

# A new brontothere from the Eocene of South China

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Averianov, A., Danilov, I., Chen, W., and Jin, J. 2018. A new brontothere from the Eocene of South China. *Acta Palaeontologica Polonica* 63 (1): 189–196.

The upper Eocene Youganwo Formation in Maoming Province, Guangdong Province, China, produced abundant remains of turtles and crocodiles, but mammalian remains are rare. The previously found mammals from Youganwo Formation include a nimravid carnivore and an amynodontid perissodactyl. Here we report on a new brontotheriid perissodactyl from the Youganwo Formation. *Maobrontops paganus* gen. et sp. nov. is described based on a maxillary fragment with P4 and M1–2 (SYSU-M-4). *Maobrontops paganus* gen. et sp. nov. is characterized by the combination of a simple P4 without a hypocone with derived molars having large molar fossae and large anterolingual cingular cusp. A parsimony implied weighting character analysis places *Maobrontops* gen. nov. in the clade Embolotheriita as a sister taxon to the terminal subclade containing *Nasamplus*, *Protembolotherium*, and *Embolotherium*. *Maobrontops paganus* gen. et sp. nov. is one of the largest Asian brontotheres. The brontotheriid fauna of South China is endemic and includes at least three valid taxa: *Dianotitan* from Brontotheriita and *Pygmaetitan* and *Maobrontops* gen. nov. from Embolotheriita.

Key words: Mammalia, Perissodactyla, Brontotheriidae, Eocene, China.

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Received 16 October 2017, accepted 16 November 2017, available online 11 January 2018.

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## Introduction

Brontotheres, or titanotheres, are extinct perissodactyls famous for their peculiar bunolophodont morphology and, in late representatives, large body size and bizarre nasofrontal horns. The phylogenetic position of brontotheres within the Perissodactyla has been debated; a recent analysis places them close to tapirs and chalicotheres (Rose et al. 2014). Brontotheres are common in the Eocene of North America and Eastern Asia (Osborn 1929b; Granger and Gregory 1943; Mhlbachler 2008). In China, most records of brontotheres come from Northern China, mainly from the Nei Mongol Province (Granger and Gregory 1943; Russell and Zhai 1987; Wang et al. 1999; Mhlbachler 2008). In South China, brontothere remains have been reported from the five intermountain basins: Lunan, Lijiang, and Yuezhong basins in Yunnan Province, Shinao Basin in Guizhou Province, and

Bose Basin in Guangxi Zhuang Autonomous Region. The brontotheriid taxa identified previously from these basins by Chinese scientists include *Dianotitan lunanensis* (Chow and Hu, 1959), *Protitan major* Huang and Zheng, 2004, *Protitan cf. robustus* Granger and Gregory, 1943, *Rhinotitan quadridens* Xu and Chiu, 1962, and Brontotheriidae indet. from the middle Eocene Lumeiyi Formation of Lunan Basin (Chow and Hu 1959; Xu and Chiu 1962; Chow et al. 1974; Zheng et al. 1978; Huang and Zheng 2004); Brontotheriidae indet. from the middle Eocene Xiangshan Formation of Lijiang Basin (Zhang et al. 1978); Brontotheriidae indet. from the upper Eocene Caijiachong Formation of Yuezhong Basin (Zhang et al. 1978); *Pygmaetitan panxianensis* Miao, 1982 from the upper Eocene Shinao Formation of Shinao Basin (Miao 1982); cf. *Protitan* sp. and *Metatelmatherium* sp. from the middle Eocene Dongjun Formation of Bose Basin (Ding et al. 1977). According to the recent revision

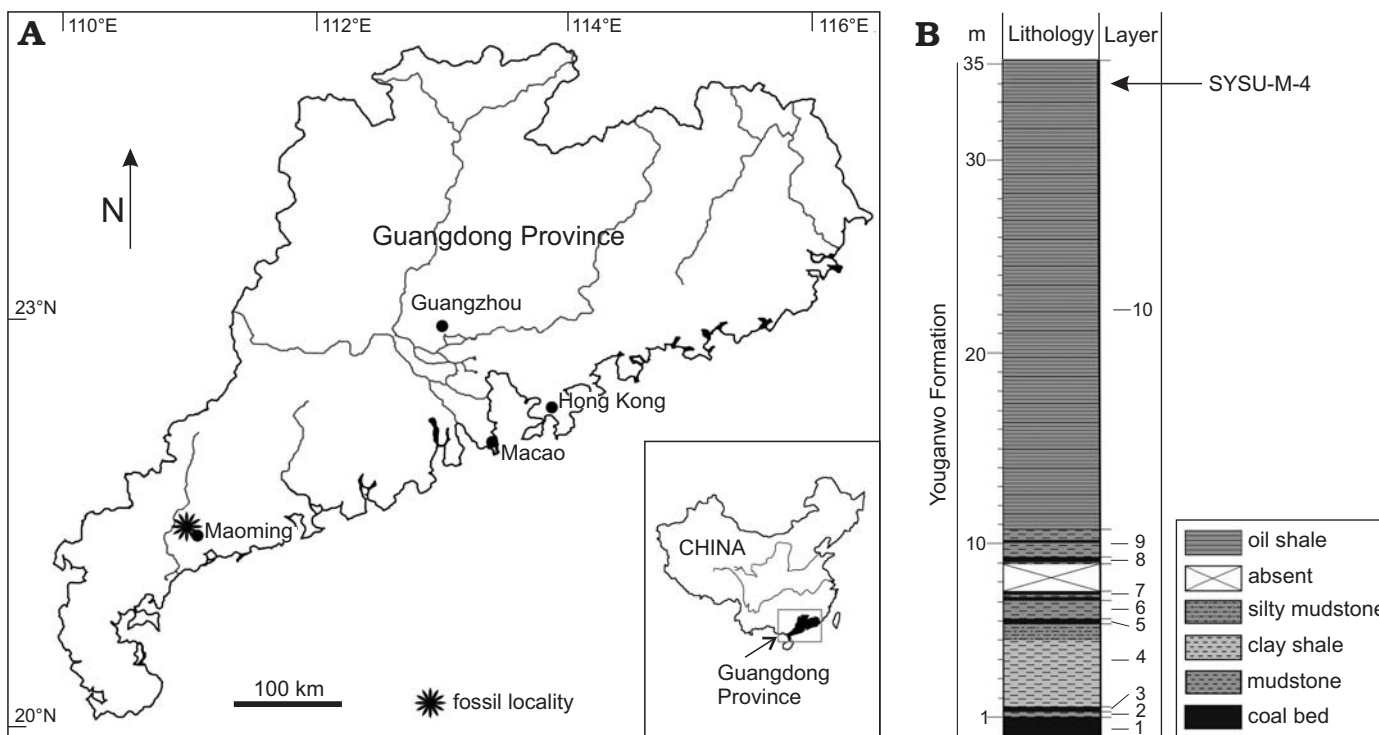


Fig. 1. A. Geographical map of the Maoming Basin, Guangdong Province, China; fossil site where SYSU-M-4 was found is indicated by a star. B. Stratigraphical column of the Youganwo Formation (position of SYSU-M-4 is indicated by an arrow).

of the brontotheriid species-level taxonomy by Mhlbachler (2008), *Dianotitan lunanensis* and *Pygmaetitan panxiensis* are valid taxa, *Protitan major* and *Rhinotitan quadridens* are nomina dubia, and the material assigned to *Protitan* cf. *robustus* from the Lumeiyi Formation lacks sufficient diagnostic characters for species or genus identification. Identification of brontotheres from the Dongjun Formation is also based on fragmentary and not diagnostic specimens.

Here we report on a brontothere record in another intermountain basin in South China, represented by a maxillary fragment with P4 and M1-2 (SYSU-M-4). It comes from the dark brown oil shales in the upper part of the Youganwo Formation (Fig. 1) of the Maoming Basin in Guangdong Province, which were deposited under lacustrine conditions. This is the southernmost record of the Brontotheriidae in China. The Youganwo Formation has been dated based on magnetostratigraphy and palynomorph assemblages as upper Eocene (Wang et al. 1994; Jin 2008; Li et al. 2016), or middle-upper Eocene (Aleksandrova et al. 2015). The previously known vertebrate assemblage of the Youganwo Formation includes cyprinid fishes, carettochelyid, adocid, trionychid, and geoemydid turtles, tomistomine and alligatorid crocodiles, nimravid carnivore, and amynodontid perissodactyls (Chow and Liu 1955; Liu 1957; Ye 1958, 1963, 1994; Chow and Ye 1962; Wang et al. 2007; Tong et al. 2010; Claude et al. 2012; Danilov et al. 2013, 2017; Skutschas et al. 2014; Chen et al. 2015; Averianov et al. 2016, 2017).

*Institutional abbreviations.*—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of

Sciences, Beijing, China; SYSU-M, Mammal fossil collection from the Maoming Basin in the School of Life Sciences, Sun Yat-sen University, Guangzhou, China.

## Systematic palaeontology

Order Perissodactyla Owen, 1848

Family Brontotheriidae Marsh, 1873

Subfamily Brontotheriinae Marsh, 1873

Tribe Brontotheriini Marsh, 1873

Subtribe Brontotheriina Marsh, 1873

Infratribe Embolotheriita Osborn, 1929a

Genus *Maobrontops* nov.

*Etymology:* From Maoming City and *Brontops*, a currently invalid genus of North American brontotheres, used as a suffix for some Asian brontotheres.

*Type species:* *Maobrontops paganus* sp. nov., by monotypy, see below.

*Diagnosis.*—Same as for the type species.

*Maobrontops paganus* sp. nov.

Fig. 2.

*Etymology:* From Latin *paganus*, rustic; an allusion to the collection of many Maoming fossils by locals.

*Type material:* Holotype: SYSU-M-4, a left maxillary fragment with P4 and M1-2.

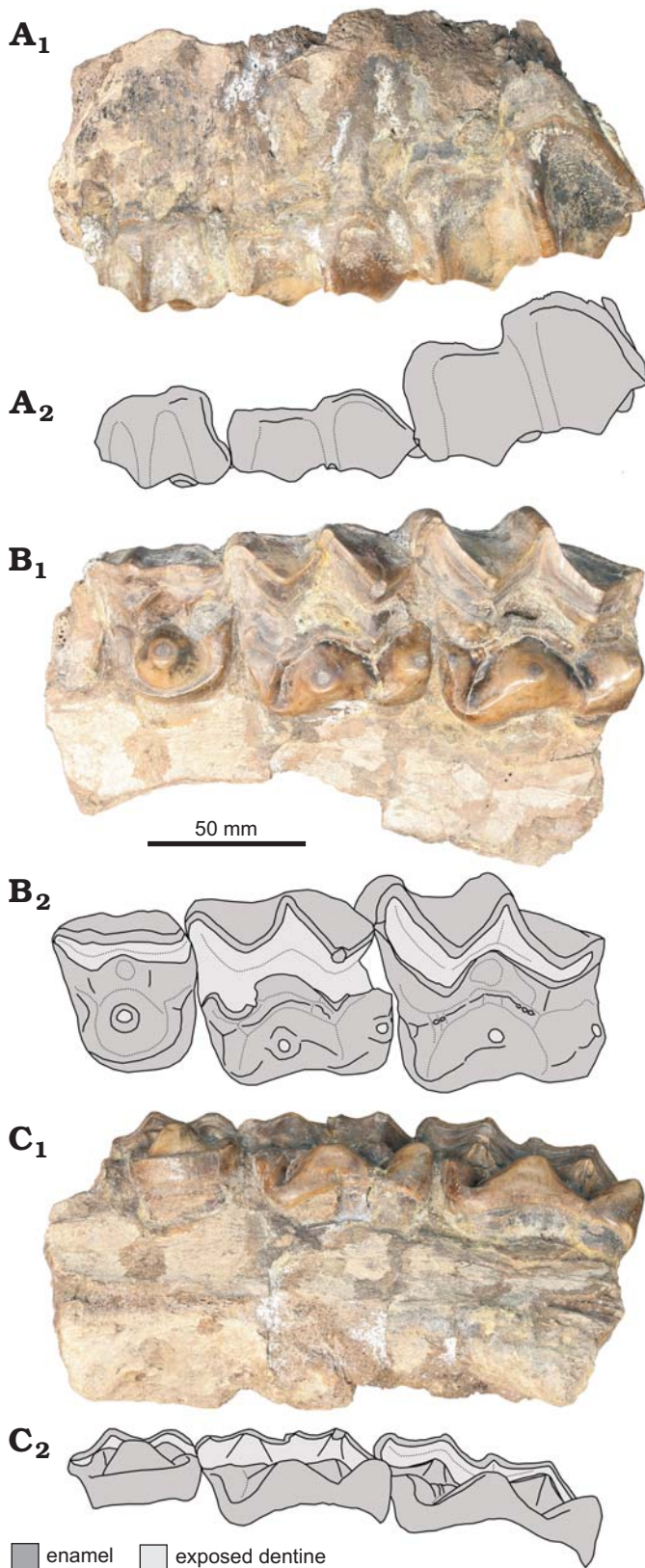


Fig. 2. Embolotheriit brontothere *Maobrontops paganus* gen. et sp. nov., SYSU-M-4 (holotype), from Maoming Basin, Guangdong Province, China; Youganwo Formation, upper Eocene. Left maxillary fragment with P4 and M1–2, in labial (A), occlusal (B), and lingual (C) views. Photographs (A<sub>1</sub>–C<sub>1</sub>) and interpretive drawings of tooth crowns (A<sub>2</sub>–C<sub>2</sub>).

*Type locality:* The oil shale quarry (21°420 N, 110°530 E) located near Maoming City, Maoming Basin, Guangdong Province, China.

*Type horizon:* Youganwo Formation, upper Eocene (Li et al. 2016).

*Diagnosis.*—Referred to the Brontotheriidae based on W-shaped ectoloph and isolated lingual cusps of upper molars. Referred to the Brontotheriinae because of tall ectoloph with functional emphasis placed on shearing on the labial enamel of the ectoloph (i.e., the labial ectoloph enamel thicker than the lingual ectoloph enamel). Differs from all Brontotheriinae except some members of Embolotheriita (*Nasamplus progressus*, *Protembolotherium efremovi*, *Embolotherium andrewsi*, and *Embolotherium grangeri*) by upper molar anterolingual cingular cusp large. Differs from the above mentioned taxa of Embolotheriita by P4 paracone rib narrow and P4 hypocone lacking.

*Description.*—The maxilla is fragmentary, poorly preserved, and offers no morphological details concerning the cranial anatomy.

*P3:* The tooth is mostly destroyed. It is evident that this tooth was slightly narrower transversely than P4.

*P4:* The tooth is of rectangular outline in occlusal view, transversely wider than long. The ectoloph is almost straight, without a mesostyle and with a rather strong labial ridge at the paracone, weaker ridge at the parastyle, and a slight labial convexity at the metacone. The wear facet of the ectoloph is widest at the paracone (13.4 mm) and the metacone (9.3 mm), and narrowest between the paracone and the metacone and labial to the central fossa (7.6 mm). The exposed enamel is thicker along the labial side (~3.8 mm). On the lingual side, the exposed enamel is thicker at the paracone and metacone apices (maximum 2.5 mm) and decreases in thickness outwards. There are strong vertical ridges on the labial side of the paracone and metacone that bracket anteriorly and posteriorly a very deep central fossa.

The lingual heel is slightly shorter anteroposteriorly than the ectoloph. It is dominated by the cone-like protocone, which is as high as the labial cusps and lacks the preprotocrista and postprotocrista. The protocone apex is slightly worn, with a small circle of exposed dentine that is flush with the surrounding exposed enamel. The protocone is surrounded by the anterior, lingual, and posterior cingula, from which it is separated by a distinct rounded groove. The anterior and posterior cingula are straight. The continuous lingual cingulum is rounded, convex lingually. There are cusp-like eminences at the anterior and posterior cingula.

*M1:* It has a quadrangular outline in occlusal view, distinctly longer and wider than P4. The W-shaped ectoloph is heavily worn, with the wear facet widest at the paracone (24 mm) and metacone (18 mm). There are strong labial ridges at the parastyle and mesostyle. The labial sides of the paracone and metacone between the labial ridges are slightly convex. The exposed enamel is thick on the labial side (~3.3 mm), and about twice as thin lingually around the paracone and metacone (~1.5 mm). There is a large central fossa of crescentic shape, which is bordered lingually by a



prominent and significantly worn ridge. This ridge extends between the anterolingual cingular cusp and vertical ridge on the lingual side of the metacone.

The lingual heel is only a little shorter anteroposteriorly than the ectoloph. The protocone and hypocone are distinctly lower than the labial cusps. Both cusps have circular wear facets at the apices with exposed dentine and enamel. On the protocone wear facet the enamel rim is raised above the adjacent dentine surface, while on the hypocone wear facet the small exposed area of dentine is flush with the enamel. This suggests that the wear on the protocone started earlier than on the hypocone. The protocone is cone like, but with a flattened to slightly concave lingual side. The hypocone is more ridge-like and resembles the enlarged posterior cingulum of P4. The anterior cingulum is similar to that of P4 but larger. It has a large cusp-like eminence that is mostly worn down (anterolingual cingular cusp). There is no lingual cingulum.

*M2*: It is distinctly larger than *M1* and is of trapezium outline in occlusal view. The anterior side is about 1.5 times wider than the posterior side, which results in an oblique position of the labial side relative to the lingual side. The W-shaped ectoloph is about twice less worn than that of the *M1*. The exposed enamel is ~3.0 mm thick along the labial side and ~2.5 mm thick around the paracone and metacone apices on the lingual side. There are strong labial ridges at the parastyle and mesostyle and a much weaker ridge at the metastyle. The labial side of the paracone and metacone is slightly convex between the ridges. There is a large central fossa of triangular shape that is bordered posteriorly by a sharp vertical ridge along the metacone lingual side and lingually by a distinct ridge.

The lingual cusps are much lower compared to the labial cusps and correspond in shape to those of the *M1*. With a flattened lingual side, the cone-like protocone is relatively larger than that of *P4*. Because of this, the size difference between the protocone and hypocone is more pronounced on *M2* compared to *M1*. The ridge-like hypocone is obliquely extended along the postero-lingual corner of the tooth. There is only slight wear on the protocone and hypocone apices. There is a large cusp-like eminence along the anterior cingulum (anterolingual cingular cusp). This eminence is connected with the base of the hypocone by a ridge extending between the central fossa and the vertical ridge on the lingual side of the metacone. This ridge is unworn and bears several prominent irregular denticles. There is no lingual cingulum.

The enamel is mostly smooth, but there are areas of pitted or wrinkled enamel on the labial side of the *P4* and molars, and on the lingual side of *P4*.

For dental measurements see Table 1.

Table 1. Measurements (in mm) of upper dentition of SYSU-M-4, the holotype of *Maobrontops paganus* gen. et sp. nov.

P4		M1		M2	
Length	Width	Length	Width	Length	Width
42.1	49.0	56.1	57.4	73.3	69.8

*Stratigraphic and geographic range.*—Eocene of South China.

## Phylogenetic analysis

*Maobrontops paganus* gen. et sp. nov. can be coded using 19 of the 91 characters (20.9%) appearing in the data matrix of Muhlbachler and Samuels (2016). The character codings are as follows:

*Character 50 (2)*: Labial upper premolar ribs: paracone rib narrow, metacone rib very weak. This character state is found in brontotheres which are more terminal than *Palaeosyops*, *Microtitan*, Brontotheriita. The terminal Embolotheriita (*Nasamplus*, *Protembolotherium*, and *Embolotherium*) have a more derived condition, all labial ribs very weak on upper premolars.

*Character 53 (1)*: Upper premolar lingual morphology: lingual side of crown is somewhat wider, protocone often associated with lingual crest. In *Maobrontops* gen. nov., there is no lingual crest on *P4*. Actually, the morphology of *P4* lingual side is intermediate between the states 0 and 1 of this character. The protocone is cone-like, but the lingual side is not narrow, although it is somewhat narrower than in most other derived brontotheres. Most of the derived brontotheres have a variously developed hypocone on *P4*. *Aktautitan hippopotamopus* Muhlbachler, Lucas, Emry, and Bayshashov, 2004 from the middle Eocene of Kazakhstan is the phylogenetically closest taxon to *Maobrontops* gen. nov. iaxon of brontotheres which lack hypocone on *P4* (Muhlbachler et al. 2004). Although the hypocone is lacking on *P4* of *Aktautitan*, the lingual side of *P4* is almost as wide as the labial side in that taxon. In *Maobrontops* gen. nov., the lingual side of *P4* is distinctly narrower than the labial side.

*Character 54 (1)*: Upper molar parastyle high. Found in all brontotheres and outgroup taxa.

*Character 55 (1)*: Upper molar parastyle mainly labial to paracone. Distribution as in the previous character.

*Character 56 (1)*: Upper molar anterior cingulum does not form parastyle shelf. Found in brontotheres more terminal than *Palaeosyops*.

*Character 57 (1)*: Upper molar metastyle angled labially. Found in all brontotheres and outgroup taxa.

*Character 58 (1)*: Upper molar ectoloph hypsodont. Found in brontotheres more terminal than *Bunobrontops*.

*Character 59 (2)*: Labial side of upper molar paracone and metacone lingually angled and convex. Found in brontotheres more terminal than *Palaeosyops*.

*Character 60 (1)*: Molar ribs weak. Found in brontotheres more terminal than *Bunobrontops*.

*Character 61 (1)*: Upper molar mesostyle present. Found in all brontotheres and outgroup taxa.

*Character 62 (1)*: Lingual margins of molar paracone and metacone wedged. Found in brontotheres more terminal than *Bunobrontops*.

*Character 63 (3)*: Thickness of the lingual enamel of

the upper molar ectoloph completely thinner than labial ectoloph enamel. Found in brontotheres more terminal than *Mesatirhinus*.

*Character 64 (2)*: Labiolingual width of upper molar ectoloph: wide. Found in brontotheres more terminal than *Eotitanops*.

*Character 65 (1)*: Central molar fossa present. Found in brontotheres more terminal than *Mesatirhinus*, but reversed in *Microtitan*, *Metatelmatherium*, *Wickia*, *Telmatherium*, and *Qufutitan*.

*Character 66 (4)*: Upper molar protoloph and paracnules absent. Found in brontotheres more terminal than *Dolichorhinus*, but reversed in *Wickia*, *Telmatherium*, and *Nanotitanops*.

*Character 67 (3)*: M1–2 metaloph absent. Found in brontotheres more terminal than *Mesatirhinus*. The second state included in this character by Mihlbachler (2008) (vestigial metaloph-like ridge) refers to the ridge extended between the anterolingual cingular cusp and the hypocone. This ridge borders the molar fossa lingually. This ridge is not connected with the hypocone apex and more likely is a neomorph character rather than the remnant of the metaloph. Mihlbachler (2008) noted the presence of this ridge in *Megacerops kuwagatarhinus* Mader and Alexander, 1995 (Mader and Alexander 1995: fig. 5) and *Pygmaetitan*, and considered this a reversal from the metaloph absence (character state 3). Based on the illustrations in Mihlbachler (2008), this ridge has a wider distribution, being present in *Dolichorhinus hyognathus* (Osborn, 1889), *Fossendorhinus diploconus* (Osborn, 1895), *Metarhinus fluviatilis* Osborn, 1908, *Metarhinus abbotti* (Riggs, 1912), *Aktautitan hippopotamopus*, *Metatitan primus* Granger and Gregory, 1943, *Metatitan relictus* Granger and Gregory, 1943, *Protembolotherium efreмовi* Yanovskaya, 1954, *Embolotherium andrewsi* Osborn, 1929a, *Embolotherium grangeri* Osborn, 1929a, and *Dianotitan lunanensis*. Distribution of this character has no clear phylogenetic pattern, but it is notably present in a clade including *Maobrontops* gen. nov., *Protembolotherium*, and *Embolotherium*.

*Character 68 (2)*: Upper molar anterolingual cingular cusp large. Present in *Maobrontops* gen. nov., *Protembolotherium*, and *Embolotherium*.

*Character 91 (1)*: M1–2 parastyle and mesostyle extend an equal distance labially.

*Character 92 (1)*: Upper molar protocone distinctly larger than the hypocone, at least 50% on M2.

The character-taxon matrix with scores for *Maobrontops paganus* gen. et sp. nov. (see SOM 1, Supplementary Online Material available at [http://app.pan.pl/SOM/app63-Averianov\\_et\\_al\\_SOM.pdf](http://app.pan.pl/SOM/app63-Averianov_et_al_SOM.pdf)) was analyzed using the traditional search option of TNT version 1.1 (Goloboff et al. 2008) with 1000 replications and 10 trees saved per replication, followed by the tree bisection and reconnection (TBR) swapping algorithm of the trees in memory; 10 000 trees were set up in memory. The tree statistics and distribution of characters were obtained using WinClada 1.00.08 (Nixon 2002).

Table 2. Statistics for equal weight and implied weighting analyses. MPT, most parsimonious tree; \* overflow.

Analysis	Number of MPT	Tree length	
Equal weight	10000*	350	
Implied weighting	K = 1	189	53.81
	K = 2	378	41.34
	K = 3	1890	33.85
	K = 4	1890	28.79
	K = 5	1485	26.06
	K = 6	1485	22.20
	K = 7	1485	19.94
	K = 8	1485	18.11
	K = 9	1485	16.59
	K = 10	99	15.31

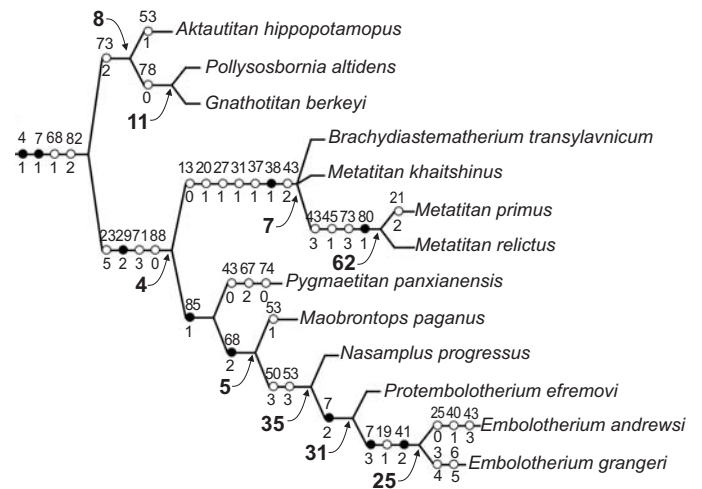


Fig. 3. Part of the strict consensus tree of 99 most parsimonious trees produced by TNT implied weighting character analysis (K = 10), showing the interrelationships within the infratribe Embolotheriita Osborn, 1929a sensu Mihlbachler (2008). Only unambiguous characters are shown (black circles are nonhomoplasies and white circles are homoplasies). The numbers next to the circles are characters (above) and states (below). The numbers at nodes in bold face are GC values for branch support.

Separate analyses were conducted under equal weights and implied weighting (Table 2). The phylogenetic position of *Maobrontops paganus* gen. et sp. nov. was unresolved in the equal weights and the implied weighting analyses with the constant K ranging from 1 to 9. Only the implied weighting analysis with the constant K = 10 produced a strict consensus tree with the resolved position of *Maobrontops paganus* gen. et sp. nov. A fragment of this tree is shown in Fig. 3. For the branch support we used the Group present/Contradict (GC) frequency values calculated on symmetric resampling with 1000 replicates using TNT software (P = 33).

## Principal component analysis

We performed a principal component analysis (PCA) to analyze variation in size dimensions of P4 and M1–2 in brontotheres based on measurements provided in Mihlbachler (2008). These teeth were chosen because only P4 and M1–2

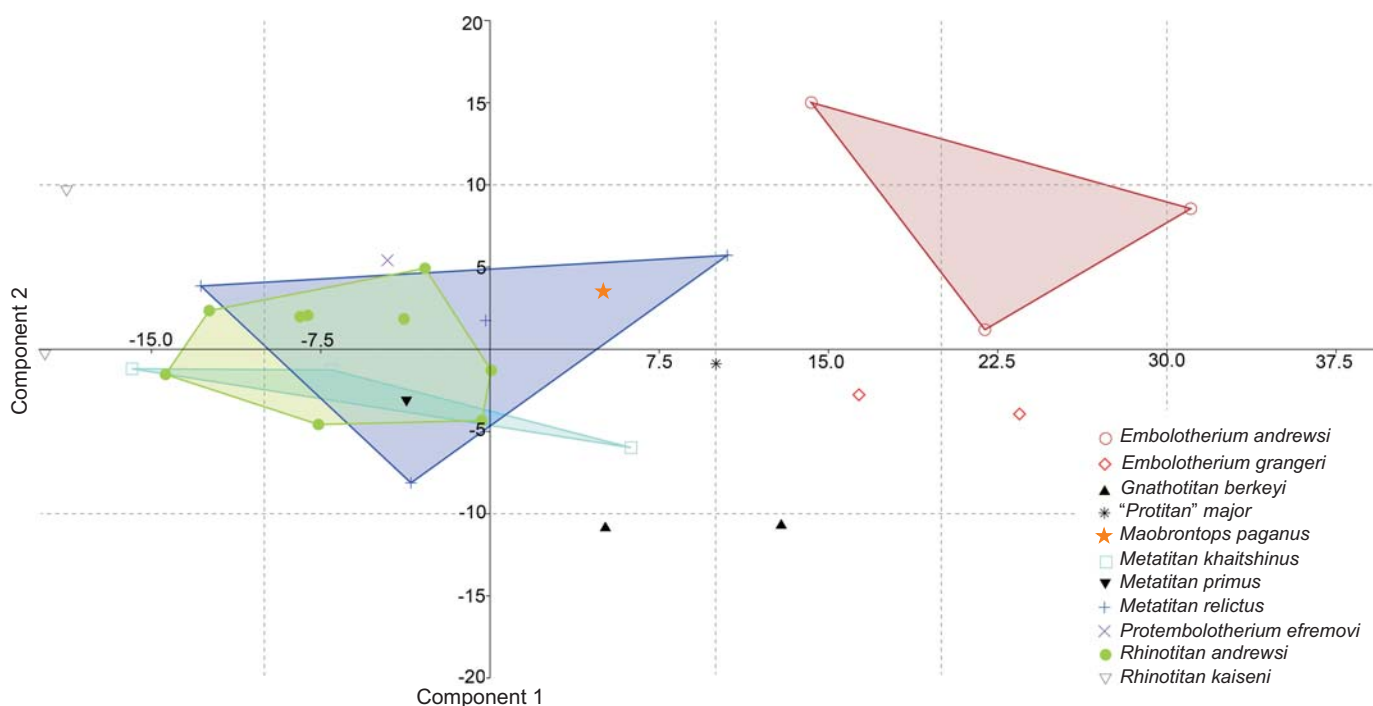


Fig. 4. Principal component analysis of 32 specimens of ten species of Embolotheriita based on measurements of P4 and M1–2 (see SOM 2).

are represented in the specimen SYSU-M-4, described in the present paper. The teeth in the middle part of the tooth row are usually less variable in size compared with the mesial and distal cheek teeth: anterior premolars or M3. Only specimens with known values for the length (L) and width (W) of all three teeth (P4, M1, and M2) were used in this study. Our dataset includes 30 specimens belonging to ten species of the Embolotheriita. *Pygmaetitan panxianensis* was excluded from this sample because it is far removed from the morphospace of other Embolotheriita owing to its very small size. The principal component analysis was performed using the software PAST version 3.01 (Hammer et al. 2001). Principal component 1 (PC 1) represents 73% of the variance in the dataset (Table 3). The length and width of M2 have the greater loadings on PC 1 (Table 3).

On the plot PC 1 versus PC 2 (Fig. 4) the holotype of *Maobrontops paganus* (SYSU-M-4) is within the morpho-

space of *Metatitan relictus*. Positionally, the holotype is located most closely to two specimens belonging to that species as well as to the holotype of "*Protitan*" *major* (IVPP V13802). The morphospaces of three species of *Metatitan* and of *Rhinotitan andrewsi* Osborn, 1925 are strongly overlapped.

## Discussion and conclusions

The phylogenetic relationships within the Embolotheriita in our resulting cladogram (Fig. 3) are very similar to those found in the strict consensus of heuristic search performed with ordered multistate characters by Mihlbachler (2008: fig. 194). Except for the inclusion of the new taxon, *Maobrontops paganus* gen. et sp. nov., the only difference between the two cladograms is the position of *Pygmaetitan panxianensis*. In the strict consensus provided by Mihlbachler (2008: fig. 194) *Pygmaetitan* forms a polytomy with the clades *Brachiadiastematherium* + *Metatitan* and *Nasamplus* + (*Protembolotherium* + *Embolotherium*). In our consensus tree (Fig. 3) the position of *Pygmaetitan* is fully resolved: it is the sister taxon to the clade *Maobrontops* gen. nov. + (*Nasamplus* + (*Protembolotherium* + *Embolotherium*)). However, the resampling analysis places *Pygmaetitan* outside Embolotheriita as the sister taxon to *Sthenodectes* with a GC branch support value of 12. In our analysis, *Pygmaetitan* is united with the derived Embolotheriita by one unambiguous synapomorphy, lower molar occlusal basins deep (character 85[1]). This unique character is present also in *Embolotherium*, but unknown for *Nasamplus*, *Protembolotherium*, and *Maobrontops* gen.

Table 3. Principal component loadings of teeth variables in analyzed sample of brontotheres. PC, Principal Component.

Variable		PC 1	PC 2
P4	length	0.1274	0.04419
	width	0.026053	0.2259
M1	length	0.20221	-0.41584
	width	0.41112	0.50834
M2	length	0.61	-0.63253
	width	0.57783	0.33999
Eigenvalue		165.009	32.4286
Variance		72.96%	14.34%



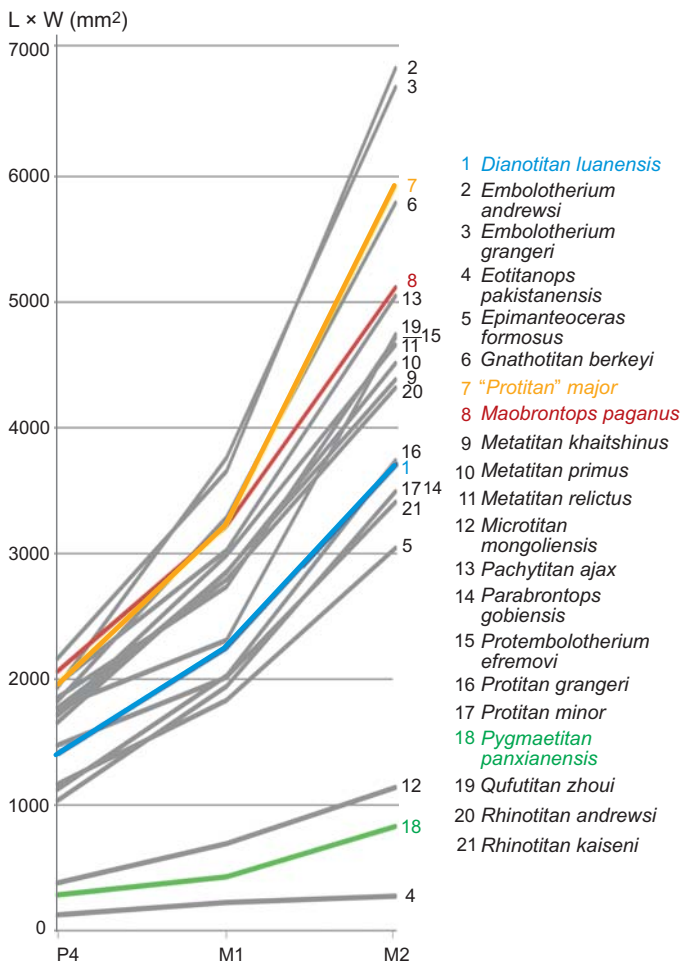


Fig. 5. The size of middle cheek teeth, P4 and M1–2 (L × W), in Asian brontotheres (based on data present in SOM 2). Taxa found in South China are *Dianotitan luanensis* (1), “*Protitan*” *major* (7), *Maobrontops paganus* gen. et sp. nov. (8), and *Pygmaetitan panxianensis* (18).

nov. *Pygmaetitan* comes from the Shinao Basin of Guizhou Province, which is relatively close to the Maoming site. In spite of its close geographic and phylogenetic position relative to *Maobrontops* gen. nov., *Pygmaetitan* is markedly different from the latter having a much smaller size (Fig. 5), P4 hypocone, and relatively short M1 compared to other molars. Another brontothere from South China, *Dianotitan*, is nested within the sister clade to the Embolotheriita, the Brontotheriita, in our analysis and in Muhlbachler (2008: fig. 194). It is also different from *Maobrontops* gen. nov. by having a smaller size (Fig. 5) and P4 hypocone.

There is a single unambiguous synapomorphy that unites *Maobrontops* gen. nov. with derived Embolotheriita: the upper molar anterolingual cingular cusp is large (character 68[2]; Fig. 3). This character is present also in *Protembolotherium* and *Embolotherium*.

*Maobrontops paganus* gen. et sp. nov. is similar to “*Protitan*” *major* from the middle Eocene Lumeiyi Formation of Lunan Basin in Southern China (Huang and Zheng 2004; Muhlbachler 2008) in its large size and lack of hypocone on P4. However, *Maobrontops paganus* gen. et sp. nov. is

clearly different from that taxon in having a much more pronounced antero-lingual cusp and deep furrows between the lingual cusps of the upper molars. The latter character is found also in *Embolotherium* and may be structurally related to the deep lower molar basins found in that taxon and related taxa. This character was not included in the data matrix provided by Muhlbachler (2008) or Muhlbachler and Samuels (2016). However, its presence in *Maobrontops* gen. nov. and derived Embolotheriita supports the inclusion of the new taxon in that clade.

*Maobrontops paganus* gen. et sp. nov. is one of the largest known brontotheres from Asia, being inferior in size only to *Embolotherium* (Fig. 5). Janis (1990) published equations relating body mass to M2 area (length × width) in hyracoids and perissodactyls. Based on those formulas, the body mass of the holotype of *Maobrontops paganus* gen. et sp. nov. was approximately 792 kg. However, this increase in size was likely evolved in southern Chinese brontotheres independently of those living in northern China, as *Protembolotherium* is smaller than *Maobrontops* gen. nov.

In spite of a far less abundant record of brontotheres in South China compared to North China and Mongolia, the brontothere fauna of that geographic region is quite diverse. It includes at least three taxa (*Dianotitan*, *Pygmaetitan*, and *Maobrontops* gen. nov.), and possible one more taxon (“*Rhinotitan quadridentis*”). *Dianotitan* (Brontotheriita) was likely derived from a North American immigrant (Muhlbachler 2008), while *Pygmaetitan* and *Maobrontops* gen. nov. were parts of the endemic radiation (Embolotheriita). Embolotheriita is mostly an Asian clade with a single North American representative (*Pollyosbornia*). *Brachydiastematherium* comes from eastern Europe, which was biogeographically part of Asia in the Eocene (Muhlbachler 2008). The Embolotheriita might have originated in Southern China, and from there, more derived members of the group dispersed to the northern parts of eastern Asia.

## Acknowledgements

We thank Matthew Muhlbachler (New York Institute of Technology, Old Westbury, USA) and Bryn Mader (Queensborough Community College, Bayside, USA) for reading the manuscript and providing useful comments. This study was supported by the National Natural Science Foundation of China (Grant No. 41210001), the Key Project of Sun Yat-sen University for inviting foreign teachers. AA was supported by Zoological Institute, Russian Academy of Sciences (project AAAA-A17-117022810195-3) and Russian Foundation for Basic Research (project 16-04-00294). The work is performed according to the Russian Government Program of Competitive Growth of Kazan Federal University.

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