

An Asian origin for *Sinomastodon* (Proboscidea, Gomphotheriidae) inferred from a new Upper Miocene specimen from Gansu of China

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We report a fossil specimen referable to *Sinomastodontinae* gen. et sp. indet. from the Neogene strata at Yanghecun locality, Xihe County, Gansu Province, China. The specimen is characterized by a brevirostrine mandible, complete pretrite trefoils, and relatively simple posttrite half lophids, showing typical features of *Sinomastodon*. It differs from the other known species of *Sinomastodon* by the following features: relatively short and wide m3 due to fewer lophid numbers, less inflated pretrite accessory central conules, poorly developed secondary trefoils and cementum, and relatively strong cingulid. All of these features indicate a bias towards pleisiomorphies of *Sinomastodon*, implying that this specimen is more ancestral than any known species of *Sinomastodon*. The symphysis of the new specimen is relatively long, which differs from the typical brevirostrine *Sinomastodon*, and thus we consider it a gen. et sp. indet. in the Subfamily *Sinomastodontinae*. In addition, the horizon in which the present specimen was found probably represents the Upper Miocene because it is lower than Pliocene strata yielding *Hipparion* (*Proboscidipparon*) *pater*. Generally, *Sinomastodon* is considered to have migrated from North America at about the time of the Miocene/Pliocene boundary, and to have been derived from a certain clade of American gomphotheres. However, the discovery of the Yanghecun specimen verifies that *Sinomastodon* lived in East Asia during the Late Miocene, and probably derived from Old World gomphotheres (e.g., *G. wimani*). The similarity between the members of the Subfamilies *Sinomastodontinae* and those of *Cuvieroninae* is suggested to have been the result of parallel evolution.

***Sinomastodon*, gomphotheres, *Sinomastodontinae*, *Cuvieroninae*, East Asia, biostratigraphy**

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The terminal taxon of the Old World gomphotheres—*Sinomastodon* Tobien et al., 1986—is distributed over East and Southeast Asia from the Late Miocene to the Middle(?) Pleistocene (Tobien et al., 1986; Zong et al., 1989; Chen, 1999; Kamei, 2000; Thasod et al., 2005; Wang, 2011; Wang et al., 2012). This genus possesses typical gomphotheriid bunobrachyodont cheek teeth, but is characterized by the

following features: a high-arched cranium, enamel-less and dorsally concave (in lateral view) upper tusks, and a brevirostrine mandible without lower tusks. These elephantid-like features clearly distinguish *Sinomastodon* from the other Old World gomphotheres. However, they are convergent with members of the New World Subfamily *Cuvieroninae* from the Early Pliocene to the Late Pleistocene.

The general view is that *Sinomastodon* originated from a North American taxon of *Cuvieroninae* that migrated into

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East Asia via the Bering Strait Land Bridge during the Late Neogene. This view was first presented by Tobien et al. (1986) when this genus was established, and then was adopted by many subsequent researchers (Zong et al., 1989; Flynn et al., 1991; Saegusa, 2011). However, the earliest cuvieroniines—*Stegomastodon* Pohlig, 1912—was contemporary to or only slightly later than *Sinomastodon* (Fisher, 1996; Lambert, 1996). Prodo and Alberdi (2008) and Wang (2011) considered that *Sinomastodon* and members of Subfamily Cuvieroniinae share the same North American ancestor (although not direct), *Rhynchotherium* Falconer, 1868. Recently, this American origin of *Sinomastodon* has been questioned by others (Chen, 1999; Cozzuol et al., 2012; Lucas, 2013).

Studies on *Sinomastodon* have had a long history. Teilhard de Chardin and Trassaert (1937) established “*Mastodon*” *intermedius* based on partial material from the Late Tertiary of the Yushe Basin, Shanxi Province. The holotype is a complete mandible with a moderately worn m3. Chang (1964) transferred this species into *Zygalophodon* Vacek, 1877. Tobien et al. (1986) believed that “*Mastodon*” *intermedius* from the Yushe Basin was phylogenetically interrelated to New World Cuvieroniinae and regarded it as the type species of their new genus *Sinomastodon*. They attributed other species to *Si. intermedius*, including *Trilophodon* cf. *wimani* Teilhard de Chardin et Trassaert, 1935, and *Tr. cf. spectabili* Teilhard de Chardin et Trassaert, 1935, from the Yushe Basin, as well as *Tr. yangziensis* Chow, 1959, *Tr. guangxiensis* Chow, 1959, *Tr. wufengensis* Pei, 1965, *Tr. serridenstoides* Pei, 1974, *Tetralophodon sinensis* (Koken, 1885), *Te. liuchengensis* Pei, 1974, and *Rhynchotherium huananensis* Chow et Chang, 1974 from the Early Pleistocene of South China (Tobien et al., 1986). Soon afterwards, Zong (1987) and Zong et al. (1989) established two new species—*Si. yanyuanensis* Zong, 1987 and *Si. hanjiangensis* Zong et al., 1989. The cranium of the latter also was discovered, which revealed that the cranial features of *Sinomastodon* are elephantid-like. Zong et al. (1989) also defined *Sinomastodon* to include the following species: *Si. intermedius*, *Si. wufengensis*, *Si. yangziensis*, *Si. guangxiensis*, *Si. serridenstoides*, *Si. huananensis*, *Si. wimani*, *Si. liuchengensis*, and *Si. Yanyuanensis*. Chen (1999) further studied *Sinomastodon*. She referred several previously described species to *Si. intermedius*, including *Tr. cf. wimani*, *Tr. cf. spectabili*, and “*Mastodon*” *intermedius*; the previously described *Si. yanyuanensis*, *G. yongrenensis* Zhang, 1980, and *R. huananensis* to *Si. hanjiangensis*; and the previously described *Tr. yangziensis*, *Tr. guangxiensis*, *Tr. wufengensis*, and *G. serridenstoides* to *Si. yangziensis*. *Sinomastodon* was also reported from outside of China. Kamei (2000) transferred *Tr. sendaicus* Matsumoto, 1924, from Sendai, Japan, into *Si. sendaicus*. Thasod and Ratanasthien (2005) established *Sinomastodon* sp. A and *Sinomastodon* sp. B from the Tha Chang Sandpits, Thailand. Wang (2011) systematically studied Chinese *Sinomastodon*

in his doctoral dissertation, and accepted the basic classification of *Sinomastodon* by Chen (1999). Furthermore, Wang et al. (2012) established a new species *Si. jiangnanensis* Wang et al., 2012, based on the material from Renzidong Cave, Fanchang, Anhui Province, and put *Sinomastodon* in their new Subfamily Sinomastodontinae.

In 1999, the second author of this paper discovered an almost complete gomphotheriid mandible in his field work. Unfortunately, most part of the specimen has been lost. Only the right hemimandible carrying m2 and m3, as well as an unclear photo (Figure 1), is preserved. In 2007, the third author of this paper (Xie, 2007) published this specimen under the name *Sinomastodon intermedius*. Recently, we restudied and reevaluated this specimen, and confirmed that the tooth of the specimen shows more ancestral features than any known primitive *Sinomastodon* (i.e., *Si. intermedius* and *Si. sendaicus*), and the mandibular symphysis of the specimen is moderately elongated (only based on the observation from the original photo), and thus might represent an intermediate form between longirostrine *Gomphotherium* and brevirostrine *Sinomastodon* (and here we considered it Sinomastodontinae gen. et sp. indet.). Furthermore, based on a field survey, we infer that the age of the Yanghecun specimen from the locality is probably Baodean (Chinese Neogene Land Mammal Age) of the Late Miocene or even earlier. Thus, the Yanghecun specimen is important with respect to the study of the origin, evolution, and paleogeographic distribution of *Sinomastodon*, which is an important member of the Pliocene and Early Pleistocene

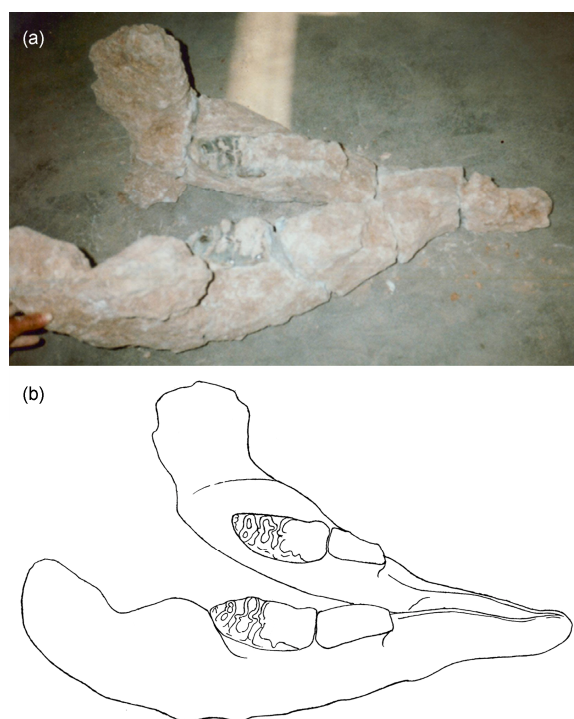


Figure 1 The original record of the Yanghecun specimen. (a) The original photo; (b) a reconstructed pencil sketch based on (a).

fauna in East Asia.

Descriptions of occlusal structures of gomphotheriid cheek teeth follow Tassy (1996).

Institutional abbreviations. GIOTC=Gansu Industrial Occupational Technology College, collection; IVPP=Institute of Vertebrate Paleontology and Paleoanthropology, vertebrate collection; THP=Tianjin Natural History, vertebrate collection.

1 Geological setting

The specimen was discovered from the Neogene strata at Yanghecun locality, Changdao Township, Xihe County (35°08'38.1"N, 105°20'29.1"E, 1706 m; Figure 2), which is situated in the middle of the Xihe-Lixian Basin in the West Qingling fold belt. Based on the geological map relevant to the study area (Regional Geological Survey Team, 1968), strata in the central Xihe-Lixian Basin are composed of the middle member of the Xihanshui Group of Middle Devonian age, as well as unnamed Paleogene, Neogene, and Quaternary deposits. The middle member of the Xihanshui Formation consists of beds of argillaceous-carbonate that make up part of the basement of the Xihe-Lixian Basin. The

Paleogene consists of fluviolacustrine deposits of brownish-red, red, and purplish-red coarse sandstone, conglomerates, and breccias, as well as impure mudstones, partially intercalated with volcanic rock. The Neogene consists of basinal accumulations of terrestrial red beds and mudstone unconformably overlying the Paleocene or Devonian strata. The Neogene is up to 1000 m thick, and can be subdivided into an upper and a lower member. The lower member consists of poorly preserved, diagenetically altered red beds and mudstone intercalated with conglomerates and sandy conglomerates, which grade upward to a suite of grey and light-grey mudstone of the upper member. The Quaternary consists of light-yellow sandy solum and clay, which overlies the Neogene or Devonian strata.

Based on our field work around the Yanghecun locality, the Devonian, Neogene and Quaternary strata are exposed to the north and south of the Yanghecun locality. The Neogene, consisting of the Upper Miocene and Pliocene strata, is composed of brownish-red silty mudstone and mudstone, partially intercalated with conglomerates, sandy conglomerates, and coarse sandstones. The Upper Miocene is distributed in a band in a gully (Figure 2), unconformably overlying the Xihanshui Group (Middle Devonian). It is also exposed on the gully and hillsides north and south of the

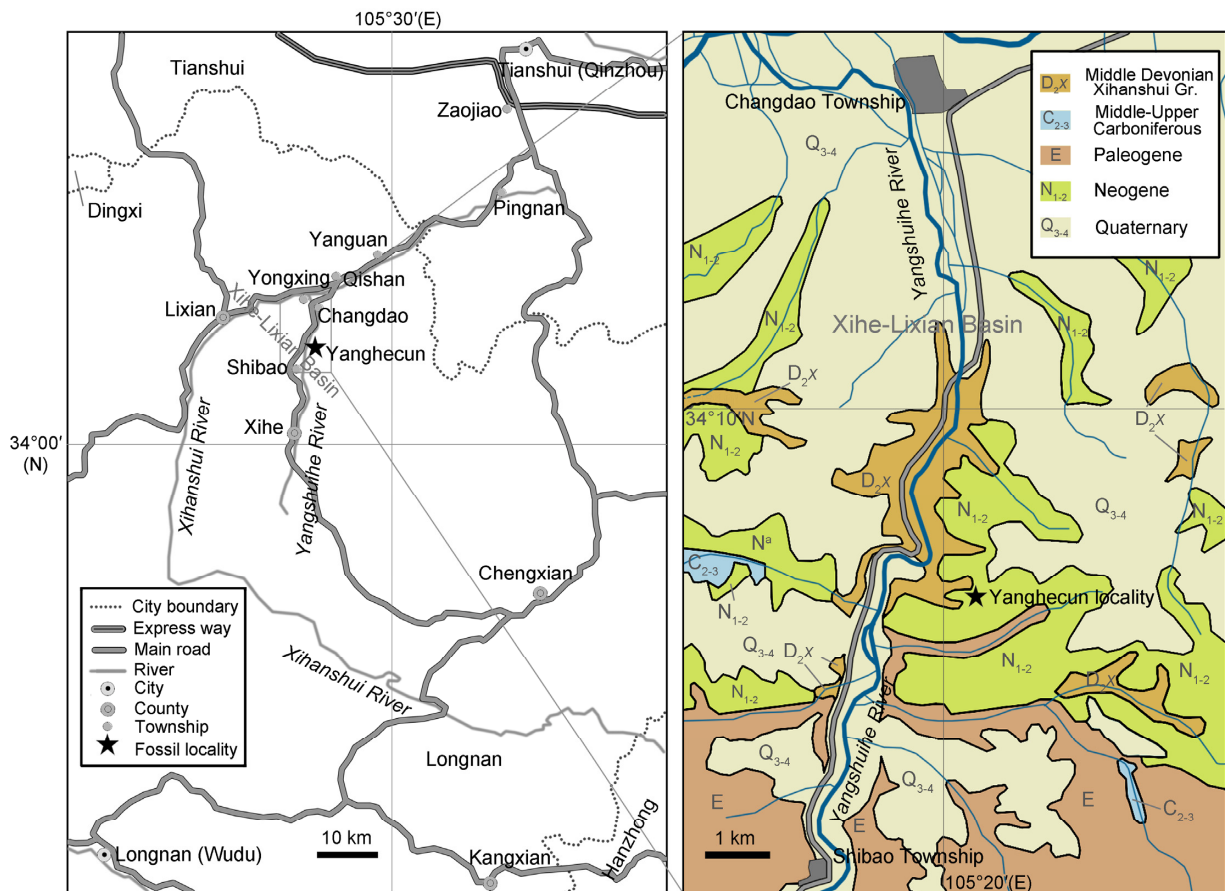


Figure 2 Geographic location of the Yanghecun site and geological map of the neighboring area.

Yanghecun locality. In contrast, the Pliocene is well exposed on the ridges. Controlled by the faulting developed in the Xihanshui Group, the brownish mudstone (palaeosol) in the lower part of the Upper Miocene is in almost continuous contact with light-grey and grayish-green sandstones and marl of the Xihanshui Group. The breccias at the base of the Upper Miocene are exposed only on the west side and close to the bottom of the gully. We infer that the Yanghecun locality is close to the margin of the depositional basin, and represents a narrow arm of a paleolake, constituting fine sandstone and marl of the Xihanshui Group, which resulted in the banded distribution of the Upper Miocene deposits.

Description of the Yanghecun section (Figure 3):

Quaternary

12 Late Pleistocene loess and modern soil; top not exposed

~~~~~Discontinuity~~~~~

Neogene

total thickness 219.4 m

Pliocene

11. Brownish-red massive silty mudstone interbedded with mudstone, calcareous muddy granules are abundant in silty mudstone. 12.1 m

10. Middle layers of light-grey caliche composed of calcareous muddy granules. 0.4 m

9. Brownish-red silty mudstone intercalated with sandy-conglomerate and coarse-sandstone lenses of variable clast sizes. The largest lens is about 15 m in length. 1.5 m

8. Thick layers of silty mudstone containing abundant calcareous muddy granules (2–6 cm in diameter). The lower part of this horizon contains *Hipparion (Proboscidipparon) pater*. 8 m

7. Brownish-red massive silty mudstone interbedded with mudstone. 82 m

6. Brownish-red massive mudstone interbedded with silty mudstone with a layer of calcareous muddy granules (30 cm) close to the base. 9 m

—————Conformity—————

Upper Miocene

5. light brownish-red massive silty mudstone intercalated with thick to thin layers of grayish-green marl. The thickest layer is 1–7 cm in thickness and 2–3 m in length. This horizon contains abundant, irregular, calcareous muddy granules with diameters mainly of 2–3 mm and up to 4 cm. In pockets within silty mudstone, light-grey calcareous concretions and granule deposits of eluvial origin developed. This unit contains a small quantity of fragmentary gastropods. 11 m

4. Brownish-red massive silty mudstone partially intercalated with calcareous muddy granules with diameters of ~1 cm, and up to 2–4 cm for larger granules. At 60 m above the base of this horizon, *Sinomastodontinae* gen. et sp. indet. was found. 85 m

3. Brownish-red massive silty mudstone and mudstone intercalated with calcareous muddy granules of irregular size and shape. The sizes of the granules are mainly 1 mm, with some reaching 2–6 cm. 7.4 m

2. Black and brownish mudstone (palaeosol), containing coal, with long tapering gastropods. 2 m

1. Well-cemented light brownish-red massive limestone and

breccias. 1 m

~~~~~Discontinuity~~~~~

Middle Devonian

Light-grey and grayish-green massive marl. Base not exposed.

2 Systematic paleontology

Order Proboscidea Illiger, 1811

Family Gomphotheriidae Hay, 1922

Subfamily Sinomastodontinae Wang et al., 2012

Genus et species indeterminata

Figures 4–5 and Table 1

Sinomastodon intermedius Xie, 2007, p. 169, fig. 31

Material. GIOTC 0984-9-178, a fragmentary right lower

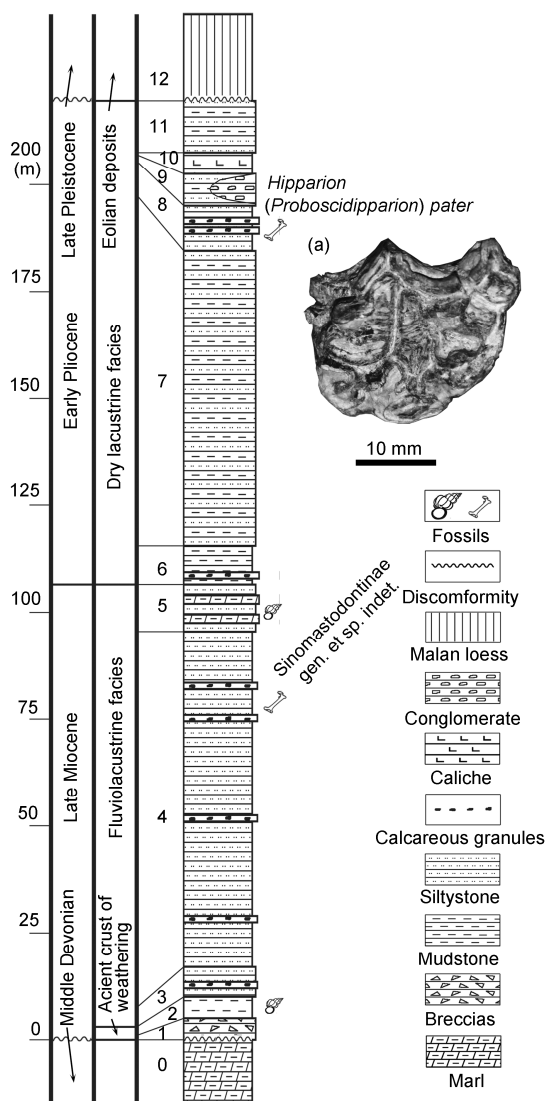


Figure 3 Composite stratigraphic column of the Yanghecun section, Xihe County. Inset panel (a), *Hipparion (Proboscidipparon) pater* (IVPP V18410), in occlusal view, discovered from the horizon 8.

hemimandible carrying fully worn m2 and moderately worn m3. A cast of the specimen (Num.: IVPP FV1967) is housed in IVPP.

Description (Figures 4 and 5). The horizontal ramus is strong with a rounded bottom surface, and laterally expanded in the posterior part, which is characterized as shortening of mandibular symphysis (Tobien, 1973). Based on the observation of the original photo, the mandibular symphysis is shorter than that in those typical trilophodont longirostrine gomphotheres, such as *Gomphotherim* and members of Amebelodontines; however, it is longer than that in any known species of *Sinomastodon*. The distal part of the mandibular symphysis is attenuated without mandibular tusks.

The m2 is broken from the anterior part and the remains have been worn to the tooth root without any observable

features. The moderately worn m3 is rectangular with a narrower posterior part and is composed of four lophids. The first lophid is completely worn out with some damage. The second lophid is deeply worn, and the enamel rings of pretrite and posttrite half lophids connect with each other. A trefoil pattern can be seen on the pretrite half lophid with relatively less inflated anterior and posterior accessory central conules, showing a bunodont rather than zygodont character. The pretrite posterior accessory central conule makes contact with the anterior accessory central conule of the third lophid, which blocks the second interlophid. The posttrite half lophid shows some damage with slightly anterior and posterior inflations of the mesoconelet, implying a rudimentary secondary trefoil. The third lophid is moderately worn. The pretrite half lophid tilts anteriorly towards

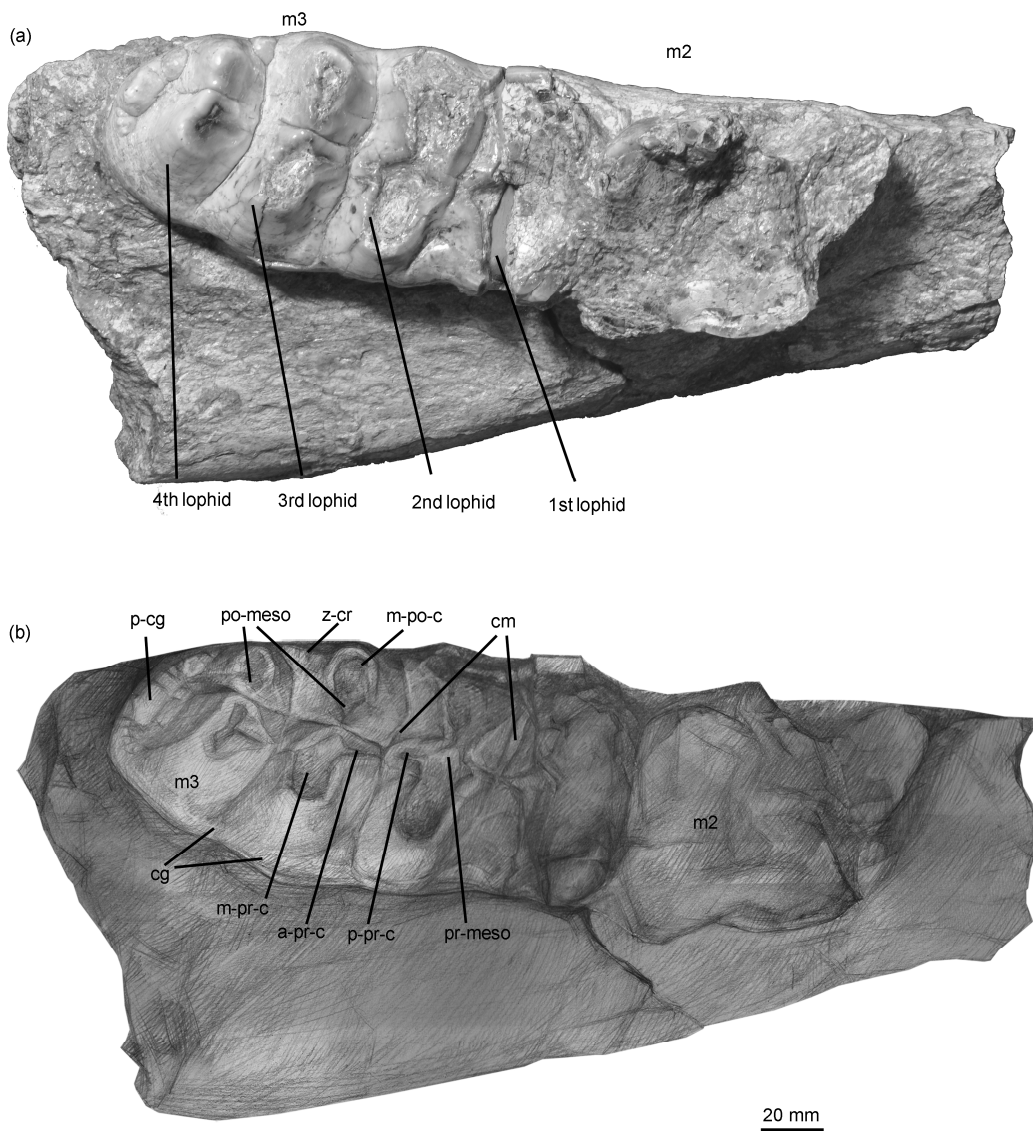


Figure 4 Right hemimandible of *Sinomastodontinae* gen. et sp. indet. (GIOTC 0984-9-178) in occlusal view. (a) Photo; (b) pencil sketch. a-pr-c, anterior pretrite accessory central conule; cg, cingulid; cm, cementum; m-po-c, main posttrite cusp; m-pr-c, main pretrite cusp; p-cg, posterior cingulid; p-pr-c, posterior pretrite accessory central conule; po-meso, posttrite mesoconelet; pr-meso, pretrite mesoconelet; z-cr, zygodont crest.

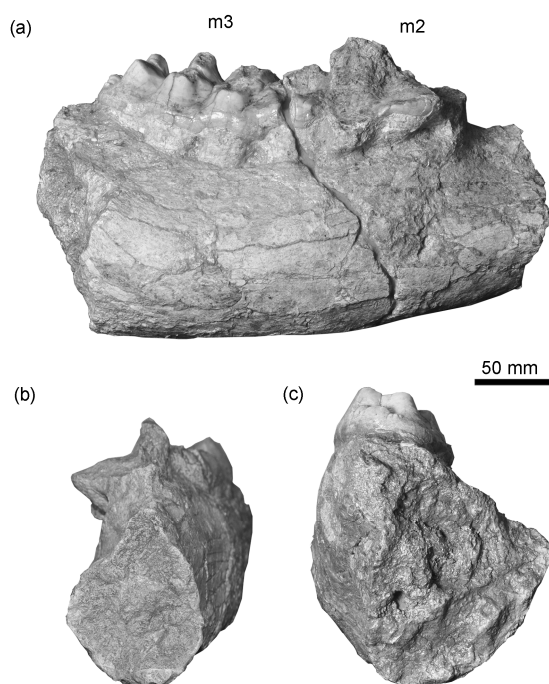


Figure 5 Right hemimandible of *Sinomastodontinae* gen. et sp. indet. (GIOTC 0984-9-178). (a) In lateral view; (b) in anterior view; (c) in posterior view.

the median sulcus. The posttrite half lophid is perpendicular to the median sulcus, which shows a slightly chevroning structure in the entire lophid. Apart from the pretrite anterior accessory central conule in contact with the posterior one of the second lophid, the posterior accessory central conule of the third lophid is weak, resulting in an open third interlophid. The posttrite half lophid shows an enamel ring composed of the main cusp and mesoconelet without accessory central conules. The zygodont crest is fairly weak,

but present. The fourth lophid is slightly worn, showing a somewhat chevroning structure. The pretrite mesoconelet and anterior accessory central conule are present, and without posttrite accessory central conule. The posttrite half lophid consists of a large main cusp and a small mesoconelet. A row of enamel conules (4–5) is arranged around the posterior margin of the tooth comprising the posterior cingulid. Although weak, the cingulid is also present on the buccal and lingual sides of the m3. A faint cementum is seen in the interlophids.

3 Discussion

The Yanghecun specimen from Xihe County, although fragmentary and worn, clearly belongs to *Sinomastodontinae*. The lateral expansion of the horizontal ramus suggests the shortening of mandibular symphysis (Tobien, 1973), and is rather different from the Eurasian longirostrines, such as *Gomphotherium* Burmeister, 1837, *Platybelodon* Borissiak, 1928, *Protanancus* Arambourg, 1945, *Stegotrabelodon*, Petrocchi, 1941, and “*Mastodon*” *grandincisivus* Schlesinger, 1917. In addition, although the structure of the m2 is unknown, the m3 has four lophids, distinct from *Tetralophodon* Falconer, 1857, *Stegolophodon* Schlesinger, 1917, and *Anancus* Aymard, 1855, in which the m3 has five or more lophids. Choerolophodony, ptychodony, and cementodony are either rudimentary or absent, also distinct from *Choerolophodon* Schlesinger, 1917, with strong choerolophodony, ptychodony, and cementodony. Furthermore, the specimen shows some convergent features with *Mammuth* Blumenbach, 1799, but differences from *Mammuth* include inflation of the pretrite accessory central conules blocking the interlophid, the rounded and separated posttrite main

Table 1 Measurements of the cheek teeth of various *Sinomastodontinae* species

| | Length (mm) | Maximal width (mm) | Width at the 1st lophid (mm) | Width at the 2nd lophid (mm) | Width at the 3rd lophid (mm) | Width at the 4th lophid (mm) |
|---|-------------|--------------------|------------------------------|------------------------------|------------------------------|------------------------------|
| <i>Sinomastodontinae</i> gen. et sp. indet. | 167 | 82.5 | 80.5 | 82.5 | 82 | 63.5 |
| | 180 | 82 | 82 | 79 | 82 | 78 |
| <i>Sinomastodon intermedius</i> | 186 | 86.5 | 75 | 82 | 86.5 | 79 |
| | 168 | 74.5 | 71 | 74.5 | 74 | 65.5 |
| <i>Sinomastodon sendaicus</i> ^{a)} | 206.8 | 87.5 | | | | |
| <i>Sinomastodon</i> sp. ^{b)} | 218 | 84 | | | | |
| <i>Sinomastodon jiangnanensis</i> ^{c)} | 204.5 | 80.1 | 78.7 | 80.1 | 75.4 | 70.6 |
| | 201.6 | 80.6 | 80.5 | 80.6 | 75.9 | 72.1 |
| <i>Sinomastodon hanjiangensis</i> ^{d)} | 196 | 71 | | | | |
| | 196 | 60.3 | | | | |
| <i>Sinomastodon yangziensis</i> ^{e)} | 185 | 65.6 | | | | |
| | 179 | 66 | | | | |

a) Data from Kamei (2000); b) data from Thasod et al. (2005); c) data from Wang et al. (2012); d) data from Zong (1987), Zong et al. (1989), and Zhang (1980); e) data from Chow et al. (1974) and Wang (2011).

cuspid and mesoconelet rather than a crest, the chevroning structure of all the lophids, as well as the weak zygodont crest (Tobien et al., 1988). The united characters of complete pretrite trefoils and relatively simple posttrite half lophids (only consisting of main cusp and mesoconelet without accessory central conules) align the Yanghecun specimen with *Sinomastodontinae*. However, based on the observation from the original photo, since the specimen possesses a relatively longer symphysis than *Sinomastodon*, we temporarily assign it as gen. et sp. indet. and put it into *Sinomastodontinae*.

The Yanghecun specimen is clearly more ancestral than any other species of *Sinomastodontinae*. Compared with the Late Pliocene-Early Pleistocene *Si. hanjiangensis*, *Si. jiangnanensis*, and *Si. yangziensis* from South China, as well as the *Sinomastodon* sp. from Thailand (Zong et al., 1989; Chen, 1999; Thasod et al., 2005; Wang, 2011; Wang et al., 2012), the m3 of the Yanghecun specimen is shorter and wider (Figure 6 and Table 1) with only 4 lophids; the pretrite accessory central conules are weaker; the cingulid is stronger; and the secondary trefoils and cementum are poorly present. These features distinguish the Yanghecun specimen from the above derived species.

Compared with *Sinomastodon intermedius* from Yushe and *Si. sendaicus* from Sendai, the m3 of the Yanghecun specimen is comparable in fairly rudimentary secondary trefoils, rudimentary zygodont crest, and rudimentary cementodontology (Tobien et al., 1986; Kamei, 2000). However, it has some different features: (1) m3 of the Yanghecun specimen is smaller and wider in size (Figure 6 and Table 1); (2) m3 of the Yanghecun specimen possesses four lophids rather than the complete five lophids as in *Si. intermedius* and *Si. sendaicus*; (3) the cingulid is stronger in the Yanghecun

specimen; (4) m2 is still preserved in the Yanghecun specimen even though m3 has been moderately worn (representing nearly the upper limit of its ontogenetic age), but in *Si. intermedius*, m2 had already shed when m3 had been comparably worn at the same stage (e.g. THP14294; IVPP V2878); (5) the pretrite accessory central conules are less inflated in the Yanghecun specimen, and the posterior pretrite accessory central conule on the fourth lophid is even absent; and (6) the lophids in the Yanghecun specimen are antero-posteriorly compressed and associated with antero-posterior expansion of the interlophids, rather than antero-posterior expansion of lophids with compressed interlophids as in *Si. intermedius* and *Si. sendaicus*. In the above listed features, the 5th and 6th are autapomorphies of the Yanghecun specimen. These features are convergent with *Mammuth borsoni* Blumenbach, 1799 (Tobien et al., 1988), which was contemporary with *Si. intermedius* in the Yushe Basin, although differential diagnosis between *Mammuth* and the Yanghecun specimen has been demonstrated herein (see above). The above listed features the 1st-4th are pleisomorphies of the Yanghecun specimen, indicating that the Yanghecun specimen is more ancestral than *Si. intermedius* and *Si. sendaicus*.

Based on biostratigraphic and paleomagnetic studies of the Yushe Basin by Flynn et al. (1991) and Tedford et al. (1991), *Sinomastodon intermedius* occurs in the Taoyang Member of the Gaozhuang Formation, corresponding to the Late Gaozhuangian (Chinese Land Mammal Age), and close to the Miocene/Pliocene boundary. However, the Mahui Formation (representing uppermost Miocene strata), which underlies the Gaozhuang Formation, yields *Gomphotherium* and *Choerolophodon*. The specimens attributed to *Gomphotherium* were originally identified as *Trilophodon* cf. *wimani* and *T. cf. spectabilis* (from Zone I, corresponding to the Late Miocene Mahui Formation) by Teilhard de Chardin and Trassaert (1937). However, the temporal distribution of *Gomphotherium* in Europe is MN4- MN9 (Gölich, 1998, 2010), and there is no evidence to indicate that it survived to the latest Miocene. In East Asia, *Gomphotherium* was limited to the Early-Middle Miocene, and was probably extinct before the Late Miocene (Tobien et al., 1986; Wang et al., 2013). The specimens attributed to *Choerolophodon* were identified by Tobien et al. (1986) from partial material of *Trilophodon* cf. *wimani*. However, the paleogeographic distribution of *Choerolophodon* in North China was even more limited, and only *Choerolophodon guangheensis* Wang et Deng, 2011, from the late Shangwangian (Chinese Neogene Land Mammal age), is definitive (Wang et al., 2011). The referral of isolated teeth to *Choerolophodon* by Tobien et al. (1986) is not reliable (Wang et al., 2011). As considered by Chen (1999), the *Gomphotherium* and *Choerolophodon* from the Yushe Basin should properly be attributed to *Si. intermedius*. Thus, if the horizon of *Trilophodon* cf. *wimani* and *T. cf. spectabilis* denoted by Teilhard de Chardin and Trassaert is precise, the first

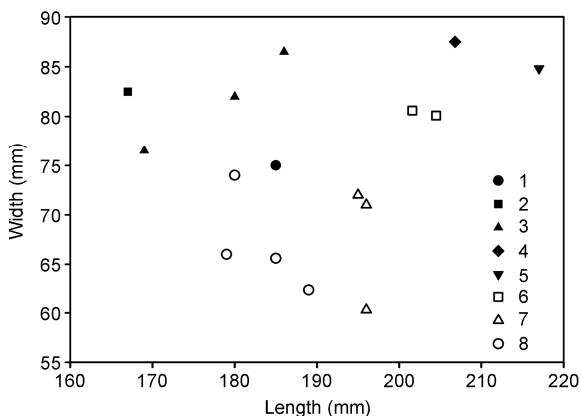


Figure 6 Bivariate plots for m3 comparison among species of *Sinomastodontinae* and *Gomphotherium wimani*. 1, *G. wimani*, data from Hopwood (1935); 2, *Sinomastodontinae* gen. et sp. indet. (Yanghecun locality); 3, *Si. intermedius* (Yushe); 4, *Si. sendaicus*, data from Kamei (2000); 5, *Sinomastodon* sp., data from Thasod et al. (2005); 6, *Si. jiangnanensis*, data from Wang et al. (2012); 7, *Si. hanjiangensis*, data from Zong (1987), Zong et al. (1989), and Zhang (1980); 8, *Si. yangziensis*, data from Chow et al. (1974) and Wang (2011).

occurrence of *Sinomastodon* in the Yushe Basin should be advanced to the latest Miocene. Furthermore, *Si. sendaicus* from Sendai, Japan, occurs in the Tatsunokuchi Formation (Kamei, 2000). Based on diatom biostratigraphy and paleomagnetism, the age of the Tatsunokuchi Formation is probably the latest Miocene (Yanagisawa, 1990; Saegusa, 2011, pers. comm.). Thus, the occurrence of *Sinomastodon* in East Asia is possibly earlier than the Miocene/Pliocene boundary, which is the time of extensive faunal interchange between Asia and North America. The pleiomorphies of the Yangheacun specimen suggest that its age is earlier than *Si. intermedius* and *Si. sendaicus*. The horizon of the Yangheacun specimen constitutes the fourth level of the section, and the overlying eighth level yields a P3 or P4 of *Hipparion* (*Proboscidihipparion*) *pater* (IVPP V18410, Figure 3(a)), which is considered a biostratigraphic marker of the Early Pliocene Gaozhuangian Stage (Qiu et al., 1987; Deng et al., 2011). The vertical distance between the two fossiliferous horizons is about 137 m. Therefore, the age of the Yangheacun specimen belongs most probably to the Baodean (Chinese Neogene Land Mammal age) of the Late Miocene, or may be even earlier.

All the members of the Subfamily Cuvieroninae occurred during the Blancan NALMA, and not earlier than the Early Pliocene (Fisher, 1996; Lambert, 1996). They were contemporary to or slightly younger than *Si. intermedius* (Chen, 1999), *Si. sendaicus*, and the Yangheacun specimen. Thus, *Sinomastodon* is not likely to have been derived from members of the Subfamily Cuvieroninae, and not likely to have migrated back from North America, contrary to what Tobien et al. (1986) stated.

Chen (1999) proposed two hypotheses for the origin of *Sinomastodon*. One was that *Sinomastodon* shared a common ancestor with members of the Subfamily Cuvieroninae. Prado and Alberdi (2008), and Wang (2010) further extended this hypothesis to *Sinomastodon* being the sister group to the Subfamily Cuvieroninae, and both of them being derived from North American *Rhynchotherium*. However, this hypothesis was questioned by Cozzuol et al. (2012) and Lucas (2013) based on morphological comparison and phylogenetic analysis. *Rhynchotherium* first appeared during the late Clarendonian NALMA, which corresponds to the late Bahean (Chinese Neogene Land Mammal age) of the Late Miocene. However, neither did *Rhynchotherium* spread to East Asia during the Late Miocene, nor have *Sinomastodon*-like proboscideans been discovered from the Hemphillian NALMA of North America. Compared with that in the Yangheacun specimen, m3 in *Rhynchotherium* possesses four well-developed lophids and commonly hosts an incipient fifth lophid, rather than merely a posterior cingulid; incipient to moderate posttrite trefoils have been developed, at least in derived forms, rather than completely absent; the anterior and posterior pretrite accessory central conules are strong and rounded, rather than weak and sharp, and thus showing some mammutid charac-

ters as in the Yangheacun specimen (Miller, 1990; Lucas et al., 2008). *Rhynchotherium* also shows some aberrant characters that are almost never observed in other gomphotheres (except partially in *Cuvieronius*), such as the spiraled enamel band on the upper tusk and presence of an enamel band on the lower tusk. These differences have hindered verification of the close relationship between *Rhynchotherium* and *Sinomastodon*.

An alternative hypothesis was proposed by Chen (1999), that *Sinomastodon* was derived from a Eurasian longirostrine gomphothere. However, no strong fossil evidence unites these two forms. One candidate that could be considered the ancestor of *Sinomastodon* is *Gomphotherium wimani* (Hopwood, 1935), which was discovered from the Middle Miocene of the Xining, Lanzhou, Linxia, and Tianshui basins (Hopwood, 1935; Qiu et al., 1997; Wang et al., 2013). The cheek tooth characters, such as the number of lophids, development of accessory central conules, cingulids, and cementum, are comparable to the Yangheacun specimen. Teilhard de Chardin and Trassaert (1937) referred some isolated teeth from the Yushe Basin to *Trilophodon* cf. *wimani*, which was subsequently synonymized into *Si. intermedius* (Chen, 1999). Teilhard de Chardin and Trassaert (1937) wrote: "By their form and dimensions, the upper teeth just described [*Trilophodon* cf. *wimani*, authors' note] fit so exactly with the holotype of *T. wimani* figured by Hopwood (Pl. V, fig. 3) that we refer our specimens to this form. Since however Hopwood's type was collected in a horizon older than the earliest Shansi formations (...), we wonder whether the analogy noted in the intermediate molars would not be contradicted by strong differences in the last molars and in the shape of the jaw." *G. wimani* is a type of longirostrine gomphothere (Wang et al., 2013). However, no complete mandibular symphysis of *G. wimani* has been discovered. Therefore, whether the mandibular symphysis of *G. wimani* is shortened, as in *Rhynchotherium*, is still unknown. Prior to the present contribution, no intermediate form between *Si. intermedius* and *G. wimani* had been discovered. Although a large temporal gap between *Sinomastodon* and *Gomphotherium* still exists, the discovery of the Yangheacun specimen at least begins to reduce this gap.

In addition to the above discussion, an important feature of the Yangheacun specimen is that the m3 only possesses four lophids. This is a very conservative feature in trilophodont gomphotheres as the increase of lophid number in m3 is only seen in later forms. In the primitive "*Gomphotherium annectens* group" such as *G. annectens* and *G. sylvaticum*, and in some "*Gomphotherium angustidens* groups" such as *G. angustidens* and *G. inopinatum*, m3 is tetralophodont, as in the Yangheacun specimen (Borrisiak, 1928; Tassy, 1985). However, in some advanced types, such as in *G. steinheimense*, a completed fifth lophid of m3 can be observed (Göhlich, 1998). In *Sinomastodon intermedius*, m3 has five lophids, and the m3 in *Si. yangziensis* even has the sixth lophid (Wang, 2011). This tendency can also be

seen in American trilophodont gomphotheres, such as m3 with four lophids in *Gomphotherium productum* and that with five lophids in the taxa of Cuvieroninae (Tobien, 1973; Prado et al., 2008).

Another interesting observation is that the Yanghecun specimen seems to possess a relatively long symphysis compared to the known species of Sinomastodontinae. This feature is observed only from the unclear original photo, and could not be confirmed (Figure 1). It also could be seen that no lower incisors were exposed from the narrow distal tip of the symphysis. In *Sinomastodon intermedius*, the symphysis is more shortened to a narrow gutter without lower tusks (Tobien et al., 1986). In American *Rhynchotherium*, although the symphysis has been shortened, the lower tusks are strong (Miller, 1990; Lucas et al., 2008). Therefore, if this feature is correct, the Yanghecun specimen shows a better intermediate stage between longirostrine trilophodont gomphotheres and brevirostrine *Sinomastodon intermedius* than *Rhynchotherium*.

The associated shortening of the mandibular symphysis with dorsal upheaval of the neurocranium in proboscideans is an important morphological event in the evolutionary history of proboscideans (Ye et al., 1990). This process has occurred repeatedly within various lineages of proboscideans, e.g., *Euzygodon*—*Zygodon*—*Mammut*, *Gomphotherium*—*Tetralophodon*—*Aanacus*, *Gomphotherium*—*Primelephas*—extant elephants, and *Gomphotherium*—*Rhynchotherium*—Cuvieroninae (Maglio, 1973; Tobien, 1973, 1978; Tassy et al., 1983; Prado et al., 2008). The underlying mechanism is very complicated, and was probably accompanied by the shifting of their masticatory function from grinding-shearing to horizontal-shearing in response to Neogene global climate change (Maglio, 1972). Thus, the similarity between *Sinomastodon* and the members of the Subfamily Cuvieroninae does not allow direct confirmation that they shared a common ancestor, as discussed by Lucas (2013). There is at least the probability that *Sinomastodon* is a native proboscidean of Asia, which was derived from longirostrine gomphotheres in the Middle Miocene, for which *G. wimani* is a potential ancestor candidate. The similarity between the members of the Subfamilies Sinomastodontinae and Cuvieroninae was likely induced by parallel evolution. The discovery of a Sinomastodontinae gen. et sp. indet. from the Yanghecun locality provides some support for this hypothesis. However, future finds of the intermediate forms between *Sinomastodon* and *Gomphotherium* from strata of the Bahean Age would be helpful in better understanding Gomphotheriidae evolution in China.

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