# A new tritylodontid synapsid from Mongolia

MAHITO WATABE, TAKEHISA TSUBAMOTO, and KHISHIGJAV TSOGTBAATAR

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The Upper Jurassic Ulaan Malgait Beds in the Shar Teg locality of southwestern Mongolia have yielded remains of a new tritylodontid therapsid (Synapsida), *Bienotheroides shartegensis* sp. nov. The specimen consists of a fragmentary skull associated with lower jaws. It is assigned to *Bienotheroides* based on its short snout, a premaxilla-palatine contact, very reduced maxilla, relatively rounded corner of upper postcanine teeth (PC), and PC cusp formula of 2-3-3. It differs from the other species of *Bienotheroides* in having a much more reduced middle mesial cusp of PC. It further differs from *B. zigongensis* and *B. ultimus* in having shorter and wider PC, from *B. ultimus* in lacking a projection at the middle mesial margin of PC, and from *B. wansienensis* in lacking the vestigialmost mesiobuccal cusp of PC and in lacking a diastema between upper I1 and I2. This is the first discovery of the Tritylodontidae in Mongolia. This discovery extends the taxonomic (morphological) diversity and geographic range of *Bienotheroides* and underlies the success of the genus in the Middle to Late Jurassic biota of eastern Eurasia.

Key words: Synapsida, Tritylodontidae, *Bienotheroides*, Jurassic, Gobi Desert, Mongolia.

*Mahito Watabe [moldavicum@pa2.so-net.ne.jp] and Takehisa Tsubamoto [sorlestes@msc.biglobe.ne.jp], Center for Paleobiological Research, Hayashibara Biochemical Laboratories, Inc., Okayama 700-0907, Japan;*
*Khishigjav Tsogtbaatar [paleolab@magicnet.mn], Mongolian Paleontological Center, Mongolian Academy of Sciences, Ulaanbaatar 46, Mongolia.*

## Introduction

The Tritylodontidae are a group of herbivorous advanced non-mammalian cynodonts and a potential sister-group of mammals (= Mammaliaformes; e.g., Kemp 1983; Rowe 1988; Wible 1991; Luo 1994). The definite tritylodontids appeared in the Early Jurassic of Europe, South Africa, Antarctica, China, and North America, and they declined in the Middle Jurassic (e.g., Fraas 1866; Owen 1856, 1884; Hennig 1922; Simpson 1928; Kühne 1956; Ginsburg 1962; Fourie 1968; Hopson and Kitching 1972; Waldman and Savage 1972; Kemp 1982; Kermack 1982; Clark and Hopson 1985; Sues 1985a, b, 1986a, b, c; Lewis 1986; Luo and Wu 1995; Hammer 1996). They survived into the Early Cretaceous through the Late Jurassic in Asia (Tatarinov and Matchenko 1999; Setoguchi et al. 1999; Maisch et al. 2004). They possess mammalian characters such as very reduced postdentary bones of lower jaws and loss of prefrontal and postorbital bones (Kemp 1982). They are characterized by possessing unique morphologies of postcanine teeth: three cusp rows in the upper teeth, and two cusp rows in the lower teeth.

Here, we describe a new tritylodontid from the Upper Jurassic Shar Teg locality of southwestern Mongolia recently discovered by the Japan (Hayashibara Museum of Natural Sciences)-Mongolia (Mongolian Paleontological Center) Joint Fossil Expedition Team during the 2002 field-season (Watabe and Tsogtbaatar 2004; Watabe et al. 2004). The specimen consists of an incomplete skull associated with right and left lower jaws. Although the tritylodontids have been found in other parts of Asia such as China, Russia (western Siberia), and Japan (Young 1940, 1947, 1974, 1982; Chow and Hu 1959a, b; Chow 1962; Hopson 1964, 1965; Cui 1976, 1981, 1986; He and Cai 1984; Sun 1984a, b, 1986; Sun and Li 1985; Sun and Cui 1986, 1987, 1989; Cui and Sun 1987; Luo and Sun 1993; Luo and Wu 1994, 1995; Tatarinov and Matchenko 1999; Setoguchi et al. 1999; Matsuoka 2000; Maisch et al. 2004; Kamiya et al. 2006), they were not hitherto reported from Mongolia.

## Material and methods

The skull material described here was enclosed in a calcareous nodule. The upper and lower teeth were tightly occluded with each other. Some breakage to the left upper and lower postcanine teeth occurred when we removed the left lower jaw and the anterior part of the right lower jaw from the skull. The postcanine part of the right lower jaw is still in occlusion with the upper jaw.

Dental cusp terminologies of the postcanine teeth of the Tritylodontidae are shown in Fig. 1. We follow the cusp identification and terminology by Setoguchi et al. (1999) and Matsuoka (2000).

*Institutional abbreviations.*—HMNS, Hayashibara Museum of Natural Sciences, Okayama, Japan; MPC, Mongolian Paleontological Center, Ulaanbaatar, Mongolia; MPC-Nd, Mongolian Paleontological Center-Non Dinosaur Reptile.

*Other abbreviations.*—I/i, upper/lower incisors; PC/pc, upper/lower postcanine teeth.

# Geologic setting and age

The specimen was discovered in a red mudstone of the lower part of the Ulaan Malgait Beds at the Ulaan Malgait Hills of the Shar Teg locality, Gobi-Altai Aimag, southwestern Mongolia (Fig. 2; Gubin and Sinitza 1996). The tritylodontid-bearing red mudstone is about 10 meters above the boundary between the Ulaan Malgait Beds and the underlying Shar Teg Beds (Watabe et al. 2004).

The Ulaan Malgait Beds consist of red mudstones, bluish-white sandstones, and red conglomerates. They conformably overlie the calcareous thick beds of the Shar Teg Beds. The Ulaan Malgait Beds yielded fossil remains of fish, turtles, crocodiles, dinosaurs, a tritylodontid, molluscs, and ostracodes (Gubin and Sinitza 1996; Watabe et al. 2004). The red mudstones include many calcareous nodules and concretions as paleosol products. The complex of red mudstones and bluish-white sandstones is considered as overbank deposits with crevasse splays, indicating a fluvial sedimentary environment (Watabe et al. 2004).

The underlying Shar Teg Beds consist of fine-grained sandstones, variegated mudstones, paper shales, and thick-bedded calcareous layers (alternation of limestones and cherts). They yielded fossils of vertebrates (such as fish, labyrinthodont amphibians, turtles, dinosaurs, and mammals), plants, molluscs, insects, conchostracans, and ostracodes (Gubin and Sinitza 1996; Watabe et al. 2004).

Based on the fossil fauna of the Shar Teg locality, Gubin and Sinitza (1996) concluded that the Ulaan Malgait and Shar Teg Beds are most probably correlated to the Upper Jurassic.

# Systematic paleontology

## Family Tritylodontidae Cope, 1884

## Genus *Bienotheroides* Young, 1982

*Type species*: *Bienotheroides wansienensis* Young, 1982; Upper Shaximiao Formation of Gaoling, Wanxian, Sichuan, China, Middle or early Late Jurassic. The species name was misspelled as "*wanhsienensis*" by Sun (1984b, 1986), Sun and Li (1985), and Maisch et al. (2004).

*Other referred species*: *Bienotheroides zigongensis* Sun, 1986; *Bienotheroides ultimus* Maisch, Matzke, and Sun, 2004; *Bienotheroides shartegensis* sp. nov.

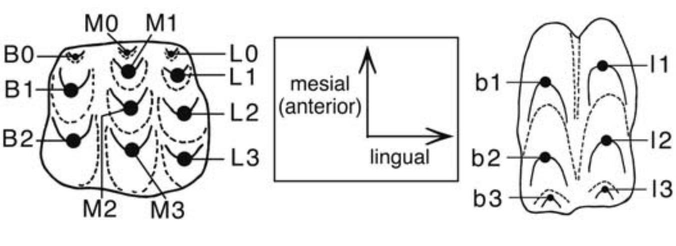


Fig. 1. Dental cusp terminologies of the postcanine teeth of the Tritylodontidae used in this paper (modified from Setoguchi et al. 1999; Matsuoka 2000).


Fig. 2. Map of Mongolia, showing the Shar Teg locality (star) of Gobi Altai Aimag (gray area). The Shar Teg locality, dated as the Upper Jurassic, has yielded the type specimen of *Bienotheroides shartegensis* sp. nov.

### *Bienotheroides shartegensis* sp. nov.

Figs. 3–6, 7C.

*Holotype and only known specimen*: MPC-Nd 10/301, an incomplete skull associated with right and left lower jaws. Casts of MPC-Nd 10/301 are deposited in HMNS (HMNS 1486 and 1491).

*Type locality*: Ulaan Malgait Hills, Shar Teg locality, Gobi-Altai Aimag, southwestern Mongolia (Fig. 2; Gubin and Sinitza 1996).

*Formation and age*: From a red mudstone bed of the lower part of the Ulaan Malgait Beds (about 10 meters above the boundary between the Ulaan Malgait Beds and the underlying Shar Teg Beds); Upper Jurassic (Gubin and Sinitza 1996).

*Derivation of the name*: Named after the type locality.

Table 1. Dental measurements (in mm) of postcanine teeth of *Bienotheroides shartegensis* sp. nov., MPC-Nd 10/301; Upper Jurassic; Shar Teg, Mongolia.

| | | Length | Width |
|---|---|---|---|
| Upper postcanine | right PC1 | 6.6 | 9.9 |
| | right PC2 | 7.3 | 10.0 |
| | right PC3 | 7.4 | 10.1 |
| | right PC4 | – | 10.3 |
| | left PC1 | 7.2 | 10.3 |
| | left PC2 | 7.6 | 10.3 |
| | left PC3 | 7.4 | 10.5 |
| | left PC4 | 7.3 | 10.8 |
| Lower postcanine | right pc1 | 9.3 | 6.7 |
| | right pc2 | 9.4 | 7.2 |
| | right pc3 | 9.7 | – |
| | right pc4 | 9.7 | – |
| | left pc1 | – | 7.1 |
| | left pc2 | 9.2 | 7.1 |
| | left pc3 | 9.3 | 7.7 |
| | left pc4 | – | 7.7 |

*Diagnosis*.—Differs from the other species of *Bienotheroides* in having a much smaller M1 cusp. Differs from *Bienotheroides zigongensis* and *Bienotheroides ultimus* in

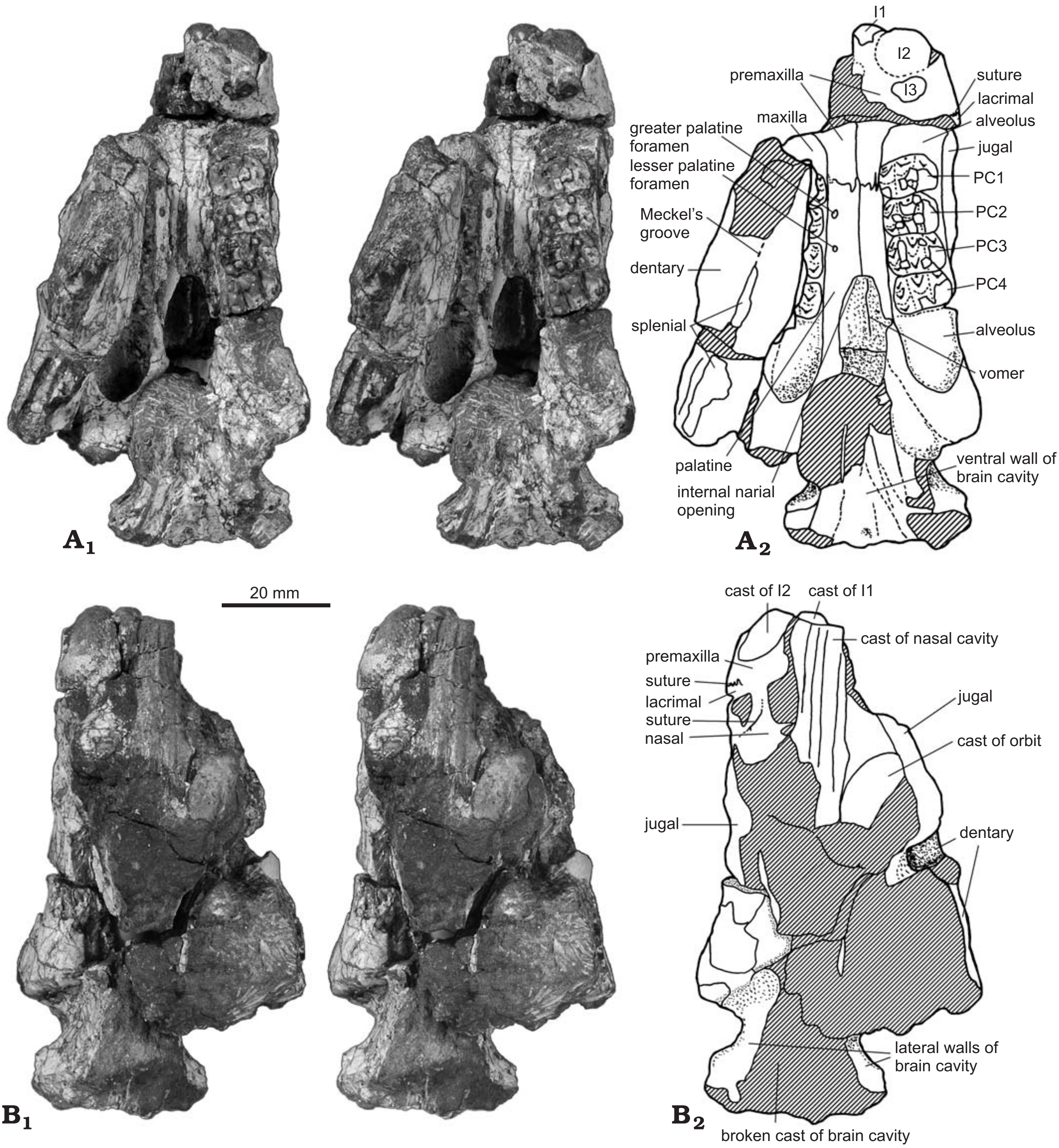


Fig. 3. Tritylodontid *Bienotheroides shartegensis* sp. nov., MPC-Nd 10/301, Upper Jurassic; Shar Teg, Mongolia. **A**. Ventral view of the skull with the posterior part of the right lower jaw; $A_1$, stereo-photograph; $A_2$, schematic drawing. **B**. Dorsal view of the skull with the posterior part of the right lower jaw; $B_1$, stereo-photograph; $B_2$, schematic drawing.

having proportionally shorter and wider PC/pc. Differs from *B. ultimus* in lacking a projection on the middle part of the mesial margin of PC. Differs from *Bienotheroides wansienensis* in lacking B0 cusp and a diastema between upper I1 and I2.

# Description

The sizes of the skull, lower jaws, incisors, and postcanine teeth of MPC-Nd 10/301 roughly correspond to those of other species of *Bienotheroides*.

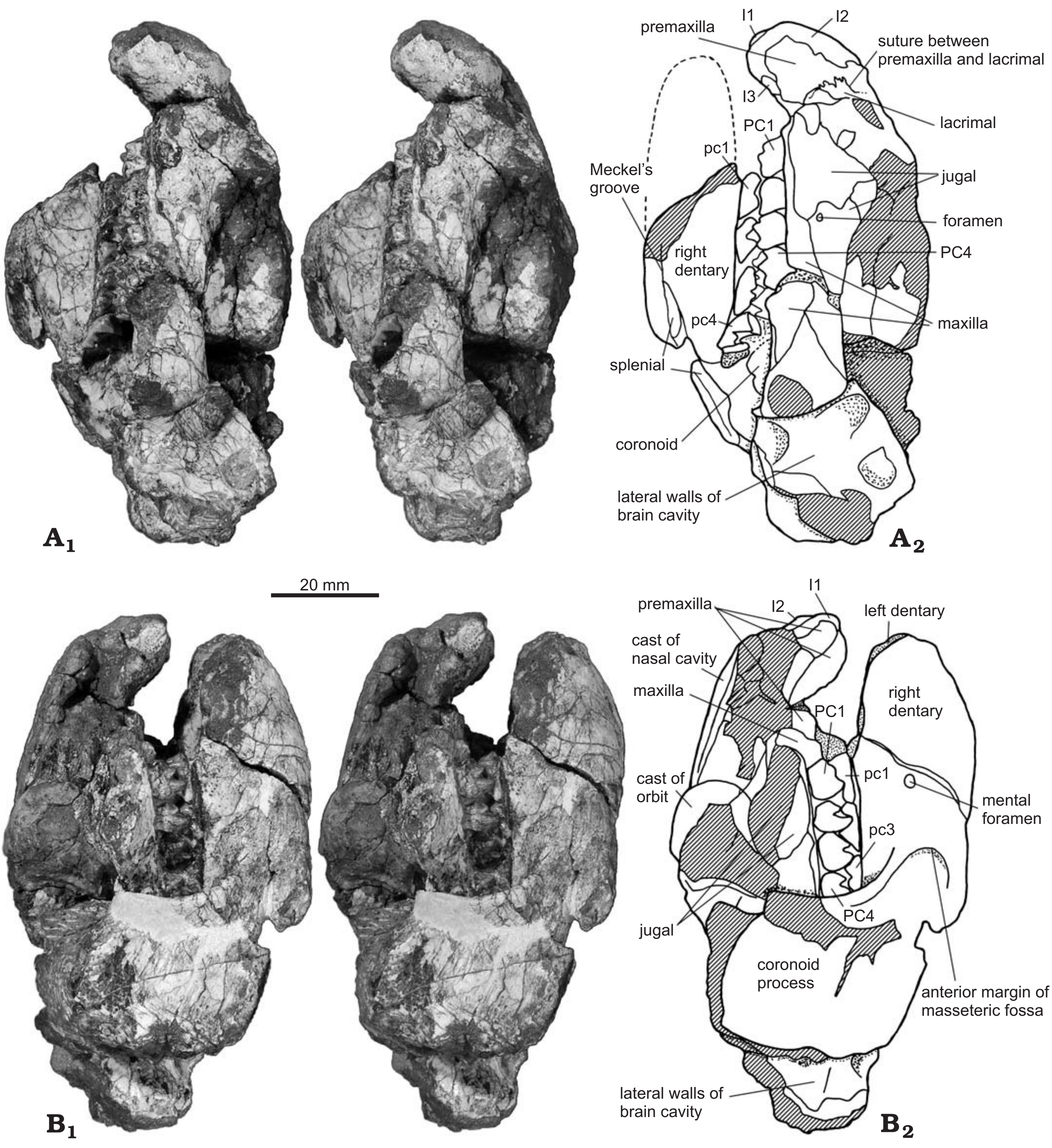


Fig. 4. Tritylodontid *Bienotheroides shartegensis* sp. nov., MPC-Nd 10/301, Upper Jurassic; Shar Teg, Mongolia. **A**. Left lateral view of the skull with the posterior part of the right lower jaw; $A_1$, stereo-photograph; $A_2$, schematic drawing. **B**. Right lateral view of the skull right and left lower jaws; $B_1$, stereo-photograph; $B_2$, schematic drawing.

**Skull**.—The skull has a short and broad snout and a relatively short postorbital region, although the skull is badly broken (Figs. 3, 4). Most of the maxilla and palatine are preserved (Fig. 3A). The premaxilla, jugal, vomer, and ventral and lateral walls of braincase (epipterygoid-pterygoid-basisphenoid region) are partly preserved. Very fragmentary parts of the lacrimal and nasal are also preserved (Figs. 3, 4). The zygomatic arch, frontal, parietal, occipital, and articulatory regions are missing. The length of the preserved part of the skull is about 99 mm. The basic structure

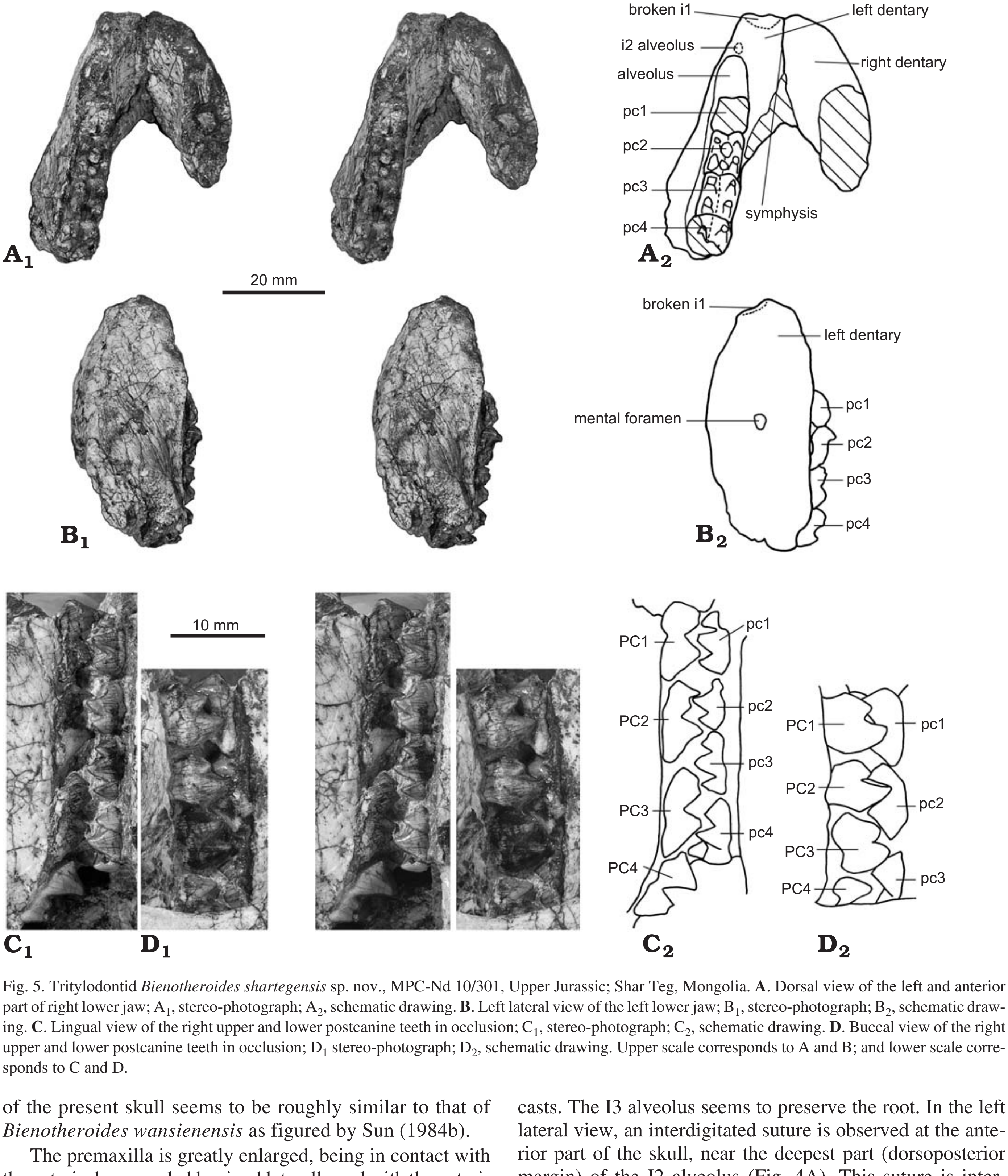


Fig. 5. Tritylodontid *Bienotheroides shartegensis* sp. nov., MPC-Nd 10/301, Upper Jurassic; Shar Teg, Mongolia. **A**. Dorsal view of the left and anterior part of right lower jaw; $A_1$, stereo-photograph; $A_2$, schematic drawing. **B**. Left lateral view of the left lower jaw; $B_1$, stereo-photograph; $B_2$, schematic drawing. **C**. Lingual view of the right upper and lower postcanine teeth in occlusion; $C_1$, stereo-photograph; $C_2$, schematic drawing. **D**. Buccal view of the right upper and lower postcanine teeth in occlusion; $D_1$ stereo-photograph; $D_2$, schematic drawing. Upper scale corresponds to A and B; and lower scale corresponds to C and D.

of the present skull seems to be roughly similar to that of *Bienotheroides wansienensis* as figured by Sun (1984b).

The premaxilla is greatly enlarged, being in contact with the anteriorly expanded lacrimal laterally and with the anteriorly expanded palatine on the secondary bony palate (Figs. 3A, 4A). The region of the incisive foramen is broken. The anterior part of the right premaxilla is missing. In the left premaxilla, three incisor alveoli are preserved (Fig. 3A). The I1 and I2 alveoli are filled with mudstone showing the endocasts. The I3 alveolus seems to preserve the root. In the left lateral view, an interdigitated suture is observed at the anterior part of the skull, near the deepest part (dorsoposterior margin) of the I2 alveolus (Fig. 4A). This suture is interpreted as the contact between the premaxilla and lacrimal. The suture between the premaxilla and palatine is deeply interdigitating. The contact between the premaxilla and the palatine is located at the level of PC1 (Fig. 3A).

The maxilla is reduced to a nearly cylindrical element holding the roots of the postcanine teeth (Fig. 3A). Therefore, the maxilla lacks the usual expansions onto the facial region dorsally, onto the secondary bony palate medially, and below the jugal laterally (Fig. 4). In both maxillae, four postcanine teeth (PC1 to PC4) are preserved (Figs. 3A, 6A). There are empty and deeply-recessed alveoli in the most mesial and most distal positions of the tooth row.

The palatine is anteriorly enlarged in contact with the premaxilla. In the right side, there are two foramina (Fig. 3A). The anterior foramen is located at the level of the mesial part of PC2 and is larger than the posterior one. This foramen can be interpreted as the greater palatine foramen. The posterior one is located at the level of the mesial part of PC3 and is smaller. This foramen can be interpreted as the lesser palatine foramen. These foramina are not observed in the left side, perhaps due to the breakage of these regions. The internal narial opening is anteriorly expanded to the level of the distal part of PC3 (Fig. 3A).

The jugal is expanded anteriorly on the lateral surface of the maxilla to form a long, flat dorsoventral (vertical) contact (Figs. 3A, 4). There is a foramen (or a small round pocket) on the left jugal above the mesial part of PC3 (Fig. 4A). This foramen is not found in the right side. The suture between the jugal and lacrimal is missing due to breakage.

The vomer is observed in ventral view (Fig. 3A). It is recognized as a median thin ridge that is located dorsal to the internal narial opening of the palatine.

The ventral and lateral walls of the brain cavity are relatively short, narrow, and symmetrical in ventral view, with laterally concave and posteriorly widening margins (Fig. 3A). There are three depressions in the left lateral side of the preserved brain cavity in lateral view (Fig. 4A). The first one is anteriorly located, dorsoposteriorly to the dorsoposterior margin of the palatine in lateral view. The second one is ventrally located and coincides with the lateral constriction of the skull behind the tooth row. The third one is located dorsoposteriorly. The third one might be due to a breakage and it is lacking in the right side (Fig. 4B). The walls of the brain cavity are badly preserved and it is difficult to describe them in detail.

Although the bones surrounding the orbit and nasal cavity are not preserved, endocasts filled with mudstone are preserved on the right and dorsal sides (Figs. 3B, 4B). The cast of the right orbit is rounded and is anteriorly and dorsally convex. Judging from the cast, the anterior rim of the orbit seems to be located at the level of PC1. The cast of the nasal cavity is anteroposteriorly elongated and is located at the dorsal side of the skull along the sagittal plane with several weak ridges running anteroposteriorly.

**Upper incisors**.—There are three upper incisors (Fig. 3A). The I2 is located lateral to I1, and I3 is located posterior to I2. The I1 alveolus is small, with a mesiodistal (transverse) diameter of about 4.5 mm. The I2 alveolus is the largest, with a mesiodistal (transverse) diameter of about 7.7 mm. The I2 is deeply rooted. The I3 alveolus is small and similar in size to the I1 alveolus with a buccolingual (transverse) diameter of about 4.2 mm and a mesiodistal (anteroposterior) diameter of about 4.6 mm. There are almost no diastemata between I1 and I2 and between I2 and I3. There is a diastema (ca. 4.5 mm) between I3 and the anterior margin of the maxilla.

**Upper postcanine teeth**.—The four upper postcanine teeth preserved on each side are almost identical in size and seem to only slightly increase in size from the most mesial to the most distal (Table 1; Fig. 6A). Their enamel is thin.

Seen in occlusal view, each upper postcanine tooth is rectangular with rounded corners and is much wider than long (Fig. 6A; Table 1). There are three mesiodistal cusp rows with two deep valleys between them. The buccal and lingual cusp rows are approximately equidistant from the middle cusp row. The mesial and distal rims of each tooth show straight relief; and the middle part of the mesial margin of the tooth is flat and does not project mesially. There is no cingulum. On the left side, several broken cusp tips of the lower postcanine teeth occlude in these deep valleys on PC1, PC2, and PC3 (Fig. 6A).

On each upper postcanine tooth, there are two buccal, three middle, and three lingual cusps; therefore, the cusp formula is 2-3-3. The cusp sizes in each row are: $B1 < B2$; $M1 \leq M2 \cong M3$; and $L1 < L3 < L2$. The largest cusp on each upper postcanine tooth is B2. M1 is the smallest and is rather vestigial. L2, L3, M2, and M3 are crescentic with two mesial cristae. B2 seems to be also crescentic, but the mesiobuccal crista is much less sharp than the mesiolingual one. L1 and B1 have only one mesial crista: the mesial crista of L1 is directed mesiobuccally, and the mesial crista of B1 extends mesiolingually. The most distal cusps (L3, M3, and B2) are arranged along a straight line buccolingually.

**Lower jaw**.—The lower jaw consists mainly of the dentary (Figs. 3A, 4, 5A, B). The depth of the right and left dentaries below pc2 is about 19.5 mm. The symphysis of the dentary is not fused, it extends back to the level of the mesial part of pc1 (Fig. 5A). The mental foramen is situated below the posterior part of pc1 on both sides (Figs. 4B, 5B). Meckel's groove is developed on the lingual side, extending to the symphysis region. On the right side, fragments of the splenial are preserved in Meckel's groove (Fig. 4A). The coronoid process of the dentary is well-developed with a vertically ascending anterior margin (Fig. 4B). The masseteric fossa extends anteriorly to the level of the mesial margin of pc3 (Fig. 4B). The lateral ridge of the dentary cannot be observed, although in *Bienotheroides wansienensis* it is developed at the external surface of the coronoid process of the dentary (Sun 1984b: 978, fig. 7). The angular process, dorsal part of the coronoid process, and articular process of the dentary are broken. The coronoid is sutured to the coronoid boss on the lingual side of the coronoid process of the dentary. The detailed morphology of the coronoid cannot be observed. The other postdentary bones of the lower jaw, the articular, prearticular, angular, and surangular, are missing. Two broken lower incisor and four lower postcanine teeth (pc1 to pc4) are preserved on the both right and left sides (Figs. 3A, 4, 5A, B, 6B).

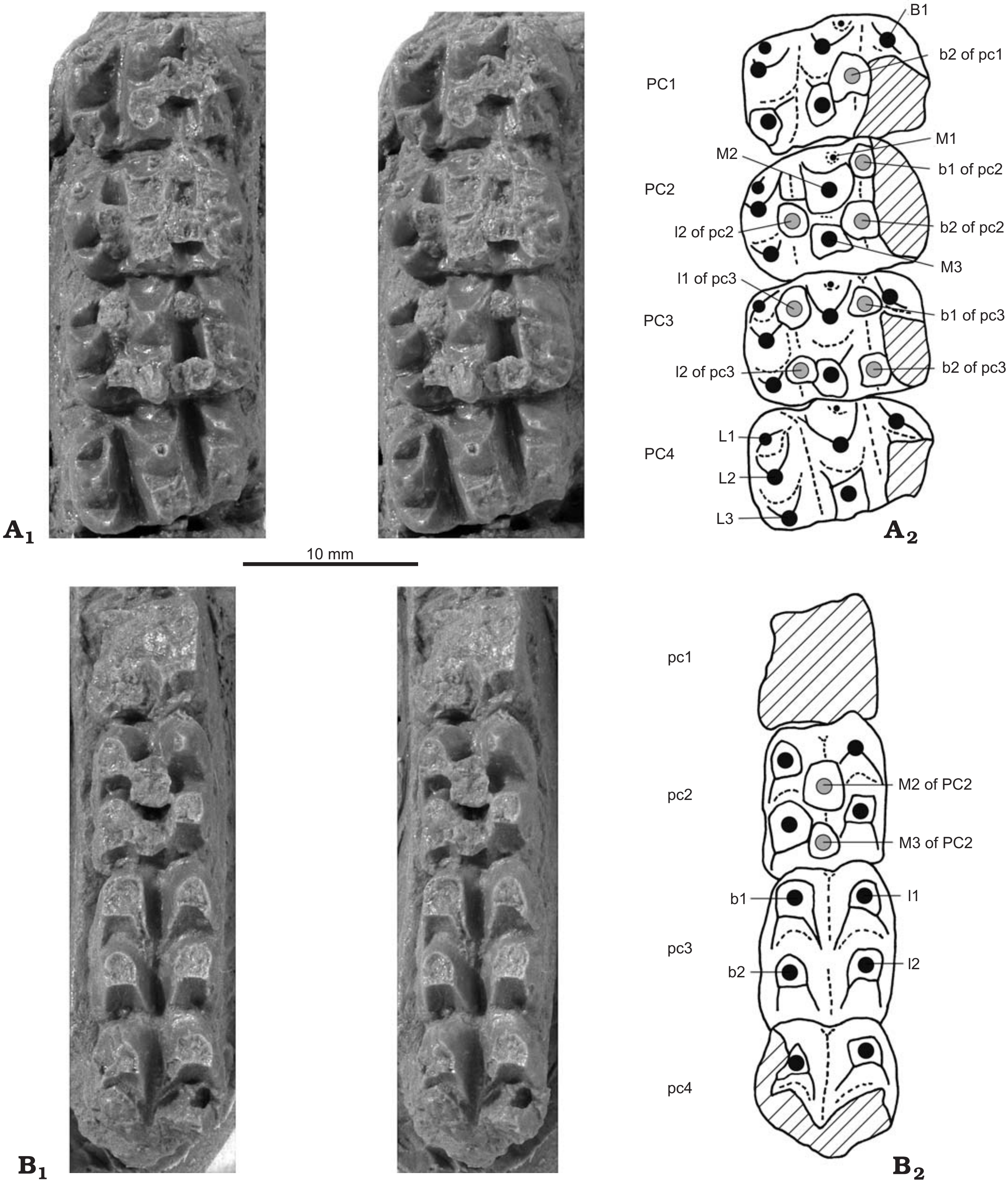


Fig. 6. Tritylodontid *Bienotheroides shartegensis* sp. nov., MPC-Nd 10/301, Upper Jurassic; Shar Teg, Mongolia. **A**. Occlusal view of the left upper postcanine dentition; $A_1$, stereo-photograph of an epoxy cast; $A_2$, schematic drawing. **B**. Occlusal view of the left lower postcanine dentition; $B_1$, stereo-photograph of an epoxy cast; $B_2$, schematic drawing.

**Lower incisors**.—There are two incisors on each sides, although their crowns are broken (Fig. 5A). The lower incisors of the right side are badly preserved and show no detail. The left i1 is procumbent and is about 6.0 mm in mesiodistal (transverse) diameter. The left i2 alveolus is filled with matrix. The left i2 seems to be much smaller than i1. There seems to be a diastema between i1 and i2, and no or only a very short diastema between i2 and the anterior margin of the alveolus of the postcanine teeth.

**Lower postcanine teeth**.—The four lower postcanine teeth preserved on each side are rectangular in occlusal view and are longer than wide (Fig. 6B). There are two mesiodistal cusp rows with a deep valley between them. There is no cingulum. The enamel is thin. On the left side, two broken cusp tips of an upper postcanine tooth occlude in this deep valley on pc2.

The lower postcanine cusp formula is 2-2: there are only b1, b2, l1, and l2. All cusps are crescentic with two distal cristids and are nearly identical in shape and size. The distolingual cristid of l1 and distobuccal cristid of b1, respectively, end at the mesiolingual base of l2 and the mesiobuccal base of the b2. The lower postcanine tooth row is gently convex lingually.

The eruption sequences of the postcanine teeth were not completely synchronous among the tooth rows in this specimen, as shown in the holotype of *Bienotheroides wansienensis* (Young 1982; Sun 1984b). The right pc4 of the present specimen is in eruption and faces diagonally to the tooth row (Figs. 4A, 5C), whereas the eruption of left pc4 is almost completed and the tooth is not so much diagonally inclined to the tooth row (Fig. 5B). On the upper dentition, on the other hand, right and left PC4 are fully erupted.

On the right side, pc4 is not occluding with PC4 (Fig. 5C). The distal part of pc3 is occluding with PC4, and the mesial part of pc3 is occluding with the distal part of PC3 (Fig. 5C, D). The distal part of pc2 is occluding with the mesial part of PC3, and the mesial part of pc2 is occluding with the distal part of PC2 (Fig. 5C, D).

**Additional fragmentary elements**.—There are five additional fragments which represent parts of the skull and lower jaw, but they are too incomplete to be interpreted with confidence. A bone fragment with unerupted and broken postcanine teeth is probably a part of the coronoid process of the left dentary. A large and thin fragment might be a part of the zygomatic arch. A small fragment has a broken tooth root. The other two fragments are indeterminate broken bones.

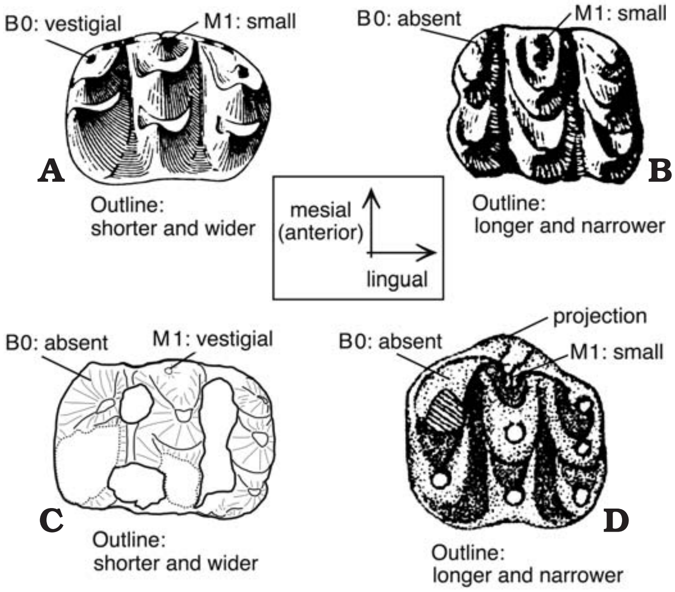


Fig. 7. Comparison of right upper postcanine teeth among the species of *Bienotheroides* in occlusal view (not to scale). **A**. *Bienotheroides wansienensis* (after Sun 1984b). **B**. *Bienotheroides zigongensis* (after Sun 1986). **C**. *Bienotheroides shartegensis* sp. nov. (reversed). **D**. *Bienotheroides ultimus* (after Maisch et al. 2004).

# Comparison and discussion

The specimen MPC-Nd 10/301 corresponds to the “advanced” tritylodontids (Clark and Hopson 1985; Sues 1986b) such as *Bienotheroides*, *Stereognathus*, *Bocatherium*, and *Dinnebitodon* based on the following cranial characteristics: (1) a short snout; (2) premaxilla in contact with the palatine on the secondary bony palate, excluding the maxilla from participation in the formation of the secondary bony palate; and (3) lateral (facial and zygomatic) extension of the maxilla much reduced due to the extension of the premaxilla, lacrimal, and jugal. MPC-Nd 10/301 has a short snout, distinguishing it from the most basal tritylodontids such as long-snout *Oligokyphus* and *Tritylodon* (Clark and Hopson 1985; Sues 1986b). It has a premaxilla in contact with the palatine and has a very much reduced lateral extension of the maxilla, distinguishing it from other relatively plesiomorphic tritylodontids such as *Bienotherium*, *Kayentatherium*, *Oligokyphus*, and *Tritylodon*, which lack a premaxilla-palatine contact and have a lateral extension of the maxilla (Clark and Hopson 1985; Sues 1986b).

The following dental characteristics of MPC-Nd 10/301 indicate that the specimen should be assigned to the genus *Bienotheroides* (Sun 1984b, 1986; Setoguchi et al. 1999; Matsuoka 2000; Maisch et al. 2004): (1) the upper postcanine cusp formula is 2-3-3 (although it is 3-3-3 in *B. wansienensis*; Sun 1984b); (2) M1 cusp is tiny; (3) L3 cusp is relatively large; (4) the most distal upper postcanine cusps (L3, M3, and B2) are arranged along a straight buccolingual line; (5) the outlines of the crowns of the upper postcanines are rectangular with rounded corners; (6) there are three upper incisors on each side, with the second being the largest; (7) the lower postcanine cusp formula is 2-2; (8) b1 and l1 cusps are as large as b2 and l2 cusps; and (9) there are two lower incisors on each side. MPC-Nd 10/301 is distinguished from *Oligokyphus* by having fewer cusps in each upper and lower postcanine teeth. It is distinguished from *Tritylodon*, *Lufengia*, *Dianzongia*, *Yunnanodon*, *Dinnebitodon*, *Bienotherium*, and *Kayentatherium* by having a much smaller M1 cusp and buccolingually arranged L3, M3, and B2 cusps. It is distinguished from *Tritylodon*, *Lufengia*, *Dianzongia*, *Yunnanodon*, and *Dinnebitodon* by having smaller L1 cusp. It is distinguished from *Yunnanodon* and *Dinnebitodon* by having L3 cusp. It is distinguished from *Bienotherium* in that b1 and l1 cusps are as large as b2 and l2 cusps (Young 1947;

Table 2. Character distribution and geological and paleontological information on the different *Bienotheroides* species (Young 1982; Sun 1984a, b, 1986; Sun and Li 1985; Sun and Cui 1989; Maisch et al. 2004; this study).

| | *Bienotheroides wansienensis* | *Bienotheroides zigongensis* | *Bienotheroides ultimus* | *Bienotheroides shartegensis* sp. nov. |
|---|---|---|---|---|
| Upper cheek tooth outline in occlusal view | short and wide | long and narrow | long and narrow | short and wide |
| Upper B0 cusp | vestigial | absent | absent | absent |
| Upper M1 cusp | small | small | small | vestigial |
| Upper L1 cusp | small | small | small | small |
| Projection at the anterior margin of upper PC | no | no | yes | no |
| Direction of stapedial process of quadrate | ? | mediodorsally | medially | ? |
| Geologic age | Middle or early Late Jurassic | Middle Jurassic | Late Jurassic | Late Jurassic |
| Formation | Upper Shaximiao Formation | Lower Shaximiao Formation and Wucaiwan Formation | Shishugou Formation | lower part of Ulaan Malgait Beds |
| Locality | Gaoling (Wanxian, Sichuan) | Dashanpu (Zigong, Sichuan) and Xinjiang | eastern Junggar Basin (Xinjiang) | Shar Teg (Gobi-Altai Aimag) |
| Region | southern China | southern and northwestern China | northwestern China | southwestern Mongolia |
| Description | Young (1982), Sun (1984a, b), Sun and Li (1985) | Sun (1986), Sun and Cui (1989) | Maisch et al. (2004) | This study |

Luo and Wu 1994). It is distinguished from more advanced tritylodontids such as *Bocatherium*, *Polistodon*, *Stereognathus*, *Xenocretosuchus*, and the unnamed Japanese tritylodontid (Setoguchi et al. 1999; Matsuoka 2000; Kamiya et al. 2006) in having M1 and L1 cusps and a more rounded corners on the upper postcanine teeth.

MPC-Nd 10/301 is assigned to a new species of *Bienotheroides*, which is named *Bienotheroides shartegensis*. Its main difference with other species resides in that M1 cusp is much more reduced, indeed vestigial (Fig. 7; Table 2). Also, the new species is distinguished from *Bienotheroides zigongensis* and *Bienotheroides ultimus* by having proportionally shorter and wider postcanine teeth, from *B. ultimus* by lacking a projection of the middle part on the mesial margin of the upper postcanine teeth (Maisch et al. 2004), and from *Bienotheroides wansienensis* in lacking both B0 cusp and a diastema between upper I1 and I2 (Sun 1984b).

Among the species of *Bienotheroides*, *Bienotheroides shartegensis* sp. nov. has two derived characteristics. One is its proportionally short and wide upper postcanine teeth; and the other is a very much reduced M1 cusp. The primitive condition of long and narrow upper postcanine teeth is seen in *Oligokyphus*, which has been considered the most basal tritylodontid (Hennig 1922; Clark and Hopson 1985; Sues 1986b), whereas the advanced condition of relatively shorter and wider upper postcanine teeth is seen in advanced tritylodontids such as *Polistodon*, *Stereognathus*, *Xenocretosuchus*, and the unnamed Japanese tritylodontid (Tatarinov and Matchenko 1999; Setoguchi et al. 1999; Matsuoka 2000). The upper postcanine teeth of *B. shartegensis* are proportionally much wider and narrower and more advanced in this character than those of the other advanced tritylodontids. On the other hand, M1 cusp is primitively large among the Tritylodontidae; it is absent in advanced forms such as *Stereognathus* and the unnamed Japanese tritylodontid (Setoguchi et al. 1999; Matsuoka 2000).

We performed a preliminary phylogenetic analysis of the Tritylodontidae to shed light on the phylogenetic position of *Bienotheroides shartegensis* sp. nov. We used 17 taxa and 11 characters (Appendices 1, 2). We have kept this analysis centered on the new species using only 11 characters, which were discussed in previous studies (Clark and Hopson 1985; Sues 1986b; Setoguchi et al. 1999; Matsuoka 2000). Despite the fact that some other groups (such as cynognathids, chiniquodontids, and traversodontids) and characters (such as postcranial features) may bring to bear information important for the resolution of the internal nodes of the tritylodontids, they are out of scope for this study. The characters comprise five cranial and six dental features. The cranial characters were compiled from Clark and Hopson (1985) and Sues (1986b) and the dental ones were complied from Setoguchi et al. (1999) and Matsuoka (2000). The character-states of each taxon except for *Bienotheroides shartegensis* were compiled from Sun (1984b), He and Cai (1984), Clark and Hopson (1985), Sues (1986b), Sun and Cui (1989), Luo and Wu (1994), Setoguchi et al. (1999), Matsuoka (2000), and Maisch et al. (2004). The data matrix was compiled using MacClade version 4.0 (Maddison and Maddison 2000) and analyzed using PAUP 4.0b10 (Swofford 2002) with the branch-and-bound search option, using *Oligokyphus* to represent an outgroup to the other tritylodontids. We performed two kinds of analysis: all characters ordered (analysis 1) and all characters unordered (analysis 2). The analysis 1 recovered 45 equally most parsimonious trees with a length of 19 steps; and the analysis 2 recovered 12 equally most parsimonious trees with a length of 17 steps. Each most parsimonious tree of the analysis 1 has a consistency index (excluding uninformative characters) of 0.7647, homoplasy index (excluding uninformative characters) of 0.2353, retention index of

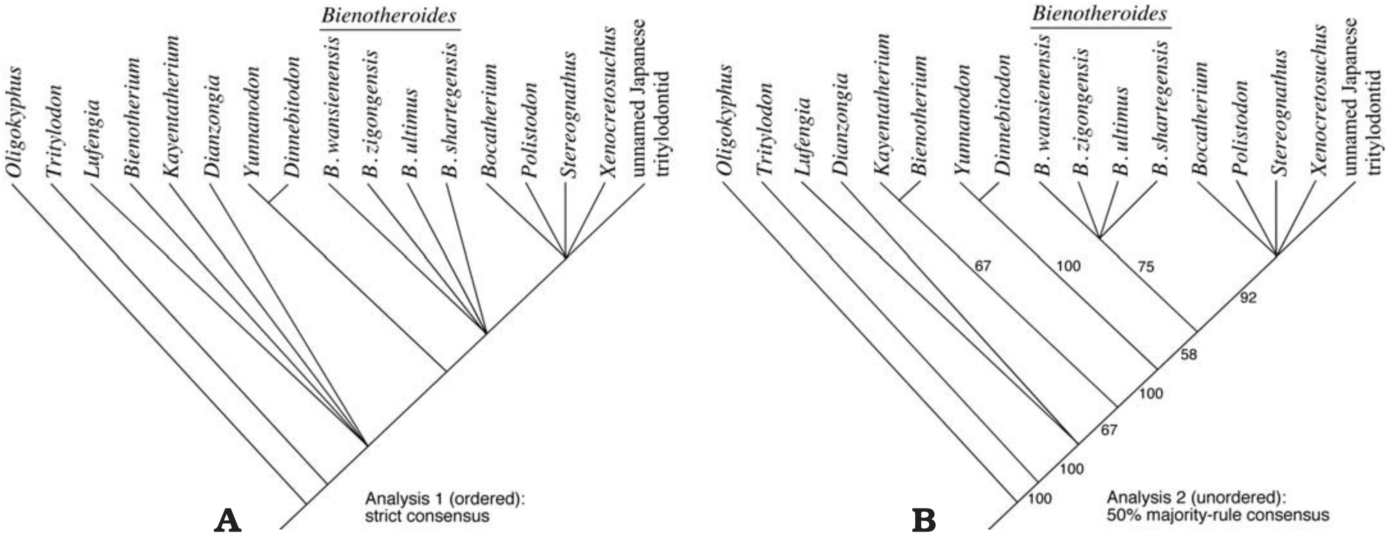


Fig. 8. The results of the preliminary parsimony analyses of the 11 character data-matrix (Appendices 1, 2). **A**. Strict consensus tree of the 45 equally most parsimonious cladogram trees recovered by the analysis 1 (all characters ordered). **B**. 50% majority-rule consensus tree of the 12 equally most parsimonious cladogram trees recovered by the analysis 2 (all characters unordered). Numbers indicate the percentages of the frequencies of occurrence. "Unnamed Japanese tritylodontid" indicates the unnamed tritylodontid reported and figured by Setoguchi et al. (1999), Matsuoka (2000), and Kamiya et al. (2006).

0.8947, and rescaled consistency index of 0.7064; that of the analysis 2 has a consistency index (excluding uninformative characters) of 0.8667, homoplasy index (excluding uninformative characters) of 0.1333, retention index of 0.9333, and rescaled consistency index of 0.8235. The strict consensus tree of the 45 trees in the analysis 1 (Fig. 8A) and the 50% majority-rule consensus tree of the 12 trees in the analysis 2 (Fig. 8B) indicate that *Bienotheroides* is the sister taxon for a clade containing *Bocatherium*, *Polistodon*, *Stereognathus*, *Xenocretosuchus*, and the unnamed Japanese tritylodontid. The 50% majority-rule consensus tree in the analysis 2 justifies the inclusion of the new species (*B. shartegensis*) into the genus *Bienotheroides*.

Although our preliminary phylogenetic analysis is based on only 11 characters, it is meaningful to test the tritylodontid phylogeny suggested by previous researchers. Clark and Hopson (1985) and Sues (1986b) suggested a phylogenetic relationships of several tritylodontids based mainly on cranial characteristics, whereas Setoguchi et al. (1999) and Matsuoka (2000) suggested a tritylodontid phylogeny based only on upper postcanine characteristics. Our analysis combined all characteristics discussed by these four studies. The resulted cladograms (Fig. 8) are consistent with that by Sues (1986b), which contains only six taxa, but are slightly different from those by Clark and Hopson (1985), Setoguchi et al. (1999), and Matsuoka (2000) in the phylogenetic relationships of plesiomorphic tritylodontids such as *Bienotherium*, *Kayentatherium*, *Lufengia*, *Dinnebitodon*, *Yunnanodon*, and *Dianzongia*. This suggests that the characteristics discussed by the above-mentioned researchers are not sufficient to resolve the phylogenetic relationships of these plesiomorphic tritylodontids and that it is necessary to identify additional useful characteristics to resolve the interrelationships.

# Concluding remarks

*Bienotheroides* has hitherto been known from the Middle to lower Upper Jurassic of Sichuan Province in southern China (*Bienotheroides wansienensis* and *Bienotheroides zigongensis*) and from the Middle and Upper Jurassic of Xinjiang Province in northwestern China (*Bienotheroides zigongensis* and *Bienotheroides ultimus*; Table 2; Yong 1982; Sun 1986; Sun and Li 1985; Sun and Cui 1989; Maisch et al. 2004). The new species described in this paper, *Bienotheroides shartegensis*, shows that the genus also occurs in the Upper Jurassic of southwestern Mongolia. This discovery extends the taxonomic (morphological) diversity and geographic range of the genus and underlies the success of the genus in the Middle to Late Jurassic biota of eastern Eurasia.

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# Appendix 1

List of characters and character definitions used in the phylogenetic analysis. The data of characters 1–5 are compiled from Clark and Hopson (1985) and Sues (1986b); those of characters 6–11 are compiled from Setoguchi et al. (1999) and Matsuoka (2000).

1. Snout: long (0); short (1).
2. Postincisive constriction of the snout: present (0); absent (1).
3. Premaxilla posterior extension on secondary palate: anteriorly (0); between incisors and the mesial cheek teeth (1); near the most mesial teeth (2).
4. Contact between premaxilla and palatine on palate: absent (0); present (1).
5. Lateral (facial and zygomatic) extension of maxilla (in *Lufengia* juveniles; adult condition uncertain): present (0); reduced or absent (1) (by extension of lachrymal, jugal, and premaxilla).
6. Upper cheek tooth B0 cusp: present (0); absent (1).
7. Upper cheek tooth M0 cusp: present (0); absent (1).
8. Upper cheek tooth L0 cusp: present (0); absent (1).
9. Upper cheek tooth M1 cusp: large (0); small (1); absent (2).
10. Upper cheek tooth L1 cusp: large (0); small (1); absent (2).
11. Upper cheek tooth L3 cusp: large (0); small (1); absent (2).

# Appendix 2

Character matrix employed in this paper for assessing the phylogenetic relationship among tritylodontids. Characters are listed in Appendix 1. Missing or unknown characters are represented by "?". The character states of each taxon except for *Bienotheroides shartegensis* sp. nov. were compiled from Sun (1984b), He and Cai (1984), Clark and Hopson (1985), Sues (1986b), Sun and Cui (1989), Luo and Wu (1994), Setoguchi et al. (1999), Matsuoka (2000), and Maisch et al. (2004). "Unnamed Japanese tritylodontid" indicates the unnamed tritylodontid reported and figured by Setoguchi et al. (1999), Matsuoka (2000), and Kamiya et al. (2006).

| Taxon | Character | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| *Oligokyphus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Tritylodon* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Lufengia* | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Bienotherium* | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Kayentatherium* | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Dianzongia* | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 |
| *Yunnanodon* | 1 | 1 | ? | ? | ? | 1 | 1 | 1 | 0 | 0 | 2 |
| *Dinnebitodon* | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 2 |
| *Bienotheroides wansienensis* | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Bienotheroides zigongensis* | 1 | ? | ? | ? | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Bienotheroides ultimus* | ? | ? | ? | ? | ? | 1 | 1 | 1 | 1 | 1 | 0 |
| *Bienotheroides shartegensis* | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Bocatherium* | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 0 |
| *Polistodon* | 1 | 1 | ? | ? | ? | 1 | 1 | 1 | 2 | 2 | 0 |
| *Stereognathus* | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 0 |
| *Xenocretosuchus* | ? | ? | ? | ? | ? | 1 | 1 | 1 | 2 | 2 | 0 |
| Unnamed Japanese tritylodontid | ? | ? | ? | ? | ? | 1 | 1 | 1 | 2 | 2 | 0 |