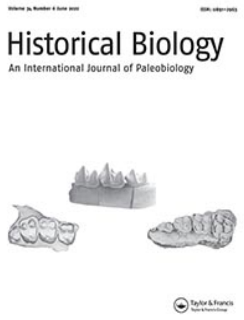

Historical Biology

An International Journal of Paleobiology

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/ghbi20

Discovery of a primitive *Gomphotherium* from the Early Miocene of northern China and its biochronology and palaeobiogeography significance

Chunxiao Li, Shi-Qi Wang & Qing Yang

To cite this article: Chunxiao Li, Shi-Qi Wang & Qing Yang (2022): Discovery of a primitive *Gomphotherium* from the Early Miocene of northern China and its biochronology and palaeobiogeography significance, Historical Biology, DOI: 10.1080/08912963.2022.2077106

To link to this article: https://doi.org/10.1080/08912963.2022.2077106

HISTORICAL BIOLOGY
https://doi.org/10.1080/08912963.2022.2077106

Taylor & Francis
Taylor & Francis Group

Discovery of a primitive *Gomphotherium* from the Early Miocene of northern China and its biochronology and palaeobiogeography significance

Chunxiao Li[a,b,c], Shi-Qi Wang[a,b] and Qing Yang[d]

[a]Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; [b]CAS Center for Excellence in Life and Paleoenvironment, Beijing, China; [c]College of Earth and Planetary Sciences, University of Chinese Academy of Sciences, Beijing, China; [d]Ningxia Geological Museum, Yinchuan, China

ABSTRACT

Gomphotheres are age-informative mammals that had widespread distribution during the Neogene. In this paper, we report new fossil *Gomphotherium* remains from the Early Miocene of Tongxin County, North China. The new material is similar to *Gomphotherium cooperi* in cheek tooth morphology and can be assigned to the same species. *Gomphotherium cooperi*, was previously reported only from Dera Bugti, the Early Miocene of South Asia. According to the research of relevant stratigraphic correlation and biostratigraphy, we estimated the age of the lower layer of the Zhangenbao Formation, where the new fossil was recovered, is approximately between 18 and 19 Ma. The occurrence of a similar Early Miocene proboscidean assemblage in both China and South Asia is further evidence that mammal dispersal between the two regions may have existed at that time. It also suggests that the Tibetan plateau was not high enough to block exchange among large animals like proboscideans. This work reveals the distribution and dispersal of *Gomphotherium* between South Asia and China through the Tibetan region during the Early Miocene and provides important biochronology and palaeobiogeography significance.

ARTICLE HISTORY
Received 7 December 2021
Accepted 8 May 2022

KEYWORDS
Gomphotherium; Early Miocene; North China; dispersal; biochronology

Introduction

Studies of *Gomphotherium* were established by the early work of Burmeister (1837). Osborn (1936) proposed to name it 'Bunomastodontidae Osborn, 1921', which belongs to the superfamily Mastodontoidea. Whereas, Simpson (1945) amended the old classification of proboscideans and revised the name to Gomphotheriidae Hay, 1922, which is followed by other scholars such as Shoshani and Tassy (1996, 2005). The stem elephantoid genus *Gomphotherium* has been found in Africa, Europe, Indian Subcontinent, the other part of Asia, North and Central Americas (Osborn 1932; Sanders et al. 2004; Aguilar and Laurito 2011; Wang et al. 2017).

Gomphotherium possibly originated from the Late Oligocene or the earliest Miocene of Africa (Kappelman et al. 2003; Sanders et al. 2004; Chen 2021). The evolution rate of *Gomphotherium* was very fast, and its diversity peaked during the Early–Middle Miocene, but after that, its diversity and abundance decreased (Wang et al. 2019). It was not until the Pliocene that *Gomphotherium* went extinct (Lambert and Shoshani 1998).

At ~19 Ma, *Gomphotherium* reached Eurasia on a large scale (Tassy 1990). In Europe and West Asia, *Gomphotherium* is represented by *G. sylvaticum, G. angustidens, G. subtapiroideum*, and *G. steinheimense* (Göhlich 1999). In South and Southeast Asia, Osborn (1932) reported two species *G. cooperi* and *G. browni*. Records of *Gomphotheirum* include *G. inopinatum, G. mongoliense*, and *G. tassyi* (Wang et al. 2017) show this group has ever existed in East and Central Asia. Research indicates *Gomphotherium* did not reach North America until ~16 Ma (Lambert 1996). Several species have been reported and were usually attributed to one species, *G. productum* (Lambert and Shoshani 1998). Very limited *Gomphotherium* material has been recovered and reported from Central America. An exceptional case is the fossil of *G. hondurensis* from the late Miocene (Aguilar and Laurito 2011), which clearly indicate that *Gomphotherium* had reached North and Central Americas.

In this paper, we report recently discovered *Gomphotherium* remains from Miaoerling sites of the Zhangenbao Formation, Tongxin County, northwestern China (Figure 1). The new fossil materials are similar to the holotype of *G. cooperi* in cheek tooth morphology and can be readily assigned to the same species. The new material is of importance in understanding the early evolution and migration of *Gomphotherium* in East Asia.

Materials and methods

The material of *Gomphotherium cooperi* described in this paper is housed in the IVPP. New materials include a complete left lower tusk and an incomplete maxillary with P4s, M1s, and M2s. The comparative materials were from previous publications (Forster-Cooper 1922; Osborn 1932). The molar measurements and terminology followed Tassy (2014) (Figure 2). Measurements were taken with digital calipers (in mm).

Abbreviations **–** **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. **NHMUK**, Natural History Museum, London. **P** & **M**, upper premolar and molar; **p** & **m**, lower premolar and molar.

Geological setting

The Tongxin Basin in the Ningxia Hui Autonomous Region, is one of the most significant Miocene fossil-rich region in China, due to its abundant and varied fossil remains. This region has been

CONTACT Shi-Qi Wang ✉ wangshiqi@ivpp.ac.cn Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; CAS Center for Excellence in Life and Paleoenvironment, Beijing 100044, China

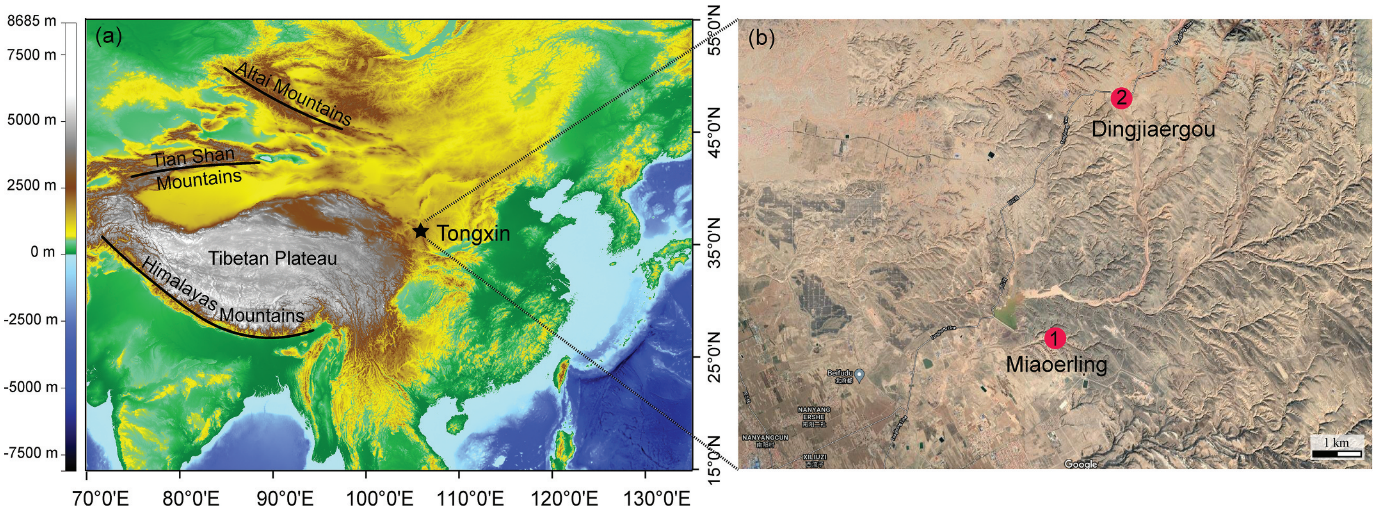

Figure 1. Geographic information of localities bearing *Gomphotherium* in China. (a) Geomorphology of East Asia. The black star denotes the location of Tongxin county. The image was generated by GEBCO (https://www.gebco.net/). (b) Fossil localities yielding *Gomphotherium cooperi* from Tongxin (Google Earth image). Number 1 in the red circle indicates the Miaoerling sites. Number 2 in the red circle indicates the Dingjiaergou sites .

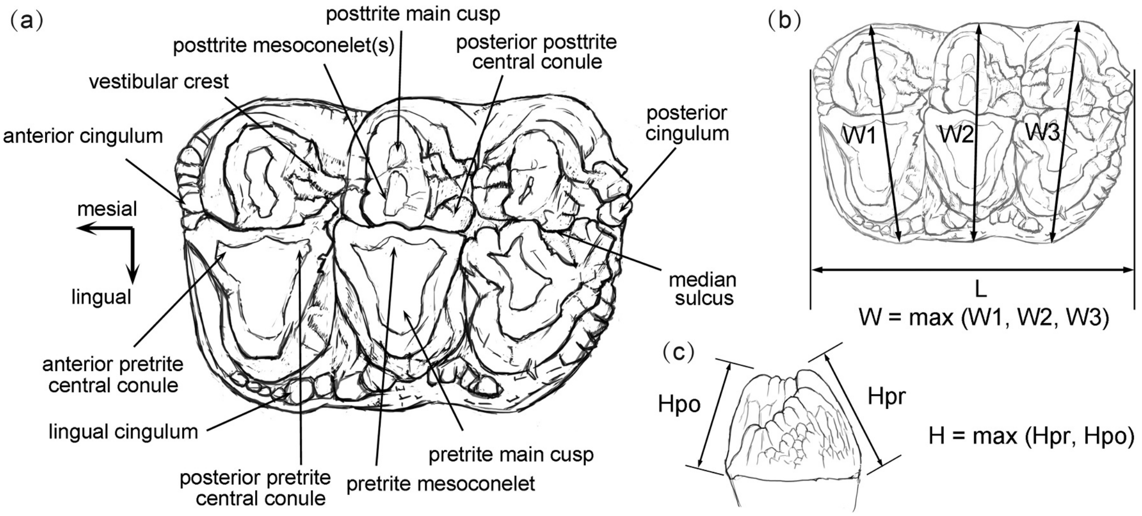

Figure 2. Tooth terminology and measurements (after Tassy 2014; Wang et al. 2019). (a) Occlusal terminology of a gomphotheriid tooth (a left M2 of *Sinomastodon praeintermedius*). (b) Length and width measurements of a left M2, occlusal view. (c) Height measurements on a molar, distal view.

intensively studied by many palaeontologists and geologists throughout China. New fossils were excavated from the Miaoerling sites (37°00′57.84″N, 106°01′17.95″E; Elevation: 1460 m) of the Early Miocene Zhangenbao Formation. This site is very close to Dingjiaergou, which is a well-known Early to Middle Miocene mammalian locality in China (Figure 1). Based on our research, most of fossils were found in the Miocene Zhangenbao Formation, which was originally named Hongliugou Formation by the Third Regional Survey Party, Ningxia Bureau of Geology in 1976, and was renamed as Zhangenbao Formation in 1999 (Zheng et al. 1999; Wang et al. 2016).

We explored several sections of fossil sites and provide a summary stratigraphic column in Figure 3. Based on the stratigraphic correlation, the fossiliferous beds of the Zhangenbao Formation are characterised by greyish-green or greyish-yellow channel sandstones. It can be divided into five sedimentary cycles, named A–E from bottom to top. Our new *Gomphotherium cooperi* material was situated at A and B sedimentary sandstone layers. We also found other proboscideans in these two lowermost layers, such as *Protanancus wimani* and *Afrochoerodon* sp. The D and E sedimentary sandstone layers are characterised by *Platybelodon*, representing the Middle Miocene age (Wang et al. 2016).

Systematic palaeontology

Order Proboscidea Illiger, 1811

Family Gomphotheriidae Hay, 1922

Genus *Gomphotherium* Burmeister, 1837

Type Species

Gomphotherium angustidens (Cuvier 1817).

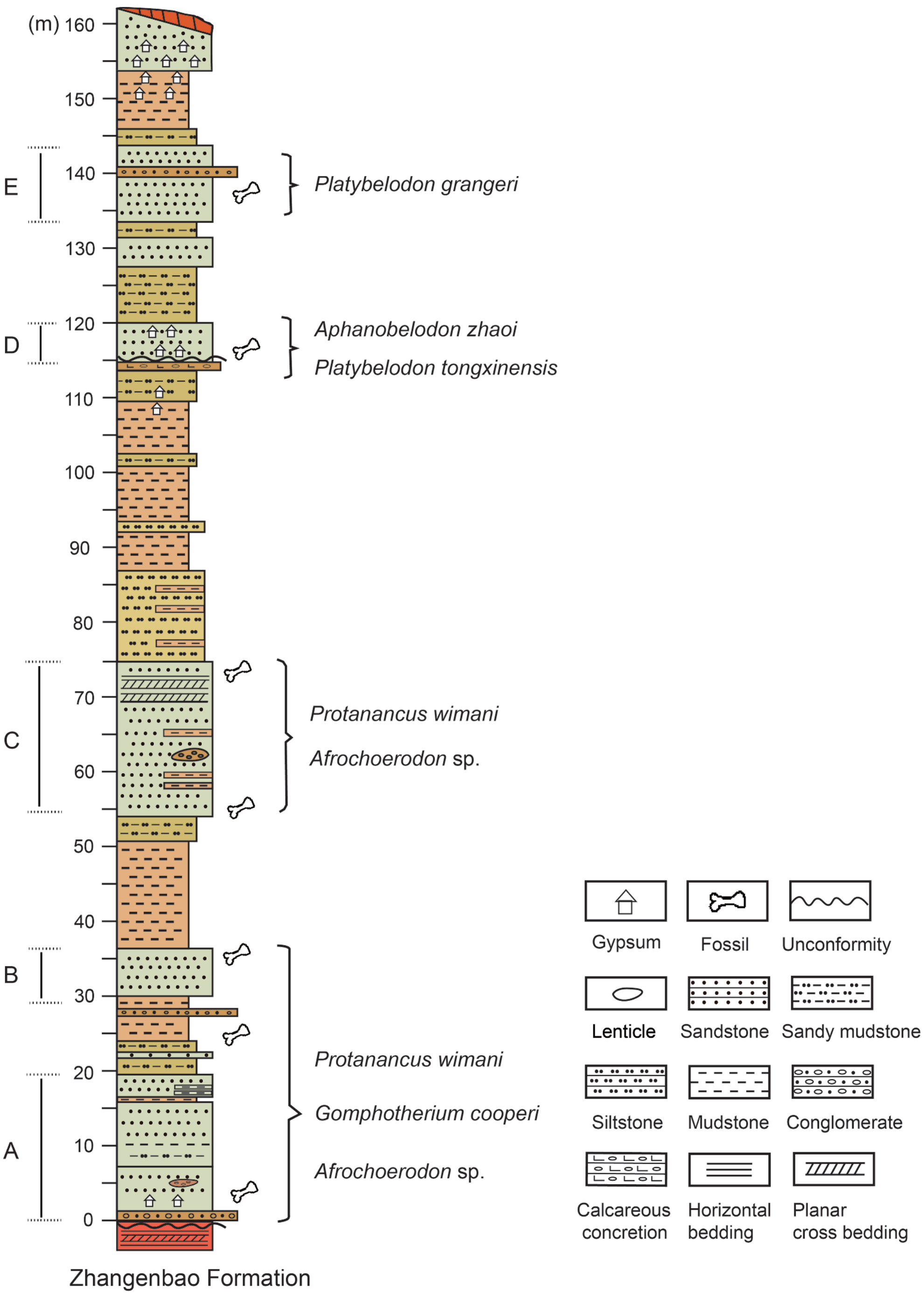

Figure 3. Stratigraphic column showing five sedimentary cycles of sandstones of the Zhangenbao Formation. The new *Gomphotherium cooperi* remains were situated at A and B sedimentary sandstones layers. Different sandstone layers are characterised by different proboscideans .

Type Locality

Simorre, France, Middle Miocene (Tassy and Göhlich 2012)

GOMPHOTHERIUM COOPERI *(Osborn 1932)*

(Figure 4, Table 1)

Bunolophodon angustidens (Cuvier 1817): Forster-Cooper 1922, see Figures 1–7, plate I
Trilophodon cooperi Osborn 1932: see Figures 1–2

Holotype

NHMUK M12181, a right hemimandible with dp4–m2, and m3 is in alveolus (Osborn 1932: see Figure 1).

Type Locality

Quarries near Gandoi or near Kumbhi, Dera Bugti, Pakistan (Osborn 1932).

Age and Occurrence

Early Miocene, ~19.5–18 Ma, South and East Asia

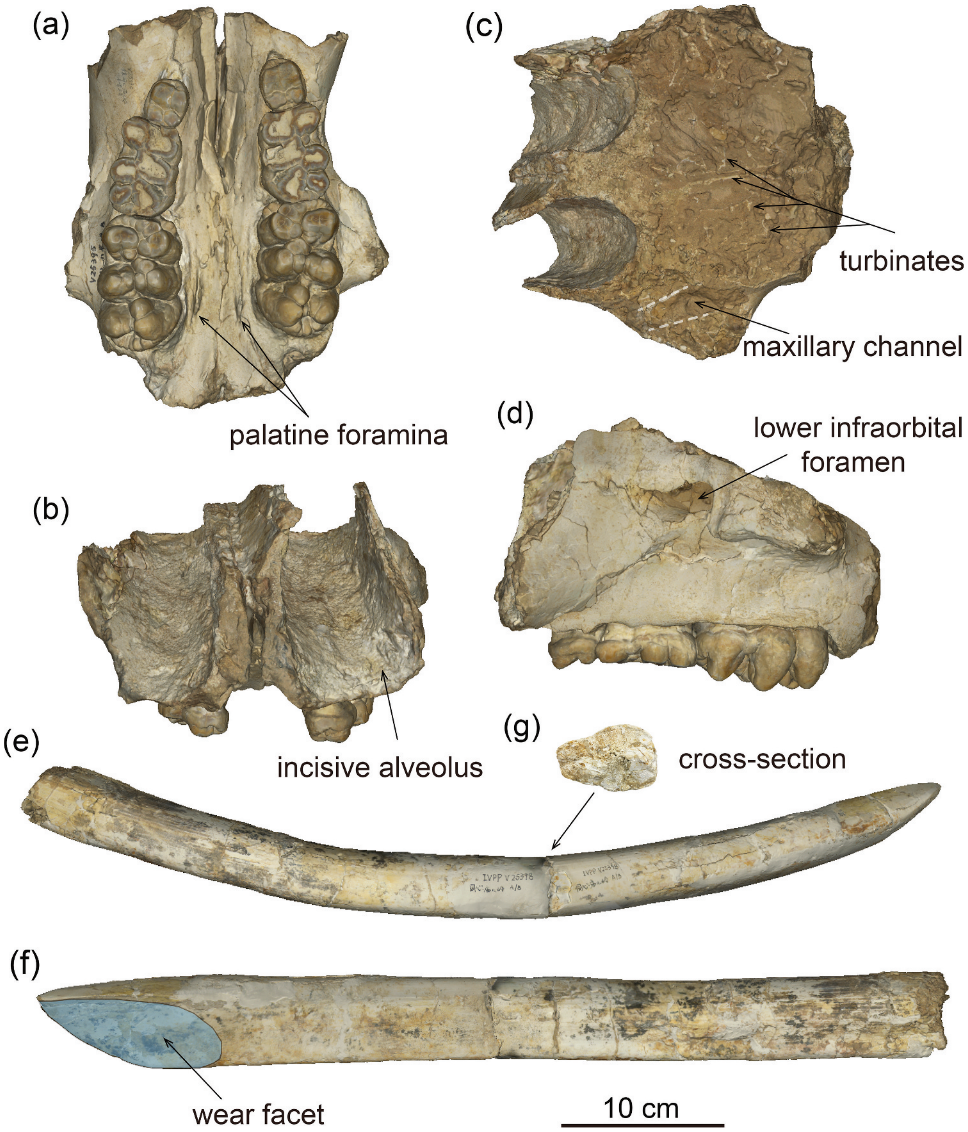

Figure 4. Lower tusk and maxillary of *Gomphotherium cooperi* from Tongxin, China. (a-d) IVPP V25395, an incomplete maxillary with P4s, M1s, and M2s. (a) ventral view; (b) front view; (c) dorsal view; (d) left lateral view. (e-g) IVPP V25398, a complete left lower tusk. (e) median view; (f) dorsal view; (g) the cross-section in the middle of the tusk. All the photos were taken from the 3D digital model .

Table 1. Tooth measurements (in mm) of new *Gomphotherium cooperi* materials from China.

	Specimen	Locus	L	W	W1	W2	W3	Hpo	I = W/L
Gomphotherium cooperi	V25395	l.P4	34.90	30.20	29.92	30.20		17.12	0.87
		r. P4	33.86	28.19	28.09	28.19		17.04	0.83
		l.M1	67.40	47.43	44.05	47.43	44.70	21.26	0.70
		r. M1	68.92	47.34	43.87	47.34	45.30	21.53	0.69
		l. M2	96.98	60.93	57.03	60.93	57.63	47.32	0.63
		r. M2	96.55	60.58	56.77	60.58	57.43	47.08	0.63
	V25398	l. i2	641.26	65.50					0.10

Parameters after Tassy (2014). Abbreviations: P, premolar; M, upper molar; i, lower incisor; l., left; r., right; L, length; W, maximal width; W1, W2, and W3: width at the first, second, and third loph(id)s; Hpo, maximal height of the posttrite side; I: index.

Emended Diagnosis

Small *Gomphotherium* with a long and dorsal-bent lower tusk, of which the cross-section is pyriform; Molar strongly bunodont; in the upper molars, second posterior pretrite central conule absent and second posttrite half loph subdivided into three conelets; in lower molars, posterior pretrite central conules strong and second anterior pretrite central conule absent.

Material in the present article

IVPP V25395, an incomplete maxillary with P4s, M1s, and M2s; IVPP V25398, a complete left lower tusk. Both from the horizon A, Xiaodiaozui Quarry (NXTX201704), Miaoerling sites, Tongxin, Ningxia Hui Autonomous Region (other specimens were found from the horizons A and B of the Miaoerling sites (e.g., Dadiaozui Quarry), but held by local farmers).

Age and Horizon

Lower Zhangenbao Formation, Early Miocene, ~19–18 Ma.

Description

Specimen IVPP 25398 (Figure 4(e–g)) is a complete left lower tusk. It is about 65 cm long and approximately 6.55 cm in width. The lower tusk is slightly upcurved, left-hand twisting when looking from back to front, and the tip tapers anteriorly. The dorsal wear facet is long and is almost flat. The shape of the cross-section is pyriform in the middle segment, and become oblate in the anterior segment. The lower tusk exhibits the similar curvature to that of *G. inopinatum* and *G. angustidens* (Tassy, 1985), compared to the relatively straight lower tusk of *G. annectens*.

Specimen IVPP 25395 (Figure 4(a–d)) is an incomplete maxillary with P4s, M1s, and M2s. In front view, it only shows two broken incisive alveoli, which are straight and ventrally declined. The bony wall of incisive alveoli is thin. In dorsal view, the turbinate, which was filled with sediments, shows complicated labyrinthine patterns. We also can see the oblique oval cross-section of the maxillary channel at the left zygomatic process. The preserved length of the channel is about 8 cm. There is a small piece of unerupted M3 that can be seen from the back view. In lateral view, the lower infraorbital foramen is relatively large, anterior to the zygomatic process, and approximately at the level of between M1 and M2. In ventral view, the anterior palatine foramina are long and backwardly extended. The palatine between the tooth rows is narrow with an elongated major palatine foramen being located at the posterior end of M2.

The left P4 is a bit bigger than the right P4. The P4s are small with only two lophs and low-crowned without wear. The first loph is larger than the second one. The protocone is smaller than paracone in the first loph, but the hypocone is almost the same size as the metacone in the second loph. There are one or two very small cones behind the second loph. The cingulum is developed.

The rectangular M1s are composed of three lophs. The anterior pretrite central conule is connected to the mesial cingulum and the first loph is deeply worn. The wear pattern of the second pretrite half-loph forms an irregular ellipse. The mesoconelet slightly inclines mesioadaxially. The posterior pretrite central conule is absent, but the posterior posttrite central conule in right M1 does exist. The third loph is moderately worn, and the anterior pretrite central conules and the mesoconelet can be recognised.

The M2s are slightly worn, and the crowns are relatively low and fall the range of *G. angustidens* M2 (42–51.5 mm, see Tassy 2014). The tooth is rectangular with three lophs and a small distal cingulum. The interlophs are relatively mesiodistally narrow. Limited cementum is deposited around the third posttrite half-loph and in the distal valleys. Alternatively, this cementum may be interpreted as dental calculus. In the pretrite half loph, the anterior pretrite central conule is relatively larger, round, and isolated, but the posterior pretrite central conule of the second loph is absent. The pretrite mesoconelet in the first loph is slightly positioned backward. In the posttrite half lophs, the typical characters are as follows: subdividing into three conelets, anterior posttrite central conules missing, posterior posttrite central conules very small. Some irregular small cusps rise on the distal cingulum. The cingula are not evident in both lingual side and buccal side.

Comparisons and discussion

Comparisons of the new material with the species of Gomphotherium

The new material represents a primitive species of *Gomphotherium*. The lower tusk is long-spike-like with a pyriform cross-section. This morphology is distinct from the *Gomphotherium* species with circular cross-sectional mandibular tusks, such as *G. pruductum* and *G. steinheimense*.

The upper molars of the new material show a distinct character, lacking the second posterior pretrite central conule. In most species of *Gomphotherium*, including *G. angustidens, G. subtapiroideum, G. steinheimense, G. browni, G. inopinatum, G. mongoliense, G. tassyi*, and *G. productum*, both the anterior and posterior pretrite central conules of the second loph are present, showing a complete pretrite trefoil. Therefore, the new material does not belong to any of the above species. We can only compare it with the species of the primitive '*Gomphotherium annectens*' group, of which the species may have an incomplete second pretrite trefoil. Furthermore, a - complete second pretrite trefoil is also present in molars of contemporary *Protanancus wimani* and *Afrochoerodon* sp. Therefore, the new material does not belong to the above taxa.

Tassy (1985) subdivided *Gomphotherium* into two groups: the primitive '*Gomphotherium annectens*' group and the advanced '*Gomphotherium angustidens*' group. The former comprises *Gomphotherium annectens, Gomphotherium sylvaticum* and *Gomphotherium cooperi*. *Gomphotherium annectens* was reported by Matsumoto (1925) from Banjoburo, Hiramaki Formation, Japan (MN3) (Tomida et al. 2013). Tassy (1994) re-evaluated the cranium of *G. annectens* based on the cast in Muséum national d'Histoire Naturelle, Paris, and mentioned a distinctively primitive character, which is the retracted nasal fossae. *G. annectens* lacks the posterior pretrite central conule, and both the half lophs do not subdivide into three conelets, representing the Early Miocene gomphotheres with simple bunodont teeth. *Gomphotherium sylvaticum* occurs in Artenay, France (MN4) (Göhlich 2010). Description of several upper and lower molars was made by Tassy (1977), who first named these specimens as '*Gomphotherium angustidens*'. The striking difference between *G. sylvaticum* and *G. annectens* is that the former has well-developed anterior and posterior pretrite central conules, which form a trefoil structure, the latter does not. *G. sylvaticum* is more derived than *G. annectens*.

Another member of '*Gomphotherium annectens*' group – *Gomphotherium cooperi*, first appeared in the Early Miocene of Dera Bugti, Pakistan (Forster-Cooper 1922; Welcomme et al. 2001). Originally referred to '*Bunolophodon angustidens*' by Forster-Cooper (1922: see Figure 2), then it was revised to '*Trilophodon cooperi*' by Osborn (1932). The posterior pretrite central conule in the lower molars of *G. cooperi* is large and looks like a big cusp in the middle of the first two interlophids, and the second posterior pretrite central conule in the upper molars is absent. One might argue that this character is variable in the hypodigm. For example, a left upper M2 (Forster-Cooper 1922: see pl. I, Figure 2) has a large second posterior pretrite central conule, but this tooth can also be interpreted as an M2 or M3 of *Afrochoerodon palaeindicus* from the same region, because in *Afrochoerodon*, the second posterior pretrite central conule of the upper molars is clearly present (Tobien 1980).

The present material from the lower Zhangenbao Formation, Miaoerling sites, Tongxin County represents a relatively primitive type of gomphotheres, of which the lower incisor curves upwardly with the shape of a slightly twisted long stick, and has a pyriform shaped cross-section. These features are close to the lower tusk of *G. inopinatum* and *G. angustidens*. The upper cheek teeth are typical bunodont gomphotheriid. Also, the absence of posterior pretrite central conule of the second loph has only been reported in the primitive '*Gomphotherium annectens*' group. Therefore, there is no doubt that these new fossil materials can be attributed to *Gomphotherium*. In the pretrite half loph, the anterior pretrite central conule is relatively larger, but the second posterior pretrite central conule loph is absent. The second posttrite half loph is subdivided into three conelets, anterior posttrite central conules are absent, and posterior posttrite central conules are small. Those upper molar morphology of new materials show strong similarities with those of *Gomphotherium cooperi*, and here we attribute the new Miaoerling material to it. Furthermore, the molar size of the Miaoerling material is close to the members of the '*Gomphotherium annectens*' group. It also falls in the range of *G. angustidens*, but considerably smaller than that of the derived *Gomphotherium*, such as, *G. tassyi, G. steinheimense*, and *G. browni* (Figure 5).

In the various species of the '*Gomphotherium annectens*' group, the dental morphology exhibits a pronounced evolutionary trend: from the absence of posterior pretrite central conule, and undivided posttrite half loph of *G. annectens*, to the absence of posterior pretrite central conule, but subdivided posttrite half loph of *G. cooperi*, and to the well-developed anterior and posterior pretrite central conule of *G. sylvaticum*. The three species of '*G. annectens*' group, positioning in the different stages along with this trend, also show an important bio-chronological significance.

The bio-chronological and paleobiogeographical significance of new **Gomphotherium cooperi** *materials*

Our new discovery indicates that *G. cooperi* from the Early Miocene of Miaoerling site is the only known species that can be classified into the '*Gomphotherium annectens*' group in China. It was found in the lowermost layers of the Zhangenbao Formation. From our bio-stratigraphical investigations and fossil identification in this region all along, the proboscidean fossil assemblage from the lowermost layers is characterised by Choerolophodontidae (*Afrochoerodon* sp.), Amebelodontidae (*Protanancus wimani*). This proboscidean fossil assemblage occurred earlier than *Platybelodon*, which was only recovered from the upper layers of the Zhangenbao Formation (D and E layers), whereas *Platybelodon* is present in the Halamagai Formation, Junggar Basin. Fossil evidence shows that the age of the lowermost layers of the Zhangenbao Formation is earlier than that of Halamagai Formation (16.9 Ma) (Ye et al. 2012; Wu et al. 2018; Li et al. 2019), and might be in a similar age to the Dalanggou and Hujiagou fossil site (Li et al.

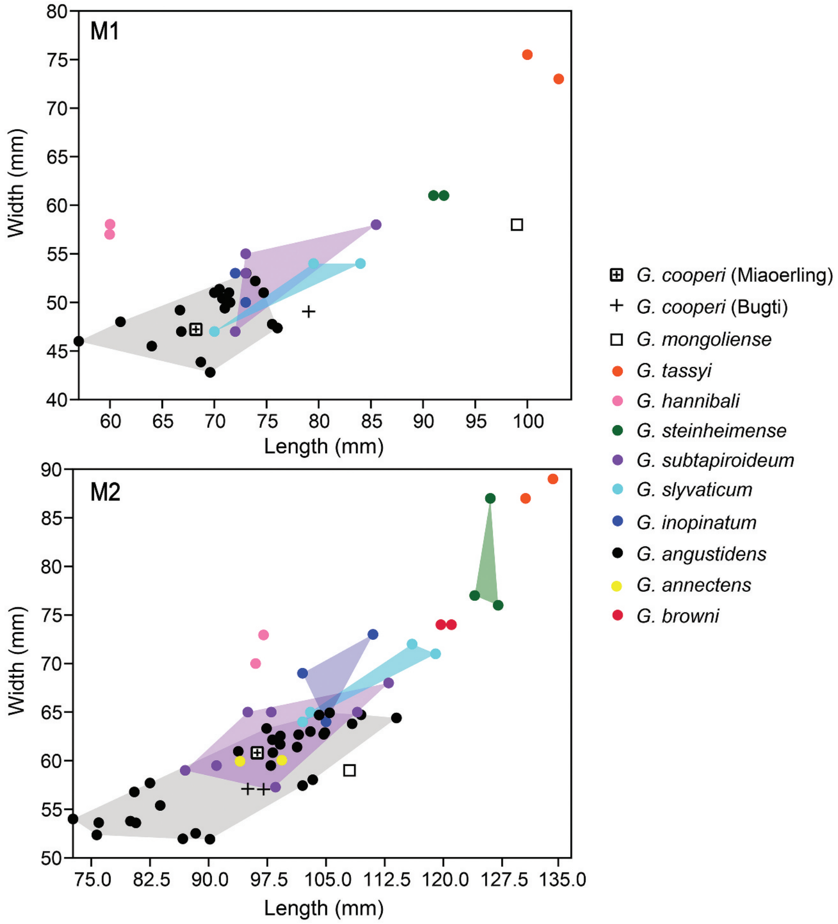

Figure 5. Scatter plot of upper molar measurements of several species of Gomphotheriidae. M1-M2: Horizontal ordinates represent molar length (in mm) and vertical ordinates represent width (in mm). Data source: *Gomphotherium cooperi* (Miaoerling), data from the present paper; *G. cooperi* (Bugti), after Forster-Cooper (1922); *G. hannibali*, after Welcomme (1994); *G. mongoliense*, after Osborn (1924); *G. slyvaticum*, after Tassy (1977); *G. inopinatum*, after Borissiak and Belyaeva (1928); *G. angustidens*, after Tassy (1977), Tassy (2014); *G. subtapiroideum*, after Göhlich (2010); *G. tassyi*, after Wang et al. (2017); *G. browni*, after Tassy (1983); *G. steinheimense*, after Göhlich (1998) .

2019), Linxia Basin, which also yields a primitive proboscidean assemblage including *Afrochoerodon guangheensis, Protanancus brevirostris*, and *Gomphotherium inopinatum*.

Based on the stratigraphic correlation and biostratigraphy that have been done by other scholars, the estimated age of *G. annectens* from Hiramaki Formation, Japan, is 19.5 Ma (MN3), and *G. sylvaticum* from Artenay, France, is 17–18 Ma (MN4); *G. cooperi* from Dera Bugti is approximately 19–20 Ma. There are other species like *Afrochoerodon palaeindicus* and cf. *Protanancus chinjiensis*, which were also reported from the Early Miocene Bugti in South Asia (Tassy 1983; Antoine et al., 2013). Combining the ages of these three species, we estimated the age of the lower layer of the Zhangenbao Formation, Tongxin, is approximately between 18 and 19 Ma. Therefore, the age of the lower layers of the Zhangenbao Formation is earlier than previously we believed (Qiu and Qiu 1995). In the previous publications, the Dingjiaergou Fauna, the representative mammalian assemblage was often correlated to MN6 or Tunggurian age, Middle Miocene. Actually, the age of the lower Zhangenbao Formation is close to the Shanwang Fauna (17–18 Ma) in the East Asia. Recently, *Plesiaceratherium* sp., a characteristic member of Shanwang Fauna, was recovered from the lower Zhangenbao Formation (Sun 2021). A very primitive giraffidae was also occurred in the same layers (Wang et al. 2016: see Figure 5a-d), which is morphologically more primitive than the earliest giraffine *Cathumeryx sirtensis* (Gebel Zelten, 18–16 Ma) in Africa. These mammals also support the middle Early Miocene age of the lower Zhangenbao Formation. Our research has important implications for understanding the Early Miocene fauna and providing the key biochronological evidence in northern China.

The proboscidean assemblage from the lowermost layers of the Zhangenbao Formation, Tongxin, represented by *Gomphotherium cooperi, Afrochoerodon* sp. and *Protanancus wimani* (Figure 3), is similar to the assemblage of Dera Bugti, including *Gomphotherium cooperi, Afrochoerodon palaeindicus* and cf. *Protanancus chinjiensis*. On the one hand, the two assemblages are probably contemporary as we have mentioned, and on the other hand, there may exist across-regional dispersal between these two assemblages (Figure 6). Deng et al. (2021) reported *Paraceratherium linxiaense* from Linxia Basin, China, which has a tight relationship with *P. bugtiense* of Oligocene Bugti by cladistic analysis. During the Late Oligocene, the evolution and dispersal of *Paraceratherium* evidence that the giant rhinoes can exchange between South Asia and North China and demonstrate that the Tibetan plateau did not reach enough high elevation at that time and was not yet a barrier to exchange of land mammals. In addition, *Parabrachyodus* has also been found in both north and south side of the Tibetan plateau in Oligocene (Wang 2021).

The similarity of the Early Miocene proboscidean assemblage in China and South Asia is further evidence that mammal dispersal may have existed during the Early Miocene. It also suggests that the plateau was not high enough to block exchange among large animals like proboscideans (Figure 6). Zhang and Wang (2021) reported *Eozygodon* in China and speculated that proboscidean was able to migrate through the Tibetan Plateau in the Early Miocene. Another possibility is that *Gomphotherium cooperi* reached northern China via Southeast Asia. However, in the Early Miocene of Southeast Asia, proboscideans were represented by *Stegolophodon* (Tassy et al. 1992) and *Gomphotherium* has not

Figure 6. Late Early Miocene dispersal of *Gomphotherium cooperi* between South Asia and China. The white stars denote the fossil locations of *Gomphotherium cooperi*. The arrow indicates the dispersal of *Gomphotherium* between South Asia and China through the Tibetan region. Palaeogeography map of the Early Miocene is modified from Paleo-digital Elevation Model (Paleo-DEM) (https://www.earthbyte.org/paleodem-resource-scotese-and-wright-2018/) .

been reported (Chavasseau et al. 2009). Therefore, the directed dispersal of *Gomphotherium cooperi* across the Tibetan Plateau is highly probable. In the Middle Miocene, *Platybelodon* did not occur in South Asia, this route possibly was already closed. The Tibetan plateau is probably higher and hinders the distribution of proboscideans.

Conclusion

The new fossil materials we described herein from the Early Miocene of Tongxin, China, present relatively primitive characters of *Gomphotherium*, such as the second posterior pretrite central conule loph is absent; the second posttrite half loph subdivided into three conelets; the elongated lower incisor curves slight upwardly. Therefore, the new materials can be attributed to *G. cooperi*, with the same characters, suggesting a wide distribution of the '*Gomphotherium annectens* group' across South and East Asia. The similarity of the Early Miocene *Gomphotherium* in China and South Asia is further evidence that proboscidean may disperse through the Tibetan region during the Early Miocene.

Acknowledgments

We thank Jie Ye for his great guidance and suggestions on stratigraphy. We thank Licheng Guo at the Institute of Geology and Geophysics, Chinese Academy of Sciences for his help and suggestions on the last figure. We are grateful to the reviewers and editor for providing constructive advice and suggestions.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA20070203, XDB26000000, XDA20070301), the Second Comprehensive Scientific Expedition on the Tibetan Plateau (2019QZKK0705), Natural science foundation of Ningxia, the Genesis of Geological Relics and Ecological Protection in the Yellow River Basin of Ningxia (2020AAC03462), and the Special Research Program of Basic Science and Technology of the Ministry of Science and Technology (-DD20190009)

References

Aguilar DH, Laurito CA. 2011. Nuevo registro de *Gomphotherium hondurensis* (Frick, 1933) (Proboscidea, Gomphoteriidae [sic.]). para el Mioceno Superior de El Salvador, América Central: Revista Geológica de América Central. 45:95–100.

Antoine PO, Metais G, Orliac MJ, Crochet JY, Flynn LJ, Marivaux L, Rajpar AR, Roohi G, Welcomme JL. 2013. Mammalian Neogene biostratigraphy of the Sulaiman province, Pakistan In: Wang XM, Flynn LJ, Fortelius M, editors Fossil mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York; p. 400–422.

Borissiak AA, Belyaeva E. 1928. *Trilophodon* (*Serridentinus*?) *inopinatum*. sp. from the Jilančik Beds of the Turgai Region. Leningrad: Bulletin de l'Académie des Sciences de l'URSS, Classe des Sciences Physico-Mathématique; p. 241–252.

Burmeister H. 1837. Handbuch der Naturgeschichte Zum Gebrauch bei Vorlesungen. Enslin, Berlin; p. 511.

Chavasseau O, Chalmanee Y, Yamee C, Tian P, Rugbumrung M, Marandat B, Jaeger JJ. 2009. New proboscideans (Mammalia) from the middle Miocene of Thailand. Zool J Linn Soc. 155:703–721. doi:10.1111/j.1096-3642.2008.00456.x.

Chen GF. 2021. Basal synapsids and mammals: hyracoidea, proboscidea, etc. In: ZX Q, CK L, editors. Palaeovertebrata Sinica. Beijing: Science Press; p. 231.

Cuvier G. 1817. Le règne animal, Vol. 1. Paris: Deterville.

Deng T, Lu XK, Wang SQ, Flynn LJ, Sun DH, He W, Chen SQ. 2021. An Oligocene giant rhino provides insights into *Paraceratherium* evolution. Commun Biol. 4:1–10. doi:10.1038/s42003-021-02170-6.

Forster-Cooper C. 1922. Miocene Proboscidia from Baluchistan. Proc Zool Soc Lond. 92(3):609–626.

Göhlich UB. 1998. Elephantoidea (Proboscidea, Mammalia) aus dem Mittel- und Obermiozän der oberen Süßwassermolasse Süddeutschlands: odontologie und Osteologie. München: Münchner Geowissenschaftliche Abhandlungen. 36:1–245.

Göhlich UB. 1999. Order Proboscidae. In: Rssner GE, Heissig K, editors. The Miocene land mammals of Europe. München: Verlag Dr. Friedrich Pfeil; p. 157–168.

Göhlich UB. 2010. The proboscidea (Mammalia) from the Miocene of Sandelzhausen (southern Germany). Paläontologische Zeitschrift. 84:163–204. doi:10.1007/s12542-010-0053-1.

Kappelman J, Rasmussen DT, Sanders WJ, Feseha M, Bown T, Copeland P, Crabaugh J, Fleagle J, Glantz M, Gordon A, et al. 2003. Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia. Nature. 426:549–552. doi:10.1038/nature02102.

Lambert WD. 1996. The biogeography of the gomphotheriid proboscideans of North America. In: Shoshani J, Tassy P, editors. The proboscidea: evolution and palaeoecology of elephants and their relatives. Oxford University Press, Oxford; p. 143–148.

Lambert WD, Shoshani J. 1998. Proboscidea. In: Janis CM, Scott KM, Jacobs LL, editors. Evolution of tertiary mammals of North America. Volume 1: terrestrial carnivores, ungulates, and ungulate like mammals. Cambridge University Press, Cambridge; p. 606–621.

Li CX, Wang SQ, Dimila M, Ni XJ. 2019. New fossils of early and middle Miocene *Choerolophodon* from northern China reveal a Holarctic distribution of Choerolophodontidae. J Vertebr Paleontol. 39(3):e1618864. doi:10.1080/02724634.2019.1618864.

Matsumoto H. 1925. Preliminary notes on two new species of fossil *mastodon* from Japan. J Geol Soc Tokyo. 31:395–414.

Osborn HF. 1924. *Serridentinus* and *Baluchitherium*, Loh fomation, Mongolia. Am Mus Novit. 148:1–5.

Osborn HF. 1932. *Trilophodon cooperi*, sp. nov., of Dera Bugti, Baluchistan. New York City: The American Museum of Natural History.

Osborn HF. 1936. Proboscidea: a monograph of the discovery, evolution, migration and extinction of the mastodonts and elephants of the world. New York: The American Museum Press; p. 577.

Qiu ZX, Qiu ZD. 1995. Chronological sequence and subdivision of Chinese Neogene mammalian faunas. Palaeogeogr Palaeoclimatol Palaeoecol. 116:41–70.

Sanders WJ, Kappelman J, Rasmussen DT. 2004. New large–bodied mammals from the late Oligocene site of Chilga, Ethiopia. Acta Palaeontol Pol. 49:365–392.

Shoshani J, Tassy P. 1996. The Proboscidea: evolution and palaeoecology of elephants and their relatives. In: Oxford University Press; Oxford. p. 472.

Shoshani J, Tassy P. 2005. Advances in proboscidean taxonomy & classification, anatomy & physiology, and ecology & behavior. Quat Int. 126:5–20.

Simpson GG. 1945. The principles of classification and a classification of mammals. Bull Am Mus Nat Hist. 85:1–350.

Sun DH 2021. A study of Rhinocerotidae fossils from the Miocene of Ningxia Tongxin and Shaanxi Dingbian. Ph.D. dissertation, Institute of Vertebrate Paleontology and Paleoanthropology, University of Chinese Academy of Sciences, Beijing. p. 211.

Tassy P. 1977. Le plus ancien squelette de gomphothère (Proboscidea, Mammalia) dans la Formation Burdigalienne des sables de l'Orléanais France. Mémoirs du Muséum National d'Histoire Naturelle (Serie C) C. 37:1–51.

Tassy P. 1983. Les Elephantoidea Miocènes du Plateau du Potwar, Groups de Siwalik, Pakistan. II^{e} Partie: choerolophodontes et gomphothères. Annales de Paléontologie. 69:235–297.

Tassy P 1985. La place des mastodontes Miocènes de l'ancien monde dans la phylogènie des Proboscidea (Mammalia): hypothèses et conjectures. unpubl. D.Sc. these, UPMC, Paris. p. 861.

Tassy P. 1990. The "proboscidean datum event:" how many proboscideans and how many events? In: EH L, Fahlbusch V, Mern P, editors. European Neogene mammal chronology. Plenum Press, Boston; p. 237–252.

Tassy P, Anupandhanant P, Ginsburg L, Mein P, Ratanasthien B, Sutteethorn V. 1992. A new *Stegolophodon* (Proboscidea, Mammalia) from the early Miocene of northern Thailand. Geobios. 25(4):511–523.

Tassy P. 1994. Gaps, parsimony, and early Miocene elephantoids (Mammalia), with a re-evaluation of *Gomphotherium annectens* (Matsumoto, 1925). Zool J Linn Soc. 112:101–117.

Tassy P, Göhlich UB. 2012. Retour sur la serie type de *Gomphotherium angustidens* (Proboscidea, Mammalia): de Daubenton a Cuvier, et apres. Estud Geol. 67:321–332.

Tassy P. 2014. L'odontologie de *Gomphotherium angustidens* (Cuvier, 1817) (Proboscidea, Mammalia): données issues du gisement d'En Péjouan (Miocène moyen du Gers, France). Geodiversitas. 36:35–115.

Tobien H. 1980. A note on the skull and mandible of a new choerolophodont mastodont (Proboscidea, Mammalia) from the middle Miocene of Chios (Aegean Sea, Greece). In: Jacobs L, editor. Aspects of vertebrate history: essays in honor of Edwin Harris Colbert. Flagstaff: Museum of Arizona Press; p. 299–307.

Tomida Y, Nakaya HS, Myata K, Fukuchi A. 2013. Miocene land mammals and stratigraphy of Japan. In: Wang XM, Fortelius M, editors. Fossil mammals of Asia: neogene biostratigraphy and chronology of Asia. New York: Columbia University Press; p. 314–333.

Wang SQ, Zong LY, Yang Q, Sun BY, Li Y, Shi QQ, Yang XW, Ye J, Wu WY. 2016. Biostratigraphic subdividing of the Neogene Dingjiaergou mammalian fauna, Tongxin County, Ningxia province, and its background for the uplift of the Tibetan Plateau. Quat Sci. 36:789–809.

Wang SQ, LI Y, Duangkrayom J, Yang XW, He W, Chen SQ. 2017. A new species of *Gomphotherium* (Proboscidea, Mammalia) from China and the evolution of Gomphotherium in Eurasia. J Vertebr Paleontol. 37(3):1–15.

Wang SQ, Li CX, Zhang XX, Qi-Gao JZ, Ye J, Li L, Li FC. 2019. A record of the early *Protanancus* and *Stephanocemas* from the north of the Junggar Basin, and its implication for the Chinese Shanwangian. Vert PalAsiat. 57 (2):133–154.

Wang SQ. 2021. The anthracotheres from northern Junggar Basin and their palaeoclimatic significance in relation to the Tibetan Plateau. Palaeobiodiv Palaeoenv. 101(3):839–852.

Welcomme JL. 1994. Le plus ancien crâne de proboscidien d'Europe, *Gomphotherium hannibali* nov. sp. (Proboscidea, Mammalia), du Miocène inférieur du Languedoc (France). Comptes rendus de l'Académie des sciences Paris, Série II. 319:135–140.

Welcomme JL, Benammi M, Crochet JY. 2001. Himalayan Forelands: palaeontological evidence for Oligocene detrital deposits in the Bugti Hills (Balochistan, Pakistan). Geol Mag. 138:397–405.

Wu Y, Deng T, Hu YW, Ma J, Zhou XY, Mao LM, Zhang HW, Ye J, Wang SQ. 2018. A grazing *Gomphotherium* in Middle Miocene Central Asia, 10 million years prior to the origin of the Elephantidae. Sci Rep. 8(1):1–8.

Ye J, Wu WY, Ni XJ, Bi SD, Sun JM, Meng J. 2012. The Duolebulejin Section of northern Junggar Basin and its stratigraphic and environmental implication. Sci China Earth Sci. 42:1523–1532.

Zhang XX, Wang SQ. 2021. First report of *Eozygodon* (Mammutidae, Proboscidea) in Eurasia. Hist Biol. 33(9):1661–1670.

Zheng JJ, He XX, Liu SW. 1999. Stratigraphical Lexicon of China, Tetiary. Beijing: Geological Publishing House. 3:1–163.