

Two new tritylodontids (Synapsida, Cynodontia, Mammaliaforma) from the Upper Jurassic, southwestern Mongolia

PAÚL M. VELAZCO,¹ ALEXANDRA J. BUCZEK,^{2,3} AND MICHAEL J. NOVACEK¹

ABSTRACT

Two new genera and species of Tritylodontidae, *Shartegodon altai* and *Nuurtherium baruunensis*, are described and compared with other known tritylodontids. The new taxa are represented by two partial skulls and, in the case of *Nuurtherium*, postcranial elements. They were collected from the lower part of the Ulan Malgait Sequence (Upper Jurassic) in the Shar Teg locality, Gobi-Altai Aimag, southwestern Mongolia. The upper postcanine teeth of these two genera have unique cusp formulae that differentiate them from other tritylodontids. As has been suggested for most tritylodontids in general, these two new genera may have been herbivorous.

INTRODUCTION

The Tritylodontidae Cope, 1844, is a highly specialized group of non-mammaliaform, herbivorous cynodonts (Kemp, 2005; Sues and Jenkins, 2006). The fossil record of this family extends from the Upper Triassic to the Lower Cretaceous and has a worldwide distribution, with fossils found in Antarctica (Hammer and Smith, 2008), Argentina (Bonaparte, 1970), Canada (Fedak et al., 2015), China (Young, 1940, 1982; Chow and Hu, 1959; Chow, 1962; Cui, 1976, 1981, 1986; Sun, 1986; He and Cai, 1984; Luo and Sun, 1993; Maisch et al., 2004; Hu et al., 2009), England (Charlesworth, 1855; Kühne, 1956), Germany (Lydekker, 1887; Hennig,

¹ Division of Paleontology, American Museum of Natural History.

² Department of Earth, Environmental and Planetary Sciences, Brown University, Providence, RI.

³ Richard Gilder Graduate School, American Museum of Natural History.

1922), Japan (Kamiya et al., 2006; Matsuoka et al., 2016), Lesotho (Owen, 1884), Mexico (Clark and Hopson, 1985), Mongolia (Watabe et al., 2007), Russia (Tatarinov and Maschenko, 1999; Lopatin and Agadjanian, 2008), South Africa (Kitching and Raath, 1984), and the United States (Kermack, 1982; Sues, 1985, 1986a). Tritylodontids varied in size from that of a small rat (100 g) to a large raccoon (10 kg), with the smallest taxon being *Lufengia delicata* (PC3 [postcanine 3]: length 2.2 mm, width 2.4 mm; Chow and Hu, 1959) and the largest being *Bienotherium magnum* (PC3: length 13 mm, width 17 mm; Chow, 1962).

The phylogenetic affinities of the Tritylodontidae have long been debated. The group has been most consistently placed close to Mammaliaformes (= crown group Mammalia and closest extinct relatives) (e.g., Wible, 1991; Rowe, 1993; Martinez et al., 1996; Luo et al., 2002; Kemp, 2005; Liu and Olsen, 2010; Ruta et al., 2013). While some authors place tritylodontids as sister to Mammaliaformes (e.g., Wible, 1991; Rowe, 1993; Martinez et al., 1996; Ruta et al., 2013), other studies have placed them within the diademodontoids, as a sister clade to cynognathids, and identified the tritheledontids as the sister group to mammaliaforms (Hopson and Barghusen, 1986; Hopson, 1991; Hopson and Kitching, 2001). The definition of Tritylodontidae depends on the choice between these two hypotheses.

The tritylodontid skull resembles that of the general condition in mammals in lacking a postorbital bar and in having confluent orbit and temporal fenestrae and a high sagittal crest (Sues, 1986c). Unlike mammals, however, the craniomandibular joint is formed by the quadrate and articular, and there is no contact between the dentary and squamosal. Well-developed coronoid and angular processes are present on the mandible (Sues, 1986c; Kemp, 2005). The inner ear of tritylodontids represents an intermediate state between nonmammalian cynodonts and mammals in having a distinct cochlear canal in an enlarged pars cochlearis and in lacking a promontorium. While the mammalian inner ear is characterized by having an elongated cochlear canal and enlarged pars cochlearis and promontorium, most nonmammalian cynodonts lack a promontorium and, if present, the bony cochlear recess is poorly developed (Luo, 2001).

Some of the most diagnostic characters of tritylodontids reside in their dentition. Tritylodontids have one to three upper procumbent incisors and one to two lower procumbent incisors. Tritylodontids lack canines, but the upper second and lower first incisors are greatly enlarged and resemble canines. Despite the lack of canines, the upper and lower cheek teeth are commonly called “postcanines.” A large diastema separates the incisors from the postcanine teeth. The maxillary postcanines have three longitudinal rows of curved cusps that face anteriorly, whereas the mandibular postcanines have two rows of cusps that are oriented posteriorly. The tooth rows are parallel and, when in occlusion, the two lower rows of cusps fit into the troughs between the three upper rows of cusps. This orientation suggests a propalinal (fore-and-aft) movement of the dentary and palinal (backward) power stroke (Kermack and Kermack, 1984), which, in many living mammals, is effective for shredding tough vegetation (Simpson, 1926; Fejfar et al., 2011; Lazzari et al., 2015). The number of postcanine teeth increases through ontogeny: when front teeth are lost, new teeth erupt at the posterior end of the tooth row (Cui and Sun, 1987; Matsuoka and Setoguchi, 2000).

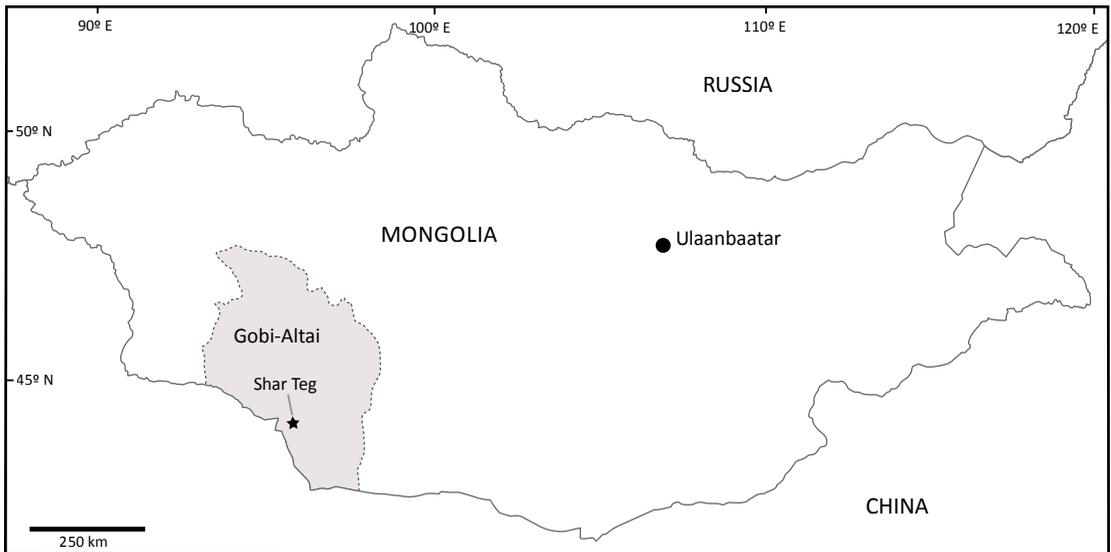


FIGURE 1. Map of Mongolia, showing the Shar Teg (filled star) locality of the Gobi-Altai Aimag (gray area).

Twenty-four species of tritylodontids are currently recognized and are grouped into 15 genera: *Bienotherium* Young, 1940; *Bienotheroides* Young, 1982; *Bocatherium* Clark and Hopson, 1985; *Dianzhongia* Cui, 1981; *Dinnebitodon* Sues, 1986; *Kayentatherium* Kermack, 1982; *Lufengia* Chow and Hu, 1959; *Montirictus* Matsuoka et al., 2016; *Oligokyphus* Hennig, 1922; *Polistodon* He and Cai, 1984; *Stereognathus* Charlesworth, 1855; *Tritylodon* Owen, 1884; *Xenocretosuchus* Tatarinov and Matchencko, 1999; *Yuanotherium* Hu et al., 2009; *Yunnanodon* Cui, 1986; and an unnamed putative tritylodontid from Argentina (Bonaparte, 1970).

Here we report on two new genera and species of tritylodontids found by the Mongolian Academy of Sciences-American Museum of Natural History expeditions (MAE) in 2010 and 2011 from the Upper Jurassic of southwestern Mongolia (fig. 1). The taxa are represented by a partial skull in one instance and by a skull and postcranial elements in the other.

MATERIALS AND METHODS

The fossils described in this paper are temporarily housed at the American Museum of Natural History (AMNH) and will be permanently deposited at the Institute of Paleontology and Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia (PSS-MAE). To assess the phylogenetic relationships of our two specimens with other tritylodontids genera, we analyzed the variation in 35 cranial and dental characters (appendices 1 and 2). The matrix includes all known genera of tritylodontids. In cases where more than one state was present in a genus, we scored that character as having a polymorphic state (appendix 2). All the characters and scorings are based on the following references: Simpson (1928); Young (1947); Kühne (1956); Chow and Hu (1959); Chow (1962); Waldman and Savage (1972); Cui (1981); Kermack (1982); He and Cai (1984); Sun (1984); Clark and Hopson (1985); Sues (1985, 1986b, 1986c); Cui and

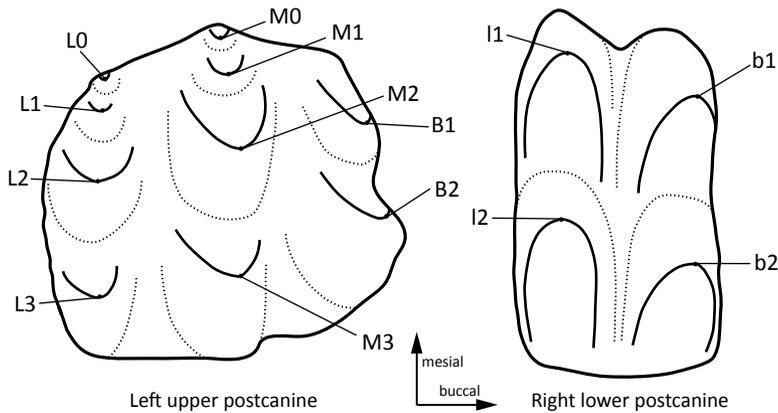


FIGURE 2. Dental cusp nomenclature of the postcanine teeth of tritylodontids used in this paper (modified from Setoguchi et al., 1999; Matsuoka, 2000; and Watabe et al., 2007). Abbreviations: B, buccal; M, medial; L, lingual; b, buccal; l, lingual.

Sun (1987); Sun and Cui (1989); Luo and Wu (1994); Setoguchi et al. (1999); Matsuoka (2000); Maisch et al. (2004); Sues and Jenkins (2006); Watabe et al. (2007); Lopatin and Agadjanian (2008); Hu et al. (2009); Jasinowski and Chinsamy (2012); Fedak et al. (2015); and Matsuoka et al. (2016). Upper and lower postcanine cusp nomenclature follows Watabe et al. (2007). In the upper postcanines (PC) tritylodontids have three cusp rows that run mesiodistally across each tooth, with two deep valleys running between them. The number of cusps in the buccal (B) medial (M), and lingual (L) rows varies in number among different tritylodontid genera. Cusps in each row are demarcated by a number as well as the initial of their row. The most mesial cusp of any given row is numbered 0 or 1, the most distal by a higher number depending on the number of cusps in the row. Thus, M0 would indicate the most mesial cusp of the medial row, and L3, the most distal cusp of the lingual row (fig. 2). In the lower postcanine teeth (pc) there are two mesiodistal cusp rows with one valley running between them. All the lower postcanine teeth have two buccal (b) and two lingual (l) cusps. Thus, b1 indicates the most mesial cusp of the buccal row, l2 the most distal cusp of the lingual row (fig. 2). We follow Setoguchi et al. (1999) in considering the position of the upper and lower postcanine cusps to be homologous among all members of the family.

The complete matrix is available at <http://www.morphobank.org> (project: P2219, Two new tritylodontids (Synapsida, Cynodontia, Mammalia-morpha) from the Upper Jurassic, southwestern Mongolia) (O’Leary and Kaufman, 2012).

We used “New Technology” search option, using sectorial search, ratchet, tree drift, and tree fusing of TNT version 1.5 (Goloboff et al., 2003, 2008) to analyze the resulting matrix of 17 taxa and 35 character states, using unordered states. *Oligokyphus* was selected as an out-group because it has been considered the most basal tritylodontid (Hennig, 1922; Clark and Hopson, 1985; Sues, 1986b; Setoguchi et al., 1999; Watabe et al., 2007).

The maximum length and width of all complete lower and upper postcanines were measured for both specimens. The upper postcanine measurements were added to the original tooth size data of Hu et al. (2009) to determine size relationships of the two new specimens

relative to other tritylodontids. The selected measurements were chosen based on the most complete and well-preserved upper postcanine. The right PC2s were chosen for both *Shartegodon altai* and *Nuurtherium baruunensis*.

SYSTEMATIC PALEONTOLOGY

Synapsida Osborn, 1903

Cynodontia Owen, 1861

Mammaliamorpha Rowe, 1988

Tritylodontidae Cope, 1844

Shartegodon, gen. nov.

Figures 3–10

TYPE SPECIES: *Shartegodon altai*, sp. nov.

ETYMOLOGY: *Sharteg-*, Mongolian, after the type locality.

AGE: As for the type and only species.

DIAGNOSIS: As for the type and only species.

Shartegodon altai, sp. nov.

HOLOTYPE: PSS-MAE 633, a badly damaged skull with cheek teeth and partial right and left dentaries with three postcanine teeth each (figs. 3–10).

TYPE LOCALITY: Shar Teg locality, Gobi-Altai Aimag, southwestern Mongolia (fig. 1).

STRATIGRAPHIC HORIZON: From a maroon bed of the lower part of the Ulan Malgait Sequence (just above the boundary with the Shar Teg Sequence); Upper Jurassic (Gereltsetseg, 1992; Ponomarenko et al., 2014).

ETYMOLOGY: The species name *altai*, derived from Mongolian, refers to the *aimag* (“province”), Gobi-Altai, in which the Shar Teg beds are located.

DIAGNOSIS: Differing from other tritylodontids in having a palatine that contacts the alveoli of the last upper postcanine teeth (PC4); a lack of interdigitations on the maxillo-palatine and premaxillo-palatine sutures; three foramina (two of which are probably just small round pockets) present on the jugal above PC2; upper postcanine teeth with four roots; and upper postcanine teeth with a cusp formula of 2-4-4. Differs from the species, *Bienotheroides shartegensis*, previously recorded at the Shar Teg locality in having a maxilla that extends laterally to contribute to the zygoma (zygomatic process of the maxilla), and in having M0 and L0 cusps on the upper postcanine (PC) teeth (Watabe et al., 2007).

DESCRIPTION: The skull of *Shartegodon altai* (PSS-MAE 633) is extensively crushed (figs. 3A–B, 4A–B), and the anterior region of the skull is badly damaged, but the nasals, maxilla, premaxilla, palatine, jugal, and lacrimal are partly preserved (figs. 3A–B, 4A–B). The nasals

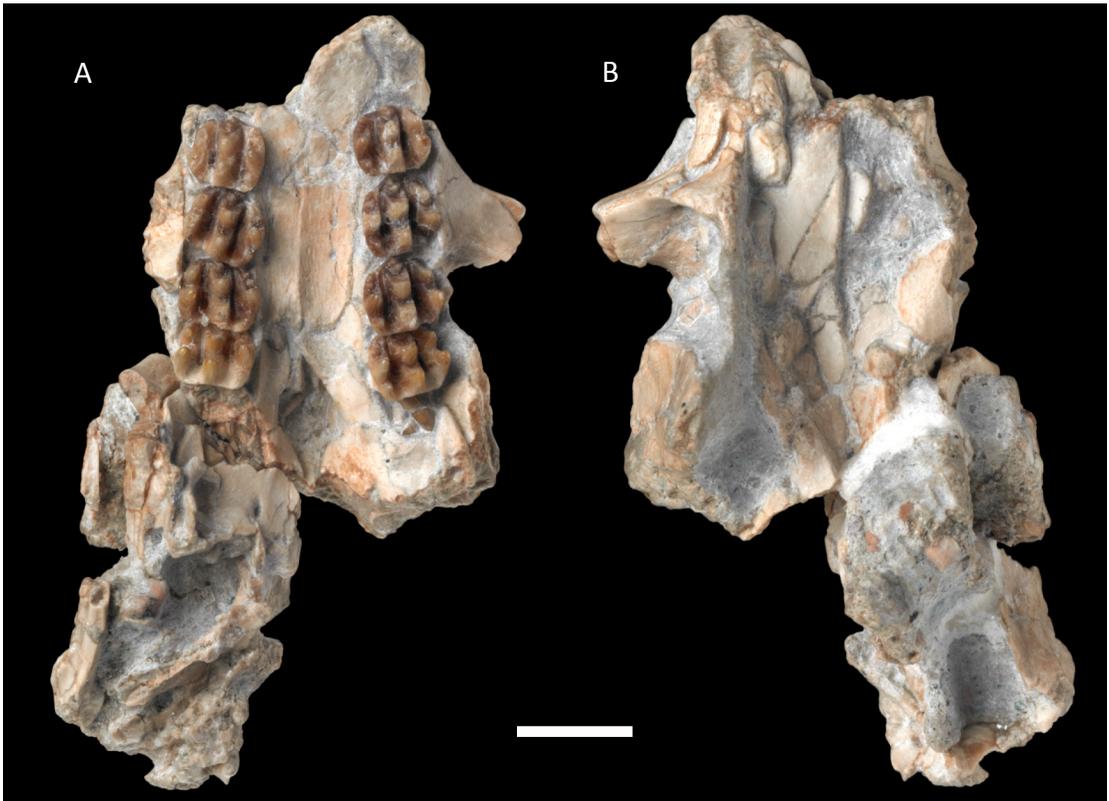
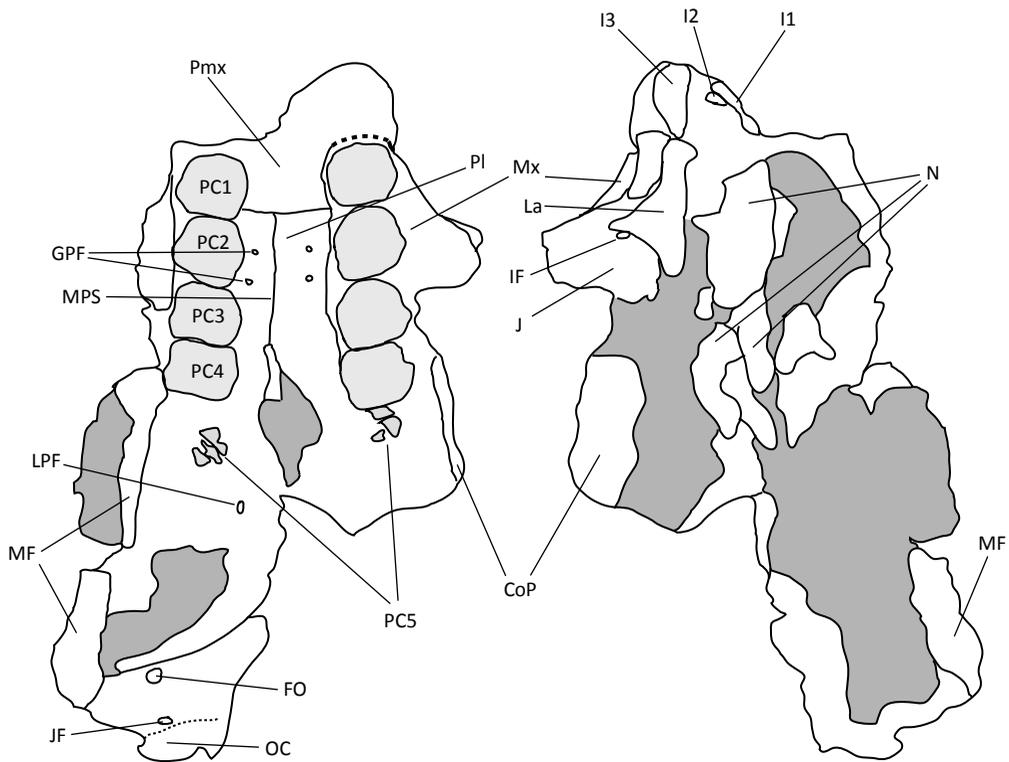


FIGURE 3. The skull of *Shartegodon altai* PSS-MAE 633 (holotype) in (A) ventral and (B) dorsal views (above) with accompanying line drawings (opposite page). Dark gray indicates matrix; light gray indicates the upper postcanines. Abbreviations: **CoP**, coronoid process of dentary; **GPF**, greater palatine foramina; **FO**, fenestra

are shattered, making it difficult to observe their contact with other bones (figs. 3B, 4B). The palate is smooth. In the palate the maxilla (preserved only on the left side) is very small and is confined to form the alveoli of PC1-PC3, with a narrow band forming the lingual margins of PC1-PC3 (fig. 3A). The maxilla extends laterally to form the zygomatic process. This process constitutes the ventral surface of the anterior root of the zygomatic arch (fig. 3A). There is no contribution of the maxilla to the orbital wall. Most of the anterior and dorsal aspects of the premaxilla are missing. Ventrally, the premaxilla is well developed and it contacts both the palatine and maxilla (fig. 3A). The premaxilla-palatine contact is a transverse suture that aligns with the posterior portion of PC1. The premaxilla-maxillary contact follows the mesio-lingual shape of PC1 (fig. 3A). In lateral view the anterior premaxilla is distinctly downturned (fig. 4A-B). On left side of the skull, damage to the dorsal premaxilla reveals the presence of two incisors (figs. 3B, 4B). Root remnants of two small mesial incisors (left I1 and I2), and a large partial alveolus for the I3 root are preserved (figs. 3B, 4B). The palatine is the best-preserved bone in the skull. Posteriorly, the palatine presents extensive horizontal processes. The suture between palatine and pterygoid cannot be observed. On the right horizontal process the lesser palatine foramen is located posteriomedial to the last postcanine tooth (fig.



ovalis; **I1**, first upper incisor partial root; **I2**, second upper incisor partial root; **I3**, partial alveolus for the third upper incisor; **IF**, infraorbital foramen; **J**, jugal; **JF**, jugular foramen; **La**, lacrimal; **LPF**, lesser palatine foramen; **MF**, masseteric fossa; **MPS**, median palatine suture; **Mx**, maxilla; **N**, nasal; **OC**, occipital condyle; **PC1-5**, upper postcanine teeth; **PI**, palatine; **Pmx**, premaxilla. Scale bar = 5 mm.

3A). The posterior margin of the horizontal process of the palatine is damaged and, therefore, the shape of its posterior margin or internal narial opening cannot be determined. Along the median palatine suture, there is a posteriorly pronounced ridge. Additionally, a caudal nasal spine is present. The posterior termination of the median palatine suture ends at the level of the posterior margin of PC3 (fig. 3A). The palatal process of the palatine is bordered anteriorly and laterally by the maxilla and anteriorly by the premaxilla. The palatine contacts the premaxilla along a transverse suture at level to the posterior margin of PC1 (fig. 3A). Laterally the palatal process of the palatine directly contacts the alveolus of PC4 and the palatal process of the maxilla (fig. 3A). The latter is a very thin process situated between PC1–PC3 and the palatine. The anterior portion of the palatine has two small foramina (greater palatine foramina) (fig. 3A). The suture between the palatal processes of the maxillary and palatine is broadly curvilinear and lacks interdigitations. Posteriorly, the lateral walls of the nasopharyngeal canal converge, nearly contacting each other.

The anterior margin of the orbit is located directly dorsal to the distal margin of PC1 (fig. 4A). The lacrimal is exposed in lateral view, and it ventrally contacts the jugal and anteriorly contacts the premaxilla (fig. 4A). These sutures are not interdigitated. The suture between the

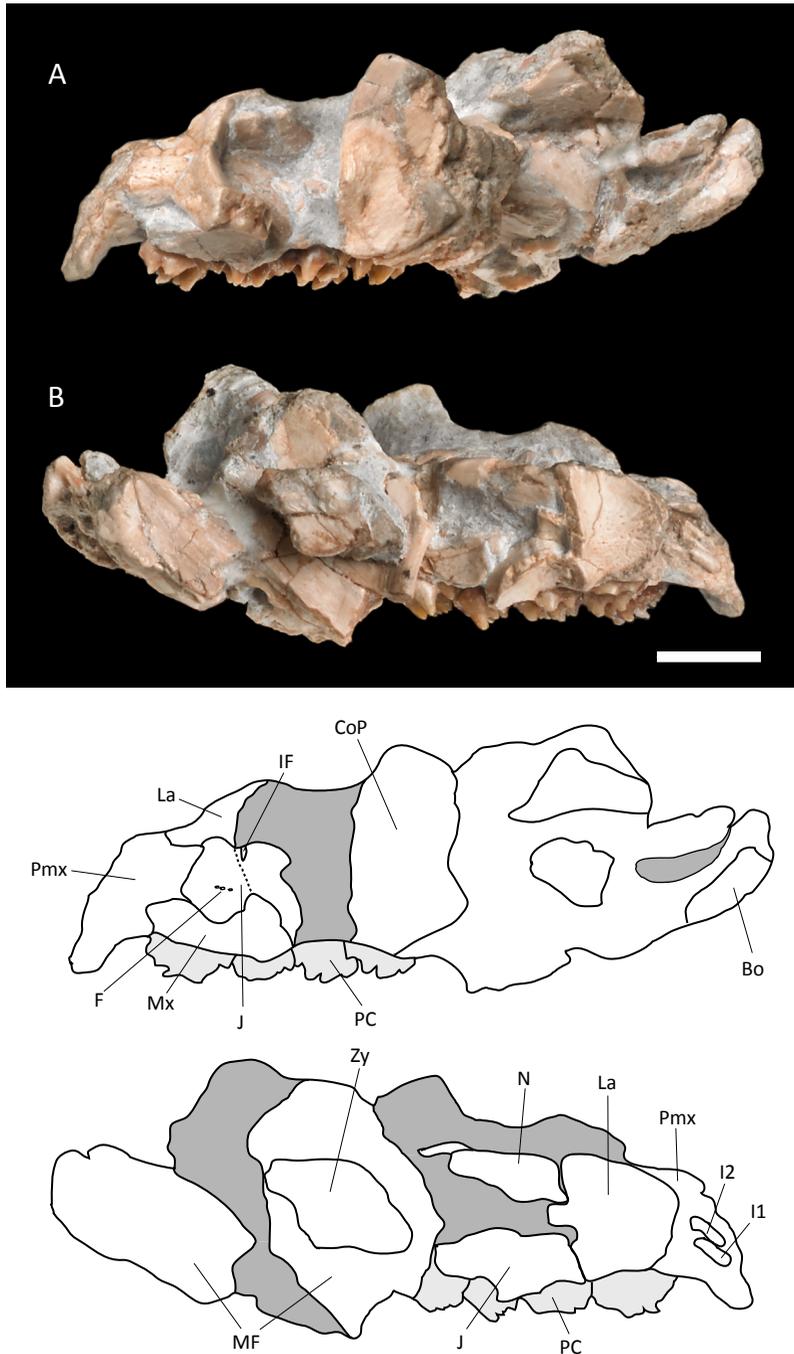


FIGURE 4. The skull of *Shartegodon altai* PSS-MAE 633 (holotype) in (A) left lateral and (B) right lateral views (top) with accompanying line drawings (bottom). Dark gray indicates matrix; light gray indicates the upper postcanines. Abbreviations: **Bo**, basioccipital; **CoP**, coronoid process of dentary; **F**, foramina; **I1**, first upper incisor partial root; **I2**, second upper incisor partial root; **IF**, infraorbital foramen; **J**, jugal; **La**, lacrimal; **MF**, masseteric fossa; **Mx**, maxilla; **N**, nasal; **PC**, upper postcanine teeth; **Pmx**, premaxilla; **Zy**, zygoma. Scale bar = 5 mm.

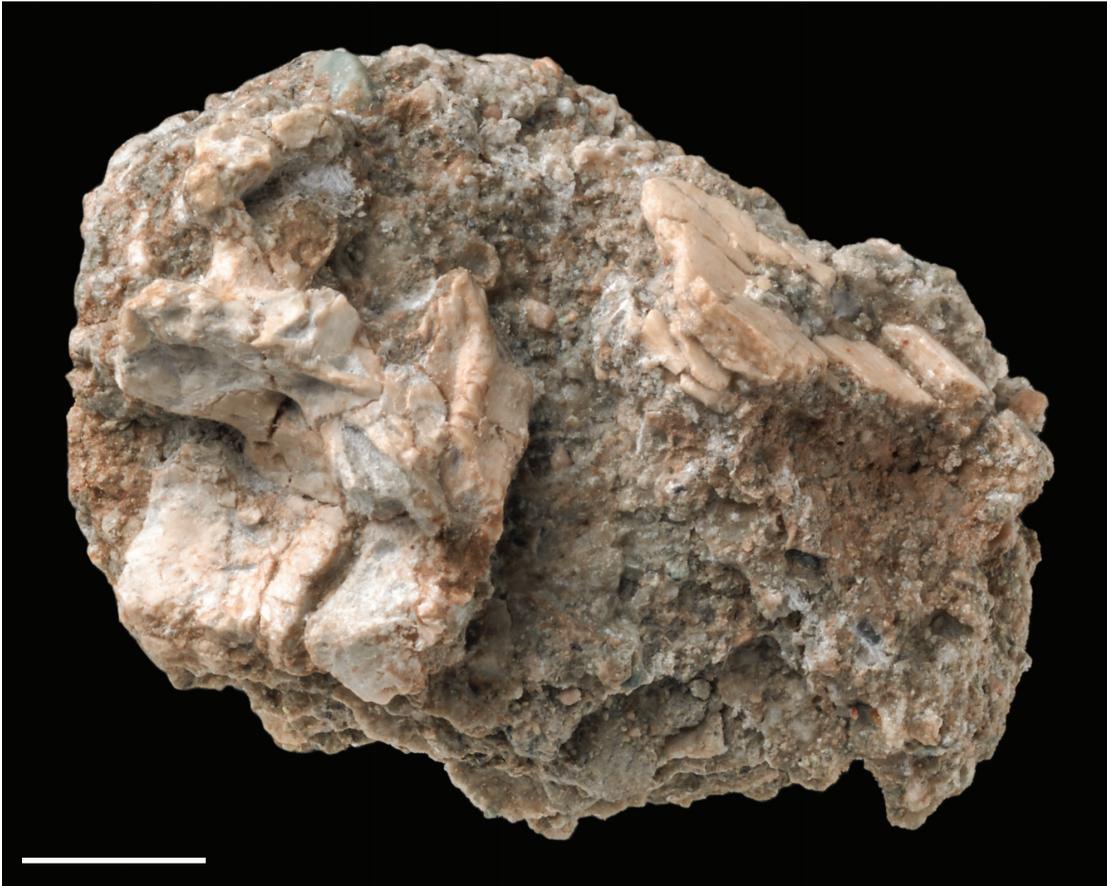


FIGURE 5. Isolated right region of the basicranium of *Shartegodon altai* PSS-MAE 633 (holotype). Scale bar = 5 mm.

lacrimal and the nasal cannot be observed due to the shattered condition of the nasals (figs. 3B, 4B). The lacrimal forms the medial orbital wall (fig. 3B). The jugal is partly preserved on the left side of the skull and its zygomatic process gently curves outward and forms the dorsal surface of the anterior root of the zygomatic arch. The jugal also forms part of the medial orbital wall and the inferior orbital wall. A large infraorbital foramen lies just below the suture between the jugal and the lacrimal (figs. 3B, 4A). There is a foramen, and two other small round depressions, possibly for muscle attachments, on the left jugal above PC2 (fig. 4A).

The basicranium is badly damaged with only a partial left region attached to the skull and an isolated portion of the right region preserved (figs. 3A–B, 4A, 5). The only identifiable structures are the left fenestra ovalis and left jugular foramen (fig. 3A). The stapedia ratio, calculated by proxy as length (1.56 mm) divided by width (0.87 mm) of the fenestra ovalis, is approximately 1.8.

Partial right masseteric fossae and left coronoid processes are preserved on both the left and right jaws (figs. 3B, 4A). The right partial dentary is preserved as a posterior fragment containing three postcanines (fig. 6A–B). The left partial dentary is also preserved only as a

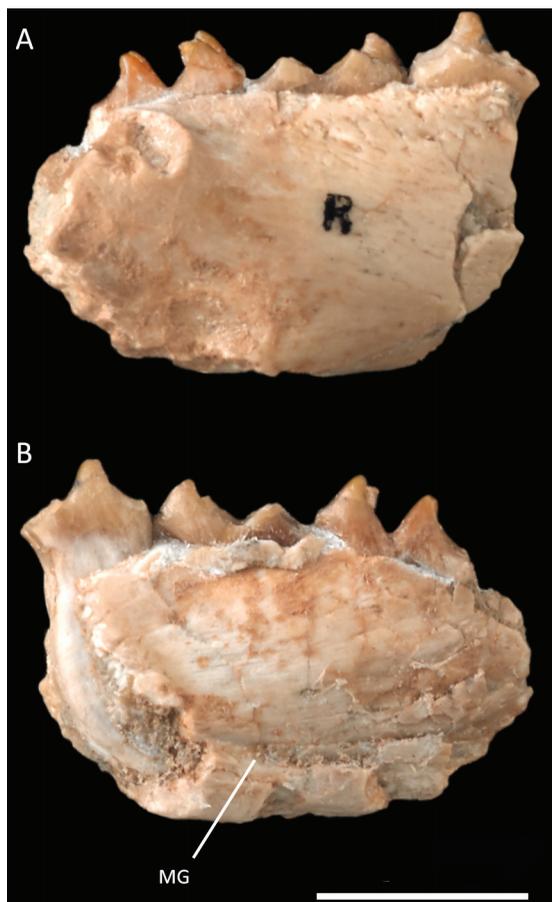


FIGURE 6. Right partial ramus of *Shartegodon altai* PSS-MAE 633 (holotype) in (A) lateral and (B) medial views. Abbreviation: **MG**, meckelian groove. Scale bar = 5 mm.

posterior fragment containing three mature postcanines (anterior most detached) and a fourth erupting postcanine (fig. 7A–B). The depths of the right and left dentaries below the penultimate postcanine are 6.7 mm and 7.1 mm respectively with the difference in depth likely due to distortion. The proximal portions of the coronoid crests are present on both fragments (figs. 6A, 7A) and both fragments show a well-defined Meckelian groove with a small portion of the splenial present in the groove of the right dentary (fig. 6B).

In the left premaxilla, there is evidence of the presences of three incisors. I1 and I2 are represented by remnants of their roots (figs. 3B, 4B). Lateral to the I1 and I2 roots, the left I3 partial alveolus suggests that I3 was at least five times the width of I1 or I2 (fig. 3B). No lower incisors are preserved (figs. 6A–B, 7A–B).

The upper postcanine alveolar tooth rows diverge posteriorly. Four upper postcanine teeth, almost identical in size, are preserved on both sides of the skull (table 1; figs. 3A, 8). On both sides, fifth postcanine teeth are erupting (fig. 3A). There are no diastemata between them. Each upper postcanine has four long and cylindrical roots, two anterior and two posterior, arranged in two

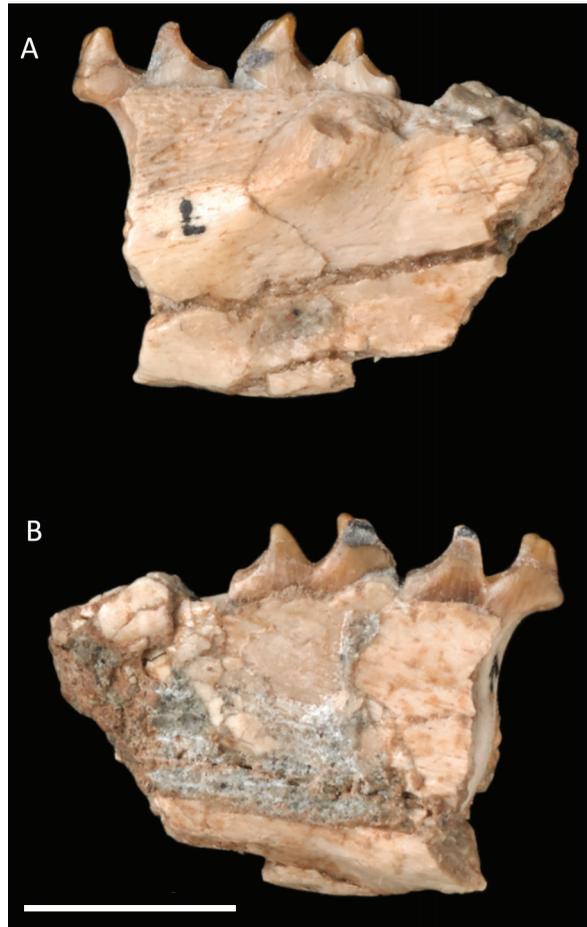


FIGURE 7. Left partial ramus of *Shartegodon altai* PSS-MAE 633 (holotype) in (A) lateral and (B) medial views. Scale bar = 5 mm.

transverse rows. The four are independent and the lingual roots are larger than the buccal ones. In occlusal view the teeth are rectangular with rounded corners and a convex mesial edge (fig. 8). There are three cusp rows that run mesiodistally across each tooth with two deep valleys running between them (figs. 3A, 8). Most of the upper postcanine teeth have two buccal, four medial, and four lingual cusps; the only exception is the right PC3, which has six lingual cusps instead of the four present in all the other teeth (fig. 8). Therefore, the generalized cusp formula is 2-4-4 (fig. 8). The cusp heights in each row are as follows (with 0 or 1 representing the most mesial cusp and 2 or 3 representing the most distal cusp): $B1 < B2$; $M0 < M1 < M2 \approx M3$; and $L0 < L1 < L3 < L2$. In the case of the right PC3 the lingual cusps heights are: $L0 < L1 \approx L2 < L4 \approx L5 < L3$. There are six broken cusp apices on the left (PC1 [B2, M2]; PC2 [L2]; and PC3 [B1, B2, M3]) side and four broken apices on the right (PC1 [B1, B2]; PC2 [B2]; and PC3 [M3]) side (fig. 8). The largest cusps on all upper postcanines, B2, M2, M3, and L2, are subequal in height. The smallest cusps on all upper postcanines are M0 and L0. Five cusps exhibit different degrees of crescentic shape: M2, M3, and L2 are

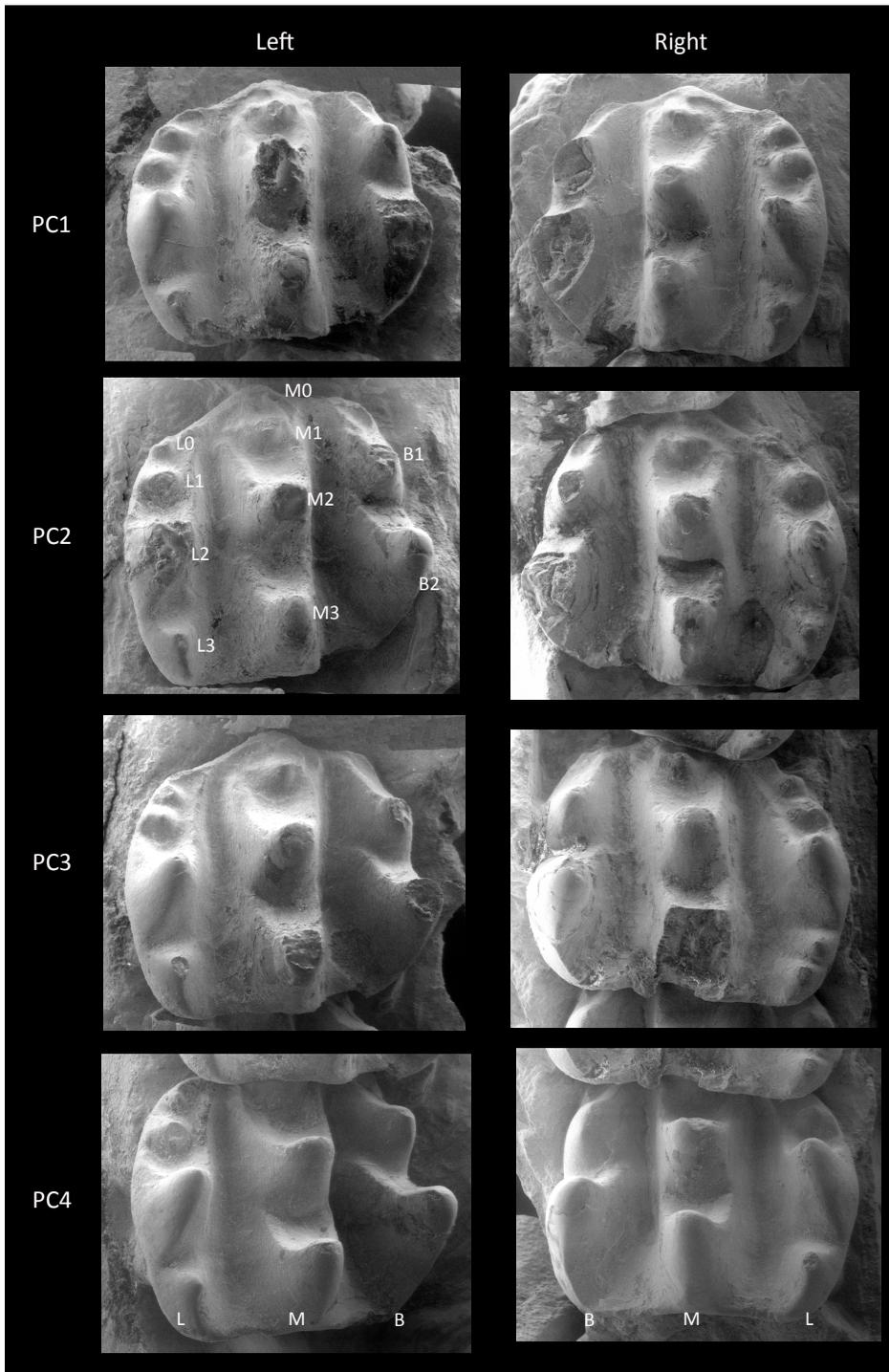


FIGURE 8. Upper postcanine dentition of *Shartegodon altai* PSS-MAE 633 (holotype) in occlusal views. The identity of the buccal, medial, and lingual cusps is labeled on the left PC2. Abbreviations: **B**, buccal; **M**, medial; **L**, lingual; **PC**, upper postcanine teeth.

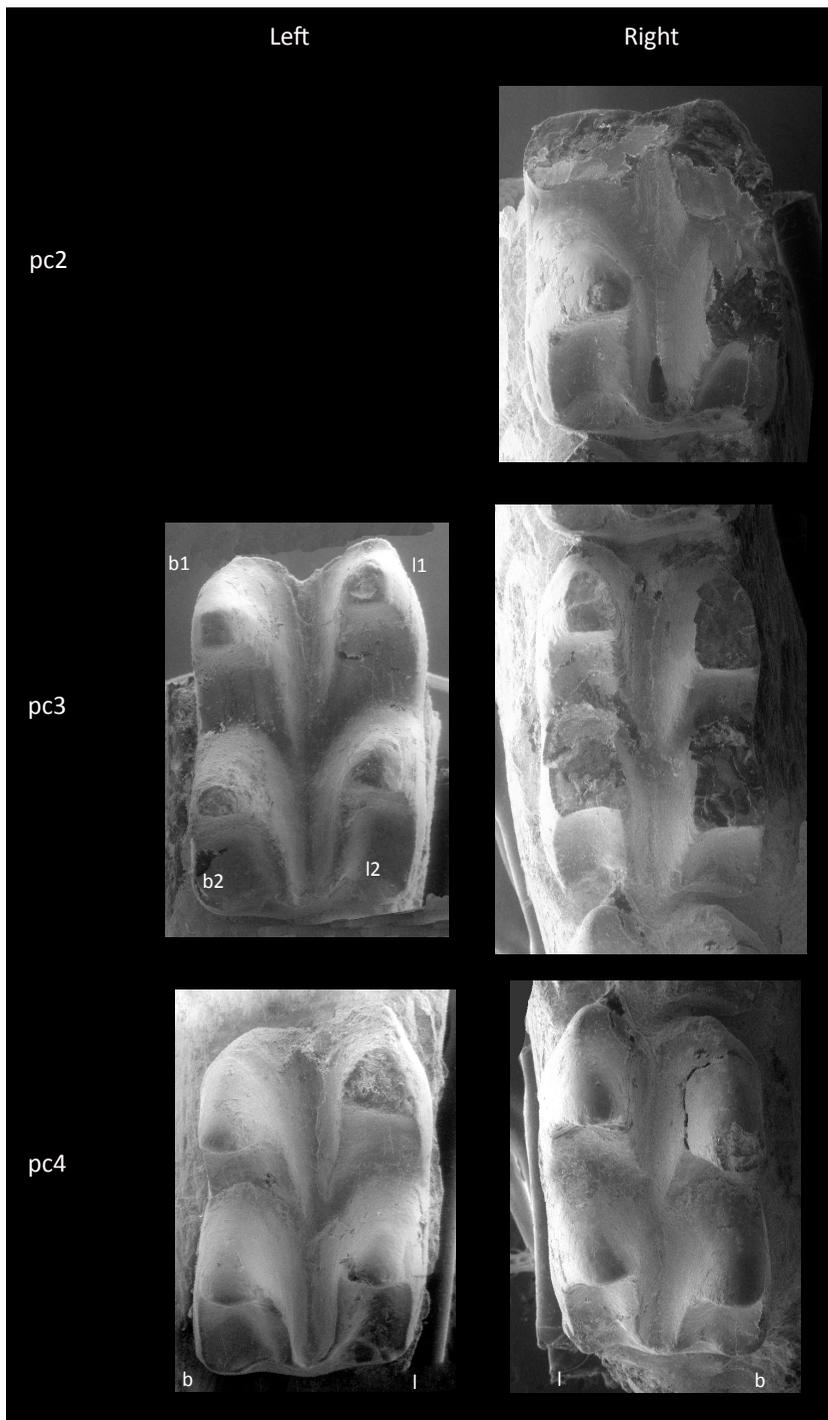


FIGURE 9. Lower postcanine dentition of *Shartegodon altai* PSS-MAE 633 (holotype) in occlusal views. Abbreviations: **b**, buccal; **l**, lingual; **pc**, lower postcanine teeth.

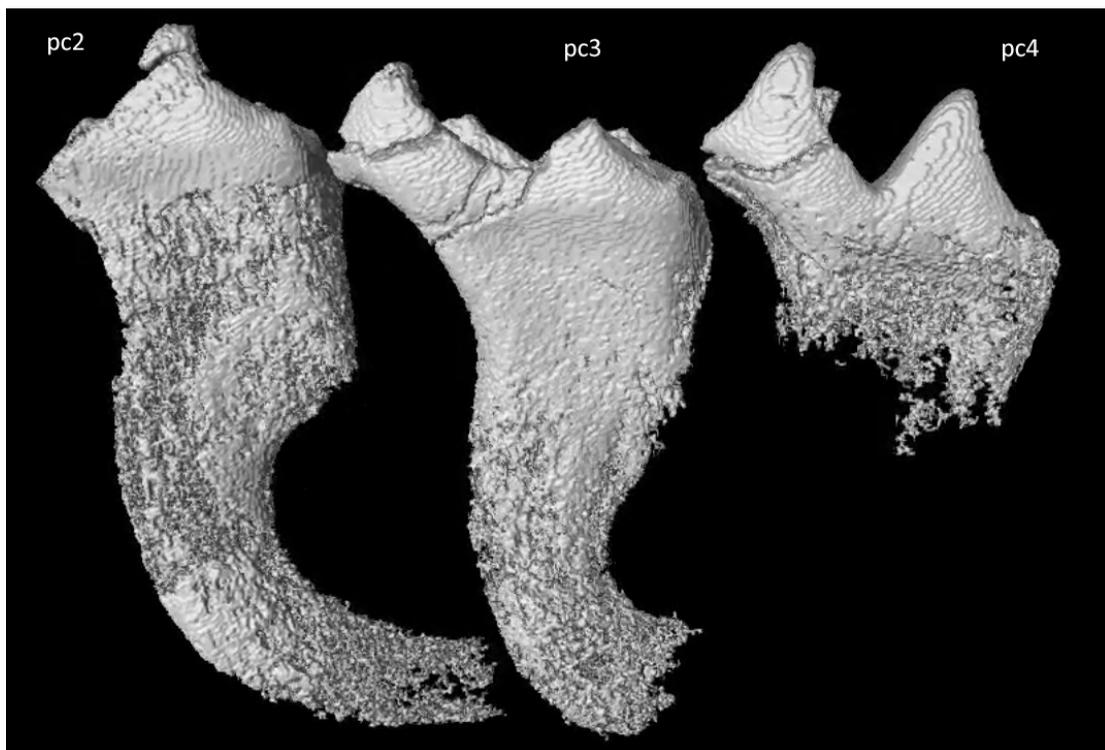


FIGURE 10. Right lower postcanine teeth of *Shartegodon altai* PSS-MAE 633 (holotype) in lingual views, illustrating the shape of the roots.

strongly crescentic and present sharp lingual and buccal cristae, whereas B1 and B2 are somewhat crescentic and have a sharp lingual and blunt buccal cristae (fig. 8).

The three posterior lower postcanines are preserved on both dentaries (figs. 6A–B, 7A–B, 9, 10), the left dentary also includes a fourth erupting postcanine. Each lower postcanine has only one root (fig. 10). The root is long and square throughout its length. The upper section of the root descends vertically from the base of the crown, while the lower two-thirds of the root forms a C-shaped curve (fig. 10). The lower postcanine tooth cusps occlude in the deep valleys of the upper postcanine (figs. 3A, 8, 9). The lower postcanine teeth are rectangular in occlusal view, being longer in length than in width. There are two mesiodistal cusp rows with one valley running between them. All the lower postcanine teeth have two buccal and two lingual cusps (fig. 9). The cusp formula for the lower postcanines is 2-2 (b1, b2, l1, and l2). All cusps are subequal in height. There are several broken cusp apices on both the left (pc2 [b1]; and pc4 [b2]) and right (pc2 [b1, b2, and l1]; pc3 [b1, b2, l1, and l2]; and pc4 [b1]) sides (fig. 9). The cusps that are unbroken show a crescentic pattern. All lower postcanine cusps (lingual and buccal) present sharp lingual and buccal cristids (fig. 9). The cusp rows are slightly offset; the lingual cusps (l1 and l2) are located more mesially than the buccal cusps (b1 and b2) (fig. 9). The eruption sequence of the lower postcanines was not synchronous between both sides of the jaw: the left dentary shows the two proximal cusps (b1 and l1) and the tip b2 of pc5 in eruption, whereas the right pc5 has not erupted.

Nuurtherium, gen. nov.

Figures 11–14

TYPE SPECIES: *Nuurtherium baruunensis*, sp. nov.

ETYMOLOGY: *Nuur-*, Mongolian, “lake,” fossils at Shar Teg were preserved in a cyclic sequence of fluvial and lake beds (see Ponomarenko et al., 2014).

AGE: As for the type and only species.

DIAGNOSIS: As for the type and only species.

Nuurtherium baruunensis, sp. nov.

HOLOTYPE: PSS-MAE 632, a damaged skull with cheek teeth, partial edentulous left dentary, partial right dentary with three postcanine teeth, left quadrate, and partial skeleton including two dorsal, and two caudal vertebrae; three ribs; right clavicle; right scapula; left ulna; left femur; right tibia; left astragalus; two metacarpals; and one metatarsal (figs. 11–14).

TYPE LOCALITY: Shar Teg locality, Gobi-Altai Aimag, southwestern Mongolia (fig. 1).

STRATIGRAPHIC HORIZON: From the lower part of the Ulan Malgait Sequence (just above the boundary with the Shar Teg Sequence); Upper Jurassic (Gereltsetseg, 1992; Ponomarenko et al., 2014).

ETYMOLOGY: The species name, *baruun-*, from the Mongolian, “west,” refers to location of the Shar Teg beds in far western Mongolia.

DIAGNOSIS: Differing from other tritylodontids in having all the upper postcanine teeth with a cusp formula of 2-3-4 (fig. 12). *Nuurtherium baruunensis* differs from the species, *Bienotheroides shartegensis*, previously recorded at the Shar Teg locality in having a different cusp formula (*B. shartegensis* = 2-3-3) and in having M0 and L0 cusps, and a much more robust M1 cusp on the upper postcanine teeth.

DESCRIPTION: The exposed portion of this crushed specimen shows only part of the palate with cheek teeth, left zygomatic arch, partial dentaries, and some postcranial elements preserved (fig. 11). The skull of *Nuurtherium* (PSS-MAE 632) is badly damaged (fig. 11), and the rostrum and basicranium are not preserved. The only partially preserved cranial elements are the palatine, maxilla, and jugal. The palatine is crushed extensively. The posterior terminus of the median palatine suture ends at the level of the fourth from the last postcanine teeth (fig. 11). The only portion of the maxilla preserved is a narrow band forming the lingual margins of the upper right postcanines (fig. 11). The upper postcanine alveolar line diverges posteriorly. Only a portion of the left jugal is preserved (fig. 11). It is long and curved outward; at the level of the fourth from the last postcanine tooth it bends to become parallel to the right jugal. Posteriorly, the jugal increases in size to 15.7 mm at the level of the last postcanine and forms a thin sheet of bone.

The right dentary is better preserved than the left dentary (fig. 11). Three postcanines are preserved in the right dentary while none remains in the left. The anterior portion of the right dentary is not preserved (fig. 11). The depth of the right dentary below the last preserved post-



FIGURE 11. The skull of *Nuurtherium baruunensis* PSS-MAE 632 (holotype; above) with accompanying line drawing (opposite page). Dark gray indicates matrix; light gray indicates the upper postcanines. Abbreviations: AP, angular process of dentary; Co, coronoid; CoP, coronoid process of dentary; crt, crypt for replacement

canine is 16 mm. The coronoid process is very tall (>45 mm), with a gently curved anterior margin (fig. 11). The tip of the coronoid process has been lost. The posterior margin of the coronoid process is concave. The tips of the articular and angular processes are broken off. The coronoid is missing and the coronoid boss is partly cracked (fig. 11). The alveolar line and the anterior margin of the coronoid process form an angle $<90^\circ$. At the anterior base of the coronoid there is a crypt for the replacement teeth (fig. 11). Both fragments show a well-defined Meckelian groove, without signs of the presence of the splenial (fig. 11). The left quadrate is



teeth; **ePC**, erupting upper postcanine teeth; **J**, jugal; **MG**, meckelian groove; **mc**, metacarpal; **Mx**, maxilla; **ID**, left dentary; **pc**, right lower postcanine; **Pl**, palatine; **ptMPS**, posterior terminus of median palatine suture; **Q**, left quadrate; **rD**, right dentary. Scale bar = 10 mm.

preserved (fig. 11). The dorsal angle of the quadrate is absent. The lateral trochlear condyle is preserved, but the medial trochlear condyle and the stapelial process are embedded in the matrix (fig. 11).

No upper or lower incisors are preserved (fig. 11). The upper postcanine alveolar tooth rows diverge posteriorly. The more posterior six right and four left upper postcanines are preserved (table 1; fig. 11). On both sides, the last postcanine teeth are in the process of erupting (fig. 11). There are no diastemata between them (fig. 12). The upper postcanine teeth have five

TABLE 1. Dental measurements (in mm) of postcanine teeth of *Shartegodon altai* (PSS-MAE 633) and *Nuurtherium baruunensis* (PSS-MAE 632). PC = upper postcanine, pc = lower postcanine.

	<i>Shartegodon altai</i>		<i>Nuurtherium baruunensis</i>	
	Length	Width	Length	Width
Right PC1	3.23	3.39	5.74	7.37
Right PC2	3.18	3.57	6.07	7.06
Right PC3	3.20	3.54	5.62	5.51
Right PC4		3.51	4.98	6.33
Right PC5			4.64	6.60
Right PC6			4.36	5.48
Left PC1	3.26	3.41		
Left PC2	3.37	3.41		
Left PC3	3.44	3.51		
Left PC4		3.37		
Right pc3	4.15	2.52		
Right pc4	3.73	2.37		
Left pc3	4.21	2.38		
Left pc4	3.74	2.45		
Right pc			6.80	5.00

long and cylindrical roots, two anterior and three posterior, arranged in two transverse rows. The anterior pair are united at their bases, whereas the posterior roots are independent throughout their length. In occlusal view, the upper postcanines are rectangular and buccolingually wider, with rounded corners. There are three cusp rows that run mesiodistally along each tooth, with two deep valleys running between them (fig. 12). The upper postcanine teeth have two buccal, three medial, and four lingual cusps (fig. 12). The generalized cusp formula is therefore 2-3-4. Most of the cusps have broken tips, but the generalized cusp heights in each row are as follows: $B_1 < B_2$; $M_0 < M_1 < M_2$; and $L_0 < L_1 < L_3 < L_2$. The largest cusps on all upper postcanine teeth are B_2 and M_2 . The smallest cusp on every upper postcanine is L_0 . Five cusps (B_1 , B_2 , M_1 , M_2 , and L_2) exhibit a small degree of crescentic shape. M_1 and M_2 present sharp lingual and buccal cristae; B_1 and B_2 present sharp lingual and blunt buccal cristae; and L_2 presents a sharp buccal and a blunt lingual cristae.

Five lower right postcanines are preserved, three are still emplaced in the dentary while two are detached and isolated (figs. 11, 13, 14). Each lower postcanine has only one root (fig. 13B). The root is long and square throughout its length. The upper third section of the root descends vertically from the base of the crown, while the lower two-thirds of the root form a C-shaped curve (fig. 13B). The lower postcanine tooth cusp rows occlude in the deep valleys of the upper postcanines. The lower postcanine teeth are rectangular in occlusal view, i.e., greater in length than in width (table 1). There are two mesiodistal cusp rows with one valley running in between them. All the lower postcanine teeth have two buccal and two lingual cusps (fig. 13A). The cusp formula for the lower postcanines is 2-2 (b_1 , b_2 , l_1 , and l_2). Most of the cusp apices are broken

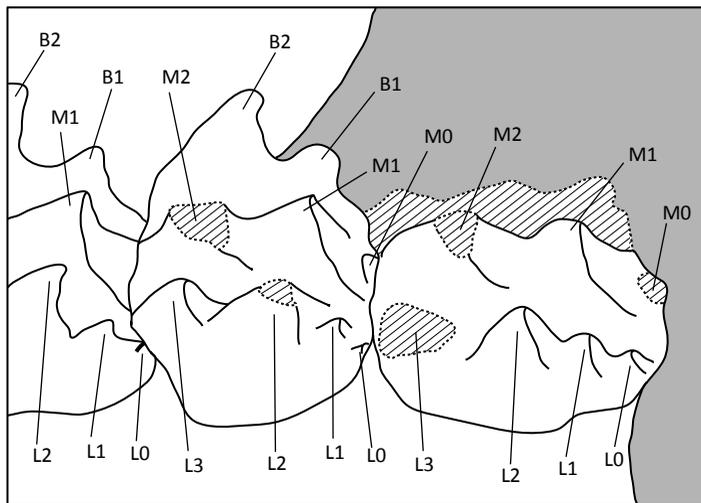


FIGURE 12. Upper right postcanine teeth of *Nuurtherium baruunensis* PSS-MAE 632 (holotype) in lingual views with accompanying line drawing. Gray indicates matrix; hatching indicates damage teeth surface. The identity of the buccal, medial, and lingual cusps are labeled on the line drawing. Abbreviations: **B**, buccal; **M**, medial; **L**, lingual.

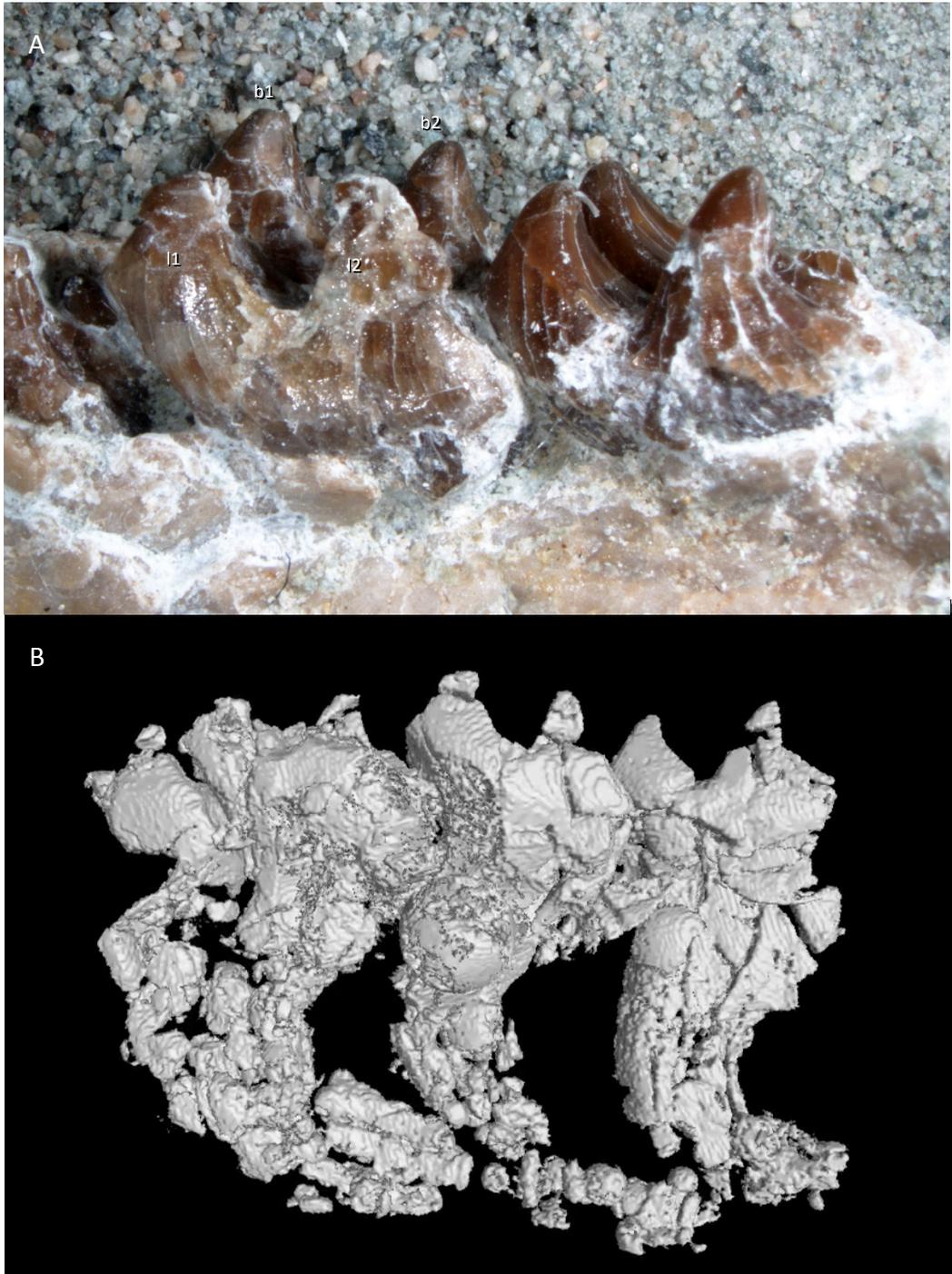


FIGURE 13. Lower right postcanine teeth of *Nuurtherium baruunensis* PSS-MAE 632 (holotype) in (A) lingual view of the crowns and (B) lingual views of crowns and roots. Abbreviations: **b**, buccal; **l**, lingual.

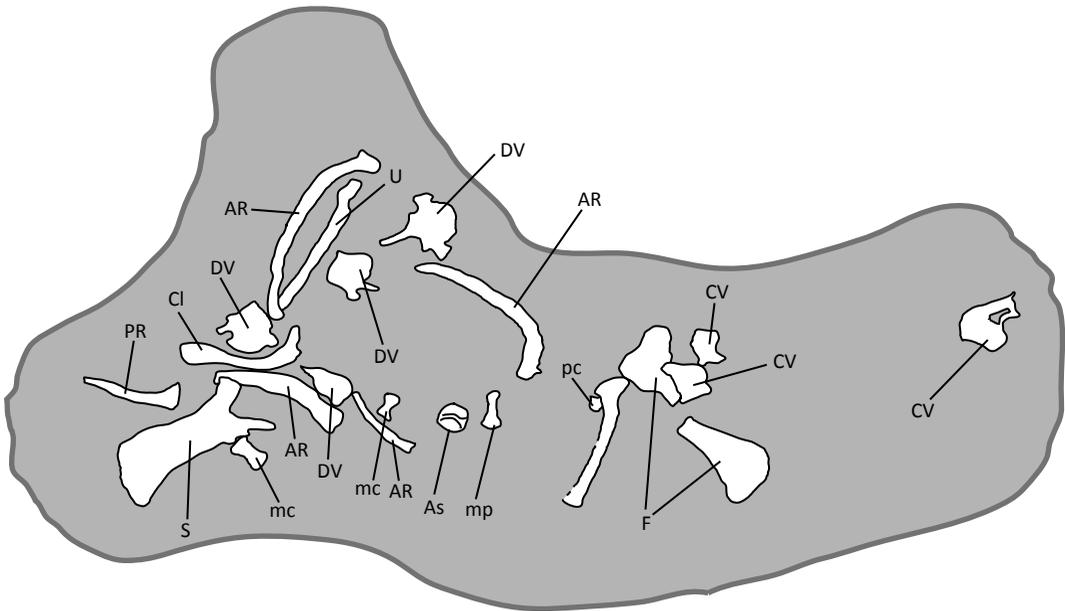


FIGURE 14. Postcranial elements of *Nuurtherium baruunensis* PSS-MAE 632 (holotype; top) with accompanying line drawing of recognizable bones (bottom). Gray indicates matrix. Abbreviations: **AR**, anterior rib; **As**, left astragalus; **CV**, caudal vertebrae; **Cl**, right clavicle; **DV**, dorsal vertebrae; **F**, left femur; **mc**, metacarpal; **mp**, metapodial; **pc**, postcanine teeth; **PR**, posterior rib; **S**, right scapula; **T**, right tibia. Scale bar = 50 mm.

off, but it can be inferred from the unbroken cusps that all the cusps on a tooth are subequal in height (fig. 13A). The cusps that are unbroken show a crescentic pattern (fig. 13A). All lower postcanine cusps (lingual and buccal) present sharp lingual and buccal cristids. l1 is located more mesially than b1, whereas l2 and b2 are mesiodistally aligned (fig. 13A).

Several postcranial elements are preserved: four dorsal, and two caudal vertebrae; five ribs; right clavicle; right scapula; left ulna; left femur; right tibia; left astragalus; two metacarpals; and one metatarsal (fig. 14).

Only the cranial and lateral aspects of the isolated dorsal vertebrae are visible (fig. 14). The neural spine is tall, narrow, and distinctively inclined posterodorsally. The centrum is wider than it is tall (12.3×7.9 mm). The neural canal is triangular. The prezygapophyses project beyond the anterior margin of the centrum. The articular processes of the prezygapophyses are oval and are inclined at about 45° from the vertical plane. The postzygapophyses are located posterodorsal to the prezygapophyses. The prezygapophyses are centric (roughly perpendicular to the plane of the lamina). The parapophyses are not preserved. Each robust transverse process is almost half the size of the centrum and does not project beyond the anterior margin of the centrum. The transverse processes are directed ventrolaterally. The diapophyses show a roughly triangular outline and are ventrolaterally oriented and flat.

The two isolated proximal caudal vertebrae are present (fig. 14). Even though the neural spines are broken off, it can be inferred from the remaining recesses that the spines are distinctively inclined posterodorsally. The centra are hourglass shaped in lateral view. The distal centrum is wider than tall (10.2×8.1 mm). The neural canal is triangular but narrower than it is in the dorsal vertebrae. The pre- and postzygapophyses are broken off. The transverse processes are broken off, but it is clear that they originate near the neurocentral junction and are positioned near the anterior part of the body. These vertebrae lack chevrons.

The rib material is poorly preserved; only five ribs, four anterior and one posterior, with the distal ends broken off are preserved (fig. 14). The anterior ribs are long and curved, (defining the surface of the thorax), and flattened anteroposteriorly. The capitular and tubercular facets are proximal to each other, with the tuberculum situated above the capitulum. The tubercular facet is circular and flat, while the capitular is round. The posterior rib is short and straight, and has only one articular facet.

Only the right clavicle is preserved (fig. 14). The medial end is spatulated and shows striations for contact with the interclavicle, which is not preserved. The lateral end presents two recesses and articular contacts for the acromion.

Only the medial surface of the right scapula is preserved, it but presents extensive damage, where both ends are missing (fig. 14). The scapular blade is slightly widened dorsally. The acromion and scapular glenoid facet are badly damaged.

The badly damaged left ulna has a long olecranon process (fig. 14). Damage obscures the facets for the ulnar condyle of the humerus, the ulnar condyle, and the distal articular. The ulnar shaft is shattered throughout its length.

Only the anterior view of the left femur is visible: it is broken in half and both ends are abraded (fig. 14). Both ends are greatly expanded (~ 20 mm) and the femur is extremely con-

stricted toward the middle of the shaft (6.4 mm). The bulbous femoral head is oriented dorso-medially relative to the long axis of the shaft. The edges of the greater trochanter are abraded, but it is apparent that the femoral head and the greater trochanter are of the same height. The lateral flaring edge of the greater trochanter is oriented dorsally. The intertrochanteric fossa is slightly concave. Both the lateral and medial condyles are abraded.

The anterior view of the right tibia is visible; it is complete, but its proximal end is abraded (fig. 14). The maximum length of the tibia is 42.9 mm. Proximally, the tibia is lateromedially expanded. Its proximal and distal thirds are triangular in transverse section, with medial, lateral and anterior sides. The distal articular surface is oval.

The plantar view of the left astragalus is preserved (fig. 14). The sustentacular facet is long and narrow, whereas the ectal facet is oval. The facets are separated by a slightly curved deep groove, the sulcus tali.

Only three isolated metapodials (two metacarpals and one metatarsal) are preserved (fig. 14). All the metapodials recovered are broadly expanded proximally and distally.

COMPARISONS OF *SHARTEGODON* AND *NUURTHERIUM* WITH OTHER TRITYLODONTS

We compared *Shartegodon altai* and *Nuurtherium baruunensis* with all the known genera within the family (Simpson, 1928; Young, 1947; Kühne, 1956; Chow and Hu, 1959; Chow, 1962; Waldman and Savage, 1972; Cui, 1981; Kermack, 1982; He and Cai, 1984; Clark and Hopson, 1985; Sues, 1985, 1986a, 1986b, 1986c; Cui and Sun, 1987; Sun and Cui, 1989; Setoguchi et al., 1999; Maisch et al., 2004; Sues and Jenkins, 2006; Watabe et al., 2007; Lopatin and Agadjanian, 2008; Hu et al., 2009; Jasinowski and Chinsamy, 2012; Fedak et al., 2015).

The snout is short and lacks a postincisive constriction in *Shartegodon*, *Bienotherium*, *Bienotheroides*, *Bocatherium*, *Dianzhongia*, *Dinnebitodon*, *Kayentatherium*, *Lufengia*, *Polistodon*, *Stereognathus*, and *Yunnanodon*, whereas it is longer and has a postincisive constriction in *Oligokyphus* and *Tritylodon*. In *Shartegodon* and *Nuurtherium* the palatal process of the maxilla is markedly reduced; it is preserved as a narrow band forming the lingual margins of the postcanine teeth, and the palatine is in contact with the premaxilla. This is similar to the condition in *Bienotheroides*, *Bocatherium*, *Dinnebitodon*, *Stereognathus*, and *Yuanotherium*. In contrast, the maxilla is large and occupies most of the area of the palate and the palatine contacts the maxilla in *Bienotherium*, *Kayentatherium*, *Oligokyphus*, and *Tritylodon*. The zygomatic process of the maxilla constitutes the ventral aspect of the anterior root of the zygomatic arch in *Shartegodon*, *Bienotherium*, *Kayentatherium*, *Oligokyphus*, *Polistodon*, and *Tritylodon*, whereas it constitutes the dorsal aspect of the anterior root of the zygomatic arch in *Yuanotherium*. The premaxilla-maxillary contact follows the mesiolingual outline of PC1 in *Shartegodon*, *Kayentatherium*, *Bienotheroides*, *Bocatherium*, and *Yuanotherium*, whereas premaxilla-maxillary contact occurs in the snout in *Bienotherium*, *Oligokyphus*, and *Tritylodon*. Anteriorly and laterally, the palatine is bordered by the maxilla and premaxilla in *Shartegodon*, *Bienotheroides*, *Bocatherium*, whereas it is bordered only by the maxilla in *Bienotherium*, *Oligokyphus*, and *Tritylodon*. In *Shartegodon* the palatine laterally contacts the alveolus of PC4 and the palatal process of the maxilla is merely a thin splint

of bone located between the lingual margins of PC1–PC3 and the palatine. The palatine does not laterally contact any PC alveoli in *Bienotherium*, *Bienotheroides*, *Bocatherium*, *Kayentatherium*, *Oligokyphus*, and *Tritylodon*. There are no interdigitations on the maxillo-palatine or premaxillo-palatine sutures in *Shartegodon*. There are no interdigitations on the maxillo-palatine suture, but there are interdigitations on the premaxillo-palatine suture in *Bienotheroides*, *Bocatherium*, and *Yuanotherium*. Interdigitations are observed only on the proximal aspect of the maxillo-palatine suture in *Bienotherium*, *Kayentatherium*, *Oligokyphus*, and *Tritylodon*. The anterior portion of the palatine has two greater palatine foramina in *Shartegodon*, *Bocatherium*, and *Yuanotherium*, but these foramina are lacking in *Oligokyphus*. Only one foramen is present in *Bienotherium*, *Kayentatherium*, and *Tritylodon*, and between one and three are present in species of *Bienotheroides*. The anterior margin of the orbit is above the distal edge of PC1 in *Shartegodon*, *Bienotherium*, *Bocatherium*, *Kayentatherium*, and *Oligokyphus*, whereas it is above the anteroposterior midpoint of PC2 in *Bienotheroides*. The lacrimal is large and forms the medial orbital wall in *Shartegodon*, *Bienotherium*, *Bienotheroides*, *Bocatherium*, *Kayentatherium*, and *Oligokyphus*, whereas it is much smaller in *Polistodon*. The lacrimal contacts the jugal ventrally and the premaxilla anteriorly in *Shartegodon*, *Bienotheroides*, and *Bocatherium*. In *Bienotherium*, *Kayentatherium*, *Oligokyphus*, *Polistodon*, and *Tritylodon*, it contacts the jugal ventrally and the maxilla anteriorly. The lacrimal lacks lacrimal foramina in *Polistodon*, whereas there is one lacrimal foramen in *Bienotherium*, *Bienotheroides*, *Bocatherium*, and *Kayentatherium*, and two lacrimal foramina in *Oligokyphus*. The jugal contributes to the medial and inferior orbital wall in *Shartegodon* and *Polistodon*, whereas it does not contribute to either wall in *Kayentatherium* and *Oligokyphus*. There is one foramen and possibly two small, round depressions for muscle attachments on the left jugal above PC2 in *Shartegodon*, whereas these foramina are absent in *Kayentatherium* and *Oligokyphus*.

The coronoid process is very tall with gently curved anterior margin in *Nuurtherium*, *Bocatherium*, *Kayentatherium*, and *Tritylodon*. The coronoid process is shorter, with gently curved anterior margin in *Polistodon*, and is shorter, with a straight anterior margin in *Oligokyphus*. The alveolar line and the anterior margin of the coronoid process form an angle of less than 90° in *Nuurtherium* and *Kayentatherium*, whereas the angle is greater than 90° in *Oligokyphus* and *Polistodon*, and the angle is roughly equal to 90° in *Bocatherium* and *Tritylodon*.

Three upper incisors are present in *Shartegodon*, *Bienotherium*, *Bienotheroides*, *Bocatherium*, *Dinnebitodon*, and *Oligokyphus*, whereas only one is present in *Kayentatherium* and *Polistodon*, and two in *Dianzhongia*. Upper postcanine alveolar tooth rows diverge posteriorly in *Shartegodon*, *Nuurtherium*, *Bienotherium*, *Bienotheroides*, *Dinnebitodon*, *Kayentatherium*, and *Oligokyphus*; whereas they are parallel in *Bocatherium*, *Dianzhongia*, and *Tritylodon*.

In upper postcanine dimensions, *Shartegodon* clusters with the smaller tritylodont species and especially with *Bienotherium minor*, *Oligokyphus minor*, and *Yunnanodon brevirostre* (table 2; fig. 15); however, *Shartegodon* differs from these latter taxa in crown morphology, including upper postcanine cusp formula. In the same dimensions, *Nuurtherium* clusters with medium-sized species, with *Bienotherium elegans* and *Montirictus kuwajimaensis* (larger type) the closest (table 2; fig. 15). *Nuurtherium* is, however, easily distinguished from those two species by the upper postcanine cusp formula (fig. 12).

TABLE 2. Measurements of upper postcanine teeth of selected tritylodontids species used in the elaboration of figure 15.

#	Taxon	Reference	Tooth #	Side	Length (mm)	Width (mm)
1	<i>Bienotherium yunnanense</i>	Chow (1962)	PC2	–	6.00	8.00
2	<i>Bienotherium magnum</i>	Chow (1962)	PC2	–	11.00	15.00
3	<i>Bienotherium minor</i>	Chow (1962)	PC2	–	3.20	3.40
4	<i>Bienotherium elegans</i>	Chow (1962)	PC2	–	5.50	6.70
5	<i>Bienotheroides wansienensis</i>	Measured from Sun (1984)	PC2	Right	5.97	8.51
6	<i>Bienotheroides zigongensis</i>	Measured from Sun (1986)	PC3	Right	4.75	7.31
7	<i>Bienotheroides shartegensis</i>	Watabe et al. (2007)	PC2	Left	7.60	10.30
8	<i>Bienotheroides ultimus</i>	Measured from Maisch et al. (2004)	Isolated tooth	–	7.89	7.79
9	<i>Bocatherium mexicanum</i>	Clark and Hopson (1985)	PC2	Right	4.10	5.10
10	<i>Dianzhongia longirostrata</i>	Cui (1981)	PC2	Left	2.40	2.80
11	<i>Dinnebitodon amarali</i>	Measured from Sues (1986c)	PC2	Right	7.92	9.12
12	<i>Kayentatherium welliesi</i>	Measured from Sues (1986b)	PC2	Right	6.67	7.76
13	<i>Lufengia delicata</i>	Chow and Hu (1959)	PC3	Left	2.20	2.40
14	<i>Montirictus kuwajimaensis</i> ^a	Matsuoka et al. (2016)	Isolated tooth	Right	6.53	6.90
15	<i>Montirictus kuwajimaensis</i> ^b	Matsuoka et al. (2016)	Isolated tooth	Right	4.17	4.23
16	<i>Oligokyphus major</i>	Measured from Kühne (1956)	PC2	Left	4.23	3.97
17	<i>Oligokyphus minor</i>	Measured from Kühne (1956)	PC2	Left	3.23	3.53
18	<i>Polistodon chuannanensis</i>	He and Cai (1984)	PC2	Left	4.60	6.90
19	<i>Stereognathus ooliticus</i>	Savage (1971)	PC2	Right	4.30	5.00
20	<i>Tritylodon longaevus</i>	Butler (1939)	PC3	–	7.40	8.10
21	<i>Xenocretosuchus sibiricus</i>	Tatarinov and Maschenko (1999)	Isolated tooth	–	3.80	4.20
22	<i>Yuanotherium minor</i>	Hu et al. (2009)	PC2	–	2.82	3.07
23	<i>Yunnanodon brevirostre</i>	Cui (1976)	PC2	Left	3.20	3.70
24	<i>Shartegodon altai</i>	This paper	PC2	Right	3.18	3.57
25	<i>Nuurtherium baruunensis</i>	This paper	PC2	Right	6.07	7.06

^a Larger type.^b Smaller type.

Each upper postcanine has four roots in *Shartegodon*, whereas five are present in *Nuurtherium*, *Bienotheroides*, *Lufengia*, *Stereognathus*, *Tritylodon*, and *Yunnanodon*, six are present in *Bienotherium*, *Montirictus*, and *Oligokyphus*, and seven in *Dianzhongia*. The upper postcanine teeth lack an anterior median root in *Shartegodon*, *Nuurtherium*, *Bienotheroides*, *Lufengia*, *Montirictus*, *Stereognathus*, and *Yunnanodon*, whereas an anterior median root is present in *Bienotherium*, *Oligokyphus*, and *Tritylodon*. The upper postcanine generalized cusp formula varies among the different tritylodontid genera: *Shartegodon* (2-4-4); *Nuurtherium* (2-3-4),

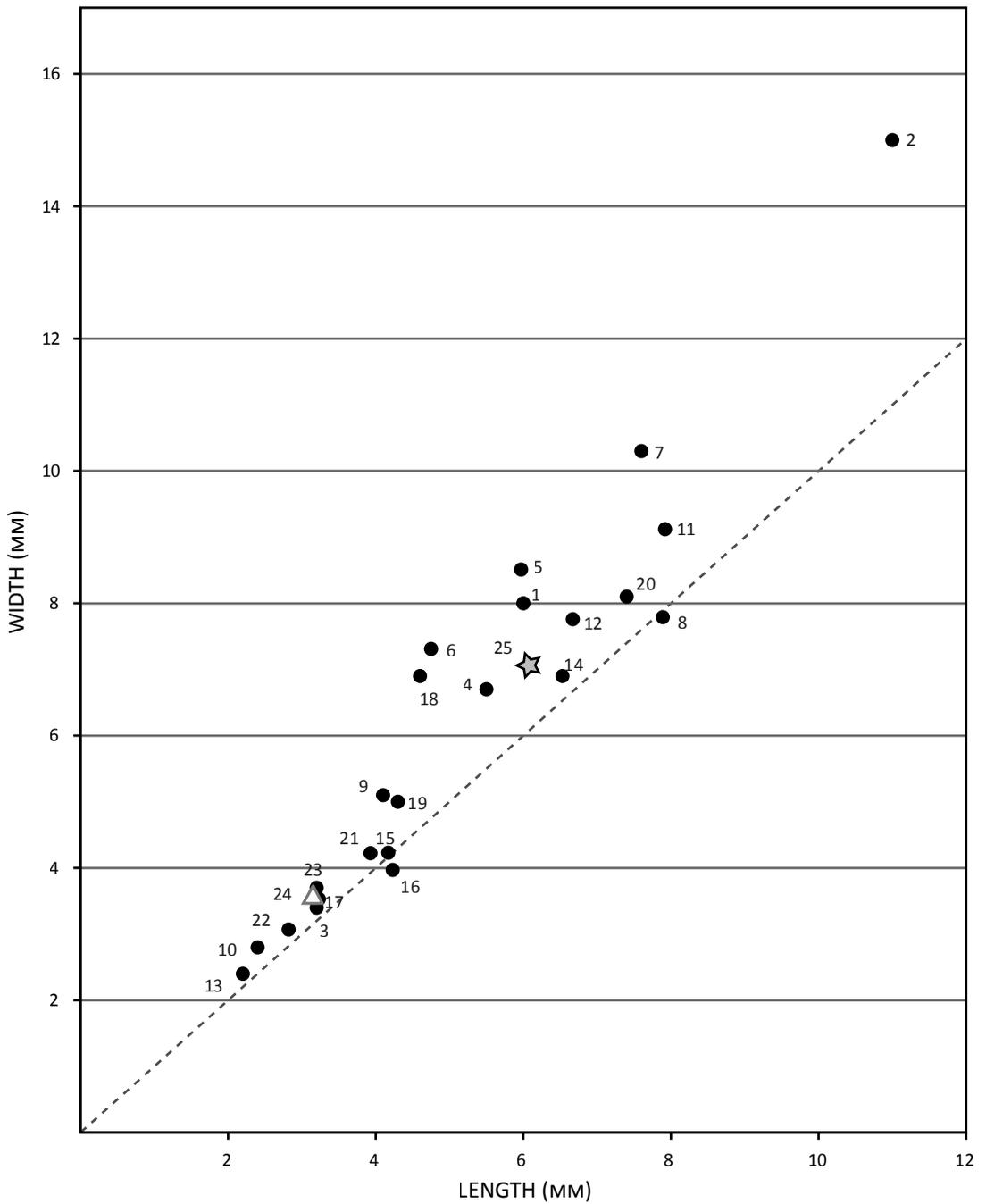


FIGURE 15. Size distribution of upper postcanines in selected tritylodontids species. Dashed line indicates location where length and width are equal. Source of measurements are provided in table 2.

Bienotherium (2-3-3), *Bienotheroides* (2-3-3 [3-3-3 in *B. wansienensis*]), *Bocatherium* (2-2-2), *Dianzhongia* (2-3-2), *Dinnebitodon* (2-3-2), *Kayentatherium* (2-3-3), *Lufengia* (2-3-3), *Montirictus* (2-2-2), *Oligokyphus* (3-4-4), *Polistodon* (2-2-2), *Stereognathus* (2-2-2), *Tritylodon* (2-3-3), *Xenocretosuchus* (2-2-2), *Yuanotherium* (2-4-3), and *Yunnanodon* (2-3-2).

The B0 cusp on the upper PC teeth is absent in *Shartegodon*, *Nuurtherium*, *Bienotherium*, *Bocatherium*, *Dianzhongia*, *Dinnebitodon*, *Kayentatherium*, *Lufengia*, *Montirictus*, *Polistodon*, *Stereognathus*, *Tritylodon*, *Xenocretosuchus*, and *Yunnanodon*, whereas it is present in *Bienotheroides* (absent only in *B. wansienensis*), *Oligokyphus*, and *Yuanotherium*. M0 and L0 cusps on the upper PC teeth are present in *Shartegodon*, *Nuurtherium*, *Oligokyphus*, and *Yuanotherium*, whereas they are absent in *Bienotherium*, *Bienotheroides*, *Bocatherium*, *Dianzhongia*, *Dinnebitodon*, *Kayentatherium*, *Lufengia*, *Montirictus*, *Polistodon*, *Stereognathus*, *Tritylodon*, *Xenocretosuchus*, and *Yunnanodon*. M1 cusps on the upper PC teeth are large in *Nuurtherium*, *Bienotherium*, *Dianzhongia*, *Dinnebitodon*, *Kayentatherium*, *Lufengia*, *Oligokyphus*, *Tritylodon*, *Yuanotherium*, and *Yunnanodon*, whereas they are small in *Shartegodon* and *Bienotheroides*, and absent in *Bocatherium*, *Montirictus*, *Polistodon*, *Stereognathus*, and *Xenocretosuchus*. L1 cusps on the upper PC teeth are small in *Shartegodon*, *Nuurtherium*, *Bienotherium*, *Bienotheroides*, *Kayentatherium*, and *Yuanotherium*, whereas they are large in *Dianzhongia*, *Dinnebitodon*, *Lufengia*, *Oligokyphus*, *Tritylodon*, and *Yunnanodon*, and absent in *Bocatherium*, *Montirictus*, *Polistodon*, *Stereognathus*, and *Xenocretosuchus*. L3 cusps on the upper PC teeth are large in *Shartegodon*, *Nuurtherium*, *Bienotherium*, *Bienotheroides*, *Bocatherium*, *Kayentatherium*, *Lufengia*, *Montirictus*, *Oligokyphus*, *Polistodon*, *Stereognathus*, *Tritylodon*, and *Xenocretosuchus*, whereas they are small in *Dianzhongia* and *Yuanotherium*, and absent in *Dinnebitodon* and *Yunnanodon*.

Each lower postcanine has one root in *Shartegodon*, *Nuurtherium*, and *Bienotheroides*, whereas two are present in *Bienotherium*, *Lufengia*, *Montirictus*, *Oligokyphus*, and *Yunnanodon*. The roots are long with the proximal section (30%) straight and the distal section (70%) curved in *Shartegodon*, *Nuurtherium*, and *Bienotheroides zigongensis* (Cui and Sun, 1987: fig. 4C), whereas the roots are long and curved throughout their entire length in *Bienotherium*, *Montirictus*, and *Oligokyphus*, and short and slightly curved in *Lufengia* and *Yunnanodon*. Most genera have a lower postcanine generalized cusp formula of 2-2 (*Shartegodon*, *Nuurtherium*, *Bienotheroides*, *Kayentatherium*, *Montirictus*, *Polistodon*, and *Xenocretosuchus*); the only genus that presents a different generalized cusp formula is *Oligokyphus* (3-3).

In addition to *Nuurtherium*, there are postcranial elements known from three genera: *Bienotheroides*, *Kayentatherium*, and *Oligokyphus* (Kühne, 1956; Maisch et al., 2004; Sues and Jenkins, 2006). The preserved postcranial elements of *Nuurtherium* do not depart from the known postcranial morphology exhibited by the other tritylodontid genera.

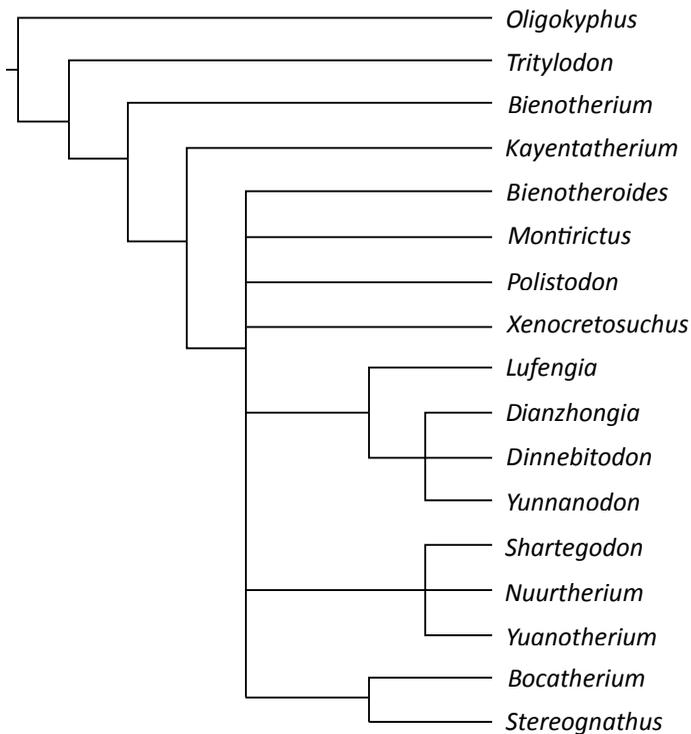


FIGURE 16. Strict consensus of four most parsimonious trees generated in a phylogenetic analysis of tritylodontid taxa. Support for nodes are shown as MP bootstrap values/Bremer support values.

PHYLOGENETIC ANALYSIS

Our phylogenetic analysis of the 35 character matrix (appendix 2) identified two most parsimonious trees of 68 steps (fig. 16). Our analysis, including all the recognized genera for the family, and using *Oligokyphus* as the outgroup, recovered *Tritylodon*, *Bienotherium*, and *Kayentatherium*, as sequential taxa. The remaining species were part of a polytomy that included three clades: (1) *Shartegodon* and *Nuurtherium* grouped together with *Yuanotherium* in a polytomy; (2) *Lufengia* sister to a polytomy containing *Dianzhongia*, *Dinnebitodon*, and *Yunnanodon*; and (3) sister relationship of *Bocatherium* and *Stereognathus* (fig. 16).

DISCUSSION

Despite their recorded occurrence from the Upper Triassic to the Lower Cretaceous and their cosmopolitan distribution, tritylodontids are not very abundant in the fossil record. Only 17 genera and 26 species are known for the family, three of these species (*Shartegodon altai*, *Nuurtherium baruunensis*, and *Bienotheroides shartegensis*) are known only from the Shar Teg locality in southwestern Mongolia. The Shar Teg locality is one of the most diverse Jurassic

fossil deposits containing a high diversity of aquatic and terrestrial plant, invertebrate, and vertebrate fossils (Ponomarenko et al., 2014).

Phylogenetic hypotheses of relationships among tritylodontid genera have been proposed by Clark and Hopson (1985), Sues (1986b), Setoguchi et al. (1999), Matsuoka (2000), and Watabe et al. (2007). These studies were based on a reduced number of taxa (e.g., six genera; Sues, 1986b) and/or characters (e.g., 11; Watabe et al., 2007). Our analysis included all the recognized genera for the family. Using *Oligokyphus* as an outgroup we identified *Tritylodon*, *Bienotherium*, and *Kayentatherium* as sequential taxa, a result similar to those of Clark and Hopson (1985) and Sues (1986b). These taxa are characterized by having: (1) a large maxilla that occupies most of the area of the palate, (2) palatine bordered only by the maxilla, (3) interdigitations on the maxillo-palatine suture, (4) a jugal that does not contribute to the medial and inferior orbital walls, (5) lack of foramina on jugal above PC2, and (6) upper postcanine teeth present and an anterior median root. The remaining genera are part of a polytomy that included three clades: the first includes *Dianzhongia*, *Dinnebitodon*, *Lufengia*, and *Yunnanodon* and is supported by having short and slightly curved lower postcanine roots; the second clade includes our new taxa *Shartegodon*, *Nuurtherium*, and *Yuanotherium* and is supported by having a contribution of the palatine to the PC4 alveoli and foramina on the jugal above PC2; and the third clade includes a sister relationship of *Bocatherium* and *Stereognathus*.

Based on their unique dental structure, tritylodontids have long been thought to be herbivorous, well adapted to plant diets rich in fibrous materials (Kühne, 1956; Kemp, 1982; Sues, 1984). However, Hu et al. (2009), based on the characteristic upper postcanines (slender cusps, with relatively weak crests, and the posterolingual cusps high and blade-like) of *Yuanotherium* that are more trenchant and fragile than other tritylodontids, suggest that this species may have been omnivorous rather than herbivorous. The dentition of *Shartegodon* and *Nuurtherium* is similar to the generalized morphology pattern (e.g., wide cusps, with strong crests) of tritylodontids and does not resemble the characteristic upper postcanine morphology of *Yuanotherium*, suggesting that *Shartegodon* and *Nuurtherium* are herbivorous like the majority of tritylodontids.

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APPENDIX 1

CHARACTERS IN THE PHYLOGENETIC ANALYSIS

List of characters and character states used in the phylogenetic analysis. Characters and scorings are based on Simpson (1928); Young (1947); Kühne (1956); Chow and Hu (1959); Chow (1962); Waldman and Savage (1972); Cui (1981); Kermack (1982); He and Cai (1984); Sun (1984); Clark and Hopson (1985); Sues (1985, 1986b, 1986c); Cui and Sun (1987); Sun and Cui (1989); Luo and Wu (1994); Setoguchi et al. (1999); Matsuoka (2000); Maisch et al. (2004); Sues and Jenkins (2006); Watabe et al. (2007); Lopatin and Agadjanian (2008); Hu et al. (2009); Jasinoski and Chinsamy (2012); Fedak et al. (2015); and Matsuoka et al. (2016).

1. Snout: **0**, longer than postcanine tooththrow length; **1**, shorter than postcanine tooththrow length.
2. Postincisive constriction of the snout: **0**, present; **1**, absent.
3. Anterior margin of orbit: **0**, directly dorsal to the distal margin of PC1; **1**, above the anteroposterior midpoint of PC2.

4. Lacrimal size: **0**, large; **1**, reduced.
5. Lacrimal foramina: **0**, absent; **1**, one; **2**, two.
6. Anterior contact of lacrimal: **0**, premaxilla; **1**, maxilla.
7. Premaxilla posterior extension on secondary palate: **0**, anteriorly; **1**, between incisors and the mesial cheek teeth; **2**, near the most mesial teeth.
8. Contact between premaxilla and palatine on palate: **0**, absent; **1**, present.
9. Premaxilla-maxillary: **0**, contact follows the mesiolingual shape of PC1; **1**, contact occurs in the snout.
10. Interdigitations on the maxillo-palatine suture: **0**, absent; **1**, present.
11. Interdigitations on the premaxillo-palatine suture: **0**, absent; **1**, present.
12. Maxilla presence on the hard palate: **0**, large and occupies most of the area of the palate; **1**, highly reduced, preserved as a narrow band forming the lingual margins of the postcanine teeth.
13. Palatine contact: **0**, anteriorly and laterally, the palatine is bordered by the maxilla and premaxilla; **1**, bordered only by the maxilla.
14. Palatine contribution to the PC4 alveolus: **0**, present; **1**, absent.
15. Greater palatine foramina: **0**, three; **1**, two; **2**, one; **3**, absent.
16. Lateral (facial and zygomatic) extension of maxilla: **0**, present; **1**, reduced or absent.
17. Zygomatic process of the maxilla: **0**, constitutes the ventral aspect of the anterior root of the zygomatic arch; **1**, constitutes the dorsal aspect of the anterior root of the zygomatic arch.
18. Jugal contribution to the medial and inferior orbital walls: **0**, present; **1**, absent.
19. Foramina on jugal above PC2: **0**, three foramina present; **1**, absent.
20. Coronoid process height: **0**, very tall; **1**, short.
21. Coronoid process anterior margin shape: **0**, gently curved anterior margin; **1**, straight anterior margin.
22. Angle of the alveolar line and the anterior margin of the coronoid process: **0**, <90°; **1**, >90°; **2**, 90°.
23. Upper postcanine alveolar tooth rows: **0**, diverge posteriorly; **1**, parallel.
24. Upper postcanine teeth generalize cusp formula: **0**, 2-2-2; **1**, 2-3-2; **2**, 2-3-3; **3**, 2-3-4; **4**, 2-4-3; **5**, 2-4-4; **6**, 3-3-3; **7**, 3-4-4.
25. Upper cheek tooth B0 cusp: **0**, present; **1**, absent.
26. Upper cheek tooth M0 cusp: **0**, present; **1**, absent.
27. Upper cheek tooth L0 cusp: **0**, present; **1**, absent.
28. Upper cheek tooth M1 cusp: **0**, large; **1**, small; **2**, absent.
29. Upper cheek tooth L1 cusp: **0**, large; **1**, small; **2**, absent.
30. Upper cheek tooth L3 cusp: **0**, large; **1**, small; **2**, absent.
31. Upper postcanine roots: **0**, four; **1**, five; **2**, six; **3**, seven.
32. Upper postcanine teeth anterior median root: **0**, absent; **1**, present.
33. Lower postcanine teeth generalize cusp formula: **0**, 2-2; **1**, 3-3.
34. Lower postcanine root number: **0**, one; **1**, two.
35. Lower postcanine root length and curvature: **0**, long with the distal 2/3 curved; **1**, long and curved throughout its entire length; **2**, short and slightly curved.

APPENDIX 2

DATA MATRIX

Character matrix employed in this paper for assessing the phylogenetic relationships among tritylodontid genera. Matrix scoring was based on Simpson (1928); Young (1947); Kühne (1956); Chow and Hu (1959); Chow (1962); Waldman and Savage (1972); Cui (1981); Kermack (1982); He and Cai (1984); Sun (1984); Clark and Hopson (1985); Sues (1985, 1986b, 1986c); Cui and Sun (1987); Sun and Cui (1989); Luo and Wu (1994); Setoguchi et al. (1999); Matsuoka (2000); Maisch et al. (2004); Sues and Jenkins (2006); Watabe et al. (2007); Lopatin and Agadjanian (2008); Hu et al. (2009); Jasinowski and Chinsamy (2012); Fedak et al. (2015); Matsuoka et al. (2016). Character description and coding are listed in appendix 1. Missing or unknown characters are represented by “?”. Polymorphisms are shown between brackets. An electronic version of this matrix is available at <http://www.morphobank.org> (project P2219, Two new tritylodontids (Synapsida, Cynodontia, Mammalia) from the Upper Jurassic, south-western Mongolia).

	5	10	15	20	25	30	35
<i>Bienotherium</i>	11001	11011	-0112	00???	??021	11010	21?11
<i>Bienotheroides</i>	11101	02100	1101(0,2)	1????	??0(2,6)(1,0)	11110	10000
<i>Bocatherium</i>	11001	02100	11011	1???0	02101	11220	?????
<i>Dianzhongia</i>	11???	?20??	?????	0????	??111	11001	3????
<i>Dinnebitodon</i>	11???	?21??	?1???	1????	??011	11002	?????
<i>Kayentatherium</i>	11001	12001	-0?12	00110	00021	11010	??0??
<i>Lufengia</i>	11???	?20??	?????	0????	???21	11000	10?11
<i>Montirictus</i>	?????	?????	?????	?????	???01	11220	20011
<i>Oligokyphus</i>	00002	10011	-0113	00111	11070	00000	21111
<i>Polistodon</i>	11?10	1????	?????	000?1	01?01	11220	??0??
<i>Stereognathus</i>	11???	?21??	?1???	1????	???01	11220	10???
<i>Tritylodon</i>	00???	10011	-0112	00??0	02121	11000	11???
<i>Xenocretosuchus</i>	?????	?????	?????	?????	???01	11220	??0??
<i>Yunnanodon</i>	11???	?????	?????	?????	???11	11002	10?11
<i>Yuanotherium</i>	?????	?2100	11??1	01???	???40	00011	?????
<i>Shartegodon</i>	1100?	02100	01001	0000?	??051	00110	00000
<i>Nuurtherium</i>	?????	???0	?1???	???0	00031	00010	10000

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