid is prominent on the posterior end, which is composed of a strong cuspid, and absent on the other margins of the tooth. Measurements (left/right, in mm): length, 185/184; width at lophid 1, 59/59; lophid 2, 61.5/58.5; lophid 3, 60/58.5; lophid 4, 57/58.5; height at the posttrite side of lophid 4, 47/50.

**Stylohyoid.** The left stylohyoid (Fig. 5K, L), the only remainder of the hyoid apparatus, looks like a bifurcated antler. The superior and the posterior rami are nearly arranged in line with one another. Both rami are strong and rod-like. The proximal end of the superior ramus is oval, and is connected to the tympanohyal cartilage. The posterior ramus is longer than the superior one, and has a groove on its lateral side. The distal end of the posterior ramus is flat, where the *m. digastricus posterior* is attached. The inferior ramus is hook-like with a tapering and slightly medially oblique tip. It is slender relative to the other two rami. The morphology of the stylohyoid is typical of gomphotheres (Shoshani & Tassy 2005).

## Comparisons and discussion

### Comparison of cranium

The cranium of *Aphanobelodon zhaoi* displays some pleiomorphies. The braincase is relatively low; the basicranium is not or only slightly erect. These features are common in trilophodont amebelodontids and trilophodont gomphotheres. In *Serbelodon barbourensis*, the basicranium is somewhat more erect, which is a slightly derived feature (Frick 1933). We do not know this feature in *Amebelodon*, in which a cranium has not been explicitly assigned. However, in *Konobelodon* from China (S.-Q. Wang *et al.* 2016a), the braincase is clearly moderately domed and the basicranium is clearly moderately erected. Therefore, these common elephantiform traits were also present in the lineage of Amebelodontidae (considered a monophyletic group).

The facial part of *Aphanobelodon zhaoi* is very developed, showing an anteriorly elongated face and a basally expanded incisive fossa. These features are also observed

in *Platybelodon grangeri* (S.-Q. Wang *et al.* 2013). In *Archaeobelodon* aff. *filholi*, the facial part is also anteriorly elongated, but the incisive fossa is not basally expanded. Sanders *et al.* (2010) considered an anteriorly elongated facial part to be a diagnostic character of Amebelodontidae. Based on this feature, they put *Progomphotherium* into Amebelodontidae. However, a relatively anteriorly elongated facial part is also observed in *Gomphotherium annectens*, a primitive species in Gomphotheriidae (Tassy 1994). In *Konobelodon* from China (S.-Q. Wang *et al.* 2016a), the facial part is substantially shortened, similar to that of *Tetralophodon longirostris*. Therefore, we consider the shortening of the facial part to be a common elephantiform trend that also occurred in Amebelodontidae.

A step-like perinasal fossa is described in *Gomphotherium angustidens* (Tassy 1994, 2013) and considered an important nasal modification in elephantiforms. This feature appears also to be present in some amebelodontids such as *Archaeobelodon* aff. *filholi* (Tassy 1986) and in *Konobelodon* from China (S.-Q. Wang *et al.* 2016a). In *Aphanobelodon zhaoi*, the nasal aperture is laterally enlarged, but no clear step-like perinasal fossa can be observed. A similar morphology is also seen in *Platybelodon grangeri* (S.-Q. Wang *et al.* 2013). The perinasal fossa may be secondarily lost with the development of the enlarged basal part of the incisive fossa.

The tympanic bulla of *Aphanobelodon zhaoi* is not laterally expanded, similar to that of *Phiomia* (Andrews 1906). This feature is also observed in *Platybelodon grangeri* (S.-Q. Wang *et al.* 2013). Except for the absence of upper tusks and the slenderness of the rostrum, the cranium of *Aphanobelodon zhaoi* resembles *Platybelodon* in all aspects.

### Comparison of mandible

As a typical amebelodontid, the mandible of *Aphanobelodon zhaoi* resembles that of *Platybelodon* more than any other. In dorsal view, the mandibular symphysis of *Aphanobelodon zhaoi* strongly expands laterally in the distal part, which is similar to that of *Platybelodon* (Osborn & Granger 1932; S.-Q. Wang *et al.* 2013), in contrast to the not or slightly laterally expanded mandibular symphysis in *Archaeobelodon*, *Serbelodon*, *Protanancus*, *Amebelodon* and *Konobelodon* (Barbour 1927; Frick 1933; Tobien 1973; Tassy 1986; S.-Q. Wang *et al.* 2015, 2016a). Furthermore, in *Aphanobelodon zhaoi*, the anterior edge of the mandibular symphysis is slightly anteriorly convex. This feature is more similar to the straight anterior end of the mandibular symphysis in *Platybelodon* and *Torynobelodon* (Barbour 1932; Osborn & Granger 1932; S.-Q. Wang *et al.* 2013) than to that of the other amebelodontids displaying an anterior apex (Barbour 1927). In lateral view, the mandibular symphysis of *Aphanobelodon zhaoi*

is deflected moderately downward, like that in *Platybelodon*; this shows a contrast to the strongly downward-deflected mandibular symphysis in *Amebelodon* and *Konobelodon* (Barbour 1927; Lambert 1990; S.-Q. Wang *et al.* 2016a). The mandibular resemblance between *Aphanobelodon* and *Platybelodon* reflects the close phylogenetic relationship of the two genera and will be further discussed below.

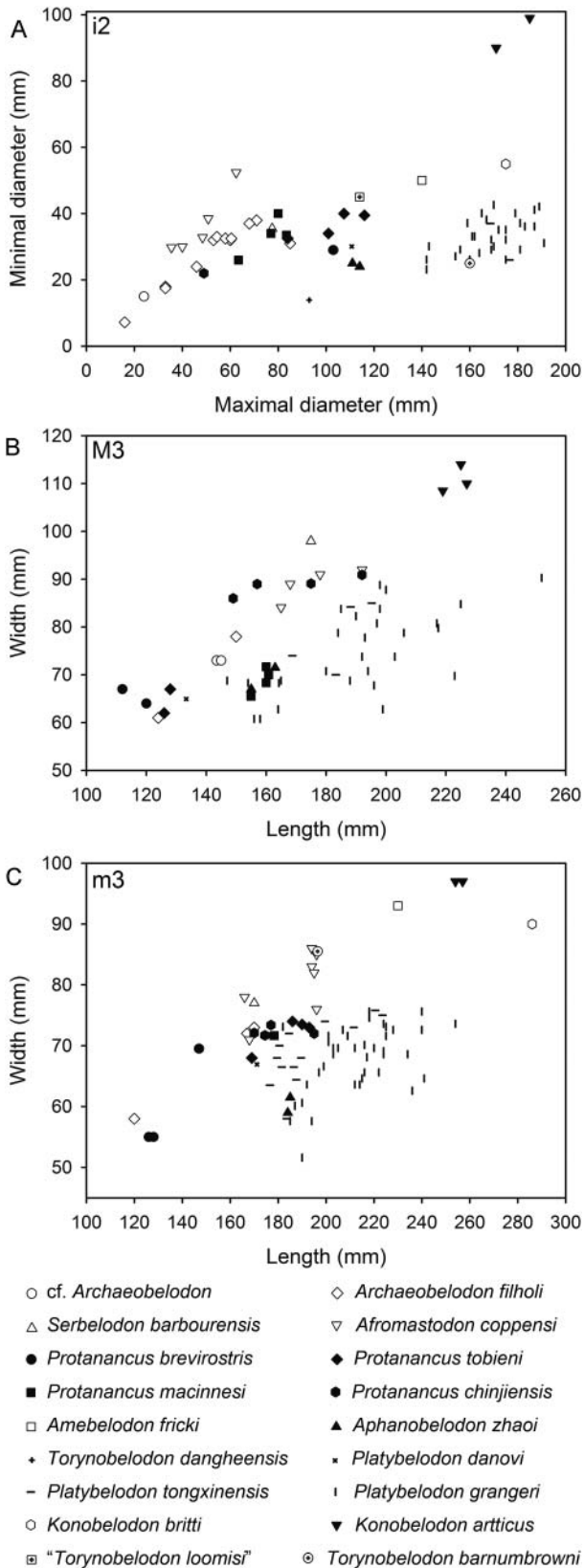
In *Aphanobelodon zhaoi*, there are also some mandibular features that are distinct from those of *Platybelodon*. For example, the ascending ramus of *Aphanobelodon zhaoi* is vertical to the occlusal plan, and this feature is shared widely among other amebelodontids. However, in *Platybelodon* (except *Platybelodon danovi* from the Caucasus), the ramus is strongly posteriorly inclined (Borriasiak 1929; S.-Q. Wang *et al.* 2013). Furthermore, in *Platybelodon grangeri* and the tetralophodont *Platybelodon*, there is a strong transverse ledge at the base of the mandibular symphysis (S.-Q. Wang *et al.* 2013). However, this ledge is likewise missing in *Aphanobelodon zhaoi* and the other amebelodontids.

### Comparison of lower tusks

In *Aphanobelodon zhaoi*, the lower tusks are extremely wide and thin. Wear facets are distributed on both dorsal and ventral sides of the tusks. The dorsal facet is long, and the ventral one short. The anterior edge of the lower tusks is sharp, forming a cutting edge, and the anteromedial and anterolateral angles are sharp, forming two nearly right angles (Fig. 5A–F). These morphologies are similar to those of *Platybelodon* and *Torynobelodon barnumbrowni*. The dimensions of the lower tusk of *Ap. zhaoi* are smaller than those of *Platybelodon tongxinensis* and *Pl. grangeri*, and similar to those of *Pl. danovi* (Fig. 6A). However, the internal structure of *Aphanobelodon zhaoi* displays concentric lamination, which is also observed in *Archaeobelodon*, *Serbelodon*, *Protanancus* and *Amebelodon*, and distinct from the tubular structure in *Platybelodon* and *Torynobelodon* (Osborn & Granger 1932; Tassy 1986; Ye & Jia 1986; Lambert 1990; S.-Q. Wang *et al.* 2013, 2015; Konidaris *et al.* 2014).

### Comparison of cheek teeth

The cheek tooth morphology of *Aphanobelodon zhaoi* is typical amebelodontid. The contours of M3 and m3 are narrow and long. Posttrite central conules and pseudo-anancoidy are developed. The cheek teeth of *Ap. zhaoi* resemble those of *Platybelodon* more than those of the other amebelodontids, because of the strong cementodontology and choerodontology. The dimensions of M3 and m3 are also in the ranges of *Pl. tongxinensis* and *Pl. grangeri* (Fig. 6B, C). In the teeth sample of *Platybelodon* we obtained, the anterior posttrite central conule is always



**Figure 6.** Bivariate plots for various amebelodontid teeth measurements. **A**, cross-section measurements of lower tusks; **B**, occlusal measurements of M3; **C**, occlusal measurements of m3.

absent in the second loph of upper molars (S.-Q. Wang *et al.* 2013). However, it is present in M3 of *Ap. zhaoi*. This element is also often present in *Protanancus* and *Amebelodon* (Barbour 1927; Lambert 1990; S.-Q. Wang *et al.* 2015). This was the only difference that we could find between the cheek teeth of *Platybelodon* and *Ap. zhaoi*; however, this difference seems not to be an important feature.

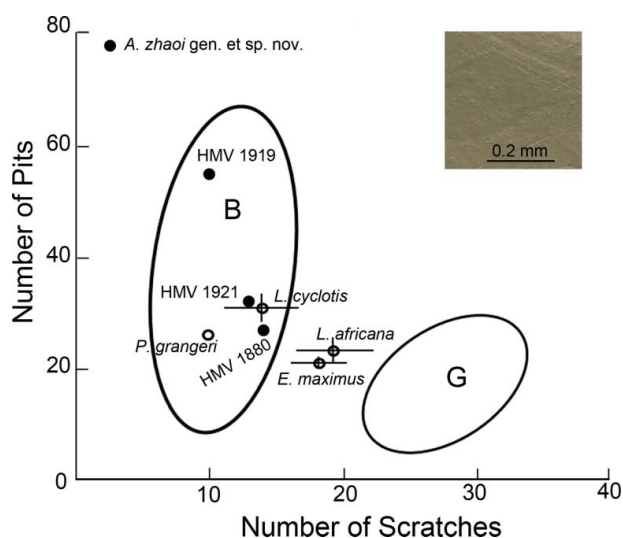
### Feeding behaviour and ecological differentiation of Amebelodontidae

Research using various approaches has been carried out to infer the feeding behaviour of shovel-tuskers. Barbour (1927), Borissiak (1929) and Osborn (1936) hypothesized that shovel-tuskers (i.e. *Amebelodon*, *Platybelodon* and *Torynobelodon*) were marsh dwellers that scooped up aquatic plants using their shovel-like tusks. Lambert (1992) opposed this hypothesis based on morphology and microwear studies of upper and lower tusks of shovel-tuskers; he considered that *Amebelodon* used its upper and lower tusks in various ways, whereas *Platybelodon* and *Torynobelodon barnumbrowni* had lower tusks that were specialized for cutting vegetation. Semperebon *et al.* (2016) reconstructed the dietary habit of *Pl. grangeri* from the Linxia Basin, China based on microwear analysis and confirmed that *Platybelodon* was generally a browser. S.-Q. Wang *et al.* (2015) discussed the competition and replacement between *Protanancus* and *Platybelodon* in East Asia, from which evidence was partly based on microwear study.

Although the sample size is limited (most specimens are not prepared), we studied the microwear of shearing surfaces of the M3 of the three adult *Aphanobelodon zhaoi*. The result showed that the diet of *Ap. zhaoi* is in the range of browsers and close to mix-feeders. However, *Platybelodon grangeri* appears to be slightly more specialized as a browser than *Ap. zhaoi* (Fig. 7).

This result can be further confirmed from the analyses of morphology of lower tusks and mandible. In *Aphanobelodon zhaoi*, the lower tusks are extremely wide and thin. The anterior edge of the lower tusks is sharp, forming

Data sources: *Aphanobelodon zhaoi* gen. et sp. nov., present paper; cf. *Archaeobelodon*, from Tassy (1986); *Ar. filholi*, from Tobien (1973); *Serbelodon barbourensis*, from Frick (1933); *Afromastodon coppensi*, from Pickford (2003); *Protanancus brevirostris* and *Pr. tobieni*, from S.-Q. Wang *et al.* (2015); *Pr. macinnesi*, from Tassy (1986); *Pr. chinjiensis*, from Tassy (1983); *Amebelodon fricki*, from Barbour (1927); *Torynobelodon dangheensis*, from B.-Y. Wang & Qiu (2002); *Pl. danovi*, from Borissiak 1929; *Pl. tonxingensis* and *Pl. grangeri* (including the tetralophodon *Platybelodon*) from S.-Q. Wang *et al.* (2013); *Konobelodon britti*, from Lambert (1990); *K. atticus*, from Schlesinger (1917, 1922) and Konidarar *et al.* (2014); *Torynobelodon barnumbrowni*, from Barbour (1932); '*T. loomisi*', from Barbour (1929).



**Figure 7.** Bivariate plot of the average scratch versus average pit results of extant elephants, *Platybelodon grangeri* and *Aphanobelodon zhaoi* gen. et sp. nov., redrawn after Sempredon *et al.* (2016, fig. 3B). Oval outlines = Gaussian confidence ellipses ( $p = 0.95$ ) on the centroid of the comparative extant grazer (G) and browser (B) samples adjusted by sample size. The insert is a photomicrograph of an enamel surface in HMV1921.

a cutting edge, and the anteromedial and anterolateral angles are sharp, forming two nearly right angles (Fig. 5A, B, F). This morphology is similar to those of *Platybelodon* and *Torynabelodon barnumbrowni*, which indicates vegetation-cutting behaviour, as Lambert (1992) stated. However, in *Amebelodon*, *Serbelodon* and *Protanancus*, the lower tusks are not as wide and thin as those in *Ap. zhaoi*. The anterior edge is blunt without sharp anteromedial and anterolateral angles. This morphology indicates that the tusks are attrited on hard substrate, possibly for digging.

### Phylogenetic position of *Aphanobelodon zhaoi* in Amebelodontidae

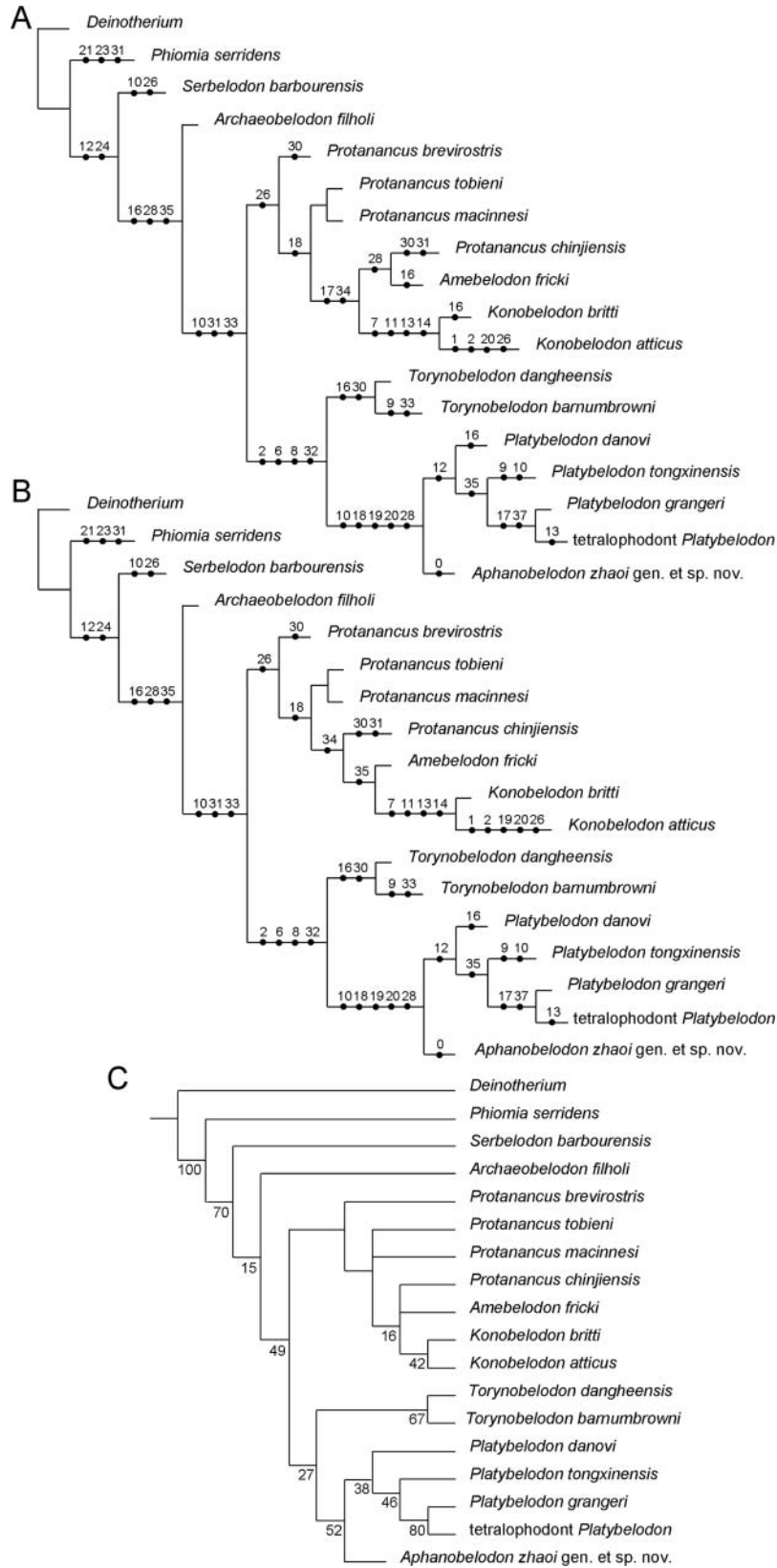
It is easy to attribute *Aphanobelodon zhaoi* to Amebelodontidae based on its flattened lower tusks. Thus far, nine genera have been attributed to the family, including seven shovel-tuskers, *Archaeobelodon*, *Serbelodon*, *Protanancus*, *Amebelodon*, *Platybelodon*, *Torynabelodon* and *Konobelodon* (Shoshani 1996; Tassy 1996; Prado & Alberdi 2008; Konidaris *et al.* 2014; S.-Q. Wang *et al.* 2015), and, controversially, two non-shovel-tuskers, *Progomphotherium* and *Afromastodon* (Sanders *et al.* 2010). Here we confine our discussion to the shovel-tuskers. Among these taxa, *Platybelodon*, *Torynabelodon* and *Konobelodon* have tubular structure in their low tusks (Osborn & Granger 1932; Ye & Jia 1986; Tassy 1986; Lambert 1990; Konidaris *et al.* 2014; S.-Q. Wang *et al.*

2015), and the others have concentric lamination. *Aphanobelodon zhaoi* has concentric lamination in its lower tusks. However, its lower tusk is more flattened than that of any members of *Archaeobelodon*, *Serbelodon*, *Protanancus* and *Amebelodon*. The width-height ratio of its lower tusk falls into the variation range of *Platybelodon* (Fig. 6A), and the mandibular shape is more similar to that of *Platybelodon* than any other genus. This makes it difficult to determine the phylogenetic relationship within Amebelodontidae.

A cladistic analysis was carried out to determine the phylogenetic position of *Aphanobelodon zhaoi* within Amebelodontidae. Two MPTs were obtained (Fig. 8A, B). The topologies of the two MPTs yielded different positions of *Protanancus chinjiensis* (as the sister group of *Amebelodon* or *Amebelodon* + *Konobelodon*). In both MPTs, the position of *Aphanobelodon zhaoi* was stable; however, it was nested into species of *Platybelodon*. '*Platybelodon*' *dangheensis*, an isolated species in the early Miocene, MN3 (B.-Y. Wang & Qiu 2002), was stably clustered with the American late Miocene *Torynabelodon barnumbrowni*, sharing two synapomorphies – the incipient posttrite trefoils and the very short and broad symphysis. Therefore, we suggest that the genus name *Torynabelodon* is valid, and only includes two species, *T. barnumbrowni* and *T. dangheensis*.

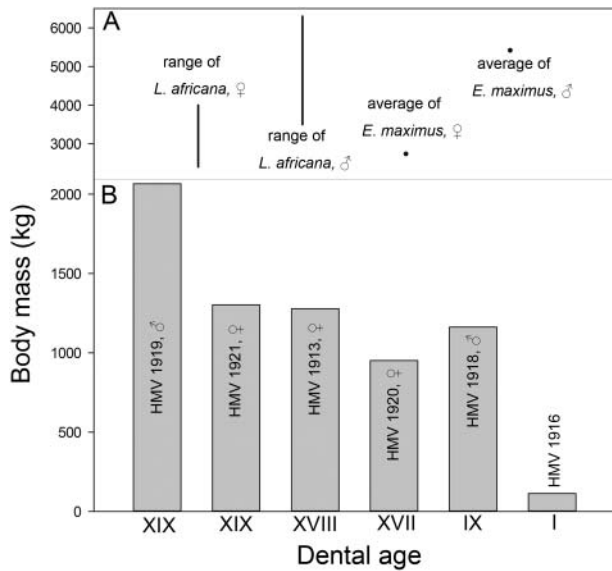
Excluding *Torynabelodon*, *Aphanobelodon zhaoi* constitutes the sister group of *Platybelodon*. Guan (1991) considered *Pl. tongxinensis* from the Dingjiaergou fauna (Ye & Jia 1986; Ye *et al.* 1989, 1990; Guan 1988) as a junior synonym of *Pl. danovi*, and this view was accepted by subsequent researchers (Qiu *et al.* 1999; S.-Q. Wang *et al.* 2013). However, based on our comparison, there are two important differences between the type mandible of *Pl. danovi* and *Pl. tongxinensis*. First, the cross section of type material is relatively narrow in *Pl. danovi* (Fig. 6A); second, the mandibular ramus of *Pl. danovi* is not posteriorly inclined (Borissiak 1929, pl. 4, fig. 3). Furthermore, the presence of tubular structure in the type specimen of *Pl. danovi* is questionable (Tobien 1973, p. 252). Therefore, it is better to revive *Pl. tongxinensis* as a valid species.

S.-Q. Wang *et al.* (2013) demonstrated the morphological differences between *Platybelodon grangeri* from the Tairum Nor Fauna (from lower horizons in the Tunggur Formation) and the Moergen Fauna (from upper horizons in the Tunggur Formation). *Platybelodon* from the Moergen Fauna differs from other species of *Platybelodon* because it possesses complete tetralophont M2 and m2. It is also distinct from other species of *Platybelodon* because it possesses a wider symphysis that is closer to the tooth rows (Osborn & Granger 1932, fig. 5). Therefore, we suggest establishing a new species for *Platybelodon* from the Moergen Fauna of Tunggur, and here we have temporarily referred to it as tetralophodont *Platybelodon*.



**Figure 8.** Phylogenetic reconstruction of shovel-tusked elephantiforms. **A**, **B**, MPTs from cladistic analysis of the proboscideans, based on the characters provided in Supplemental Appendix S1 and the data matrix in Supplemental Appendix S2. Tree length = 91, CI = 0.637; RI = 0.720; the numbers above each circle represent the supporting characters; **C**, the strict consensus tree from the two MPTs; the number at each node represents the bootstrap support value.

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**Figure 9.** Body mass estimation of *Aphanobelodon zhaoi* gen. et sp. nov. and comparison with extant elephants. **A**, body mass data of extant elephants from Norwak (1999); **B**, body mass estimation of *Aphanobelodon zhaoi* gen. et sp. nov., based on Christiansen (2004).

*Konobelodon* was first established as a subgenus of *Amebelodon* that contained shovel-tusked intermediate cheek teeth and tubular structures in the mandibular tusks (Lambert 1990), but recently was upgraded to genus level, with the taxon enlarged to include the Eurasian '*Mastodon*' *grandincisivus* (Konidaris *et al.* 2014; S.-Q. Wang *et al.* 2016a). *Konobelodon* was thought to be derived from *Platybelodon* by some researchers (Konidaris *et al.* 2014) because of the presence of tubular structures in the mandibular tusks. However, the mandibular morphology does not support a close relationship between *Konobelodon* and *Platybelodon*. In *Konobelodon*, the ramus is not posteriorly inclined and the symphysis is strongly downwardly deflected. These features are similar to those of *Amebelodon*, and our phylogenetic reconstruction also supports the close relationship of the two genera. However, it should be noted that in our phylogeny, the presence of tubular structures in the mandibular tusks is no longer regarded as a synapomorphy. S.-Q. Wang *et al.* (2015) demonstrated biomechanical advantages of the tubular structures in *Platybelodon*. Therefore, the occurrence of the tubular structure is potentially due to parallel evolution (having evolved three times, in *Torynobelodon*, *Platybelodon* and *Konobelodon*, in our phylogenetic reconstruction) induced by competition and selection pressure.

To summarize, based on our phylogenetic reconstruction, we recognized two monophyletic groups in Amebelodontidae (Fig. 8C): one includes *Protanancus*,

*Amebelodon* and *Konobelodon*; and the other includes *Torynobelodon*, *Aphanobelodon* and *Platybelodon*. The former can be referred to as Amebelodontinae and the latter as Platybelodontinae; *Archaeobelodon* and *Serbelodon* are plesions.

### Sexual dimorphism and body mass estimation

The size distribution of the three adult individuals of *Aphanobelodon zhaoi* is notably bimodal. The length of the cranium of HMV1919 is 1016 mm and those of HMV1880 and HMV1921 are 895 mm and 808 mm, respectively. The mandible length of HMV1919 is 1550 mm and those of HMV1880 and HMV1921 are 1127 mm and 1201 mm, respectively. This is easily interpreted as sexual dimorphism. The braincase of HMV1880 (and of HMV1921) is low, and the superior rim of the nasal aperture is at the level of the two postorbital processes (Fig. 1E). However, in HMV1919, the braincase is relatively domed and the superior rim of the nasal aperture is clearly posterior to the postorbital process (Fig. 1F). Similar sexual dimorphism was also observed in *Platybelodon grangeri* (S.-Q. Wang *et al.* 2013, fig. 3; S.-Q. Wang & Deng 2016), and possibly also *Gomphotherium angustidens* (Tassy 2013, fig. 15A, D; S.-Q. Wang & Deng 2016).

The body mass of the adult male (HMV1919) was estimated to be 2066.76 kg and that of the adult female (HMV1921) to be 1302.33 kg, only 63% that of the adult male, which indicates strong sexual dimorphism (Supplemental Table S1; Fig. 9). Two subadults very close to the adult dental age are estimated to be 950.98 kg and 1278.34 kg, respectively, and were identified as two females (Supplemental Table S1; Fig. 9). However, a subadult with younger dental age was estimated at 1162.53 kg, which is close to the adult female, and thus was identified as a young male (Supplemental Table S1; Fig. 9). The baby is only estimated to be 112.98 kg (Supplemental Table S1; Fig. 9). The estimated body masses of *Aphanobelodon zhaoi* are much smaller than the lower limit of extant elephants (Fig. 9). Furthermore, they are also smaller than estimated body masses of the fossil elephantiform taxa (i.e. *Mammuthus primigenius* 3179.50–9837.41 kg, *Elephas antiquus* 5762.53–12266.55 kg, *Mammut americanum* 4004.44–5390.60 kg and *Serbelodon barbourensis* 3211.10 kg); and are similar to those of *Archaeobelodon filholi* 2029.45 kg, *Gomphotherium angustidens* 2069.42 kg and *G. productum* 1309.98–1874.35 kg (Christiansen 2004).

### Conclusions

In the present study, we report an interesting proboscidean taxon, *Aphanobelodon zhaoi*, that possessed a shovel-

tusked mandible and lacked permanent upper tusks. This is a unique feature combination – like a combination of *Deinotherium* and *Platybelodon*. Based on our cladistic analysis, *Aphanobelodon zhaoi* is the sister group of *Platybelodon* and, along with *Torynobelodon*, constitutes a monophyletic group in Amebelodontidae. The mandible of *Aphanobelodon* is not as specialized as that of *Platybelodon*, which is more suitable for cutting vegetation. This study enhances our knowledge regarding the evolutionary diversification of proboscideans in terms of morphology, taxonomy and biology.

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## Supplemental data

Supplemental material for this article can be accessed online at: <http://dx.doi.org/10.1080/14772019.2016.1208687>.

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