

# *Gomphotherium inopinatum*, a basal *Gomphotherium* species from the Linxia Basin, China, and other Chinese members of the genus

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**Abstract** An incomplete right dentary retaining m2 and m3 was recovered from the upper Lower Miocene of Ganchiliang, in the Linxia Basin. The part of the corpus anterior to the molars is strongly elongated, but not inclined or deflected downward. The mandibular angle of the ramus is in a low position. The molars are small and morphologically primitive. The interlophids are moderately anteroposteriorly open. Clear indications of further subdivision are absent in the posttrite half lophids and in the pretrite central conules. The major characters of the partial dentary correspond to those of *Gomphotherium inopinatum* from the Lower Miocene of the Turgai region of Kazakhstan, and the new Ganchiliang specimen is accordingly referred to this species. This is the first report of *G. inopinatum* from China, and *G. inopinatum* in turn represents the most basal species of *Gomphotherium* so far known in the Chinese record. Among other *Gomphotherium* species known from China, *G. wimani* represents a derived east Eurasian form that appears to be closely related to the European species *G. steinheimense*. *Gomphotherium connexum* seems to be a member of the “*G. angustidens* group”, given its strong morphological resemblance to *G. angustidens*. *G. subtapiroideum* may represent another evolutionary branch of the “*G. angustidens* group”, distinct from *G. angustidens*. “*G. shensiensis*” may represent a variation of *G. subtapiroideum*.

**Key words** Eurasia, China, Miocene, *Gomphotherium inopinatum*, *G. angustidens* group, phylogeny

## 1 Introduction

*Gomphotherium* Burmeister, 1837 is the most conservative genus in Gomphotheriidae (Lambert, 1996), and indeed one of the most conservative among all Miocene proboscideans. The only synapomorphy of *Gomphotherium* is the pyriform or subcircular cross-section of the lower tusks (Tobien, 1973a; Tassy, 1985). Since Cuvier described several isolated teeth from the Middle Miocene of Simorre, South France as “mastodontes à dents étroites” in 1806

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国家重点基础研究发展计划项目(编号:2012CB821900)、中国科学院战略性科技先导专项(编号:XDB03020104)和国家自然科学基金(批准号:41372001,41002010,40730210)资助。

收稿日期:2013-08-12

(Osborn, 1936; Tassy and Göhlich, 2012), many taxa have been established in the genera *Gomphotherium*, *Trilophodon*, and *Serridentinus* (Osborn, 1936; Simpson, 1945; Tassy, 1985; Tobien, 1972; Wang et al., 2013a). The last two of these genera are now considered junior synonyms of the first. Tobien (1973a) amended the genus *Gomphotherium* to include all of the European taxa in one species, *Gomphotherium angustidens*. He also considered other Asian and African gomphothere species to belong to the “*Gomphotherium angustidens* group.” This classic work created a useful framework for research on *Gomphotherium*. Tassy (1985) subdivided *Gomphotherium* species having lower tusks with a pyriform cross-section into the “*Gomphotherium annectens* group” and the “*Gomphotherium angustidens* group.” Members of the former (*G. annectens*, *G. sylvaticum*, and *G. cooperi*) exhibit more plesiomorphies than members of the latter (*G. angustidens*, *G. subtapiroideum*, and *G. inopinatum*). Sanders et al. (2010) recognized an additional “‘pygmy’ *Gomphotherium* group” including the African species *G. pygmaeus*. However, neither of these authors discussed *Gomphotherium* species from China, which remain in need of further attention.

Recently, our field team discovered a fragmentary gomphothere right lower jaw in the Lower Miocene of Ganchiliang in the Linxia Basin, Gansu, China (Fig. 1). The cheek tooth pattern is primitive and exhibits none of the derived characteristics known in other Chinese species (e.g., narrowness of m3 as in *G. connexum*, or subdivision of posttrite half loph(id)s as in *G. wimani*). However, this specimen is a good match for *G. inopinatum* Borissiak & Belyaeva, 1928 from the Lower Miocene Jilančik Beds of the Turgai region of Kazakhstan (Borissiak and Belyaeva, 1928). This important find helps us further elucidate the phylogenetic relationships among *Gomphotherium* species from China and elsewhere and understand the dispersal throughout the Holarctic of *Gomphotherium*, an important basal genus within the Elephantidae.

**Institutional abbreviations** AMNH, American Museum of Natural History, New York, USA; BSP, Bayerische Staatssammlung für Historische Geologie und Paläontologie, Munich, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; LZU, Key Laboratory of Western China’s Environmental Systems, Research School of Arid Environment and Climate Change, Lanzhou University, Lanzhou, China; MNHN, Muséum National d’Histoire Naturelle, Paris, France; PMU, Palaeontological Museum, Uppsala, Sweden.

## 2 Systematic paleontology

### Order Proboscidea Illiger, 1811

#### Family Gomphotheriidae Hay, 1922

#### Genus *Gomphotherium* Burmeister, 1837

#### *Gomphotherium inopinatum* (Borissiak & Belyaeva, 1928)

(Figs. 2–3; Tables 1–2)

*Trilophodon* (*Serridentinus*?) *inopinatus* Borissiak & Belyaeva, 1928, p. 241, pl. I-II

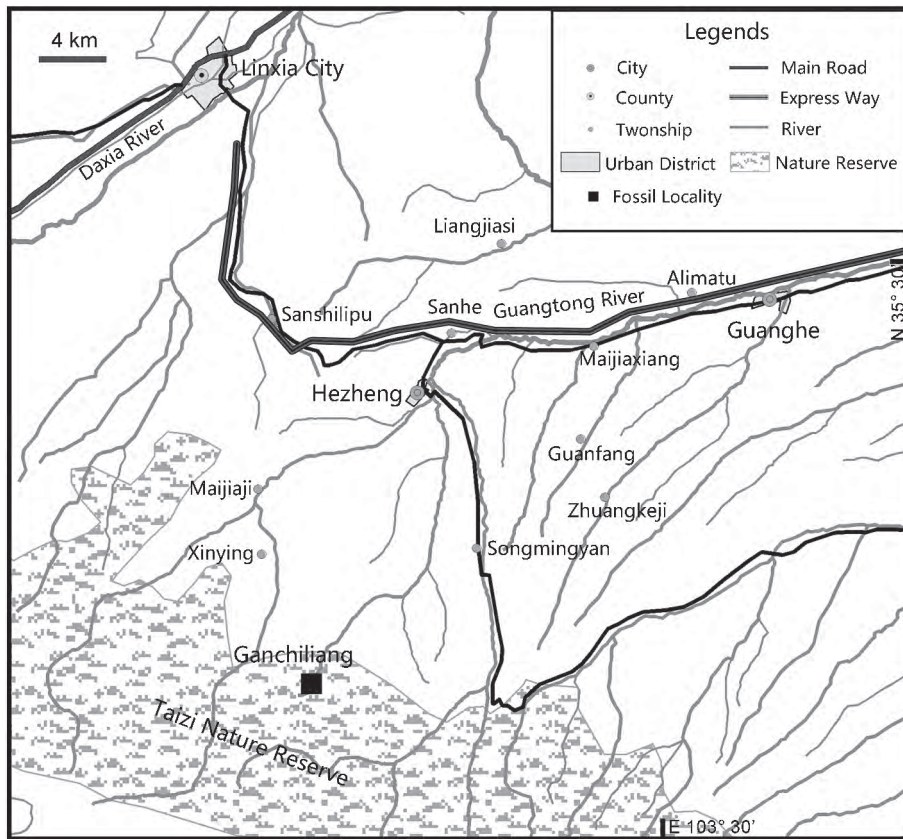


Fig.1 Map of the Ganchiliang locality in the Linxia Basin

**Syntypes** Two maxillae with M2 and M3 (specimens no.: 1401/614 and 1401/1152) belonging to one skull; two pairs of incomplete mandibular rami, both having m2 and m3 (1401/606+1401/607; 1401/608+1401/602); isolated M3 (1401/642, 1401/602), M2 (1401/643, 1401/618), P4 (1401/623, 1401/629), I2 (1401/598, 1401/1328), m3 (1401/619, 1401/639), m2 (1401/640, 1401/644), m1(1401/645), and i2 (1401/597, 1401/599) (Borissiak and Belyaeva, 1928).

**Type locality** Jilančik Beds, Turgai region, Kazakhstan (Borissiak and Belyaeva, 1928), Lower Miocene (Tassy, 1985).

**New referred specimen** IVPP V 18700, an incomplete right dentary with a greatly worn m2 and a slightly worn m3.

**Locality and horizon of IVPP V 18700** Ganchiliang (N 35° 17' 59.4", E 103° 17' 30.1", H 2530 m, loc. No. LX200802), Linxia Basin, Gansu, China (Fig. 1), Dongxiang Formation, upper Lower Miocene. The accompanying fauna (Shinanu Fauna) indicates a possible correspondence in age to MN5 (Deng et al., 2013). A fragmentary mandibular symphysis of *Platybelodon danovi* was discovered at the same locality (Wang et al., 2013b).

**Remarks** Three species of *Gomphotherium* have been previously reported from China.

The Ganchiliang specimen differs from *G. connexum* in having more open interlophids, lower central conules, and a wider m3; differs from *G. wimani* in having more open interlophids and central conules that are not subdivided, and in lacking posttrite central conules; also differs from “*G. shensiensis*” in having 2<sup>nd</sup> posterior pretrite central conules, and posttrite half lophids that are not subdivided (Hopwood, 1935; Chow and Zhang, 1974; Chang and Zhai, 1978; Tobien et al, 1986; Chen, 1988; Wang et al., 2013a). Resemblances in the mandible and teeth link the Ganchiliang specimen to the primitive *G. inopinatum* from Kazakhstan, and support its referral to this species (see below). Thus, the Ganchiliang specimen represents the most primitive species of *Gomphotherium* so far known from China.

**Description** All but the posteriormost portion of the symphyseal area is broken away in the right dentary (Fig. 2). The mandibular condyle and adjacent ramus are broken. The surface of the bone is deeply weathered, exhibiting many long cracks along the corpus and some reticulated areas.

No remnant of the lower tusk or alveolus can be observed. The distance between the anteriormost preserved tooth and the posterior border of the symphysis is considerable (117 mm). The interalveolar crest anterior to the dentition is high and sharp. The corpus has a rounded ventral surface, and is expanded neither laterally in the posterior part nor ventrally in the anterior part. The apex of the retromolar trigon is broken. The ramus is low, with a rounded angular process. The anterior and posterior borders of the ramus are almost perpendicular to the corpus, rather than posteriorly inclined as in *Platybelodon*. The coronoid process protrudes dorsally and slightly anteriorly, forming a deep mandibular notch. The masseteric fossa is dorsoventrally compressed, but very deep. In medial view, a triangular groove is visible posterior to the opening of the mandibular foramen, close to the posterior part of the ramus.

**Table 1** Measurements (after Tassy, 1996a) of the dentary of *Gomphotherium inopinatum* from Ganchiliang, IVPP V 18700

	(mm)
preserved length of dentary	642
alveolar distance (from most salient point of trigonum retromolare to symphyseal border of corpus) (3)	ca. 389
width of corpus measured at root of ramus (7)	102
width of corpus measured at anterior alveolus (or at grinding tooth if alveolus entirely resorbed) (8)	82
maximum height of corpus (measurement taken perpendicular to the ventral border of the corpus) (16)	117
height of corpus measured at the root of the ramus (measurement as above) (17)	108
rostral height measured at the symphyseal border (measurement taken perpendicular to the ventral border of the symphyseal rostrum) (18)	107
maximum depth of ramus (21)	236
depth between gonion and coronoid processes (22)	270
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 (24)	240

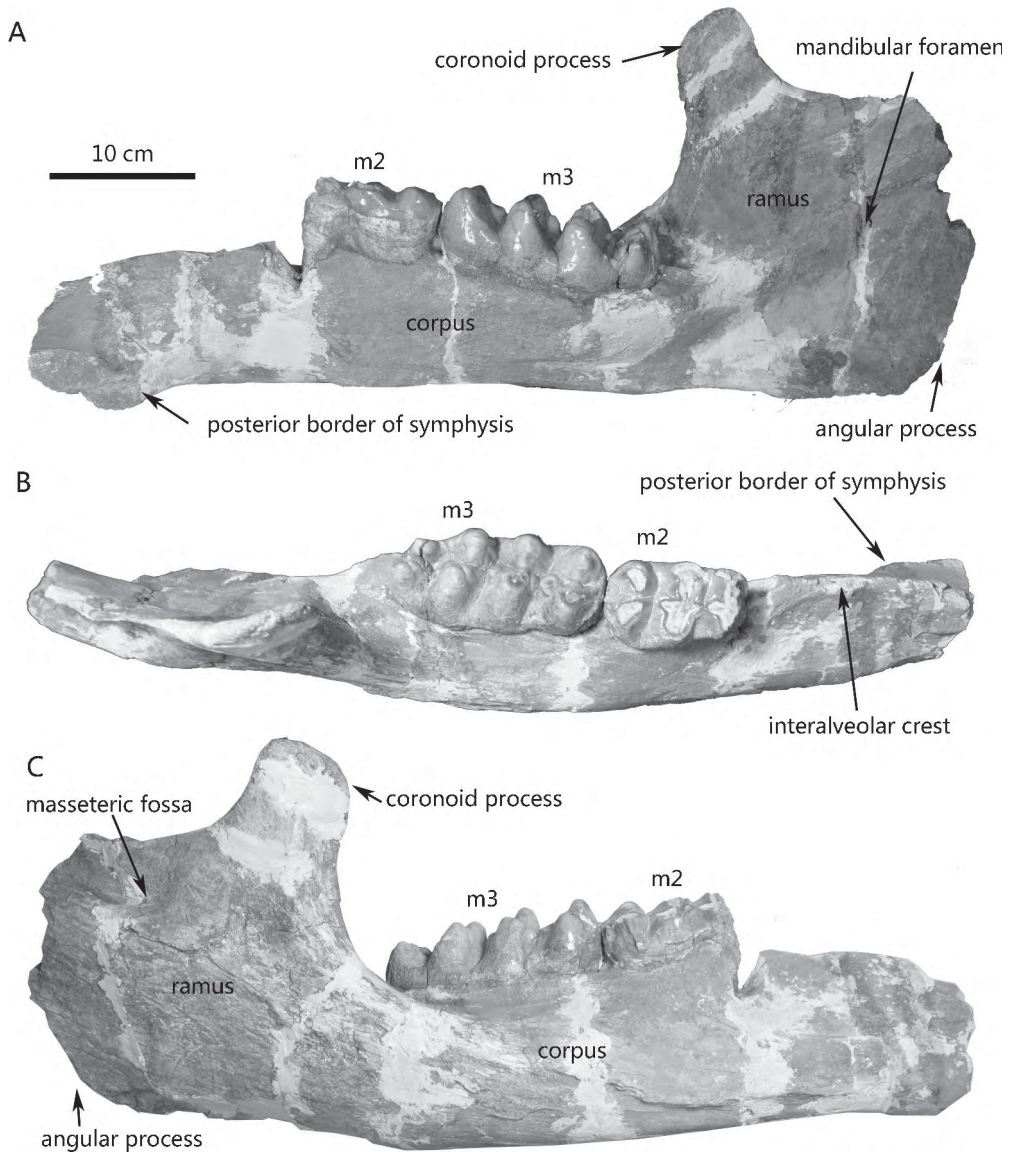


Fig. 2 Right dentary of *Gomphotherium inopinatum* (IVPP V 18700)  
A. medial view; B. dorsal view; C. lateral view

The trilophodont m2 (Fig. 3) is deeply worn, and has a broken anterior edge. The first lophid is narrow, and only a strong posterior pretrite central conule can be observed. The second and third lophids are widened. The second posterior pretrite central conule is larger than the anterior one, and no posttrite central conules are present. The third pre- and posttrite half lophids form a chevron structure. Only two low enamel cusps arise from the posterior cingulid of the tooth. Cingulids are absent on the other margins of the tooth, except at the posterior border, and almost no cementum exists.

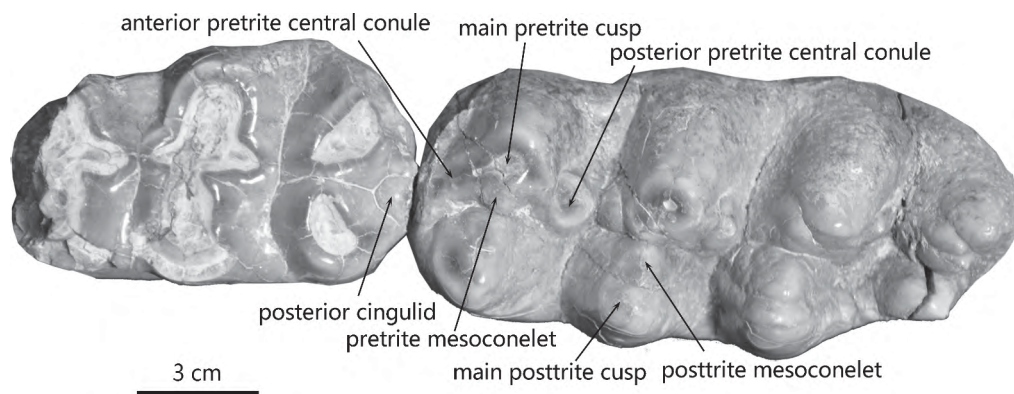


Fig. 3 Lower right cheek teeth of *Gomphotherium inopinatum* (IVPP V 18700) in occlusal view

**Table 2** Measurements of the right lower cheek teeth of *Gomphotherium inopinatum* from Ganchiliang, IVPP V 18700 (mm)

Type	L	W	H	W1	W2	W3	W4
m2	92+	56	—	45+	54	56	
m3	149	68	49	60	65.5	68	52.5

Abbreviations: L. length; W. maximal width; H. height; W1, 2, 3, and 4. width at the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> loph(id)s, respectively.

The tetralophodont m3 (Fig. 3) is only slightly worn, and the tooth is widest at the level of the third lophid. The cusps of each half lophid are blunt and rounded, as is typical in *G. angustidens*, and not compressed and subdivided. However, the interlophids are moderately anteroposteriorly widened, showing a degree of similarity to the condition in *G. subtapiroideum*. The first pretrite mesoconelet is much smaller than the main cusp. The first anterior pretrite central conule extends anterolingually, connecting to the anterior cingulid. The first posterior pretrite central conule is low but broad, and is separated from the main cusp but linked to it by an enamel ridge. The second pretrite mesoconelet is enlarged and anteriorly displaced, and tends to fuse with the anterior pretrite central conule. The second posterior central conule is morphologically identical to (but a little smaller than) the anterior one, and is linked to the main cusp in much the same manner as the first lophid. The central conule on the third lophid is weak, but the pretrite mesoconelet is strong. Two half lophids form a chevron as in m2. The posttrite half lophids of the first three lophids are all simple in that they each comprise only a large main cusp and a smaller mesoconelet, without any trace of posttrite central conules. The fourth lophid is incomplete, consisting of four irregular enamel cusps. As in m2, almost no cingulid (except on the anterior border) or cementum can be seen.

### 3 Discussion

#### 3.1 Affinities of the Ganchiliang specimen

The Ganchiliang specimen is undoubtedly referable to *Gomphotherium*, as indicated by several taxonomically significant features. First, the lower jaw is typical of longirostrine trilophodont gomphotheres, and shows that the specimen does not belong to a tetralophodont (i.e., *Tetralophodon*, *Paratetralophodon*, *Anancus*, *Stegolophodon*, or “*Mastodon*” *grandincisivus*) or brevirostrine (i.e., *Sinomastodon* or a cuvieronine)(Lucas, 2013; Lucas and Morgan, 2008; Prado and Alberdi, 2008; Schlesinger, 1917; Tassy, 1983a,b,c, 1985, 1986; Tobien, 1973a,b, 1975, 1978; Tobien et al., 1986, 1988). Second, the anterior part of the corpus is not deflected downward, excluding the specimen from *Rhynchotherium* (Lucas and Morgan, 2008; Miller, 1990; Tobien, 1973a). Third, the evident lack of strong chevroning, choerolophodony, ptychodonty, or cementodonty on the cheek teeth excludes the specimen from the Choerolophodontinae (i.e., *Choerolophodon*, *Afrochoerodon*, or *Synconolophus*) (Pickford, 2001; Tassy, 1983b, 1985, 1986; Tobien, 1973a; Wang and Deng, 2011). Fourth, although m3 exhibits anteroposteriorly widened interlophids, the posterior half lophids display no trace of either anteroposterior compression or subdivision. This feature distinguishes the Ganchiliang specimen from Mammutidae (i.e., *Eozygodon*, *Zygodolophodon*, or *Mammut*)(Tassy, 1985; Tassy and Pickford, 1983; Tobien, 1975). Finally, the cheek teeth in this specimen exhibit none of the synapomorphies seen in the Amebelodontinae (i.e., *Archaeobelodon*, *Protanancus*, *Platybelodon*, *Afromastodon*, *Amebelodon*, and *Torynobelodon*), such as narrow molars or the presence of posttrite central conules and pseudo-anancoidy in the cheek teeth. The ramus is not posteriorly inclined, in contrast to the condition in most amebelodontines (Pickford, 2003; Tassy, 1983a, 1984, 1985, 1986; Wang et al., 2013b). However, the primitive structure of the cheek teeth supports referral of this specimen to *Gomphotherium*, even though no information on the lower tusks is available. It is difficult to compare the Ganchiliang specimen to the African *Progomphotherium* (for which few lower teeth have been found), but the Ganchiliang specimen seems not belong to this genus given the very primitive stage of horizontal accession of the cheek teeth (P3–M3 in wear at the same time) that is characteristic of *Progomphotherium maraisi* (Pickford, 2003).

The incomplete mandible of the Ganchiliang specimen exhibits some features that are unusual for *Gomphotherium*. First, the distance between the posterior border of the symphysis and the anteriormost of the preserved cheek teeth is similar to that seen in *G. inopinatum* from the Turgai region of Kazakhstan (Borissiak and Belyaeva, 1928). Second, the anterior part of the corpus (anterior to the dentition) neither slopes gradually downward as in *G. annectens*, *G. angustidens*, and *G. subtapiroideum*, nor is deflected downward as in *G. browni*, *G. steinheimense*, and *G. productum* (Osborn, 1926, 1936; Tassy, 1985, 1994; Göhlich, 1998, 2010). The corpus remains almost straight along its entire length, again as in *G. inopinatum* (Fig. 4).

Third, although it is slightly damaged, the posterior border of the ramus is almost perpendicular to the corpus. As a result, the mandibular angle is in a relatively low position as in *G. inopinatum* from the Turgai region, as opposed to the relatively high position seen in *G. angustidens* (Borissiak and Belyaeva, 1928; Tassy, 1985)(Fig. 4). However, the strong, protruding, and rounded coronoid process differs from both the small, non-protruding process of *G. angustidens* and the hook-like process of *G. steinheimense*, *G. subtapiroideum*, and *G. inopinatum* from the Turgai region, Kazakhstan (Borissiak and Belyaeva, 1928; Göhlich, 1998, 2010)(Fig. 4), but is morphologically similar to the type of process that is present in *G. productum*. Thus, except for the shape of the coronoid process, the Ganchiliang specimen is almost identical to *G. inopinatum*.

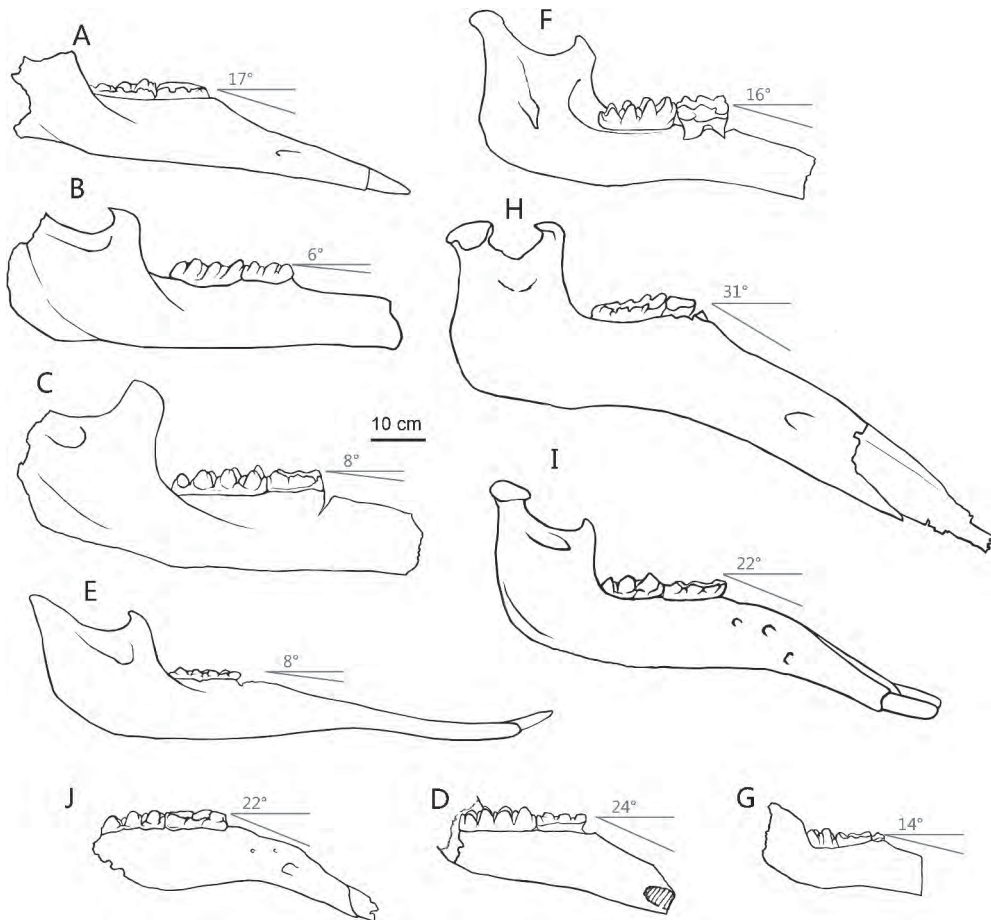


Fig. 4 Comparison among gomphothere mandibles

A. *Gomphotherium annectens*, Banjôburo, a cast of the holotype in MNHN; B. *G. inopinatum*, Turgai, 1401/606–607 (holotype), after Borissiak and Belyaeva, 1928; C. *G. inopinatum*, Ganchiliang, IVPP V 18700; D. *G. connexum*, Xining, cast of PMU-M 3047 (holotype); E. *G. angustidens*, En Péjouan, cast of MNHN SEP137; F. *G. subtapiroideum*, Sandelzhausen, BSP1959 II 384, after Göhlich, 2010; G. *G. wimani*, Nanyucun, LZU201002, after Wang et al., 2013a; H. *G. steinheimense*, Mühlendorf, BSP1971/275, after Göhlich, 1998; I. *G. productum*, AMNH10582, after Osborn, 1936; J. *G. browni*, AMNH19417 (holotype), after Osborn, 1926. Angles accompanying drawings represent symphyseal deflection. Except in G, all mandibles represent adults.

B and I are horizontally reversed. D and F are in medial view, and all others are in lateral view



Tassy (1985) subdivided *Gomphotherium* into the “*Gomphotherium annectens* group” (including *G. annectens*, *G. sylvaticum*, and *G. cooperi*), representing an “archaic” type of *Gomphotherium*, and the purportedly aberrant “*Gomphotherium angustidens* group” (*G. angustidens*, *G. subtapiroideum*, and *G. inopinatum*). Furthermore, Sanders et al. (2010) postulated a “‘pygmy’ *Gomphotherium* group” including the African species *G. pygmaeus*. Because of the presence of a synapomorphy—a subcircular cross-section of the lower tusks—the remaining species (*G. productum*, *G. browni*, and *G. steinheimense*) seemingly constitute another natural group of *Gomphotherium*, and I refer to them here as the “*Gomphotherium productum* group”. It will be informative to compare the tooth crown patterns of different groups in *Gomphotherium* to that of the Ganchiliang specimen. Furthermore, I provisionally assign the Chinese species *G. connexum* to the “*Gomphotherium angustidens* group” and *G. wimani* to the “*Gomphotherium productum* group” based on preliminary comparisons of tooth crown morphology (for detailed reasons given below).

The Ganchiliang specimen exhibits more plesiomorphies in tooth crown morphology than members of the “*Gomphotherium productum* group”, in which the interlophids are anteroposteriorly compressed by the rounded cusps of pre- and posttrite half lophids rather than relatively open as in the Ganchiliang specimen. Some derived crown features, such as posttrite central conules, subdivision of the posttrite half lophids, and a pentalophodont m3, are occasionally or often present in the “*Gomphotherium productum* group” (Göhlich, 1998; Hopwood, 1935; Osborn, 1926, 1936; Tassy, 1985; Tobien, 1972, 1973a; Tobien et al., 1986). However, none of these structures can be observed in the Ganchiliang specimen.

The Ganchiliang specimen has relatively open interlophids and rounded main cusps, similar to members of the “*Gomphotherium annectens* group.” In all taxa of the “*Gomphotherium annectens* group”, the anterior pretrite central conules of the lower molars are seemingly poorly developed (Osborn, 1932, 1936; Tassy, 1977, 1985, 1994), but these structures are relatively strongly developed in the Ganchiliang specimen. In the “*Gomphotherium annectens* group” the tooth crowns are more rounded and their boundaries are less clear than in the Ganchiliang specimen. Furthermore, in the Ganchiliang specimen the fourth lophid of m3 is poorly developed as in *G. annectens*, in contrast to the well-developed fourth lophid seen in *G. cooperi* and *G. sylvaticum* (Osborn, 1932, 1936; Tassy, 1977, 1985, 1994).

The systematic position of *G. pygmaeus* is debated (Osborn, 1936; Tobien, 1973a; Roger et al., 1994; Pickford, 2004; Sanders et al., 2010), with this species typically either assigned to *Choerolophodon* or regarded as a *nomen dubium*. However, Sanders et al. (2010) considered *G. pygmaeus* to belong to a distinct “‘pygmy’ *Gomphotherium* group”, and *G. pygmaeus* is indeed very small (Fig. 5; Table 3). Furthermore, in this species the interlophids are relatively compressed and covered by strong cementum. These characters clearly distinguish *G. pygmaeus* from the Ganchiliang specimen.

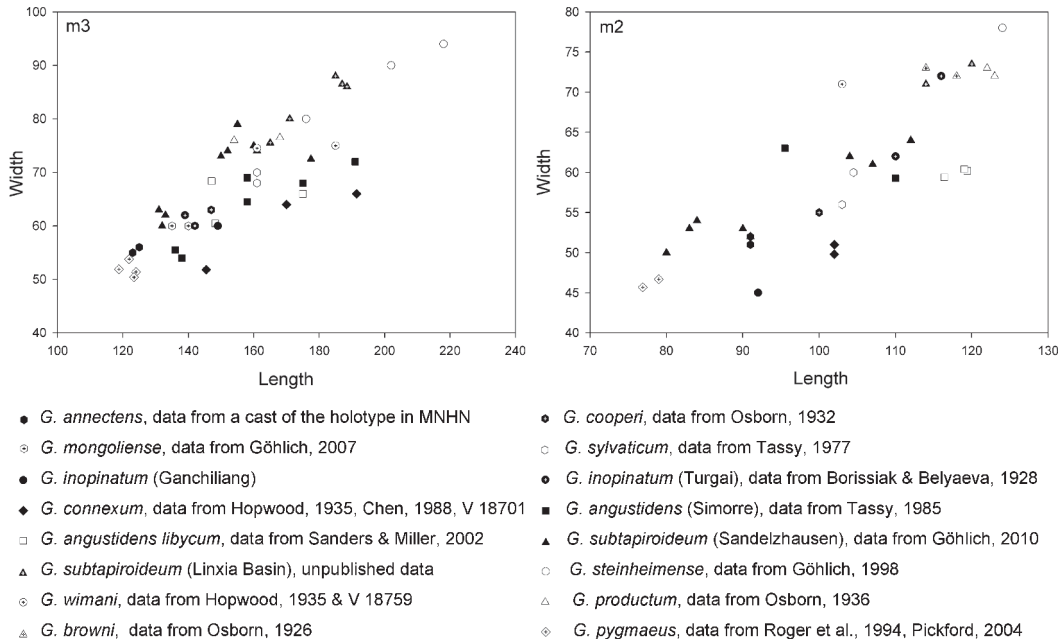


Fig. 5 Scatter plots showing the proportions of m2 and m3 in various *Gomphotherium* species

In the “*Gomphotherium angustidens* group”, the Ganchiliang specimen differs from *G. angustidens* and *G. connexum* in having relatively open interlophids and low central conules (Hopwood, 1935; Tassy, 1985, Tobien et al., 1986). The Ganchiliang specimen has open interlophids resembling those of *G. subtapiroideum*, but in *G. subtapiroideum* the lophids (especially the posttrite half lophids) are generally more anteroposteriorly compressed than in the Ganchiliang specimen (Göhlich, 2010; Schlesinger, 1917). Some derived features, such as subdivisions of both the posttrite half lophids and the pretrite central conules, are often present in the cheek teeth of *G. subtapiroideum* (Schlesinger, 1917; Göhlich, 2010). However, these features are definitely lacking in the Ganchiliang specimen.

The Ganchiliang specimen resembles *G. inopinatum* from the Turgai region, Kazakhstan, in lower cheek tooth morphology and other mandibular features. The m3 is almost identical in both cases. Only the third anterior pretrite central conule exists in the Ganchiliang specimen (although it is fairly weak), whereas even this conule is absent in the holotype of *G. inopinatum* (Borissiak and Belyaeva, 1928). This is a small and probably unimportant variation compared to others existing in *Gomphotherium*. The two specimens are also close in m2 structure, though the Ganchiliang specimen is slightly larger and has a smaller m2 (Fig. 5; Table 3). Despite these minor differences, there appears to be no clear basis for assigning these specimens to different species.

Another species that should be mentioned is *Gomphotherium mongoliense* from the Lower Miocene of Loh, Mongolia. The holotype comprises a series of teeth including the left

**Table 3** Measurements of the cheek teeth of various *Gomphotherium* species (mm)

	m2			m3		
	Length	Width	Index <sup>1)</sup>	Length	Width	Index <sup>1)</sup>
<i>G. annectens</i> <sup>2)</sup>	91–91	51–52	56.0–57.1	123–125	55–56	44.7–44.8
<i>G. cooperi</i> <sup>3)</sup>	100	55	55.0	147	63	42.9
<i>G. mongoliense</i> <sup>4)</sup>	—	—	—	135–140	60–60	42.9–44.4
<i>G. sylvaticum</i> <sup>5)</sup>	103–104.5	56–60	54.4–57.4	161–161	68–70	42.2–43.5
<i>G. inopinatum</i> <sup>6)</sup>	92–116	45–72	48.9–62.1	139–149	60–62	42.3–44.6
<i>G. connexum</i> <sup>7)</sup>	102–102	49.8–51	48.8–50.0	145.5–191.5	51.8–66	34.4–37.6
<i>G. angustidens</i> (Simorre) <sup>8)</sup>	95.5–110	59.3–63	53.9–66.0	136–191	54–72	37.7–43.7
<i>G. angustidens libycum</i> <sup>9)</sup>	116.4–119.4	60.2–59.4	50.4–51.0	147.1–175	60.5–68.4	37.7–46.5
<i>G. subtapiroideum</i> (Sandelzhausen) <sup>10)</sup>	80–112	50–64	57.1–64.3	131–177.5	60–79	40.8–51.0
<i>G. subtapiroideum</i> (Linxia Basin) <sup>11)</sup>	114–120	71–73.5	61.3–62.3	165–188.5	75.5–88	45.6–47.6
<i>G. steinheimense</i> <sup>12)</sup>	124	78	62.9	176–218	80–94	43.1–45.5
<i>G. wimani</i> <sup>13)</sup>	103	71	68.9	161–185	74.5–75	40.5–46.3
<i>G. productum</i> <sup>14)</sup>	122–123	72–73	58.5–59.8	154–168	76–76.5	45.5–49.4
<i>G. browni</i> <sup>15)</sup>	114–118	72–73	61.0–64.0	—	—	—
<i>G. pygmaeus</i> <sup>16)</sup>	76.9–79	45.7–46.7	59.1–59.4	118.8–124	50.4–53.8	40.8–43.7

1) Index =  $100 \times \text{Width/Length}$ ; 2) data from a cast of the holotype in MNHN; 3) data from Osborn, 1932; 4) data from Göhlich, 2007; 5) data from Tassy, 1977; 6) data from Borissiak and Belyaeva, 1928 and the present article; 7) data from Hopwood, 1935, Chen 1988, and IVPP V 18701; 8) data from specimens in MNHN; 9) data from Sanders and Miller, 2002; 10) data from Göhlich, 2010; 11) unpublished data; 12) data from Göhlich, 1998; 13) data from Hopwood, 1935 and IVPP V 18759; 14) data from Osborn, 1936; 15) data from Osborn, 1926; 16) data from Pickford, 2004 and Roger et al., 1994.

upper DP4–M2, in addition to a right upper M3<sup>1)</sup>). Göhlich (2007) reported another two m3 teeth referable to the species. This species is generally primitive but nevertheless displays some aberrant features, perhaps explaining why it has been considered *incertae sedis* by some authors (Shoshani and Tassy, 1996; Tassy, 1985). The cusps of the half loph(id)s are even more robust than those in *G. annectens* (also more robust than *G. inopinatum*), and the interloph(id)s are compressed as a result of expansion of the loph(id)s. The pretrite central conules are anteroposteriorly compressed, and in the upper cheek teeth they are distant from the median

1) The anatomical positions of these teeth are controversial. Osborn (1924:1) published them as right lower dp4 (?p4), m2, m3, and left lower m1; Tobien (1973a:213) considered them right lower dp4–m3; Göhlich (2007:273) considered them left dp4 and m1, and right m2 and m3; while Tassy (1985:710) considered them upper teeth. Here I agree with Tassy (1985) because the teeth are short and broad, and because the pretrite half lophs are anteriorly displaced relative to the corresponding posttrite half lophs. I consider the M2 to be from the left side, because the strong anterior central conule in the first loph resembles the corresponding one in the M3. Thus this should be a synapomorphy of the species rather than an enamel cusp on the posterior cingulum.

sulcus. The mesoconelets are also strong. The first anterior pretrite central conules of the upper cheek teeth are extremely large, being equal in size to the first pretrite main cusps. These features are distinct from *G. inopinatum*. As Göhlich (2007) proposed, this species should be attributed to the “*Gomphotherium annectens* group.”

### 3.2 On Chinese *Gomphotherium*

*Gomphotherium* specimens from China have not been extensively studied, and require further attention. Because of its primitive morphology, *Gomphotherium* is considered to represent the ancestral stock of many derived proboscideans, such as Cuvieroniinae, tetralophodont gomphotheres, Stegodontinae, and true elephantids (Shoshani, 1996; Tassy 1982, 1988, 1996b). A great contribution was made by Tobien et al. (1986), who considered 20 putative species and concluded that only the three listed ones were valid (i.e., *G. connexum*, *G. wimani*, and “*G. shensiensis*”) from nearly 20 established species (Chow and Zhang, 1974). However, no detailed evaluation of the phylogenetic relationships among these species has ever been carried out, possibly because these Asian forms display some features that appear aberrant in the light of comparisons with their contemporaneous European cousins. *Gomphotherium inopinatum* is clearly the most basal species so far reported from China, but it will be helpful to further discuss the phylogenetic relationships among the Chinese species.

The basic crown pattern of *G. inopinatum* is primitive, and comparable to the pattern in the “*Gomphotherium annectens* group.” However, features of the upper and lower tusks (i.e., torsion in the upper tusks with slightly spiral enamel bands, and a ventral groove in the lower tusks) found at the type locality (Borissiak and Belyaeva, 1928) indicate that *G. inopinatum* is related to *G. angustidens* and *G. subtapiroideum*. *G. inopinatum* is probably the most basal member of the “*Gomphotherium angustidens* group” (Tassy, 1985). Tassy (1977, 1985) considered “*G. subtapiroideum*” either a morphotype or a subspecies of *G. angustidens*, and a potential candidate for the ancestor of typical *G. angustidens*. However, some derived features, such as subdivided posttrite half lophids and the presence of anterior and posterior pretrite central conules, often occur in *G. subtapiroideum* (Göhlich, 2010; Schlesinger, 1917). These features weigh against the interpretation that *G. subtapiroideum* is a primitive form of *G. angustidens*. Like the Ganchiliang specimen, *G. subtapiroideum* occurs in the Linxia Basin. However, *G. subtapiroideum* occurs in a higher horizon—the Hujialiang Formation—and is contemporary with *Platybelodon grangeri* (unpublished data). This formation corresponds to MN7/8, the late Middle Miocene (Deng et al., 2013)(Fig. 6). *G. subtapiroideum* from China has a larger m3 than that in European specimens (Fig. 5; Table 3). Therefore, *Gomphotherium angustidens* and *G. subtapiroideum* may have evolved in divergent directions—in the former the interloph(id)s became compressed and rounded cusps were retained, whereas in the latter the lo-ph(id)s became compressed and the cusp summits became divided. Because *G. inopinatum* exhibits moderately open interloph(id)s, it is likely to be the ancestor of both *G. angustidens* and *G. subtapiroideum*.

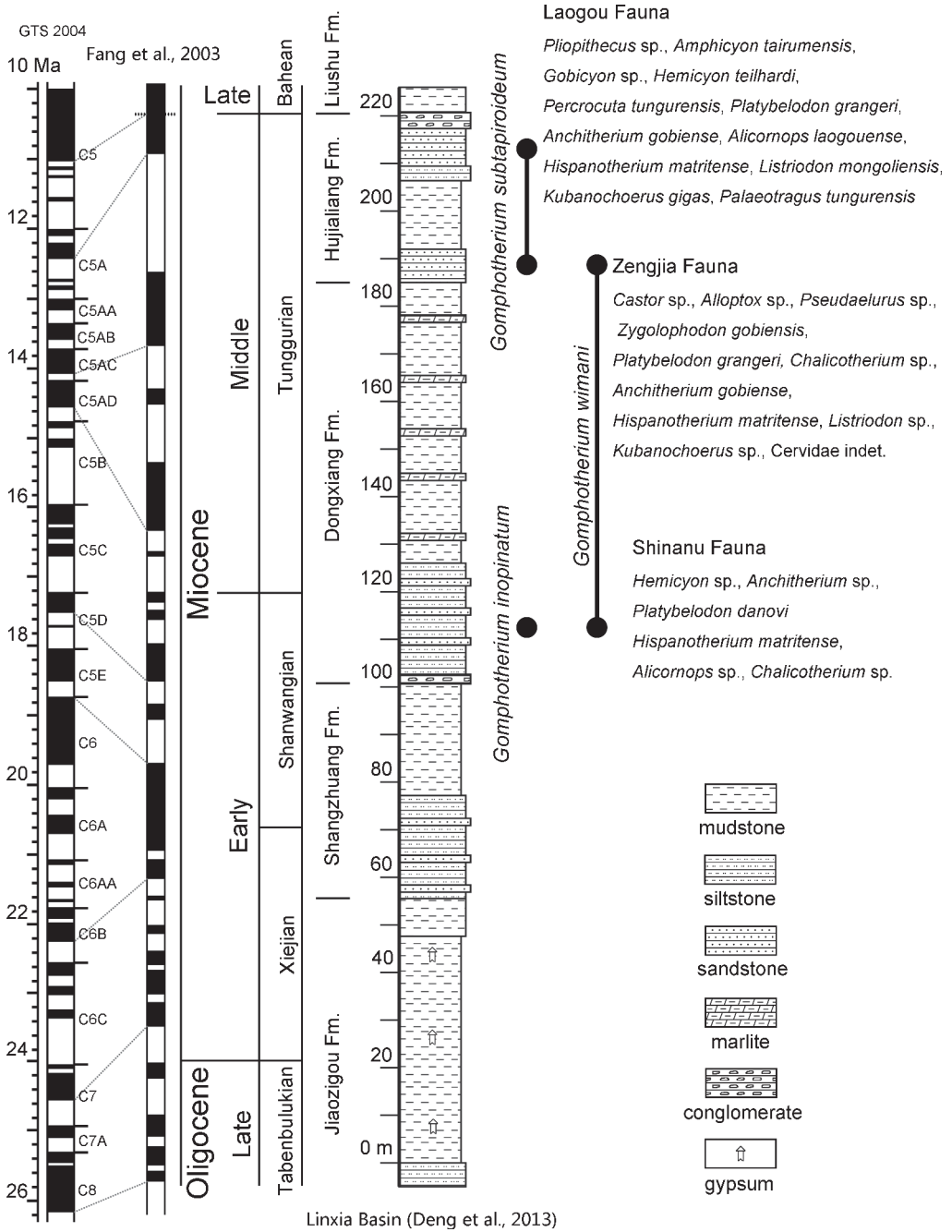


Fig. 6 Partial stratigraphic section of the Linxia Basin (after Deng et al. 2013, revised), showing the distribution of *Gomphotherium* in the Linxia Basin

*Gomphotherium wimani* has been considered an advanced form of *Gomphotherium* from the Middle Miocene of China (Hopwood, 1935; Tobien et al., 1986; Wang et al., 2013a). I align it with the “*Gomphotherium productum* group” based on the fact that it displays a tendency toward elaboration (presence of posttrite central conules, subdivision of posttrite half lophids) and subhypsodonty of the molars, but no tendency to widen the interloph(id)s (Tobien et al., 1986; Wang et al., 2013a). However, the symphysis and lower tusk of this species are still unknown. In the Linxia Basin, the stratigraphic range of *G. wimani* extends from the Dongxiang Formation to the Hujialiang Formation (unpublished data), so this species overlapped temporally with both *G. inopinatum* and *G. subtapiroideum* (Fig. 6).

Another “advanced form” of *Gomphotherium* in China considered by Tobien et al. (1986) was “*G. shensiensis*”, represented only by a fragmentary cranium with M2 and M3 from the Middle Miocene Lengshuigou Formation (possibly corresponding to MN6 or later)(Chang and Zhai, 1978; Qiu and Qiu, 1995). The interloph(id)s of the teeth are moderately open, and the posttrite half lophs are anteroposteriorly compressed and subdivided. The first posterior pretrite central conule (more properly termed the posterior crescentoid; Tobien, 1975) is triplicated, increasing the morphological complexity of the occlusal surface. In these features “*G. shensiensis*” is almost identical to the type specimen of *G. subtapiroideum* (Schlesinger, 1917: pl. 7, fig. 3), but in “*G. shensiensis*” the cusps on the pretrite half lophs are slightly more robust. The second anterior pretrite central conule is very strongly developed and is not subdivided, but the posterior central conule has been lost, in contrast to the condition in the holotype of *G. subtapiroideum*. The cementum is relatively heavy. Despite these differences, I consider “*G. shensiensis*” to be a variety of *G. subtapiroideum*. Tobien et al. (1986) considered “*G. shensiensis*” to lack enamel bands on the upper tusk. However, this conclusion is not reliable, as the only known pair of upper tusks of “*G. shensiensis*” is very fragmentary in that only the most proximal part is preserved.

The remaining “archaic” form of *Gomphotherium* in China is *G. connexum* from the Miocene (Hopwood, 1935; Tobien et al., 1986). This species resembles taxa from the “*Gomphotherium annectens* group” in that the tooth cusps are slightly more robust, and in that the lower molars lack anterior pretrite central conules. However, the molars also display some derived features. The interloph(id)s are less open than *G. subtapiroideum* and *G. inopinatum*, as in *G. angustidens*. The m3 is very narrow, and indeed is narrower than in *G. angustidens* (Fig. 5; Table 3). The posterior pretrite central conules of the upper molars are more strongly developed than the anterior ones, a feature that is clearly characteristic of *G. angustidens*. Thus, *Gomphotherium connexum* may be close related to *G. angustidens*, and represent another member of the “*G. angustidens* group”. This taxon is more specialized than the European *G. angustidens* in having extremely narrow molars, but other derived features are seemingly less well developed than in the European *G. angustidens*. Chen (1988) referred specimens from the Halamagai Formation of the northern Junggar Basin to “*G. cf. shensiensis*” and *Gomphotherium* sp. In my view, most if not all of these specimens should be attributed to

*G. connexum*, because they resemble the holotype of this taxon in the narrowness of the m3 (Fig. 5; Table 3) and the presence of strongly developed second posterior pretrite central conules (sometimes duplicated) in most examples of M3. However, no second posterior pretrite central conule is present in the type specimen of “*G. shensiensis*”. The posttrite half lophs of these Junggar specimens are not subdivided. The Junggar specimens were discovered in sandstones at the bottom of the Halamagai Formation, corresponding to MN5 and MN6 (Ye et al., 2012).

#### 4 Conclusion

A new *Gomphotherium* specimen from the upper Lower Miocene of the Ganchiliang locality shows important resemblances in mandibular and dental morphology to *G. inopinatum* from the Turgai region. The new specimen can therefore be referred to *G. inopinatum*, which represents the most basal *Gomphotherium* species known from China.

In “*Gomphotherium angustidens* group”, *G. subtaapiroideum* and *G. angustidens* represent distinct branches. Both species are seemingly derived from *G. inopinatum*.

Among Chinese species, *Gomphotherium wimani* represents a derived form and is probably closely related to the European *G. steinheimense*. *G. connexum* seems to be a true member of the “*Gomphotherium angustidens* group”, given its morphological resemblance to undoubted group members. “*Gomphotherium shensiensis*” may represent a variety of *G. subtaapiroideum*.

**Acknowledgements** I thank U. Göhlich and P. Tassy for much help in comparing European specimens and providing literature; Qiu Zhan-Xiang, Chen Guan-Fang, Deng Tao, Ye Jie, and Zheng Jia-Jian for useful advice and all kinds of help; C. Sullivan for improvement of English writing; Su Dan for preparing the specimen.

## 中国最原始的嵌齿象——意外嵌齿象(*Gomphotherium inopinatum*) 在临夏盆地的发现兼论中国的嵌齿象

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**摘要:** 临夏盆地下中新统的甘池梁地点发现了一件残破下颌带有m2和m3齿列。在齿列前方, 其水平支伸长, 并且不向下转折或倾斜。下颌角位置较低。颊齿小, 冠面结构特征原始。齿谷在前后方向宽度中等, 副齿柱侧及主齿柱中心小尖不分裂, 副齿柱中心小尖不发育。这些特征与哈萨克斯坦图尔盖地区早中新世的意外嵌齿象(*Gomphotherium inopinatum*)相同, 应归为该种。这是该种在中国的首次报道, 并且是中国发现的最原始的种。进一

步讨论了中国的嵌齿象各种的系统关系。维曼嵌齿象(*G. wimani*)代表了一种在欧亚大陆东部发现的进步类型,可以与欧洲的施泰因海姆嵌齿象(*G. steinheimense*)相联系。间型嵌齿象(*G. connexum*)则似乎是属于真正的“狭齿嵌齿象类群”,因为其与狭齿嵌齿象(*G. angustidens*)的颊齿具有相似性。亚似獬型嵌齿象(*G. subtapiroideum*)或许代表了一个与狭齿嵌齿象不同的分支,而陕西嵌齿象(“*G. shensiensis*”)则可能是其中的一种变异。

关键词: 欧亚大陆, 中国, 中新世, 意外嵌齿象, 狭齿嵌齿象类群, 系统发育

中图法分类号: Q915.878 文献标识码: A 文章编号: 1000-3118(2014)02-0183-18

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