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

PAÚL M. VELAZCO, 1 ALEXANDRA J. BUCZEK, 2, 3 AND MICHAEL J. NOVACEK 1

ABSTRACT

Two new genera and species of Tritylodontidae, *Shartegodon altai* and *Nuurtherium barunensis*, 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,
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).
Twenty-four species of tritylodontids are currently recognized and are grouped into 15 genera: Bienotherium Young, 1940; Bienotheroides Young, 1982; Bocatherium Clark and Hop-son, 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 that 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
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). 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, Mammaliamorpha) 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 outgroup 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 sharte-gensis*, 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
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.

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
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 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

---

**Key:**
- **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
- **Pl**: palatine
- **Pmx**: premaxilla

Scale bar = 5 mm.
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.
lacrima 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 stapedial 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
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 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.
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 = M3; and L0 < L1 < L3 < L2. In the case of the right PC3 the lingual cusps heights are: L0 < L1 = L2 < L4 = 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 altae* 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-
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°. 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
The dorsal angle of the quadrate is absent. The lateral trochlear condyle is preserved, but the medial trochlear condyle and the stapedial 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 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.
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: B1 < B2; M0 < M1 < M2; and L0 < L1 < L3 < L2. The largest cusps on all upper postcanine teeth are B2 and M2. The smallest cusp on every upper postcanine is L0. Five cusps (B1, B2, M1, M2, and L2) exhibit a small degree of crescentic shape. M1 and M2 present sharp lingual and buccal cristae; B1 and B2 present sharp lingual and blunt buccal cristae; and L2 presents a sharp buccal and a blunt lingual cusp.

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 (b1, b2, l1, and l2). Most of the cusp apices are broken.

### 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.

| Shartegodon altai | Nuurtherium baruunensis |
|-------------------|------------------------|
| **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 | 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 | 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 | 6.80 | 5.00 |
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; CI, right clavicle; DV, dorsal vertebrae; F, left femur; mc, metacarpal; mp, metapodial; pc, postcanine teeth; PR, posterior rib; U, left ulna; 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. \(l_1\) is located more mesially than \(b_1\), whereas \(l_2\) and \(b_2\) 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; Jasinoski 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 palate 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 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).
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*, *Monticticus*, and *Oligokyphus*, and seven in *Dianzhongia*. The upper postcanine teeth lack an anterior median root in *Shartegodon*, *Nuurtherium*, *Bienotheroides*, *Lufengia*, *Monticticus*, *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),

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

*a* Larger type.  
*b* Smaller type.
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 (2-3-3), 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, 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, 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.
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 bladelike) 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.

ACKNOWLEDGMENTS

We thank members of the 2010 and 2011 field crew for their hard work. Amy Davidson prepared the specimens. Guillermo Rougier and Mahito Watabe provided helpful reviews of the manuscript. Henry Towbin and Morgan Hill assisted with the CT and SEM images. Credits for illustrations are: Mick Ellison (photographs of figs. 3A–B, 4A–B, 5–7, 11, and 14) and Nicole Wong (line drawings of figs. 3, 4, 11, 12, and 14). Research was supported by the Frick Laboratory Endowment. Research by P.M.V. was also supported by the Margaret and Will Hearst Paleontological Research Fund.
REFERENCES

Bonaparte, J.F. 1970. Annotated list of the South American Triassic tetrapods. Second Gondwana Symposium, Proceedings and Papers 1: 665–682.

Butler, P.M. 1939. XLI.—The post-canine teeth of Tritylodon longevus Owen. Annals and Magazine of Natural History 4: 514–520.

Charlesworth, E. 1855. Notes and abstract of miscellaneous communications to the sections (Geology). In Report of the twenty-fourth meeting of the British Association for the Advancement of Science: 80. London: John Murray.

Chow, M. 1962. A tritylodont specimen from Lufeng, Yunnan. Vertebrata PalAsiatica 4: 365–367.

Chow, M.-Z., and C.-Z. Hu. 1959. A new tritylodontid from Lufeng, Yunnan. Vertebrata PalAsiatica 3: 7–10.

Clark, J.M., and J.A. Hopson. 1985. Distinctive mammal-like reptile from Mexico and its bearing on the phylogeny of the Tritylodontidae. Nature 315: 398–400.

Cope, E.D. 1844. The Tertiary Marsupialia. American Naturalist 18: 686–697.

Cui, G.-H. 1976. Yunnania, a new tritylodontid from Lufeng, Yunnan. Vertebrata PalAsiatica 14: 85–90.

Cui, G.-H. 1981. A new genus of Tritylodontidae. Vertebrata PalAsiatica 19: 5–10.

Cui, G.-H. 1986. Yunnanodon, a replacement name for Yunnania Cui, 1976. Vertebrata PalAsiatica 24: 9.

Cui, G.-H., and A.L. Sun. 1987. Postcanine root system in tritylodonts. Vertebrata PalAsiatica 25: 245–259.

Fedak, T.J., H.-D. Sues, and P.E. Olsen. 2015. First record of the tritylodontid cynodont Oligokyphus and cynodont postcranial bones from the McCoy Brook Formation of Nova Scotia, Canada. Canadian Journal of Earth Sciences 52: 244–249.

Fejfar, O., W-D. Heinrich, L. Kordos, and L.C. Maul. 2011. Microtoid cricetids and the early history of arvicolids (Mammalia, Rodentia). Palaeontologia Electronica 14: 27A.

Gereltsetseg, L. 1992. Jurassic charophytes from the lacustrine beds of the Shara Teg locality (Transaltai Gobi, Mongolia). Biulleten Moskovskogo Obshchestva Ispytatelei Prirody. Otdel Geologicheskii 67: 122–125.

Goloboff, P.A., J.S. Farris, and K.C. Nixon. 2003. TNT: Tree analysis using new technology. Version 1.0. Program and documentation, available from the authors.

Goloboff, P.A., J.S. Farris, and K.C. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24: 774–786.

Hammer, W.R., and N.D. Smith. 2008. A tritylodont postcanine from the Hanson Formation of Antarctica. Journal of Vertebrate Paleontology 28: 269–273.

He, X.-L., and K.-J. Cai. 1984. The tritylodont remains from Dashanpu, Zigong. Journal of Chengdu College of Geology (Special Paper on Dinosaurian Remains of Dashanpu, Zigong, Sichuan [II]) Supplement 2 (Sum 33): 33–45.

Hennig, E. 1922. Die Säugethrämhe des würtembergischen Rhät-Lias-Boneneds. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 46: 181–267.

Hopson, J.A. 1991. Systematics of the nonmammalian Synapsida and implications for patterns of evolution in synapsids. In H.P. Schultze and L. Trueb (editors), Origins of the higher groups of tetrapods: controversy and consensus: 635–693. Ithaca: Cornell University Press.

Hopson, J.A., and H.R. Barghusen. 1986. An analysis of therapsid relationships. In N. Hotton III, P.D. MacLean, J.J. Roth, and E.C. Roth (editors), The ecology and biology of mammal-like reptiles: 83–106. Washington, D.C.: Smithsonian Institution Press.
Hopson, J.A., and J.W. Kitching. 2001. A probainognathian cynodont from South Africa and the phylogeny of nonmammalian cynodonts. Bulletin of the Museum of Comparative Zoology 156: 5–35.

Hu, Y., J. Meng, and J.M. Clark. 2009. A new tritylodontid from the Upper Jurassic of Xinjiang, China. Acta Palaeontologica Polonica 54: 385–391.

Jasinoski, S.C., and A. Chinsamy. 2012. Mandibular histology and growth of the nonmammaliaform cynodont Tritylodon. Journal of Anatomy 220: 564–579.

Kamiya, H., T. Yoshida, N. Kusuhashi, and H. Matsuoka. 2006. Enamel texture of the tritylodontid mammal-like reptile, occurred from the lower Cretaceous in central Japan. Materials Science and Engineering: C 26: 707–709.

Kemp, T.S. 1982. Mammal-like reptiles and the origin of mammals. London: Academic Press.

Kemp, T.S. 2005. The origin and evolution of mammals. New York: Oxford University Press.

Kermack, D.M. 1982. A new tritylodontid from the Kayenta formation of Arizona. Zoological Journal of the Linnean Society 76: 1–17.

Kermack, D.M., and K.A. Kermack. 1984. Specialised cynodont derivatives. In D.M. Kermack and K.A. Kermack (editors), The evolution of mammalian characters: 37–47. Washington, D.C.: Springer US.

Kitching, J.W., and M.A. Raath. 1984. Fossils from the Elliot and Clarens Formations (Karoo Sequence) of the northeastern Cape, Orange Free State and Lesotho, and a suggested biozonation based on tetrapods. Palaeontologia Africana 25: 111–125.

Kühne, W.G. 1956. The liassic therapsid Oligokyphus. London: Trustees of the British Museum.

Lazzari, V., et al. 2015. Convergent evolution of molar topography in Muroidea (Rodentia, Mammalia): connections between chewing movements and crown morphology. In P.G. Cox and L. Hautier (editors), Evolution of the rodents: advances in phylogeny, functional morphology and development: 448–477. Cambridge: Cambridge University Press.

Liu, J., and P. Olsen. 2010. The phylogenetic relationships of Eucynodontia (Amniota: Synapsida). Journal of Mammalian Evolution 17: 151–176.

Lopatin, A.V., and A.K. Agadjanian. 2008. A tritylodont (Tritylodontidae, Synapsida) from the Mesozoic of Yakutia. Doklady Biological Sciences 419: 107–110.

Luo, Z.-X. 2001. The inner ear and its bony housing in tritylodontids and implications for evolution of the mammalian ear. Bulletin of the Museum of Comparative Zoology 156: 81–97.

Luo, Z.-X., Z. Kielan-Jaworowska, and R.L. Cifelli. 2002. In quest for a phylogeny of Mesozoic mammals. Acta Palaeontologica Polonica 47: 1–78.

Luo, Z.-X., and A.-L. Sun. 1993. Oligokyphus (Cynodontia: Tritylodontidae) from the Lower Lufeng Formation (Lower Jurassic) of Yunnan, China. Journal of Vertebrate Paleontology 13: 477–482.

Luo, Z.-X., and X.-C. Wu. 1994. The small tetrapods of the lower Lufeng Formation, Yunnan, China. In N.C. Fraser and H.-D. Sues (editors), In the shadow of the dinosaurs: Early Mesozoic tetrapods: 251–270. Cambridge: Cambridge University Press.

Lydekker, R. 1887. Catalogue of the fossil mammals in the British Museum (Natural History), Part V. Containing the group Tillodontia, the orders Sirenia, Cetacea, Edentata, Marsupialia, Monotremata, and supplement. London: Trustees of the British Museum.

Maisch, M.W., A.T. Matzke, and G. Sun. 2004. A new tritylodontid from the Upper Jurassic Shishugou Formation of the Junggar Basin (Xinjiang, NW China). Journal of Vertebrate Paleontology 24: 649–656.

Martinez, R.N., C.L. May, and C.A. Forster. 1996. A new carnivorous cynodont from the Ischigualasto Formation (Late Triassic, Argentina), with comments on eucynodont phylogeny. Journal of Vertebrate Paleontology 16: 271–284.
Matsuoka, H. 2000. Tritylodonts (Synapsida, Therapsida). In H. Matsuoka (editor), Fossils of the Kuwajima 'Kaseki-kabe'(Fossil-bluff). Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan: 53–74. Ishikawa Prefecture, Japan: Shiramine Village Board of Education.

Matsuoka, H., and T. Setoguchi. 2000. Significance of Chinese tritylodontids (Synapsida, Cynodonta) for the systematic study of Japanese materials from the Lower Cretaceous Kuwajima Formation, Tetori Group of Shiramine, Ishikawa, Japan. Asian Paleoprimatology 1: 161–176.

Matsuoka, H., N. Kusuhashi, and I.J. Corfe. 2016. A new Early Cretaceous tritylodontid (Synapsida, Cynodonta, Mammaliamorpha) from the Kuwajima Formation (Tetori Group) of central Japan. Journal of Vertebrate Paleontology 36: e1112289.

O'Leary, M.A., and S.G. Kaufman. 2012. MorphoBank 3.0: Web application for morphological phylogenetics and taxonomy. Online resource (http://www.morphobank.org).

Osborn, H.F. 1903. On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. Science 17: 275–276.

Owen, R. 1884. On the skull and dentition of a Triassic Mammal (Tritylon longævus, Owen) from South Africa. Quarterly Journal of the Geological Society 40: 146–152.

Owen, R. 1861. Palaeontology, or a systematic summary of extinct animlas and their geological relations, second edition. Edinburgh: Adam and Charles Black.

Ponomarenko, A.G., et al. 2014. Upper Jurassic Lagerstätte Shar Teg, southwestern Mongolia. Paleontological Journal 48: 1573–1682.

Rowe, T. 1988. Definition, diagnosis, and origin of Mammalia. Journal of Vertebrate Paleontology 8: 241–264.

Rowe, T. 1993. Phylogenetic systematics and the early history of mammals. In F.S. Szalay, M.J. Novacek, and M.C. McKenna (editors), Mammal phylogeny: Mesozoic differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials: 129–145. New York: Springer-Verlag.

Ruta, M., J. Botha-Brink, S.A. Mitchell, and M.J. Benton. 2013. The radiation of cynodonts and the ground plan of mammalian morphological diversity. Proceedings of the Royal Society B 280: 20131865.

Savage, R.J.S. 1971. Tritylodontid incertae sedis. Proceedings of the Bristol Natural History Society 32: 80–83.

Setoguchi, T., H. Matsuoka, and M. Matsuda. 1999. New discovery of an Early Cretaceous tritylodontid (Reptilia, Therapsida) from Japan and the phylogenetic reconstruction of Tritylodontidae based on the dental characters. In Y.-Q. Wang and T. Deng (editors), Proceedings of the seventh annual meeting of the Chinese Society of Vertebrate Paleontology: 117–124. Beijing: China Ocean Press.

Simpson, G.G. 1926. Mesozoic Mammalia, IV: the multituberculates as living animals. American Journal of Science 11: 228–250.

Simpson, G.G. 1928. A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. London: British Museum (Natural History).

Sues, H.-D. 1984. Inferences concerning feeding and locomotion in the Tritylodontidae (Synapsida). In W.-E. Reif and F. Westphal (editors), Third symposium on Mesozoic terrestrial ecosystems, short papers: 231–236. Tübingen, Germany: Tübingen University Press.

Sues, H.-D. 1985. First record of the tritylodontid Oligokyphus (Synapsida) from the Lower Jurassic of western North America. Journal of Vertebrate Paleontology 5: 328–335.

Sues, H.-D. 1986a. Dinnebitodon amarali, a new tritylodontid (Synapsida) from the Lower Jurassic of western North America. Journal of Paleontology 60: 758–762.
Sues, H.-D. 1986b. Relationships and biostratigraphic significance of the Tritylodontidae (Synapsida) from the Kayenta Formation of northeastern Arizona. In K. Padian (editor), The beginning of the age of dinosaurs: faunal change across the Triassic-Jurassic boundary: 279–284. Cambridge: Cambridge University Press.

Sues, H.-D. 1986c. The skull and dentition of two tritylodontid synapsids from the Lower Jurassic of western North America. Bulletin of the Museum of Comparative Zoology 151: 217–268.

Sues, H.-D., and F.A. Jenkins, Jr. 2006. The postcranial skeleton of Kayentatherium wellesi from the Lower Jurassic Kayenta Formation of Arizona and the phylogenetic significance of postcranial features. In M.T. Carrano, T.J. Gaudin, R.W. Blob, and J.R. Wible (editors), Amniote paleobiology: perspectives on the evolution of mammals, birds, and reptiles: 114–152. Chicago: University of Chicago Press.

Sun, A.-L. 1984. Skull morphology of the tritylodont genus Bienotheroides of Sichuan. Scientia Sinica, Series B 27: 970–984.

Sun, A.-L. 1986. New material of Bienotheroides (tritylodontid reptile) from the Shaximiao Formation of Sichuan. Vertebra PalAsiatica 24: 165–170.

Sun, A.-L., and G.H. Cui. 1989. Tritylodont reptile from Xinjiang. Vertebra PalAsiatica 27: 1–8.

Tatarinov, L.P., and E.N. Maschenko. 1999. A find of an aberrant Tritylodont (Reptilia, Cynodontia) in the Lower Cretaceous of the Kemerovo Region. Paleontologicheskii Zhurnal 33: 422–428.

Waldman, M., and R.J.G. Savage. 1972. The first Jurassic mammal from Scotland. Journal of the Geological Society 128: 119–125.

Watabe, M., T. Tsubamoto, and K. Tsogtbaatar. 2007. A new tritylodontid synapsid from Mongolia. Acta Palaeontologica Polonica 52: 263–274.

Wible, J.R. 1991. Origin of Mammalia: the craniodental evidence reexamined. Journal of Vertebrate Paleontology 11: 1–28.

Young, C.-C. 1940. Preliminary notes on the Mesozoic mammals of Lufeng, Yunnan, China. Bulletin of the Geological Society of China 20: 93–111.

Young, C.-C. 1947. Mammal-like Reptiles from Lufeng, Yunnan, China*. Proceedings of the Zoological Society of London 117: 537–597.

Young, C.-C. 1982. On a Bienotherium-like tritylodont from Szechuan, China. In Selected works of Yang Zhongjian: 10–13. Beijing: Science Press.

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 toothrow length; 1, shorter than postcanine toothrow 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. Angle of the alveolar line and the anterior margin of the coronoid process: 0, <90º; 1, >90º; 2, 90º.
22. 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.
23. Upper postcanine root number: 0, one; 1, two.
24. Lower postcanine teeth generalize cusp formula: 0, 2-3; 1, 3-3.
25. Lower postcanine root number: 0, one; 1, two.
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, 1986a, 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); 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, Mammaliamorpha) from the Upper Jurassic, southwestern Mongolia).

| Character | 5 | 10 | 15 | 20 | 25 | 30 | 35 |
|-----------|---|----|----|----|----|----|----|
| Bienotherium | 11001 | 11011 | -0112 | 00?? | ??021 | 11010 | 21?11 |
| Bienotheroides | 11101 | 02100 | 1101(0,2) | 1??? | ??0(2,6)(1,0) | 11110 | 10000 |
| Bocatherium | 11001 | 02100 | 11011 | 1???0 | 02101 | 11220 | ???? |
| Dianzhongia | 11??? | ?20?? | ????? | 0???? | ??111 | 11001 | 3??? |
| Dinnebitodon | 11??? | ?21?? | ?1?? | 1???? | ??011 | 11002 | ???? |
| Kayentatherium | 11001 | 12000 | -0?12 | 00110 | 00021 | 11010 | ??? |
| Lufengia | 11??? | ?20?? | ????? | ????? | ??01 | 11000 | 10?11 |
| Montirictus | ????? | ????? | ????? | ????? | ??01 | 11220 | 20011 |
| Oligokyphus | 00002 | 10011 | -0113 | 00111 | 11070 | 00000 | 21111 |
| Polistodon | 11?10 | 1??? | ????? | 000?1 | 01?01 | 11220 | ?0?0 |
| Stereognathus | 11??? | ?21?? | ?1?? | 1???? | ??01 | 11220 | 10??? |
| Tritylodon | 00??? | 1000 | -0112 | 00??0 | 02121 | 11000 | 11??? |
| Xenocretosuchus | ????? | ????? | ????? | ????? | ??01 | 11220 | ?0?0 |
| Yunnanodon | 11??? | ????? | ????? | ????? | ??1 | 11002 | 10?11 |
| Yuanotherium | ????? | ?2100 | 11?1 | 01??? | ???40 | 00011 | ????? |
| Shartegodon | 1100? | 02100 | 01000 | 00000 | ??051 | 00110 | 00000 |
| Nuurtherium | ????? | ?1?? | ????? | ????? | 00031 | 00010 | 10000 |
All issues of *Novitates* and *Bulletin* are available on the web (http://digitallibrary.amnh.org/dspace). Order printed copies on the web from:
http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html

or via standard mail from:
American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).