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# The gomphotheriid mammal *Platybelodon* from the Middle Miocene of Linxia Basin, Gansu, China

SHIQI WANG, WEN HE, and SHANQIN CHEN



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In this paper, we report on abundant fossils of *Platybelodon* from the Middle Miocene of the Linxia Basin, China. Most of the fossils were discovered at two localities (Laogou and Zengjia) in the upper Middle Miocene Hujialiang Formation, and possess derived characters for the genus, including a relatively slender upper incisor, the development of a transverse ledge on the narrowest part of the mandibular symphysis, narrow, elongate and hypsodont third molars, the development of fourth loph(id)s on the second molars, and the development of small enamel conules and cementum in the interloph(id)s. Following comparisons with other Eurasian platybelodonts, we assign these remains to *Platybelodon grangeri*, and demonstrate that they are morphologically intermediate between *P. grangeri* from the Tunggurian localities of Tarim Nor and *Platybelodon* Quarry in Inner Mongolia. We suggest that the locality of Laogou may be younger than that of Zengjia, based on the occurrence of platybelodonts showing a suite of more derived characters. In addition, we assign two further specimens of *Platybelodon* from the lower Middle Miocene Dongxiang Formation of the Linxia Basin to *Platybelodon danovi*, owing to their retention of plesiomorphic characters distinguishing them from other Linxia *Platybelodon* fossils. Based on a cladistic analysis, we propose an evolutionary sequence of platybelodonts in Eurasia, and discuss potential functional adaptations.

Key words: Mammalia, Gomphotheriidae, *Platybelodon*, morphology, cladistics, Miocene, Linxia Basin, China, Eurasia.

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## Introduction

The Linxia Basin is famous for its abundance of fossils of *Platybelodon*, which is a representative of the local Middle Miocene fauna (so-called "*Platybelodon* fauna") (Deng 2004b; Deng et al. 2004a). Fossil platybelodonts from this area are more numerous and generally better preserved than those from the classic Tunggur localities of Inner Mongolia (Osborn and Granger 1931, 1932), and comprise a complete ontogenetic series of skulls and mandibles of both sexes, thus providing a large amount of morphological, physiological, and behavioral information about this taxon. Previous studies referred the Linxia material to *Platybelodon grangeri* (Deng 2004a, b; Deng et al. 2004a, b, 2007), *P. tongxinensis* (Guan 1988), or *P. danovi* (Guan 1996), but made no detailed comparisons with other taxa. In addition, recent years have seen the discovery of additional and seemingly less derived fossil material of *Platybelodon* in older, early Middle Miocene horizons in the same area.

The Linxia Basin is located in the northeastern corner of the Tibetan Plateau in western China, where Cenozoic strata form a nearly uninterrupted sequence ranging from the Early Oligocene to the Early Pleistocene (Deng et al. 2004b). The Middle Miocene sediments are divided into the lower Dongxiang Formation and upper Hujialiang Formation (Deng 2004a). Most of the fossils were recovered from the localities of Zengjia and Laogou in the Hujialiang Formation, with Zengjia having yielded several nearly complete skulls and mandibles, while the finds from Laogou consist mainly of isolated cheek teeth. Mandibles were also discovered at the localities of Ganchiliang and Citan in the Dongxiang Formation (Fig. 1).

Here, we present a comprehensive revision of the Middle Miocene *Platybelodon* material from the Linxia Basin, including detailed descriptions of morphological characters and comparisons of the specimens with a range of Eurasian taxa, especially from the Tunggur and Tongxin areas of China. Our results show that the fossil platybelodonts from



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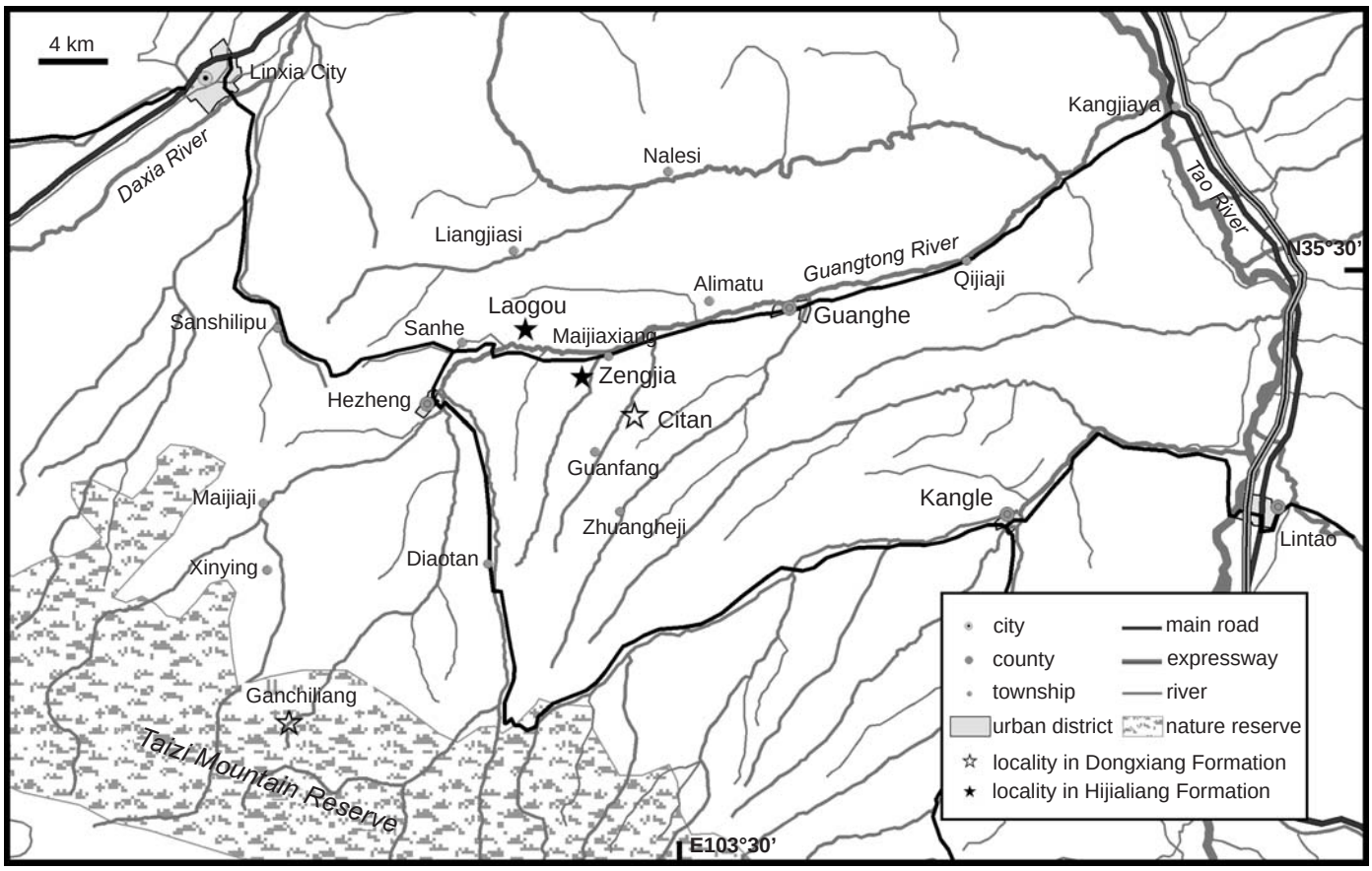



Fig. 1. Map showing fossil platybelodont localities in the Linxia Basin, Gansu, western China.

the Hujialiang Formation are generally similar to those from Tunggur, while being more derived than those from Tongxin. Furthermore, we demonstrate that the all of the Hujialiang fossils should be referred to *Platybelodon grangeri*, even though the specimens from Zengjia are apparently more archaic than those from Laogou. By contrast, the fossil remains from localities in the Dongxiang Formation possess more primitive features and are more appropriately assigned to *Platybelodon danovi*. Finally, we provide a discussion of evolutionary trends and functional adaptations of Eurasian platybelodonts.

*Institutional abbreviations*.—AMNH, American Museum of Natural History, vertebrate collection, New York, USA; BPV, Beijing Natural History Museum, vertebrate collection, Beijing, China; HMV, Hezheng Paleozoological Museum, vertebrate collection, Hezheng, China; IVPP V, Institute of Vertebrate Paleontology and Paleoanthropology, vertebrate collection, Beijing, China.

*Other abbreviations*.—CAE, Central Asiatic Expedition.

# Material and methods

Descriptions of occlusal structures of gomphotheriid cheek teeth (Fig. 2), as well as cranial and mandibular measurements follow Tassy (1983: fig. 4, slightly revised; 1996b: fig. 11.1, 11.2; see also the captions of Tables 1 and 2). In the present article, we defined juveniles as individuals preserving the premolars, and adolescents as those in which the premolars were shed but M3 or m3 have not yet been used. We also collectively refer to both of the former as immature individuals. A question mark following the catalogue number indicates that the locality from which the specimen was collected is uncertain.

We performed a cladistic analysis in order to investigate the interrelationships of Eurasian platybelodonts. The data matrix contained 24 unordered characters and 11 taxa, with the amebelodontine *Archaeobelodon filholi* (Tassy 1984, 1986) serving as outgroup (see Appendix 1). Characters 3, 7, 9, 12, 13, 16–19, and 24 in particular were chosen based on their previously suggested importance to platybelodont phylogenetics (Borissiak 1929; Osborn and Granger 1931, 1932; Ye and Jia 1986; Ye et al. 1989, 1990; Wang and Qiu 2002), whereas the remaining characters were included because they captured distinct variation among the platybelodontid taxa examined in this study. The analysis was carried out in PAUP 4.0b10 using the branch-and-bound search option, and the results reported in form of the strict consensus of all most parsimonious trees (MPTs).

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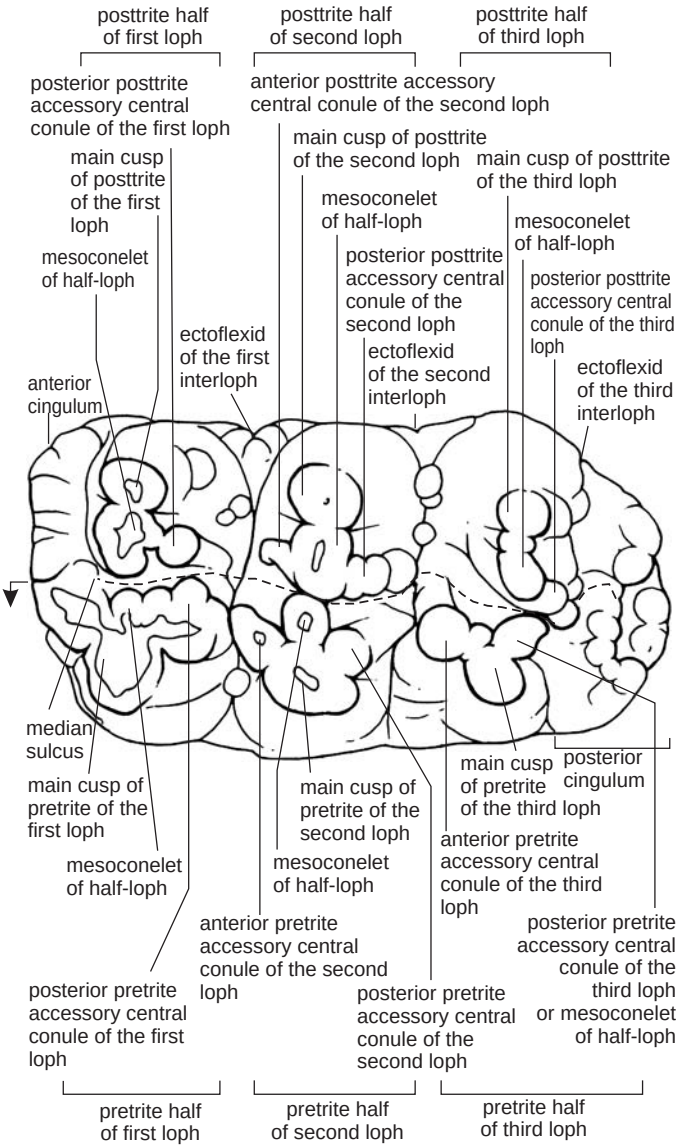



Fig. 2. Gomphotheriid dental nomenclature (left M2 of *Protanancus chijiensis*), from Tassy (1983: fig. 4, slightly revised).

# Geological setting

The material described in this paper was recovered from the localities of Zengjia (N 35°26'23.1", E 103°26'37.6", H 2150 m, loc. No. LX200002, ca. 12.6 Ma) and Laogou (N 35°28' 05.3"; E 103°24'50.5"; H 2200 m, loc. No. LX200003, ca. 12.3 Ma) in the Hujialiang Formation, and Citan (N 35°26' 43.4", E 103°29'02.8", H 2075 m, loc. No. LX200210) and Ganchiliang (N 35°17'59.4", E 103°17'30.1", H 2530 m, loc. No. LX200802) in the Dongxiang Formation, as exposed in the Linxia Basin of western China (Fig. 1). The Hujialiang Formation consists of grey-green sandstone and beds of conglomerate, and has been estimated at ca. 12.6 Ma (late Middle Miocene) based on magnetostratigraphic correlation (Deng et al. 2012). By contrast, the underlying Dongxiang Formation consists of brownish red mudstones and siltstones intercalated with bluish grey or greyish white marlite beds of 0.5–1 m thickness, and has been estimated at ca. 16–13.5 Ma (lower Middle Miocene), also based on magnetostratigraphic correlation (Deng et al. 2012).

# Systematic paleontology

## Order Proboscidea Illiger, 1811

## Family Gomphotheriidae Hay, 1922

## Subfamily Amebelodontinae Barbour, 1927

## Genus *Platybelodon* Borissiak, 1928

*Type species*: *Platybelodon danovi*, Kuban region of the North Caucasus, Chokrak beds, Middle Miocene.

### *Platybelodon grangeri* (Osborn, 1929)

Figs. 3–7, Tables 1 and 2.

*Referred material*.—Laogou locality (LX200002): juvenile skulls (HMV0049, 0050, 1812?, and 1837); juvenile skull associated with mandible (HMV1813?); adolescent skulls (HMV0019, 1815?, 1828?, and 1839?); adult skulls (HMV0014–0018, 0020–0027, 1840?, and 1841?); adult skulls associated with mandibles (HMV0939 and 0940); juvenile mandibles (HMV0045–0048); adolescent mandibles (HMV0029, 0040, 0041, and 0044); adult mandibles (HMV0030–0039, 0042, 0043, 1830, 1836, and 1842?); jaw remains (HMV1800, fragmentary right maxilla with M2 and M3; HMV1801, fragmentary maxillae with M3s; HMV 1798, fragmentary right dentary with m2 and m3); isolated cheek tooth (HMV1799, right m3); incisor remains (HMV1266–1269, and 1863, left I2s; HMV1275 and 1862, left i2s; HMV1272, right i2). Laogou locality (LX200003): jaw remains (HMV1797, fragmentary maxillae with DP4s and right M1; HMV1793, fragmentary dentaries with right m1; HMV1263 and 1795, fragmentary left dentary with m2 and m3; HMV1784 and 1794, fragmentary right dentary with m2 and m3; HMV1786, fragmentary left dentary with m3; HMV1785 and 1796, fragmentary right dentary with m3); isolated cheek teeth (HMV1859, right M2; HMV1788 and 1845?, right M3s; HMV 1787, 1802?, 1803?, and 1846?, left m3s; HMV1783, 1804?, 1847?, and 1852?, right m3s); incisor remains (HMV1270, right I2; HMV1274, 1789, 1790, and 1792, left i2s).

*Emended diagnosis*.—The diagnosis of *Platybelodon grangeri* by Osborn and Granger (1931: 4) was mainly based on the mandible and the lower incisors. Here, we add some features pertaining to the cranium and the molars: the neurocranium is low and elongated, with a narrow and long dorsal table in females, and a relatively broad and short one in males. In adults, the posterior border of the external nares is located posterior to the postorbital process, while the anterior border of the orbit is situated posterior to the anterior border of M3. The alveolus of the incisor is slender, and the upper tusk is relatively weak and lacking enamel bands in most cases. The elongated and extremely flattened mandibular

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Table 1. Cranial measurements (in mm) of *Platybelodon grangeri* from the Linxia Basin. Measurements follow Tassy (1996).

| | HMV0940 adult male | HMV0023 adult female | HMV1813 juvenile |
|---|---|---|---|
| Maximal length measured from the occipital border | 1107 | 882 | 523 |
| Length of cerebral part | 227 | 334 | 235 |
| Length of premaxilla | 877 | – | 287 |
| Length of incisive fossa | 829 | – | 261 |
| Length of nasal bones from the tip to the upper border of the nasal fossa | 40 | 36 | 28 |
| Maximal supraorbital width | 494 | 387 | 151 |
| Posterior rostral width (as measured between the infraorbital foramina) | 207 | 230 | 120 |
| Anterior rostral width | 198 | 135 | 61 |
| Width of nasal bones at the upper border of the nasal fossa | 113 | 102 | 44 |
| Width of nasal fossa | 345 | 243 | 84 |
| Minimal cerebral width between temporal lines | 240 | 209 | 93 |
| Maximal length measured from the condyles | 1120 | 858 | – |
| Length of zygomatic arch measured from the processus zygomaticus of the maxilla to the posterior border of the glenoid fossa | 551 | 417 | 242 |
| Length of orbitotemporal fossa measured at the level of the zygomatic arch | 317 | 285 | 151 |
| Palatal length from the anterior grinding tooth to the choanae | – | 344 | – |
| Length of basicranium from the choanae to the foramen magnum | – | 264 | – |
| Thickness of processus zygomaticus of the maxilla | 190 | 125 | 63 |
| Maximal cranial width across the zygomatic arches | – | 460 | – |
| Width of basicranium between the lateral borders of the glenoid fossae | 466 | 362 | – |
| Maximal width of choanae | 64 | 79 | – |
| Internal maximal width of the palate | 154 | 102 | 25 |
| External maximal width of the palate | 272 | 214 | 114 |
| Internal width of the palate measured at the anterior grinding teeth | 58 | 34 | 40 |
| Minimal palatal width between the inter-alveolar cristae (maxillary ridges) | – | 52 | 29 |
| Sagittal height of occipital | 356 | 229 | 153 |
| Occipital width | 586 | 444 | – |
| Height of premaxilla | 76 | 65 | 42 |
| Facial height measured at the anterior grinding tooth | 131 | 55 | 56 |
| Height of the maxilla ventral to the processus zygomaticus | 107 | 43 | 40 |
| Height of the orbit | – | 100 | 51 |
| Cranial height measured from the top of the cranium to the pterygoid process | 500 | 347 | 235 |
| Length of basicranium from the condyles to the pterygoid process | 393 | 251 | – |
| Facial length measured from the tip of the rostrum to the pterygoid process | 710 | 621 | 354 |
| Length of the orbitotemporal fossa measured from the squamosal to the anterior border of the orbit | 364 | 389 | 251 |
| Mid-cranial length measured from the external auditory meatus to the ventral border of the orbit | 400 | 379 | 244 |
| Mid-cranial height measured from the pterygoid process to the dorsal border of the orbit | 317 | 266 | 182 |

symphysis is relatively long in males, but short in females. In adults, a robust transverse ledge is developed at the narrowest part of the mandibular symphysis (Fig. 5A, D). The ascending ramus of the mandible is directed posteriorly, and the mandibular angle is blunt and rounded. Cementum and small enamel conules are well developed in the interloph(id)s of the upper and lower molars, whereas their cingula and cingulids are relatively weak. Pretrite trefoils are developed on at least the first two loph(id)s of all molars and the last deciduous premolars. While the pretrite trefoils are relatively symmetrical on the upper molars, advanced forms are marked by relatively weak posterior lobes (posterior pretrite accessory central conules) and the presence of posterior posttrite accessory central conules. On the lower molars, the pretrite trefoils tilt anteromedially, and are marked by strong and individualized accessory conules tending to invade the neighboring entoflexids, as well as the presence of anterior posttrite accessory central conules. The pretrite and posttrite half-lophids of the lower molars occupy alternate positions. The intermediate cheek teeth (DP4–M2, and dp4–m2, respectively) tend to have four loph(id)s, with complete fourth loph(id)s present on M2 and m2 in the more advanced forms. By contrast, M3 and m3 are relatively narrow and possess more than four loph(id)s.

## *Description*

*Skull*.—In dorsal view (Figs. $3D_1$, 4B), the alveolus for the incisor is slender and long. The incisive fossa between the

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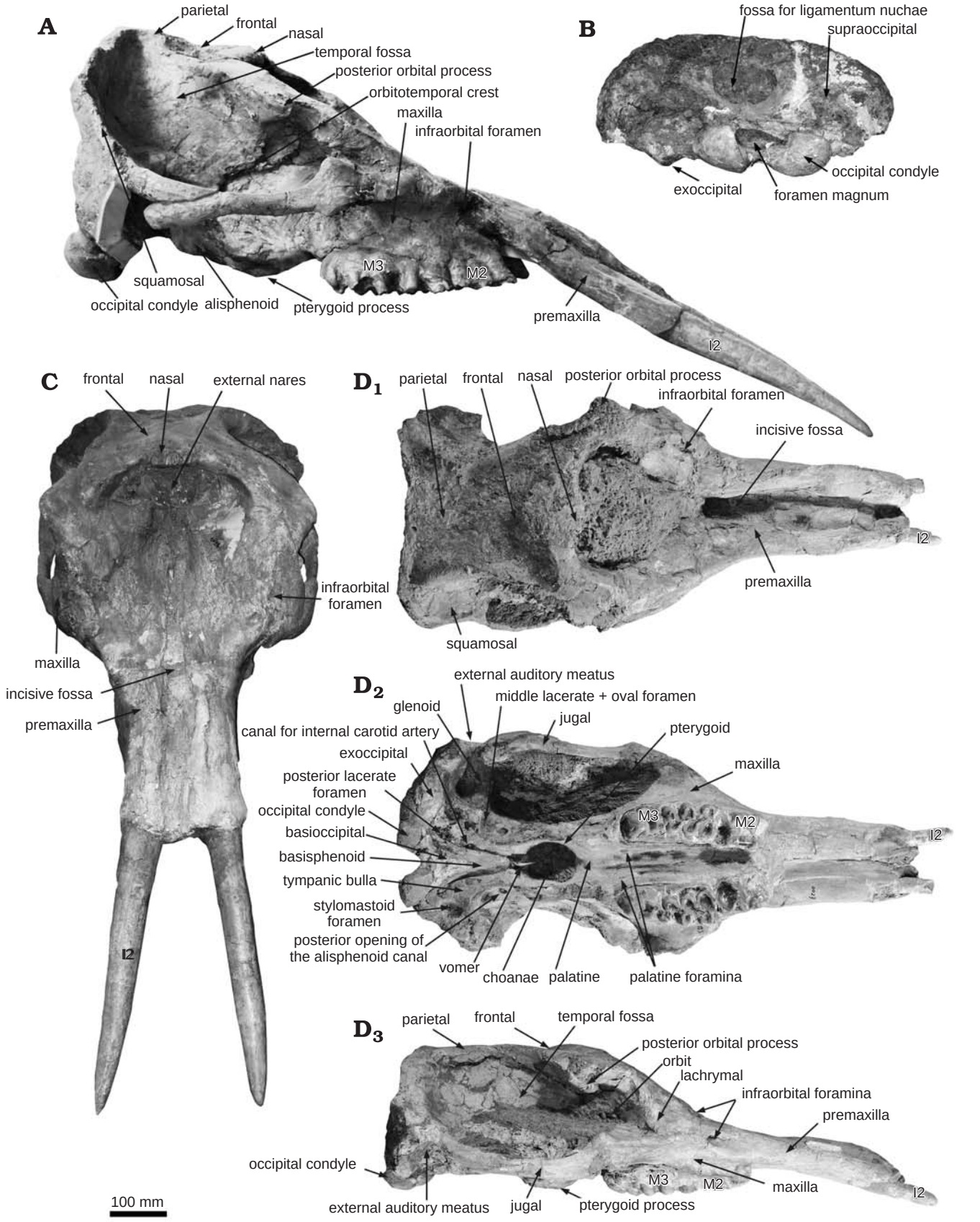



Fig. 3. Skull of the gomphotheriid mammal *Platybelodon grangeri* (Osborn, 1929) from locality LX200002 of the Linxia Basin, Middle Miocene. **A**. Adult male (HMV0940), lateral view (horizontally reversed). **B**. Adolescent (HMV0021), distal view. **C**. Adult male (HMV0024), anterior view. **D**. Adult female (HMV0023), dorsal ($D_1$) and ventral ($D_2$), and lateral ($D_3$) views.

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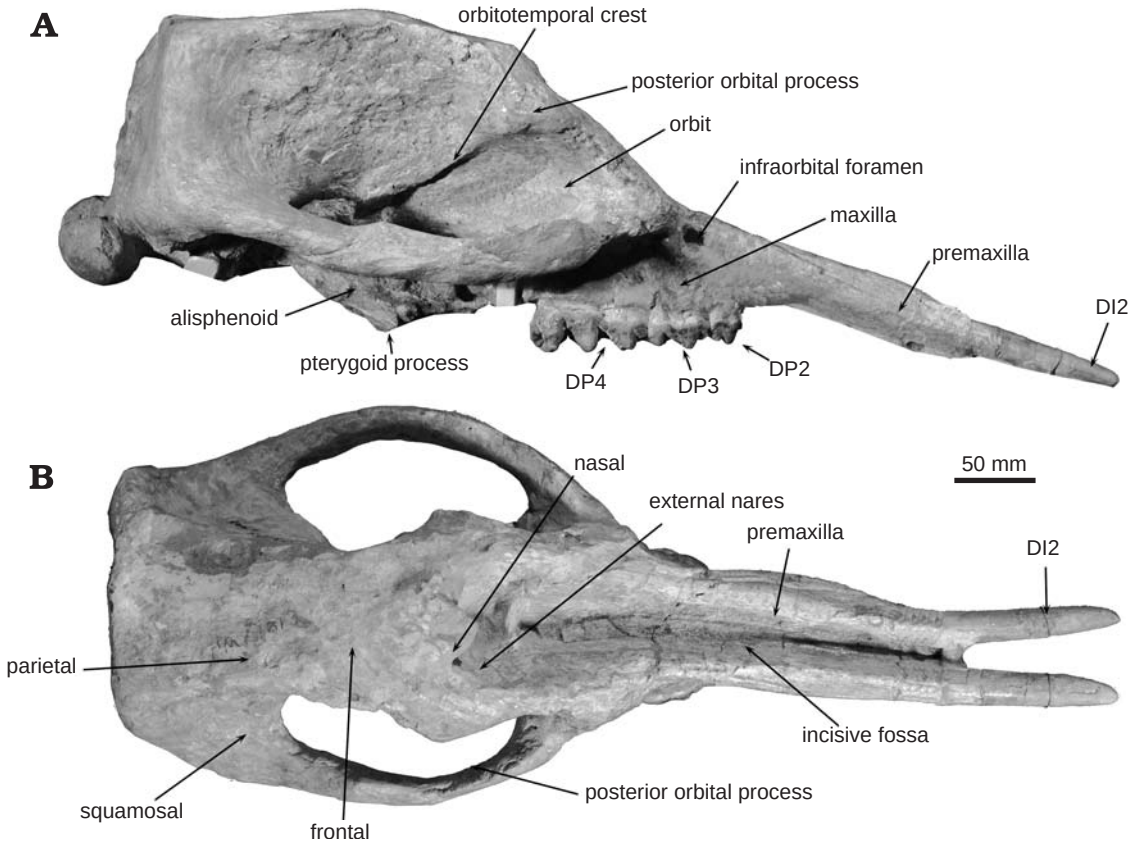



Fig. 4. Juvenile skull of the gomphotheriid mammal *Platybelodon grangeri* (Osborn, 1929) (HMV1813) from locality LX200002 of the Linxia Basin, Middle Miocene; lateral (**A**) and dorsal (**B**) views.

premaxillae is narrow and deep, and its posterior convex ledge is located deep within the external nares. The anterior end of the nasal is blunt. The posterior border of the external nares is located between the postorbital processes in the juvenile specimens, whereas it is situated more posteriorly in adults. The latter feature is particularly well developed in males, resulting in a relatively broad and short dorsal table of the neurocranium in these individuals, as opposed to the narrow and long dorsal table found in juveniles and females. Anteriorly, the temporal lines are directed anterolaterally, thus connecting the postorbital processes. Further posteriorly they converge to form an intertemporal constriction, before extending posterolaterally to merge with the occipital crest. The zygomatic process of the squamosal is relatively weak in juveniles and females, but strong in males.

In anterior view (Fig. 3C), the transversely elliptical opening of the external nares is wide and low. The rough surface of the dorsal part of the premaxilla for the attachment of maxillo-labialis is broader in males than in females and juveniles, suggesting that the former might have possessed a stronger trunk. In ventral view (Fig. $3D_2$), the incisive alveolus is slender and long, and converges distally in females, whereas it diverges in males. The triangular zygomatic process of the maxilla is relatively small and does not extend far laterally. The palate is narrow, flattened, and slightly arched upward. The suture between the palatine bone and the maxilla is visible, and anteriorly terminates in a small, slit-like palatine foramen. The posterior edge of the last functional upper check tooth is located anterior to the rounded anterior border of the choanae. The latter are elliptical and have two sharp lateral edges, forming the pterygoid processes. The posterior opening of the alisphenoid canal is large, oval, and located in the posteromedial part of the alisphenoid. The sharp crest of the pterygoid process extends backwards to connect with a crest located on the anterior border of the tympanic bulla, with the confluent openings of the oval and middle lacerate foramina located in a deep groove situated dorsal to the former crest.

The tympanic bulla is triangular and extends laterally and posteriorly, with a concave and vertical posterolateral edge. There is a large, rounded opening on the medial side of the tympanic bulla, representing the canal of the internal carotid artery, while a depression located posterior to the medial side of the tympanic bulla marks the position of the posterior lacerate foramen. The stylomastoid foramen is located in a deep fossa developed posterolateral to the tympanic bulla. The glenoid fossa is relatively flattened, lacks a prominent postglenoid process, and is anterolaterally connected to the posterior end of the jugal. On the posterior part of the ventral surface of the squamosal there is a depressed region, representing the external auditory meatus. The portion of the exoccipital posterior to the squamosal is more convex ventrally than the more medial part of the exoccipital. The occipital condyles are large and triangular, and directed posterolaterally. The basioccipital is triangular posteriorly, and attaches to the cylindri-

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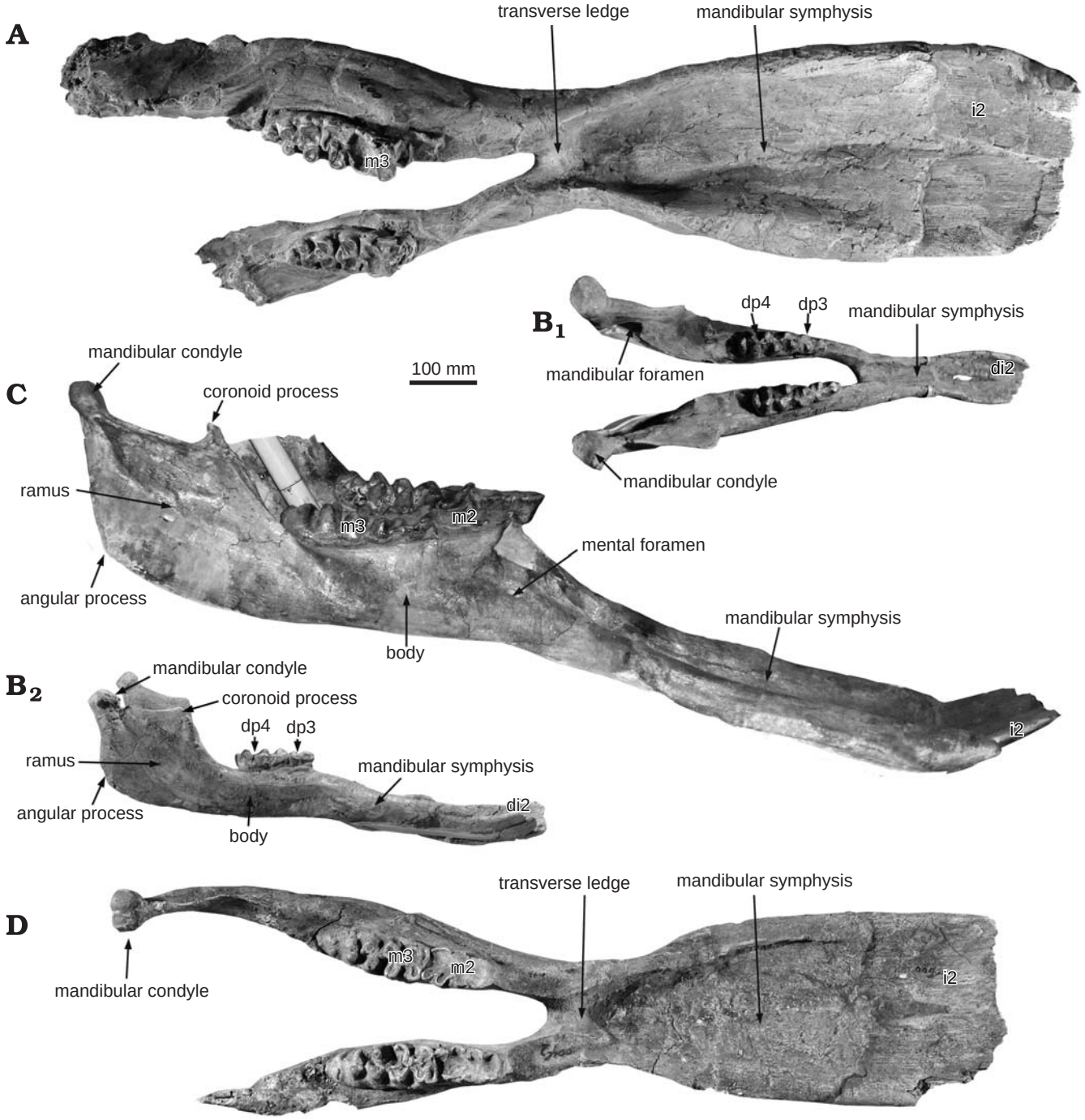



Fig. 5. Mandible of the gomphotheriid mammal *Platybelodon grangeri* (Osborn, 1929) from locality LX200002 of the Linxia Basin, Middle Miocene. **A**. Adult male (HMV0031), dorsal view. **B**. Juvenile (HMV1813), dorsal ($B_1$) and lateral ($B_2$) views. **C**. Adult male (HMV0940), lateral view (horizontally reversed). **D**. Adult female (HMV0042), dorsal view.

cal basisphenoid. The vomer is sharp and extends anteriorly into the choanae.

In posterior view (Fig. 3B), the occipital surface is transversely elliptical and nearly perpendicular to the dorsal and ventral sides of the skull. The fossa for the ligamentum nuchae is large and rounded, and marked by a thin external sagittal crest running through its center. The occipital condyles are rounded ventrolaterally, and border a dorsoventrally compressed foramen magnum. In lateral view (Figs. 3A, $D_3$, 4B), the neurocranium is generally flattened, though in some males it may be slightly arched. The basicranium (the part of the cranium located posterior to the pterygoid processes) and palate (the part located anterior to the pterygoid processes) are located almost in the same horizontal plane. The slender and long alveoli for the incisors have strong crests developed on their dorsal faces, and are located almost in the same plane as the palate in juveniles and females, while sloping further downwards in males. The lateral, facial part of the maxilla is

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Table 2. Mandibular measurements (in mm) of *Platybelodon* from the Linxia Basin. Measurements follow Tassy (1996).

| | *Platybelodon grangeri* | | | *Platybelodon danovi* | |
|---|---|---|---|---|---|
| | HMV0940 adult male | HMV0042 adult female | HMV1813 juvenile | HMV1829 | IVPPV18015 |
| Maximal length | 1655 | 1234 | 679 | – | – |
| Symphyseal length | 737 | 490 | 182 | – | – |
| Alveolar distance (from the most salient point of the trigonum retromolare to the symphyseal border of the corpus) | 517 | 409 | 247 | 477 | – |
| Ventral length measured from the gonion (angulus mandibular) to the tip of the symphysis | 1394 | 997 | 544 | – | – |
| Maximal width | 410 | 410 | 185 | 330 | – |
| Mandibular width measured at the root of the rami | 430 | 306 | 160 | 316 | – |
| Width of corpus measured at the root of the ramus | 100 | 113 | 55 | 117 | – |
| Width of corpus measured at the anterior alveolus (or the grinding tooth if the alveolus is entirely resorbed) | 75 | 61 | 36 | 61 | – |
| Posterior symphyseal width | 194 | 173 | 91 | 144 | – |
| Anterior symphyseal width | 336 | 286 | 134 | – | – |
| Maximal symphyseal width | 333 | 286 | 134 | – | – |
| Minimal symphyseal width | 176 | 159 | 85 | 137 | 140 |
| Maximal width of rostral trough | 250 | 243 | 120 | – | – |
| Minimal width of rostral trough | 69 | 50 | 36 | 23 | – |
| Internal width between anterior alveoli (or grinding teeth if the alveoli are resorbed) | 76 | 86 | 42 | 71 | – |
| Maximal height of corpus (measurement taken perpendicular to the ventral border of the corpus) | 198 | 129 | 74 | 177 | – |
| Height of corpus measured at the root of the ramus (measurement as above) | 144 | 109 | 74 | 119 | – |
| Rostral height measured at the symphyseal border (measurement taken perpendicular to the ventral border of the symphyseal rostrum) | 76 | 55 | 54 | 132 | 105 |
| Rostral height measured at the tip of rostrum (measurement as above) | 45 | 34 | 11 | – | – |
| Maximal mandibular height measured at the condyle perpendicular to the ventral border of the corpus | 341 | 250 | 183 | 250 | – |
| Maximal depth of ramus | 266 | 185 | 153 | 252 | – |
| Depth between gonion and coronoid processes | 277 | 210 | 155 | 231 | – |
| Height between gonion and condyle | 300 | 181 | 116 | 223 | – |
| Mid-alveolar length measured on the buccal side between the anterior alveolus (or grinding tooth if the alveolus is resorbed) and the root of the ramus | 371 | 284 | 113 | 281 | – |

low and elongated. The anterior border of the orbit is located in line with the middle or anterior part of M3 in fully adult individuals. The rounded lower infraorbital foramen is relatively large and situated just in front of the zygomatic process of the maxilla, while the upper infraorbital foramen is slit-like and located on the anteromedial side of the orbit. The orbitotemporal crest extends posteroventrally from the strongly developed postorbital process, with the ethmoidal and optic foramina occurring as small openings below the central part of the crest overlapping the sutura sphenofrontalis. The lower part of the orbitotemporal crest is located dorsal to a deep groove containing the anterior lacerate and round foramina, and forms the anterior edge of the alisphenoid, with the latter overlapping the posterior part of the maxilla. The temporal fossa is fan-shaped and bordered by a short zygomatic process of the squamosal, with the external auditory meatus visible as a small opening in the ventral part of the latter. The jugal is slender.

*Mandible*.—In dorsal view (Figs. 5A, $B_1$, D), the body of the mandible is well developed and connected by a trough-shaped symphysis, with the latter being concave dorsally and convex ventrally, and terminating in a straight anterior edge. A robust transverse ledge is developed at the narrowest portion of the symphysis in adolescents and adults, while being more poorly developed in juveniles. The ascending ramus is thin and the mandibular foramen large and triangular. In immature individuals, deciduous molars are present anterior to the mandibular foramen. In lateral view (Figs. $5B_2$, C), the body of the mandible is high and steeply descends from the anterior border of the postcanine tooth row to form the extremely flattened and elongated mandibular symphysis. Laterally, the symphysis is bordered by a well-developed crest. A large, rounded mental foramen is located close to the anterior edge of the postcanine tooth row, with a second, slit-like foramen located anterior to the first one near the narrowest part of the mandibular symphysis. The ascending ramus tilts backwards, and terminates in a blunt and rounded angular process. The coronoid process is rounded and directed dorsally, while the mandibular condyle has the shape of a transversely oriented, cylindrical bar.

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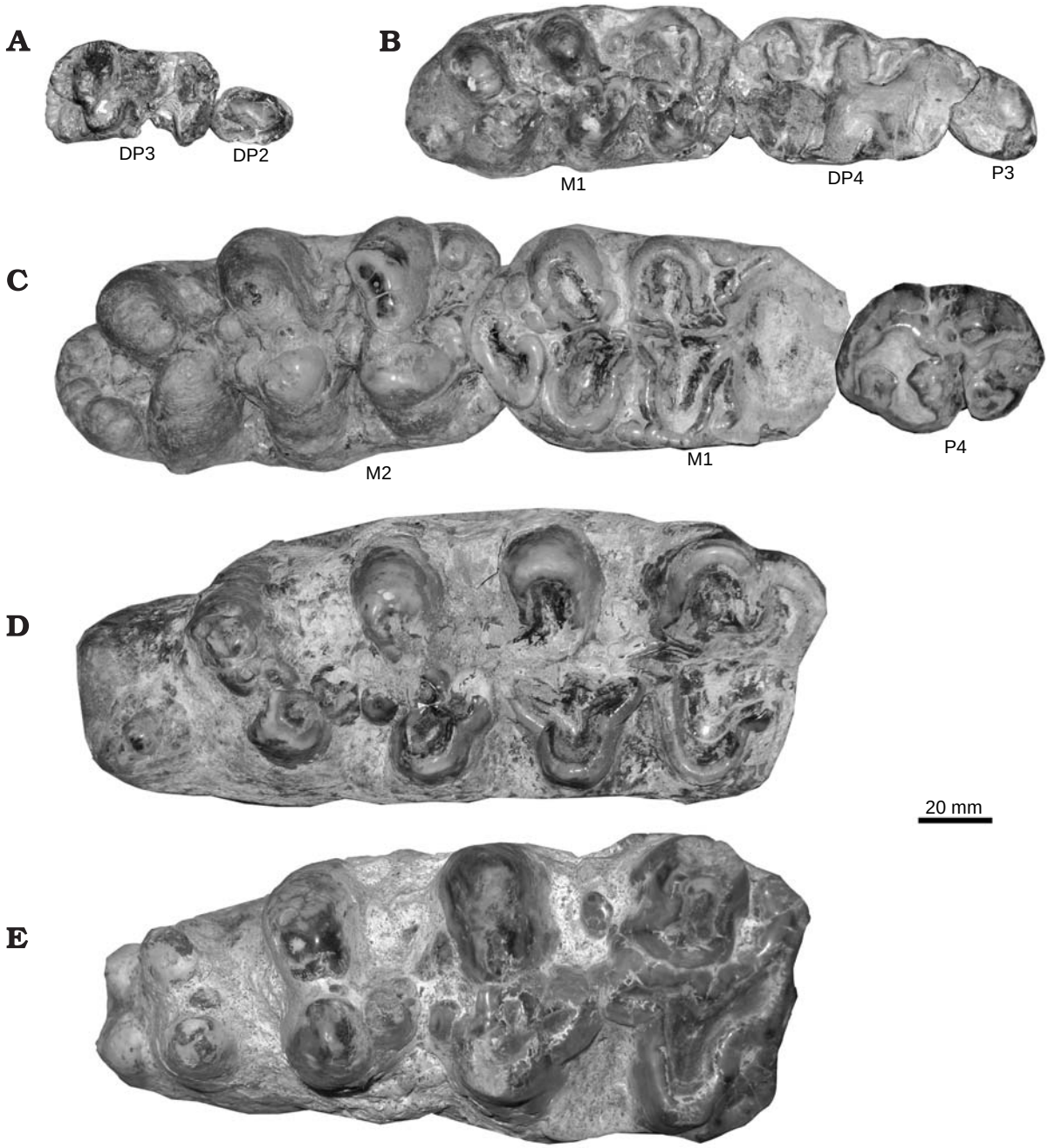



Fig. 6. Upper cheek teeth of the gomphotheriid mammal *Platybelodon grangeri* (Osborn, 1929) from localities LX200002 (A–C, E) and LX200003 (D, F), the Linxia Basin, Middle Miocene, occlusal view. **A**. Left DP2 and DP3 (HMV0050), horizontally reversed. **B**. Right P3, DP4, and M1 (HMV1812). **C**. Right P4, M1, and M2 (HMV1828). **D**. Right M3 (HMV0014). **E**. Right M3 (HMV1788).

*Incisors*.—Only specimen HMV1813 preserves DI2 (Fig. 4), which is long and slender, and covered by a layer of enamel. The distal end is blunt, and the tooth is rounded or oval in cross section. By contrast, I2 (Fig. 3A, C, D) ranges in development from slender to strongly columniform, and develops either a sharp or blunt distal end after wear. While short in females (exposed length generally < 300 mm), the tooth is long in males (exposed length generally > 300 mm), although in life it did not protrude beyond the tip of the lower tusk. Though nearly straight, the teeth point slightly ventrally and diverge laterally, allowing left and right fragments to be distinguished. There is no enamel band on the upper incisors from the Linxia Basin; however, at least one I2 from the Tunggur area (AMNH26567) preserves vestiges of enamel at the tip.

Both HMV0047 and HMV1813 preserve di2 (Fig. 5$B_1$, $B_2$), which is flattened and thin, with an upwardly concave cross section. The anterolateral corner of the distal end of this tooth is relatively rounded, while its lateral edge is serrated. Similarly, i2 (Fig. 5A, C, D) is flattened, shovel-shaped, and upwardly concave in cross section. The tooth is furthermore slightly outwardly twisted, with its medial side being perpen-

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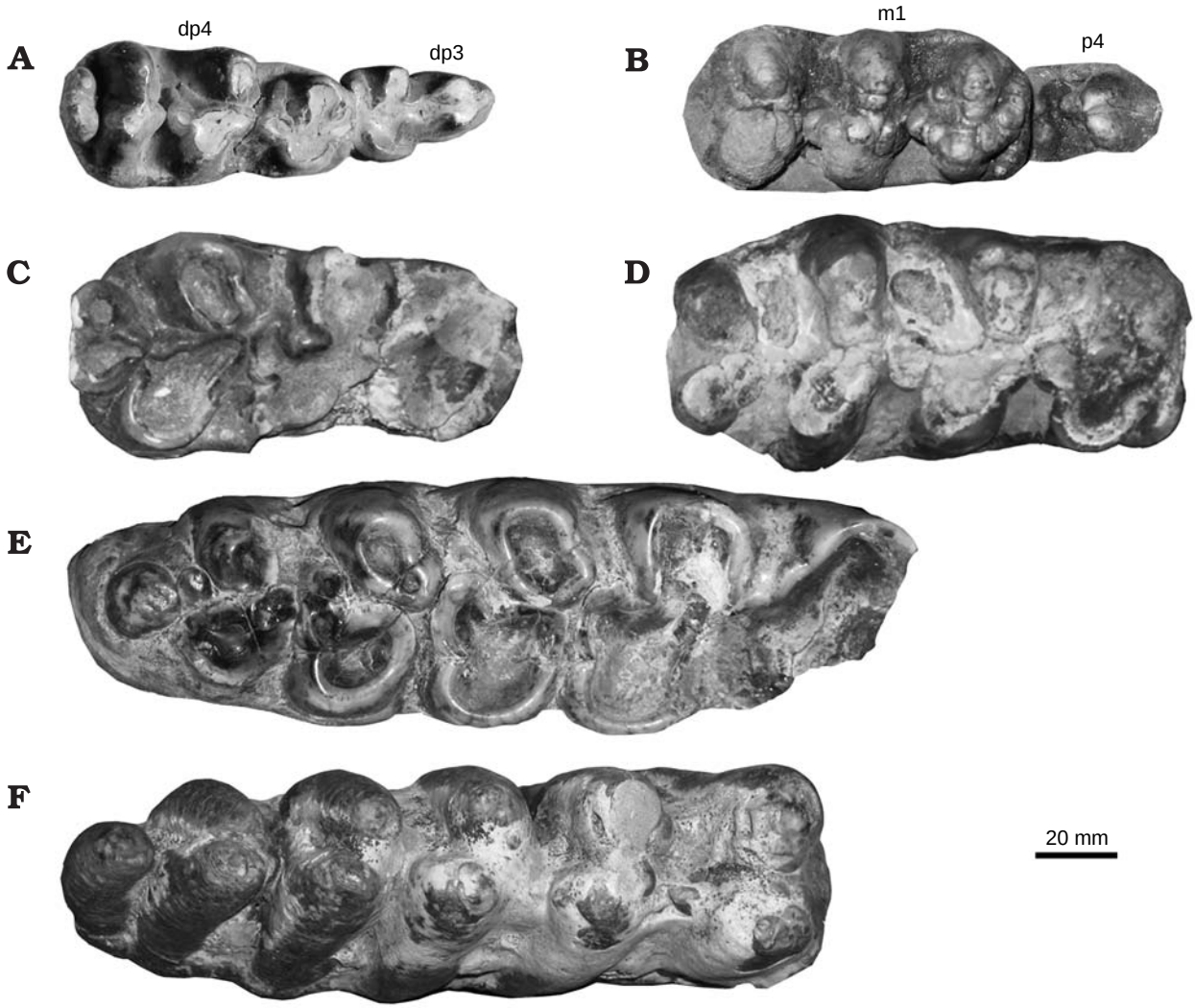



Fig. 7. Lower cheek teeth of the gomphotheriid mammal *Platybelodon grangeri* (Osborn, 1929) fromf localities LX200002 (A–C, E) and LX200003 (D, F), the Linxia Basin, Middle Miocene, occlusal view. **A**. Left dp3 and dp4 (HMV1813). **B**. Right p4 (not fully erupted) and m1 (HMV0044). **C**. Right m2 (HMV1798). **D**. Right m2 (HMV1784). **E**. Right m3 (HMV1799). **F**. Left m3 (HMV1787), horizontally reversed.

dicular to both its ventral and dorsal surfaces, and a little thicker than the rounded lateral side. In cross section, i2 is composed of multiple layers of dentinal tubules, which are enclosed in a layer of dentine. In some specimens, the tubules are strong but the number of layers is relatively low (6–7 layers), whereas in others the tubules are thin but arranged in a greater number of layers (~10 layers).

*Cheek teeth*.—DP2 (Fig. 6A) is preserved in HMV0050 and HMV1813. The tooth is oval and composed of two lophs, with the second loph being stronger. The first pretrite main cusp (protocone) is smaller and more posteriorly positioned than the posttrite one (paracone). The second pretrite (hypocone) and posttrite (metacone) main cusps are almost the same size. The anterior cingulum is more developed than the posterior one. DP3 (Fig. 6A) is moderately to strongly worn in all specimens in which it is preserved (HMV0049, HMV0050 and HMV1813). The tooth has a rectangular outline in occlusal view and is composed of two lophs, with the second loph being stronger. The wear patterns of the pretrite half-lophs are shaped like a trefoil, while the posttrite half-lophs are marked by elliptical wear surfaces oriented perpendicular to the long axis of the crown. The structure of the second loph is similar to that of the first one. Small enamel conules are developed in the interloph, and the anterior and posterior cingula are equally developed. DP4 (Fig. 6B) is rectangular and composed of three lophs oriented perpendicular to the long axis of the tooth, plus a posterior cingulum. The first pretrite trefoil is well developed, with a serrated anterior accessory central conule linked to the anterior cingulum, a simple posterior accessory central conule, and a weak mesoconelet. The first posttrite half-loph comprises a mesoconelet and a posterior accessory central conule. The second pretrite trefoil is symmetrical, with equal development of the anterior and posterior accessory central conules and a weak mesoconelet. The second posttrite half-loph is similar to the first one. The third pretrite half-loph consists of a mesoconelet and an anterior accessory central conule, with the former often shift-

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ed anteriorly to fuse with the latter. The third posttrite half-loph only has an anteriorly located mesoconelet. The posterior cingulum is composed of a row of enamel conules. Small enamel conules are also well developed in the interlophs, which are covered by a thin layer of cementum. The cingulum is developed along the anterior border of the tooth and the lingual side of the first interloph.

P3 (Fig. 6B), preserved in HMV1837 and HMV1812, is weak and oval in occlusal view. Two nearly isometric cusps form a middle loph. Weak anterior and strong posterior cingula are present and composed of a series of small conules, with the outermost two conules being the largest in both cingula. By contrast, P4 (Fig. 6C), preserved in HMV1839, HMV1815, and HMV1828, is rectangular in occlusal view and composed of two lophs. The anterior loph is a little stronger than the posterior one, and on each loph there are two main cusps. Rudimentary pretrite trefoils are present, while the posttrite half-lophs are simple. The posterior cingulum is stronger than the anterior one.

The structure of M1 (Fig. 6B, C) is similar to that of DP4, but the tooth is larger and has a better developed posterior cingulum and cementum in the interlophs, with the latter also bearing small, well-developed enamel conules. M2 (Fig. 6C) resembles DP4 and M1, but is larger, hypsodont (here defined as having an unworn crown height of more than 50 mm, almost the same as its width), and has a better developed posterior cingulum and thicker cementum in the interlophs than M1. By contrast, the development of small enamel conules in the interlophs is somewhat diminished. M3 (Fig. 6D, E) is rectangular in occlusal view and marked by a wide anterior portion. It is hypsodont and consists of 4–5.5 lophs. The first two lophs are similar to those of M2, with well-developed pretrite trefoils, posttrite half-lophs comprising mesoconelets and posterior accessory central conules, and the first anterior pretrite accessory central conule being linked to the anterior cingulum. On the third, fourth, and fifth lophs, only anterior pretrite accessory central conules are developed, and tend to diminish in size from the anterior to the more posterior lophs, or are absent altogether. The posterior posttrite half-lophs are simple, bearing only anteriorly shifted mesoconelets, but no posterior accessory central conules. The posterior cingulum is generally composed of two large cusps, of which the pretrite is the larger. There is always an anterior cingulum, and the cementum in the interlophs is strongly developed. Some small conules are present in the interlophs, but they are more weakly developed than on the more anterior teeth. The above observations are based on the specimens from Zengjia. By contrast, the posterior pretrite accessory central conules on the anterior lophs are somewhat reduced, and the cementum in the interlophs is even more developed in the specimens from Laogou.

Unlike in specimens from Tunggur (Osborn and Ganger 1931), dp2 is not preserved in any of the Linxia specimens. Only HMV0050 has an alveolus for a single root in front of dp3, implying that dp2 is only weakly developed in this group. By contrast, dp3 (Fig. 7A) is preserved in four specimens (HMV0047, HMV0048, HMV1813, and HMV0045), and is long, triangular, and composed of two lophids. Double trefoils are developed on the first lophid, with the posterior pretrite accessory central conule being distinct from the main cusp and connected to the latter via an enamel crest. The second lophid is wider than the first and the second pretrite trefoil is developed, while the posttrite half-lophid is rather simple. The anterior cingulid is relatively weak, whereas the posterior one is stronger. Compared to the corresponding upper tooth, dp4 (Fig. 7A) is narrower and longer. It is rectangular and composed of three lophids plus a posterior cingulid, with the lophids, especially the anterior two, being tilted both anteriorly and lingually. The first pretrite is trefoliate, with the anterior pretrite accessory central conule being linked to the anterior cingulid, while the posterior pretrite accessory central conule is individualized and has a tendency to invade the neighboring entoflexid. The mesoconelet is weak. The first posttrite half-lophid has a mesoconelet and weakly outlined anterior and posterior accessory central conules. The second pretrite half-lophid is also trifoliate, comprising a strong anterior and posterior pretrite accessory central conule and a weak mesoconelet. The second posttrite half-lophid has a mesoconelet and an anterior accessory central conule. The third pretrite half-lophid also has a mesoconelet and an anterior pretrite accessory central conule, with the former often shifting anteriorly to fuse with the latter. By contrast, the third posttrite half-lophid only has an anteriorly located mesoconelet. The posterior cingulid is relatively strong, with two main cusps and other smaller conules. Small enamel conules are well developed in the interlophids, and are covered by a thin layer of cementum. The cingulid is developed along the anterior border of the tooth and the buccal side of the first interlophid.

No specimens of p3 were found. There is no evidence that this tooth existed in platybelodonts from the Linxia Basin, and p3 has not been reported in *Platybelodon grangeri* from elsewhere. Only specimen HMV0044 preserves a partially erupted p4, the posterior part of which is still partially obscured by m1 (Fig. 7B). While the structure of this tooth can thus not be clearly observed, it seems to resemble specimens from Tunggur showing a double-lophed p4 with rudimentary pretrite trefoils, which is similar to P4 except for being narrower and longer. The structure of m1 (Fig. 7B) is similar to that of dp4, except for a larger and more developed posterior cingulid and cementum in the interlophids. Small enamel conules are well developed in the interlophids. Similarly, m2 (Fig. 7C, D) also resembles dp4 and m1, but is larger and more hypsodont than the latter, while the small conules in the interlophids tend to be reduced. The posterior cingulid is strong and better developed in the specimens from Laogou than those from Zengjia, and consequently a complete fourth lophid mainly tends to be present in the former. Finally, m3 (Fig. 7E, F) is long anteroposteriorly, hypsodont, and has 4.5–6.5 lophids. Generally, the pretrite half-lophids are marked by well-developed trefoils on the first three lophids, in which the mesoconelets shift anteriorly to merge with the an-

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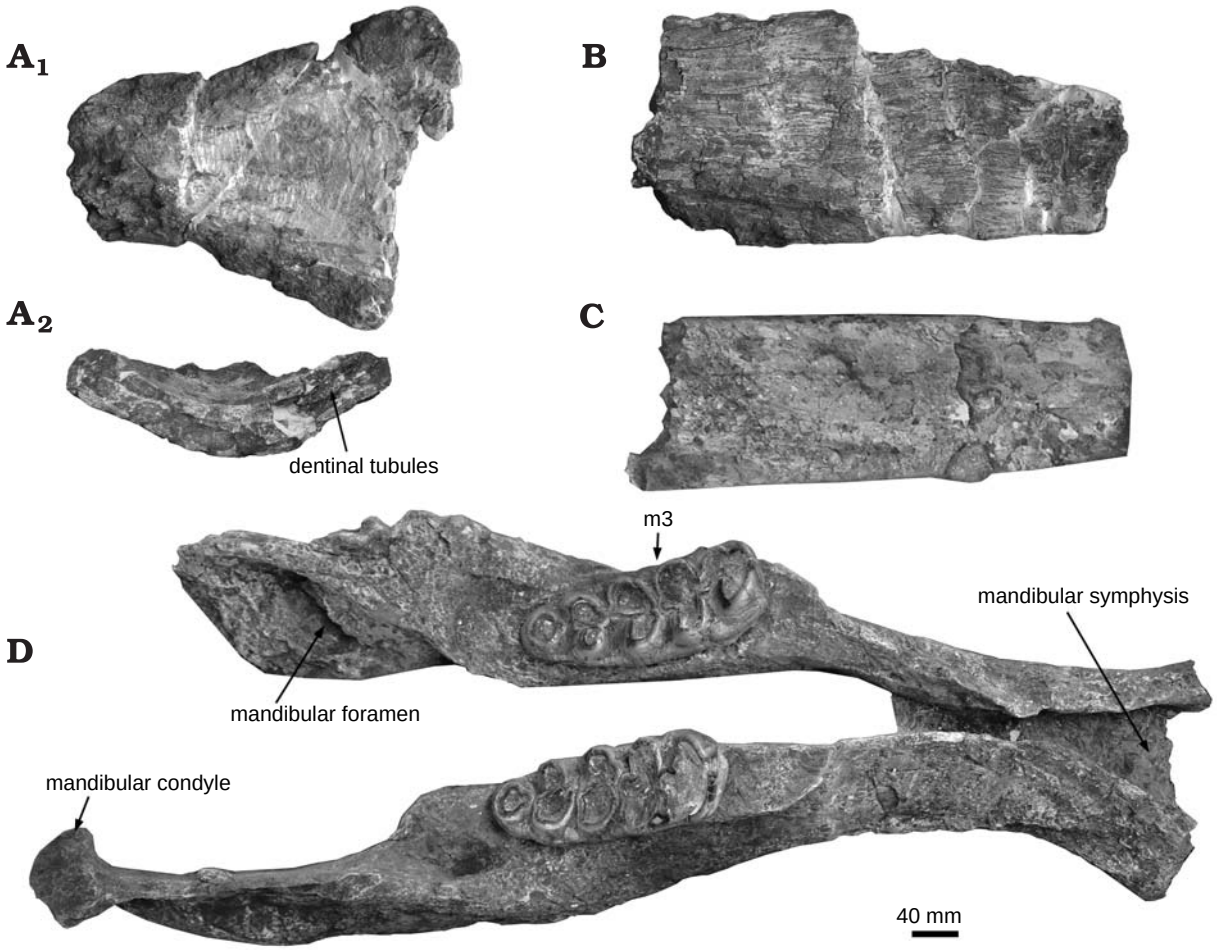



Fig. 8. Gomphotheriid mammal *Platybelodon danovi* Borissiak, 1928 from localities LX200802 (A, B) and LX200210 (C, D), the Linxia Basin, Middle Miocene. **A**. Posterior portion of mandibular symphysis (IVPP V18015), dorsal ($A_1$) and anterior ($A_2$) views. **B**. Fragmentary right lower tusk (IVPP V18015), dorsal view. **C**. Fragmentary left lower tusk (HMV1829), dorsal view. **D**. Fragmentary mandible (HMV1829), dorsal view.

terior accessory central conules, while the strong, serrated and individualized posterior accessory central conules tend to invade the neighboring entoflexid. The corresponding posttrite half-lophids have mesoconelets and anterior accessory central conules. On the posterior lophids, the mesoconelets and anterior accessory central conules of the pretrite and posttrite half-lophids can be either separated or fused, but tend to diminish in size or may even be entirely absent. The pretrite and posttrite sides of the same lophid show alternate positions. The posterior cingulid is composed of one or two large cusps, and the cingulid is generally also developed on the anterior border of the tooth. The cementum in the interlophs is strongly developed, especially in specimens from Laogou. Compared to the more anterior teeth, the development of small conules in the interlophids is weak. Specimens from Laogou are generally narrower than those from Zengjia.

*Stratigraphic and geographic range*.—Haramagai Formation, Xinjiang; Hujialiang Formation, Gansu; Zhongning area (formation not yet established), Ningxia; and Tunggur Formation, Inner Mongolia, all from the Middle Miocene of northern China (Osborn and Granger 1931, 1932; Tobien 1973; Chen 1978, 1988; Tobien et al. 1986; Ye and Jia 1986; Guan 1988, 1996; Ye et al. 1989; Wang and Qiu 2002).

## *Platybelodon danovi* Borissiak, 1928

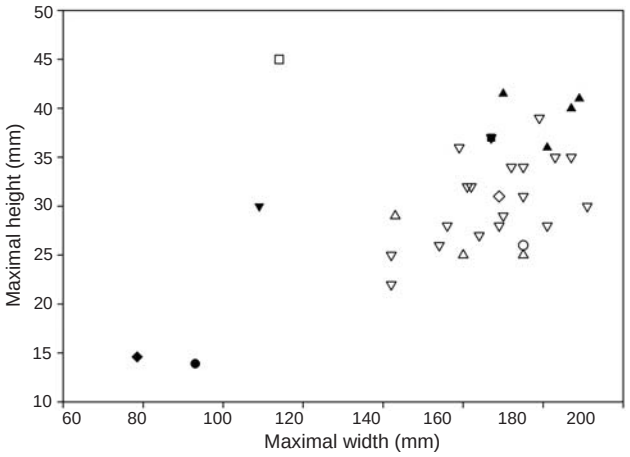
Fig. 8, Table 2.

*Referred material*.—HMV1829, a relatively complete, but not yet fully prepared mandible from Citan locality (LX200210); IVPP V18015, the posterior part of a fragmented mandibular symphysis and a fragmented right lower incisor presumably belonging to the same individual, from Ganchliang locality (LX200802).

*Diagnosis*.—See Borissiak (1929: 22).

*Description*.—IVPP V18015 (Fig. 8$A_1$, $A_2$, B): the fragmented mandibular symphysis is flattened and deeply weathered. There is no transverse ledge developed at the root of the symphysis. The fragmented i2 is flattened and relatively wide, and in cross section exhibits 3–5 layers of dentinal tubules. HMV1829 (Fig. 8C, D): the mandibular symphysis is extremely elongated and, compared to *Platybelodon grangeri*, relatively narrow. No obvious transverse ledge is developed at the root of the symphysis. The dorsal crest running along the

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- *Platybelodon dangheensis*, Danghe area
- *Platybelodon* sp., Loperot area, data from Maglio (1969)
- *Platybelodon danovi*, Caucasus area (type), data from Borissiak (1929)
- *Platybelodon danovi*, Tongxin area
- *Platybelodon danovi*, LX200802
- *Platybelodon grangeri*, Tunggur I
- *Platybelodon grangeri*, LX200002
- *Platybelodon grangeri* , LX200003
- *Platybelodon grangeri*, Tunggur II
- *Torynobelodon loomisi*, data from Barbour (1929)

Fig. 9. Bivariate plot of platybelodont lower tusk measurements.

lateral border of the symphysis is higher and sharper than in *P. grangeri* (Fig. 8D). The i2 is flattened, upwardly concave and long, but narrower than in *P. grangeri* (Fig. 8C). Its anterior edge is somewhat damaged, exposing 3–4 layers of dentinal tubules. The m3 is deeply worn and consists of 4.5 lophids (Fig. 8D), with the posterior cingulid forming a large ring of enamel. While this tooth resembles the m3 of *P. grangeri*, it is also morphologically somewhat simpler in possessing weakly developed posttrite accessory central conules, as well as in the virtual absence of small enamel conules in the interlophids.

*Stratigraphic and geographic range*.—Chokrak beds, Kuban region of the North Caucasus; Galata, Varna, Bulgaria; Araph, Turkey; Hongliugou Formation, Ningxia, and Dongxiang Formation, Gansu, both northern China. All of the localities are Middle Miocene (Borissiak 1929; Beliajeva and Gabunia 1960; Gaziry 1976; Ye and Jia 1986; Guan 1988, 1996; Ye et al. 1989; Markov 2008).

# Comparisons and discussion

The subfamily Amebelodontinae, which includes the shovel-tusked gomphotheres, contains two clades (Tassy 1986): one being characterized by concentric laminations in the lower tusk, and including the genera *Archaeobelodon*, *Protanancus*, *Amebelodon*, and *Serbelodon*; and a second one united by the occurrence of dentinal tubules in the lower tusk, and including the genera *Platybelodon* and *Torynobelodon* (Barbour 1929: fig. 2; Osborn and Granger 1931: fig. 98). In North America, the distinction between the two clades is not clear. For example, Lambert (1990) reported the subgenus *Amebelodon* (*Konobelodon*), in which incisive dentinal tubules, which he considered independent of the structures seen in *Platybelodon* and *Torynobelodon*, are enclosed in the lamination. However, in Eurasia, no lower tusk with dentinal tubules has been reported from the first clade of Amebelodontinae, suggesting that the Linxia specimens belong to the second clade including *Platybelodon* and *Torynobelodon*. Within the latter, the specimens from Linxia with their broad and flattened lower tusks clearly differ from *Torynobelodon*, which is marked by narrow and dorsally concave lower tusks (Barbour 1929; Lambert 1996; Fig. 9), and has so far only been reported from North America (Tobien 1973; Lambert 1996). By contrast, the Linxia specimens resemble *Platybelodon* in their rather broad and flattened mandibular symphysis, and lower tusks with numerous dentinal tubules.

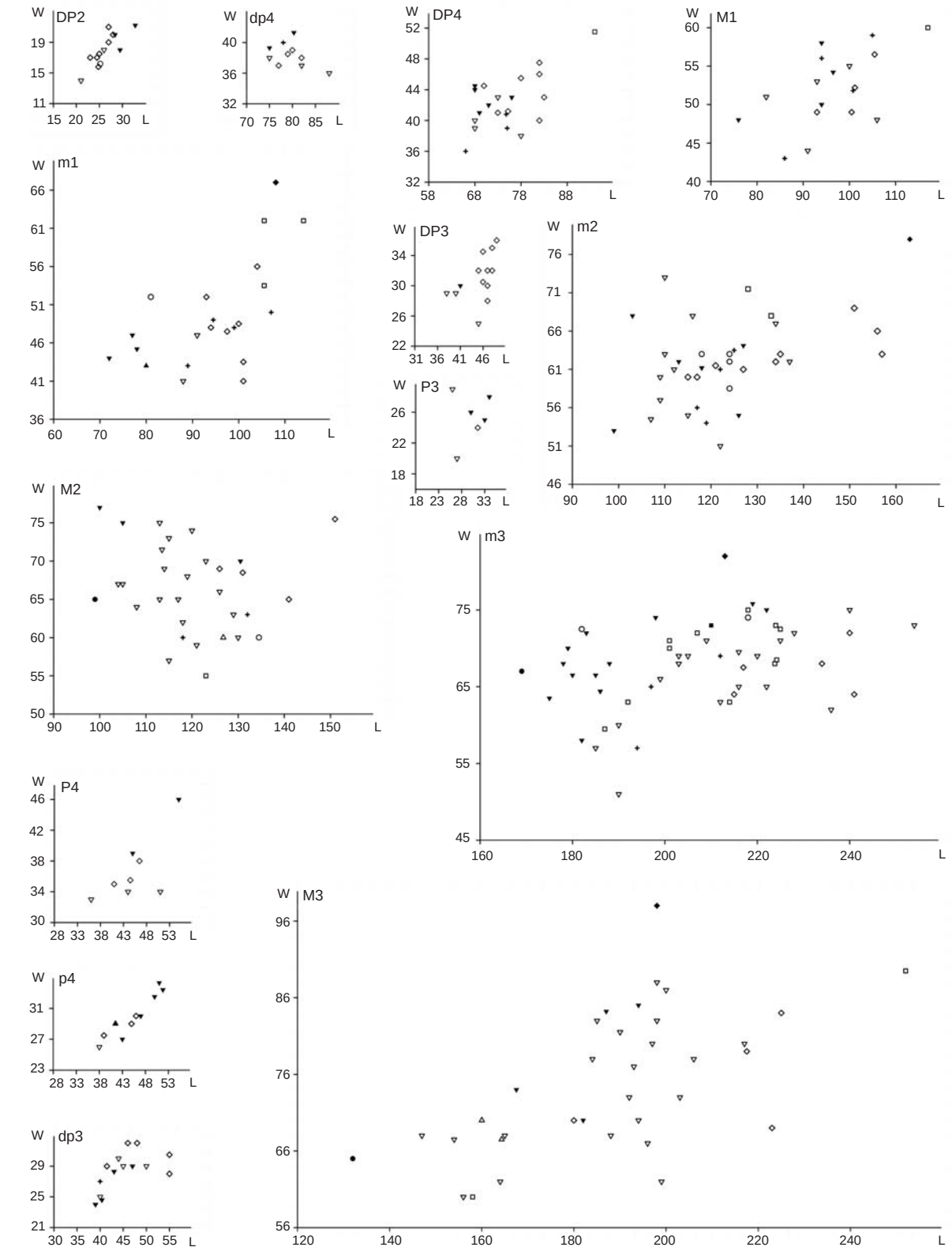
However, the fossils from Zengjia and Laogou in the Linxia Basin slightly differ from each other: compared with the material from Zengjia, the specimens from Laogou possess a relatively complete fourth lophid on m2, reduced posterior pretrite accessory central conules, a relatively larger i2, dp4, m1, M1, and m2, and a narrower M2 (Figs. 9, 10). These characters suggest the individuals from Laogou to be more derived (Ye and Jia 1986; Ye et al. 1989), and therefore possibly geologically somewhat younger. However, these differences do not exceed the range of variation observed in *Platybelodon grangeri* specimens from two horizons in the Tunggur area (discussed below in more detail). We therefore consider them to belong to the same species.

Six species of *Platybelodon* have so far been described, including *P. danovi* Borissiak, 1928; *P. grangeri* (Osborn, 1929); *P. jamandzhalgensis* Beliajeva and Gabunia, 1960; *P. beliajevae* Alexeeva, 1971; *P. tongxinensis* Chen, 1978; and *P. dangheensis* Wang and Qiu, 2004. These species are distributed mainly in the Early and Middle Miocene of Eastern Europe and Asia (except the Indian Subcontinent) (Borissiak 1929; Osborn and Granger 1931, 1932; Beliajeva and Gabunia 1960; Alexeeva 1971; Tobien 1973; Gaziry 1976; Chen 1978, 1988; Tobien et al. 1986; Ye and Jia 1986; Guan 1988, 1996; Ye et al. 1989; Wang and Qiu 2002; Markov 2008). In addition, *Platybelodon* sp. was reported from the Early Miocene of Africa by Maglio (1969), based on an isolated flattened lower incisor with dentinal tubules. *Platybelodon jamandzhalgensis* was established on the basis of a juvenile lower jaw from the same locality as *P. danovi*, leading Tobien (1973: 253) to suggest that the two taxa actually represent a single species.

*Platybelodon dangheensis* was discovered in deposits from the Early Miocene (about 20 Ma) of the Danghe area, Gansu, China (Wang and Qiu 2002), making it the oldest member of the genus. Although the species is only known from the lower jaws of a juvenile, the mandibular symphysis is fairly short and wide, and the lower tusk is thin. In addition, this species still retains p3, which is absent in later platybelodont species. These characters are obviously dis-

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▲ *Platybelodon dangheensis,* Danghe area
● *Platybelodon danovi,* Caucasus area (type), data from Borissiak (1929)
▼ *Platybelodon danovi,* Tongxin area, data from Ye and Jia (1986)
■ *Platybelodon danovi,* LX200210
○ *Platybelodon grangeri,* Tunggur I
△ *Platybelodon grangeri,* Junggar Basin, data from Chen (1988)
▽ *Platybelodon grangeri,* LX200002
+ *Platybelodon grangeri,* Zhongning area
□ *Platybelodon grangeri,* LX200003
◇ *Platybelodon grangeri,* Tunggur II
◆ *Platybelodon beliajevae,* data from Alexeeva (1971)

Fig. 10. Bivariate plots of platybelodont cheek tooth measurements (in mm). Abbreviations: L, length; W, width.

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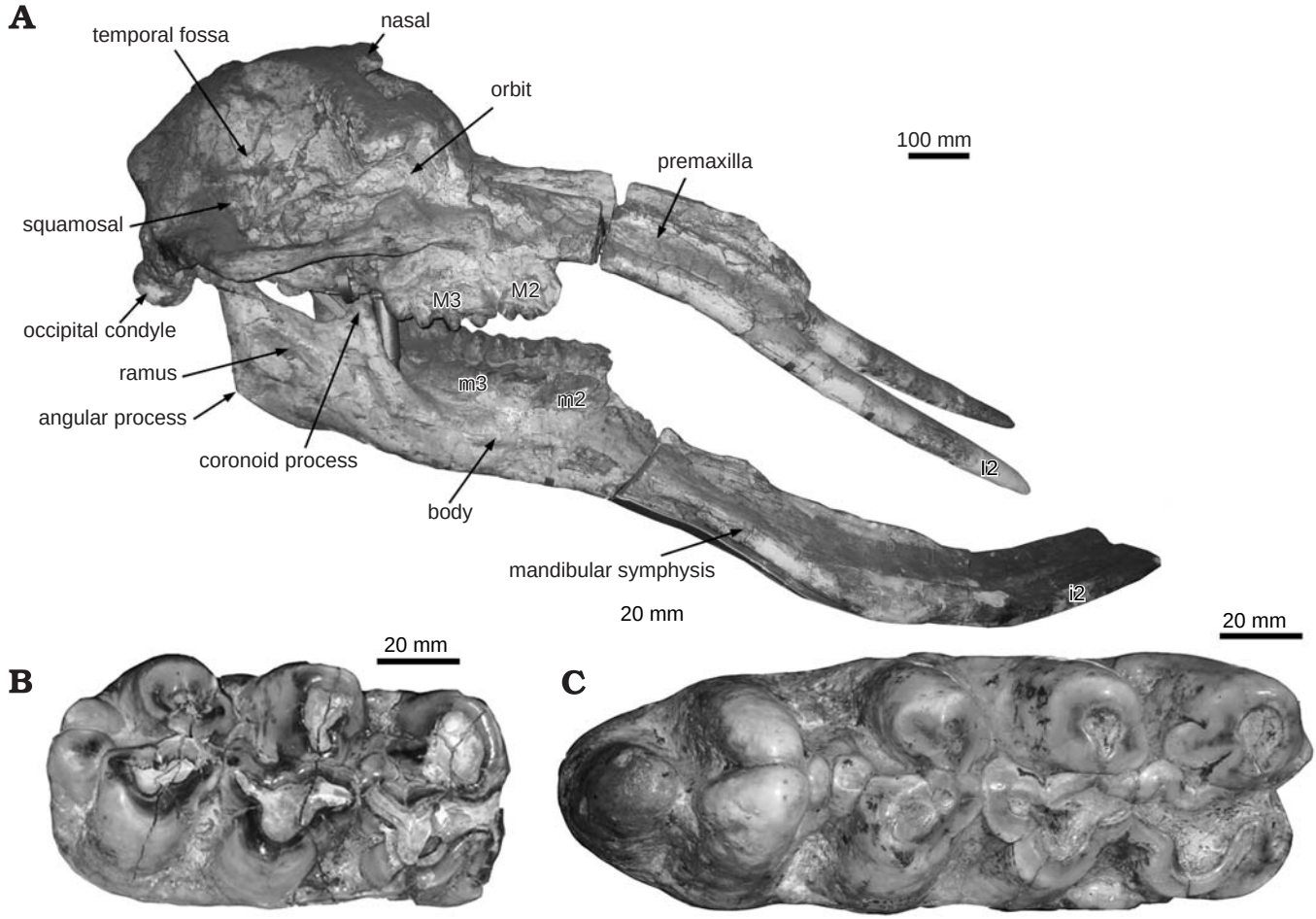



Fig. 11. Gomphotheriid mammal *Platybelodon danovi* Borissiak, 1928 from the Tongxin area, Middle Miocene. **A**. Adult male skull and associated mandible (BPV2000), lateral view. **B**. Left m2 (IVPP V8039), occlusal view (horizontally reversed). **C**. Right m3 (IVPP V5572), occlusal view.

tinct from other species including the Linxia specimens, with the latter further differing from *P. dangheensis* in their relatively smaller p4 and relatively larger m1 (Fig. 10). The only material of *Platybelodon* sp. from the Early Miocene (about 17 Ma) of the Loperot area, eastern Africa, is fragmentary and consists of a thin and narrow lower tusk composed of 3–4 layers of dentinal tubules (Maglio 1969: figs. 1, 2). The latter is smaller than the specimens from Linxia in all dimensions (Fig. 9), and hence likely to belong to a different taxon.

*Platybelodon danovi* is the type species of the genus and was first described by Borissiak (1929: pls. 3, 4) from the Chokrak Beds of the Kuban region of the Caucasus. Further finds were reported from the localities of Araph in Western Asia, and Galata, Varna, in Eastern Europe (Gaziry 1976; Markov 2008). Later, Ye and Jia (1986: pls. 1, 2) and Ye et al. (1989: figs. 1–5, pls. 1, I2) described *P. tongxinensis* from the Tongxin area, China. However, *P. tongxinensis* was subsequently reassigned to *P. danovi* (Qiu et al. 1999). Most of the specimens from Linxia differ from *Platybelodon danovi* in: a lesser degree of skull arching; the anterior border of the orbit being located behind the anterior edge of M3 in adult individuals (as opposed to being aligned with the boundary of M2 and M3 in *P. danovi*); a shorter zygomatic process of the squamosal; the larger size of the dorsal portion of the premaxilla attaching to the maxillo-labialis, possibly implying a better developed trunk; a smaller and straighter upper incisive alveolus and I2, which may be related to a rapidly developing nose partially replacing functions of the upper incisors (see below) (Figs. 3, 4, 11A); a robust transverse ledge located at the narrowest portion of the symphysis in adult individuals, which is only weakly developed in *P. danovi* from Tongxin, and altogether absent in the type specimen from the Caucasus; and a more posteriorly directed ascending ramus of the mandible (Figs. 5, 11A). In addition, the molars of the specimens from Linxia are more hypsodont, have thicker cementum in the interlophs, more complete fourth loph(id)s on M2 and m2, and a larger number of loph(id)s on M3 and m3 (Figs. 6, 7, 11B, C). All of the molars (except m2) and deciduous fourth premolars from Linxia are longer and narrower than those of *P. danovi*, with the difference being particularly marked in m3, while exactly the opposite is true for the premolars (Fig. 10). Both the increase in the size of the molars and the decrease in the size of the premolars indicate that the cheek teeth of the specimens from Linxia are more derived than those of *P. danovi*, as the loss of premolars is a common phenomenon in proboscideans (Tassy 1996a). Finally, the

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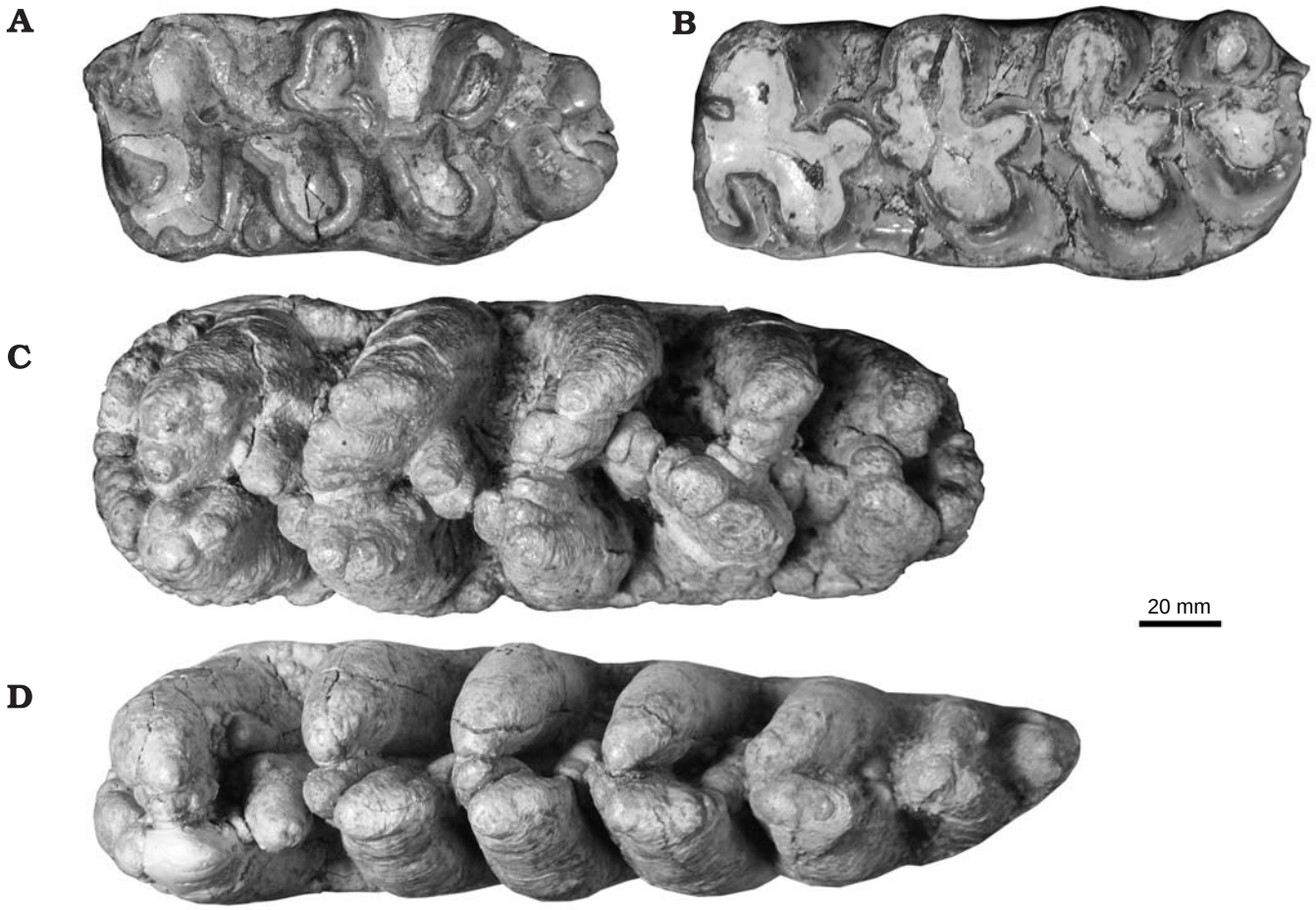



Fig. 12. Cheek teeth of the gomphotheriid mammal *Platybelodon grangeri* (Osborn, 1929) from Tunggur II, Middle Miocene, occlusal view. **A**. Left M2 (AM26479). **B**. Left m2 (AM26574). **C**. Right M3 (AM26473), horizontally reversed. **D**. Left m3 (AM26475).

specimens from Linxia have a smaller DP2 that found in *P. danovi* (Fig. 10).

*Platybelodon grangeri* is a well-known species first discovered by the Central Asiatic Expedition (CAE) in Tairum Nor, Tunggur area (in this paper, we use Tunggur I to denote this locality), Inner Mongolia. While Osborn (1929) originally assigned the name *Amebelodon grangeri* to these specimens, Osborn and Granger (1931: fig. 1) subsequently transferred the species to the genus *Platybelodon*, comparing it with *P. danovi*. The type of *P. grangeri* comprises the lower jaws of an adult lacking the cheek teeth. In 1930, CAE discovered two further localities in the Tunggur area (*Platybelodon* Quarry and Wolf Camp Quarry, here denoted as Tunggur II), which yielded a series of well-preserved fossils assigned to *P. grangeri* by Osborn and Granger (1932: figs. 1–7). The material from Linxia shares with *P. grangeri* from Tunggur the following diagnostic synapomorphies to the exclusion of other species of *Platybelodon*: (i) a strong transverse ledge developed at the narrowest part of the mandibular symphysis; and (ii) relatively narrow, elongate and hypsodont molars with strong cementum in the interlophs. Based on these features, we refer the specimens from Linxia to *P. grangeri*.

Interestingly, later work (Wang et al. 2003; Deng et al. 2007) showed Tunggur II (belonging to the upper Tunggurian Stage, Chinese NMU7) to be younger than Tunggur I (belonging to the lower Tunggurian Stage, Chinese NMU6) (Qiu et al. 1999). The fossil platybelodonts from Tunggur I and II also show some differences, with the specimens from Linxia in many regards seemingly representing a morphological intermediate. Thus, while the molars from Linxia are larger than those from Tunggur I, they are smaller than those from Tunggur II (Fig. 10). Similarly, the fourth loph(id)s on m2 and M2, hypsodonty, and the cementum in the interlophs are all better developed in the material from Linxia than in the specimens from Tunggur I, but less so than in those from Tunggur II. Furthermore, the fossils from Tunggur II differ from the specimens from both Tunggur I and Linxia in having strongly developed posterior cingulids forming complete fourth loph(id)s on m2 and M2, and, in some cases, even the development of a fourth pretrite trefoil (Fig. 12A, B). Finally, the posterior pretrite accessory central conules on M3 and the anterior posttrite accessory central conules on m3 are secondarily diminished in the Tunggur II specimens (Fig. 12C, D), while dp3 is almost rectangular in occlusal view, rather than triangular as in the material from Linxia.

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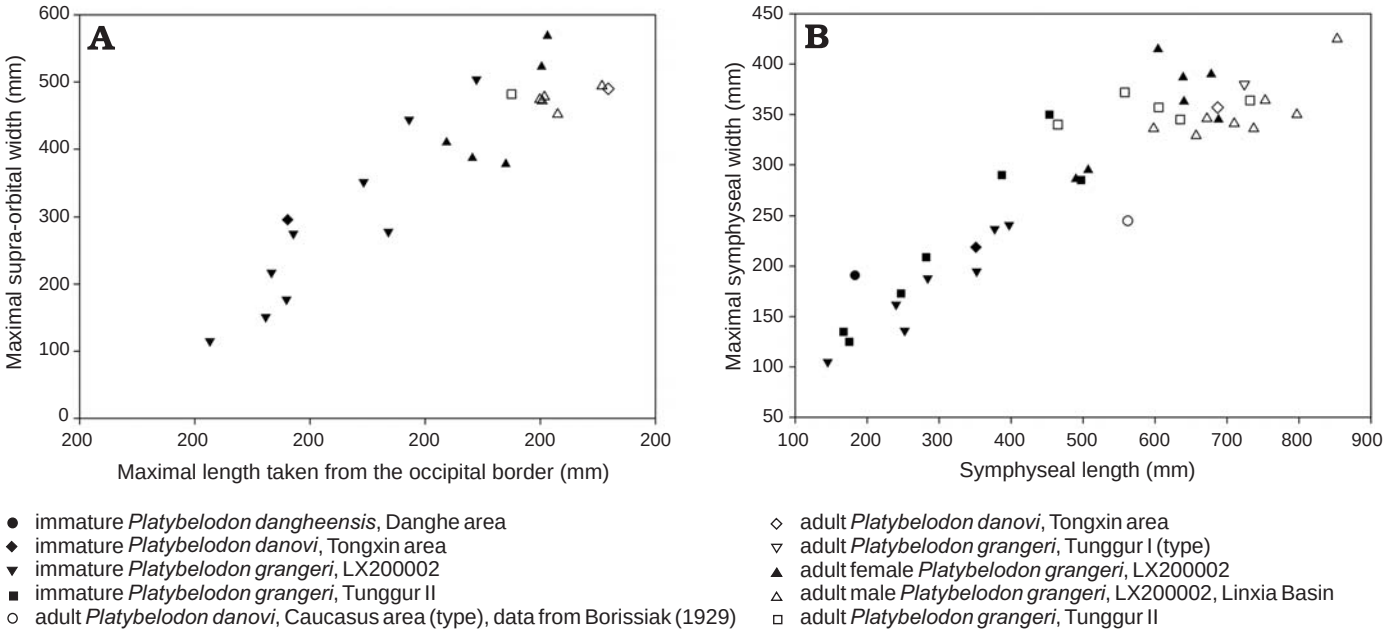



Fig. 13. Bivariate plots of platybelodont cranial and mandibular measurements. Skull (**A**) and mandible (**B**).

In terms of size, the platybelodont crania and mandibles from Tunggur I and II are comparable to those from Linxia (Fig. 13). In addition, male skulls from Tunggur (AMNH 26480) have a relatively shorter dorsal part of the neurocranium than female ones (AMNH26462), as also observed in the specimens from Linxia. Based on their broad and short mandibular symphyses, Wang and Qiu (2002) proposed that *Platybelodon dangheensis* and *P. grangeri* may form a clade to the exclusion of *P. danovi*, which in turn is characterized by a long and narrow symphysis. However, both mandibular types have been found not only in the Linxia Basin, but also in the Tunggur area, with immature individuals displaying an intermediate state. The mandibular symphysis in platybelodonts from Tunggur is on average a little wider, but does not significantly differ from that found in specimens from Linxia (Fig. 13B). The two types of mandible may therefore represent sexual, rather than interspecific, differences.

Chen (1988: pls. 2–4) reported specimens of *Platybelodon* sp. from the northern Junggar Basin, and interpreted them to represent an intermediate evolutionary stage between the material from Tongxin and Tunggur, based on their smaller size, a smaller number of lophs on M3, a weaker fourth loph on M2, and weaker development of posttrite accessory central conules relative to *P. grangeri* from Tunggur (Chen 1988). The size of these specimens falls within in the range of variation of the Zengjia specimens (Fig. 10). Chen (1978: pls. 1, 2) also reported *P. grangeri* from the Zhongning area. The molars of these fossils resemble those from Laogou, but are generally somewhat smaller (Fig. 10). Furthermore, Alexeeva (1971: pls. 1–3) reported several platybelodont molars from Oshi, Western Mongolia, and assigned them to the new species *P. beliajevae*. While this new taxon requires further study owing to the small amount of material referred to it, the teeth themselves are fairly large, with a length-width ratio similar to those from Tongxin, and hence rather different from *P. grangeri* (Fig. 10).

Apart from the specimens recovered from Zengjia and Laogou, two further platybelodont mandibles were found at localities LX200210 and LX200802 in the Linxia Basin, which belong to the lower Middle Miocene Dongxiang Formation. Although the specimens from LX200210 have not yet been fully prepared, preliminary observations show that these platybelodonts had long, narrow, and thin lower incisors, as well as a deeply worn M3 falling within the size range of *Platybelodon danovi* (Fig. 10). The specimens from LX200802 are very fragmented, and only a wide and thin right i2 and the posterior portion of a mandibular symphysis lacking the transverse ledge typical of *P. grangeri* are preserved. Based on these observations, we refer these specimens to *P. danovi*.

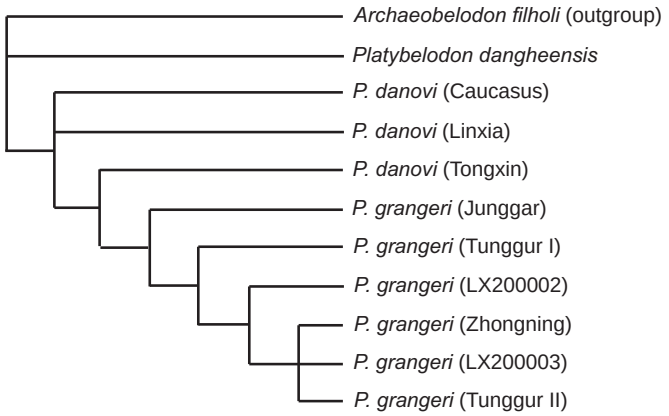



Fig. 14. Strict consensus of the nine most parsimonious trees recovered in the cladistic analysis of the genus *Platybelodon*, based on the data matrix provided in Appendix 1.

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**Evolutionary sequence**.—We performed a cladistic analysis in order to test the systematic affinities of the material from Linxia, and explore the evolutionary interrelationships of the Eurasian occurrences of *Platybelodon*. The strict consensus (Fig. 14) of the nine most parsimonious trees recovered in the cladistic analysis is relatively well resolved. Our results suggest that *P. danovi* may be paraphyletic, while supporting the notion of a monophyletic *P. grangeri*, as well as our assignment of the Linxia material to this species. Based on these results, we propose the following set of potential evolutionary trends for this genus: enlargement of the trunk; reduction of the upper incisor; posterior orientation of the ascending ramus; development of a transverse ledge on the narrowest part of the mandibular symphysis; increase in the number of layers of dentinal tubules in the lower tusk; reduction of the premolars, DP2, and dp2; molars becoming enlarged, narrower and more hypsodont; increase in the number of loph(id)s on the last molars; development of fourth loph(id)s on the second molars; and increase in the number of small conules and stronger development of cementum in the interlophs.

**Functional adaptations**.—According to Lambert (1992) there is currently no evidence that the platybelodont lower tusk was employed in either the aquatic or the terrestrial substrate. However, it is possible that some of the morphological modifications of *Platybelodon* may represent functional adaptations to a specific environment. In the Linxia Basin, the Hujialiang Formation consists of a set of fluvial strata composed of grayish-yellow conglomerates and sandstone (Deng 2004a), suggesting that *Platybelodon* might have lived near rivers or swamps, as earlier suggested by Borissiak (1929). This interpretation is further supported by the occurrence of several other (mostly brachyodont) fossils occurring in the same strata, including *Alloptox* sp., *Pliopithecus* sp., *Hemicyon teilhardi*, *Amphicyon tairumensis*, *Percrocuta tungurensis*, *Gomphotherium wimani*, *Zygolophodon* sp., *Anchitherium gobiense*, *Alicornops laogouense*, *Hispanotherium matritense*, *Kubanochoerus gigas*, *Listriodon mongoliensis*, *Palaeotragus tungurensis*, and *Turcocerus* sp. (Deng 2004a), implying a warm and humid environment.

In proboscideans possessing both upper and lower tusks, the upper and lower incisors are usually oriented in roughly parallel or somewhat convergent directions, with the upper incisors generally directed downwards. This implies that the upper and lower tusks may have been employed against each other during foraging. By contrast, those proboscideans lacking lower tusks (mostly derived taxa, including extant elephants) always possess upper incisors which are straight or curved upwards, and it is possible that an enlarged nose partially replaced the functions of ventrally pointing upper tusks in those taxa. With the aid of an enlarged trunk, the elongated mandibular symphysis and the shovel-like lower tusk may have assisted *Platybelodon* in the harvest of marshy weeds, while the posteriorly tilted ramus and the robust transverse ledge on the mandibular symphysis ensured mechanical stability of the lower jaws. Furthermore, the multi-loph(id)ed, hypsodont molars with numerous small enamel conules and strong cementum may have helped to grind food containing small sediment particles (Borissiak 1929). Thus, *Platybelodon* was well adapted to marshy environments, and by the late Middle Miocene was widespread throughout eastern Asia. However, at the end of the Middle Miocene, the genus went extinct in Eurasia, possibly owing to environmental changes and competition from "true" elephantids. By contrast, *Torynobelodon*, a likely descendant of *Platybelodon*, moved into North America, where it survived until the Late Miocene (Tassy 1986).

# Conclusions

In the present article, we describe the fossil remains of platybelodonts from the Linxia Basin of China. The animals were discovered in the upper Middle Miocene Hujialiang Fomation and the lower Middle Miocene Dongxiang Formation, respectively. While the former yielded abundant specimens that we attribute to the derived *Platybelodon grangeri*, the latter yielded only two specimens referable to the more ancestral *P. danovi*. These fossils provide a great deal of information important not only in the exploration of the phylogenetic relationships of *Platybelodon*, as we do in this article, but also to our understanding of sexual dimorphism and the patterns of ontogenetic development of these animals. Thus, for example, the nasal bones are more posteriorly positioned in males than in females, thus implying a more progressed trunk in males, and indicating that nose evolution was asynchronous. In addition, immature individuals resemble females in their morphology, thus further suggesting an asynchronous growth pattern in the two sexes. These interesting topics will be studied in more depth as part of future research.

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# Appendix 1

Cladistic data matrix of 24 characters scored for 11 platybelodont taxa in the ingroup and the outgroup *Archaeobelodon filholi*. A question mark in the matrix indicates that the character state is unknown.

Taxa and sources of data:

A, *Archaeobelodon filholi*, data from Tobien, 1973;
B, *Platybelodon dangheensis*, data from IVPP V13322;
C, *Platybelodon danovi* (Caucasus), data from Borissiak, 1929;
D, *Platybelodon danovi* (Linxia), data from IVPP V18015 and HMV1829;
E, *Platybelodon danovi* (Tongxin) data partly from BPV2000, HMV1838, and 1825, partly from Ye and Jia 1986;
F, *Platybelodon grangeri* (Junggar), data from Chen, 1988;
G, *Platybelodon grangeri* (Tunggur I), data from AMNH26200-5;
H, *Platybelodon grangeri* (LX200002), data from HMV0014–27, 0029–50, 0939, 0940, 1266–1269, 1272, 1275, 1798–801, 1812, 1813, 1815, 1828, 1830, 1836, 1837, 1839–42 , 1862, and 1863;
I, *Platybelodon grangeri* (Zhongning) data from IVPP V5573–8;
J, *Platybelodon grangeri* (LX200003), data from HMV1263, 1270, 1274, 1783–90, 1792–7, 1802–4, 1845–7, 1852, and 1859;
K, *Platybelodon grangeri* (Tunggur II), data from AMNH26462, 26465, 26469–75, 26477–82, 26488, 26490, 26497, 26498, 26500, 26560–8, 26570, 26572, 26575, 98696, 98697, and 98699.

| Characters | Taxa | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | C | D | E | F | G | H | I | J | K |
| 1 | 0 | ? | ? | ? | 0 | ? | ? | 1 | ? | ? | 1 |
| 2 | 0 | ? | 1 | ? | 1 | ? | 1 | 2 | ? | 2 | 2 |
| 3 | 0 | ? | 1 | ? | 1 | ? | 1 | 1 | ? | 1 | 1 |
| 4 | 0 | ? | 1 | ? | 1 | ? | ? | 2 | ? | ? | 2 |
| 5 | 0 | ? | 1 | ? | 1 | ? | ? | 2 | ? | ? | 2 |
| 6 | 0 | ? | ? | ? | 1 | ? | ? | 2 | ? | ? | 2 |
| 7 | 0 | ? | ? | ? | 0 | ? | ? | 1 | ? | ? | 1 |
| 8 | 0 | ? | 1 | 1 | 1 | ? | 2 | 2 | ? | ? | 2 |
| 9 | 0 | 2 | 1 | 1 | 1 | ? | 2 | 2 | ? | ? | 2 |
| 10 | 0 | 0 | 0 | 0 | 1 | ? | 2 | 2 | ? | 2 | 2 |
| 11 | 0 | 1 | 1 | 1 | 1 | ? | 1 | 1 | ? | ? | 1 |
| 12 | 0 | 1 | ? | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 13 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14 | ? | ? | ? | ? | 0 | ? | 1 | 1 | ? | ? | 1 |
| 15 | ? | ? | ? | ? | 0 | ? | ? | 0 | ? | ? | 1 |
| 16 | ? | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 17 | ? | 0 | ? | ? | 0 | ? | ? | 1 | ? | ? | 1 |
| 18 | ? | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 |
| 19 | 0 | ? | 0 | ? | 0 | 0 | 1 | 1 | 2 | 2 | 3 |
| 20 | 0 | ? | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 |
| 21 | 1 | 0 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 |
| 22 | 0 | ? | 0 | ? | 0 | 0 | 0 | 0 | ? | 1 | 2 |
| 23 | 0 | 0 | 0 | 0 | 1 | ? | 2 | 2 | 2 | 2 | 2 |
| 24 | 0 | 0 | ? | 0 | 0 | 1 | 1 | 1 | 2 | 2 | 2 |

Characters are defined as follows:

1. Development of the dorsal part of the premaxilla: weak (0); strong (1);
2. Upper incisive alveolus and tusk: strong and exceeding the lower tusk (0); strong (1); weak (2);
3. Enamel bands on the upper tusk: present (0); absent (1);
4. Dorsal table of the neurocranium in males: long (0); intermediate (1); short (2);
5. Position of the anterior border of the orbits: anterior to the M2–M3 boundary (0); at the M2–M3 boundary (1); posterior to the M2– M3 boundary (2);
6. Temporal fossa: long (0); intermediate (1); short (2);
7. Cranium: arched (0); low (1);
8. Ramus: vertical (0); slightly tilted posteriorly (1); strongly tilted posteriorly (2);
9. Shape of the mandibular symphysis: high and narrow (0); intermediate (1); low and wide (2);
10. Transverse ledge on the mandibular symphysis: absent (0); weakly developed (1); strong (2);
11. Anterior border of the mandibular symphysis: pointed anteriorly (0); straight (1);
12. Inner structure of the lower tusk: laminated (0); consists of one or more layer(s) of dentinal tubules (1);
13. Cross-section of the lower tusk: relatively rounded (0); flattened (1);
14. DP2 and dp2: large (0); small (1);
15. DP3 and dp3: small (0); large (1);
16. p3: present (0); absent (1);
17. P3, P4, and p4: large (0); small (1);
18. Width of the molars, DP4, and dp4: wide (0); medium (1); narrow (2);
19. Fourth loph(id)s on M2 and m2: weak (0); strong (1); complete (2); pretrite trefoils present (3);
20. Loph(id)s on M3 and m3: few (0); medium (1); numerous (2);
21. Secondary trefoils on the molars, DP4, and dp4: absent (0); weakly developed (1); strong (2);
22. Posterior accessory central conules of the pretrite trefoils on the upper molars and DP4: present (0); weakly developed (1); absent (2);
23. Alternating positions of the half-lophids of the lower molars and dp4: absent (0); weak (1); strong (2);
24. Development of cement and small enamel cones: weak (0); medium (1); strong (2).

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