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Authors: Hu, Yaoming, Meng, Jin, and Clark, James M.

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A new tritylodontid from the Upper Jurassic of Xinjiang, China

YAOMING HU*, JIN MENG, and JAMES M. CLARK

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A new genus and species of Tritylodontidae, *Yuanotherium minor,* is described and compared with other known tritylodontids. The new taxon is represented by a partially preserved upper jaw with three postcanines, collected from the upper part of the Shishugou Formation (Oxfordian, Late Jurassic) in the Wucaiwan area of the Junggar Basin, northwestern Xinjiang, China. Like other tritylodontids its maxillary teeth have three rows of blade-like trenchant cusps separated by deep furrows. The new species differs from other tritylodontids mainly in having posteriormost two cusps of the median row on upper postcanines closely placed. The new tritylodontid may have been omnivorous rather than herbivorous, as previously suggested for tritylodontids in general.

Key words: Tritylodontidae, Cynodontia, Upper Jurassic, Xinjiang, China.

*Yaoming Hu, Institute of Vertebrate Paleontology and Paleoanthropology, 142 Xiwaidajie, P.O. Box 643, Beijing 100044, China; (*Deceased on April 12th, 2008)*
Jin Meng [jmeng@amnh.org], Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA;
James C. Clark [jclark@gwu.edu], Department of Biological Sciences, George Washington University Washington DC 20052, USA.

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Introduction

Tritylodontidae are a group of highly derived nonmammalian cynodonts living in the middle Mesozoic (Kemp 1982, 2005; Watabe et al. 2007). Fossil remains of definite tritylodontids have been found in terrestrial sediments of Early Jurassic to Early Cretaceous age from England, South Africa, Antarctica, North America, China, western Siberia, Japan, and Mongolia (Watabe et al. 2007; Hammer and Smith 2008). The family Tritylodontidae Cope, 1884 are characterized by an aberrant and stereotyped dentition that has enlarged incisors, no canine but a distinct diastema, and squarish postcanines with three rows of crescent cusps on upper teeth and two rows on the lowers. During mastication, leading edges on cusps of the lower postcanines moved posteriorly relative to opposing surfaces of the uppers, producing shearing action (Crompton 1972; Sues 1986a). The peculiar dental structures of tritylodontids are somewhat multituberculate-like and, to a less extent, rodent-like, and were presumably suitable for an herbivorous diet (Kemp 1982). Because tritylodontids possess some mammal-like dental, cranial and postcranial features, they were considered a group within mammals in early studies (see Simpson 1928 for a summary). The group was later removed from Mammalia because a mammalian jaw joint is lacking (Kühne 1956). Some workers recognize a close relationship between tritylodontids and mammals (Kemp 1982; Rowe 1988), whereas most studies of advanced synapsids favor the hypothesis that tritylodontids belong to a clade of largely herbivorous cynodonts, of which no branch led to mammals (Crompton and Ellenberger 1957; Hopson and Crompton 1969; Crompton 1972; Sues 1985a; Hopson 1991; Sidor and Hopson 1998; Hopson and Kitching 2001; Bonaparte et al. 2003, 2005). Regardless of their affinities, tritylodontids have a cosmopolitan distribution and are very abundant in terms of specimens in many Jurassic localities, indicating a degree of evolutionary success for the group in the middle Mesozoic.

Here we report a new genus and species of Tritylodontidae, represented by a partial left upper jaw with three postcanines. The specimen was collected from the Upper Jurassic part of the Shishugou Formation in the Wucaiwan area of the Junggar Basin in Xinjiang, northwestern China (Clark et al. 2006). Other tritylodontids, e.g., *Bienotheroides zigongensis* Sun, 1986, *B. ultimus* Maisch, Matzke, and Sun, 2004, and *B. shartegensis* Watabe, Tsubamoto, and Tsogtbaatar, 2007, have been reported from the Middle and Upper Jurassic of the Junggar Basin (Sun and Cui 1989; Maisch et al. 2004) and neighboring southwestern Mongolia (Watabe et al. 2007).

Institutional abbreviation.—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

Materials and methods

The fossil described in this paper is housed at the IVPP. Although the canines were absent in tritylodontids, we follow the convention of referring to cheek teeth of tritylodontids as postcanines. Cusps on the tooth crown are described based on their relative positions (buccal, median and lingual; anterior, middle and posterior). The photographs were taken using a Nikon digital camera mounted to Nikon SMZ-U microscope.

Systematic paleontology

Synapsida Osborn, 1903

Cynodontia Owen, 1861

Tritylodontidae Cope, 1884

Genus *Yuanotherium* nov.

Etymology: Yuan Fuli was a pioneer Chinese geologist and paleontologist who worked in Xinjiang early in the last century; *therion* (L.), beast.

Type species: *Yuanotherium minor* sp. nov.

Diagnosis.—The same as for the type and only species.

Stratigraphic and geographic range.—The upper part of the Shishugou Formation, Oxfordian of the Late Jurassic.

Yuanotherium minor sp. nov.

Figs. 1, 2.

Etymology: From Latin *minor*, small.

Holotype: IVPP V15335, a partial left upper jaw with anterior three postcanines (Figs. 1, 2).

Type locality: Wucaiwan area of Junggar Basin in northeastern Xinjiang, China.

Type horizon: The upper part of the Shishugou Formation, radiometrically dated as between 161.2±0.2 Ma and 158.7±0.3 Ma (Eberth et al. 2001, 2006; Clark et al. 2006), within the Oxfordian stage of the Late Jurassic.

Diagnosis.—Upper cheek tooth with a cusp formula 2:4:3 on the second and third postcanines. Differing from other tritylodontids in having posteriormost two cusps of the median row on upper postcanines closely placed; cusps high and slender (potentially owing to lack of wear), buccolingually compressed; posterobuccal cusp with a prominent posterior crest.

Description.—The specimen is preserved in matrix, with only the palatal side being exposed (Fig. 1), and represents the middle section of the left upper jaw, including much of the palatal portion of the highly reduced maxilla and palatine, a small portion of the premaxilla, the root of the zygomatic arch, and three anterior upper postcanines, denoted as PC1, PC2, and PC3. In ventral view, the maxilla comprises only a thin bone forming the alveoli of postcanines, as in derived tritylodontids such as *Bienotheroides*. A narrow band of the maxilla forms the lingual margins of the alveoli and separates them from the premaxilla and palatine; the latter two elements contact each other along a transverse, interdigitating suture at a level medial to the anterior portion of PC2. Only a small portion of the premaxilla medial to the suture is preserved. The preserved portion of the palatine is a thin, slightly concave plate bearing two small foramina, one being about 1.5 mm medial to the middle lingual cusp of PC2 and the other 2.0 mm medial to the middle lingual cusp of PC3. Watabe et al. (2007) identified similar foramina on a specimen of *Bienotheroides shartegensis* Watabe, Tsubamoto, and Tsogtbaatar, 2007 as the greater and lesser palatine foramina, respectively. Due to the damage of the premaxilla, the maxilla anterior and medial to PC1 is exposed ventrally. The medial edge of the bone does not contact its counterpart on the other side of the skull. It appears that the maxilla is reduced in size, but is not completely excluded from the secondary palate. Instead, the premaxilla ventrally overlaps the reduced palatal process of the maxilla and contacts the palatine. The stout zygomatic process of the maxilla forms the anterior root of the zygomatic arch laterodorsal to PC 2 and 3. The surface of the maxilla between the postcanines and the zygomatic arch is concave. A triangular but uneven facet on the ventral side of the maxilla root of the zygomatic arch is probably for the jugal.

Upper postcanines of *Yuanotherium* have a sub-quadrangular outline in occlusal view with rounded and convex buccal and, to a less extent, lingual margins (Figs. 1, 2). Measurements of these teeth are (length/width in mm): PC1, 2.63/2.76; PC2, 2.82/3.07; and PC3, ?/3.48, respectively. Each tooth has three anteroposterior rows of cusps, which are separated by two deep longitudinal furrows. Apices of cusps are knob-like (Fig. 2A, B). Cusps of the median row are nearly symmetrical relative to the longitudinal axis, and those of lingual and buccal rows are asymmetrical. All cusps are slightly compressed linguobuccally and most of them form crescents facing anteriorly (Fig. 2D). The posterior buccal cusp is the tallest and anteroposteriorly longest cusp on the crown.

In crown view, PC1 has a rounded anterior edge and a transversely straight posterior one. The PC1 cusp formula is 2:3:3. Three cusp rows are subequal in length although the anterior cusp on the median row is more anteriorly positioned than those of the other two rows. The anterior cusps of all three rows are small and similar in size. The buccal and lingual anterior cusps are somewhat crescentic and strongly asymmetrical in that the buccal cusp has a sharp lingual crest and a blunt buccal one, whereas the lingual one has the reverse condition. The median anterior cusp is nearly symmetrical but is not crescentic. There are four accessory cuspules along the anterior margin of the crown, two of which are at the anterior ends of the longitudinal furrows and are smaller than other cuspules. Within the buccal row, the posterior cusp is similarly asymmetrical to, but much taller than, the anterior one. Its lingual crest extends anteriorly to the base of the anterior cusp but does not embrace it. In buccal and lingual views, the cusp is triangular in outline, with the apex of the cusp being positioned almost at the transverse axis of the tooth. The buccal surface of the cusp is convex, contrasting the flat lingual one that forms most of the lateral wall of the buccal furrow. The

Fig. 1. Tritylodontid cynodont *Yuanotherium minor* gen. et sp. nov. from the upper part of the Shishugou Formation (Oxfordian, Late Jurassic), Junggar Basin, northwestern Xinjiang, China. IVPP V15335 (holotype), fragment of upper jaw and three anterior postcanines in occlusal view. Stereo pair (**A**) and explanatory drawing (**B**). 1–3, the first, second and third left upper postcanines.

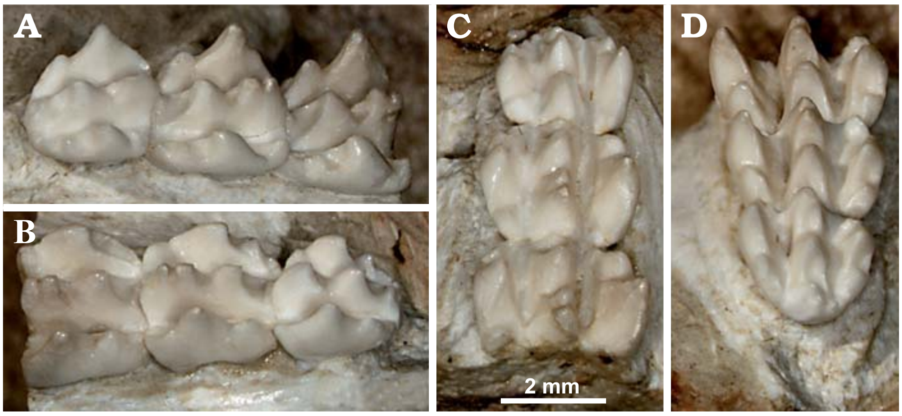

Fig. 2. Tritylodontid cynodont *Yuanotherium minor* gen. et sp. nov. from the upper part of the Shishugou Formation (Oxfordian, Late Jurassic), Junggar Basin, northwestern Xinjiang, China. IVPP V15335 (holotype), showing details of PC1–3 in occlusolingual (**A**), occlusobuccal (**B**), occlusodistal (**C**), and occlusomesial (**D**) views.

cusp possesses a distinct posterior crest that extends from the apex to the posterobuccal corner of the tooth, forming the posterobuccal margin of the tooth crown. The middle and posterior cusps of the median row are similar in size and shape; each is slightly shorter than the posterior cusp on the buccal row. The middle median cusp has symmetric buccal and lingual crests that enclose a steep crescent surface anteriorly and form a convex posterior surface. The crests reach anteriorly to the base of the anterior median cusp and slightly embrace it. In buccal or lingual view each crest is steep near the apex of the cusp and gently sloped approaching the base of the preceding cusp. The posterior median cusp is somewhat asymmetrical due to wear, deeper on its buccal side than on the lingual. Its crests extend to the base of the preceding cusp but do not embrace it. The posterior surface of the cusp protrudes slightly posteriorly beyond the posterior edge of the tooth and partially overlaps the anteromedian cusp of PC2. The middle lingual cusp is strongly asymmetrical, somewhat crescentic, and slightly smaller than the posterior two cusps of the median row. Its apex levels with that of the posterior cusp on the buccal row and its buccal crest extends anteriorly to a point lingual to the base of the anterior cusp on the lingual row. The buccal and lingual furrows are deep, roughly V-shaped in transverse cross section, anteroposteriorly straight, and widened posteriorly. The buccal furrow is wider and deeper than the lingual one, probably owing to deeper wear. The crests of crescentic cusps do not reach the bottom of either furrow, nor were they eliminated by wear.

PC2 is about 10% longer and wider than PC1 and has the cusp formula 2:4:3. The anterior and posterior edges of its crown are nearly straight and parallel to each other. The tooth is similar to PC1 in general morphology. The most obvious difference is that its median row has four rather than three cusps, of which the two posterior cusps are closely packed so that they share a common base. PC2 also differs from PC1 in several detailed aspects: (i) the anterior cusp on the median row is at the anterior edge of the tooth and buttresses the corresponding cusp of PC1; (ii) the notch separating the posterolingual and mediolingual cusps is wider than that on PC1; and (iii) there are only two cuspules, instead of four, on the anterior edge of the tooth crown.

PC3 was broken at its posterior end. The preserved tooth is almost identical to PC2 in crown morphology, except for its slightly larger size. Trivial differences from PC2 include that the lingual crest of the anterior cusp on the buccal row almost reaches the anterior edge of the tooth and that the buccal crest of the middle lingual cusp embraces the anterolingual cusp.

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IVPP V15335 probably belongs to a young adult individual because PC1–3 display some wear. All wear facets are limited to the anterior edges of crescents, suggesting that the crescents functioned as a cutting apparatus, as commonly seen in tritylodontids.

Stratigraphic and geographic range.—The upper part of the Shishugou Formation, Oxfordian of the Late Jurassic.

Comparison and discussion

As in *Bienotheroides*, *Stereognathus*, *Dinnebitodon*, and *Bocatherium* (Sun 1984; Clark and Hopson 1985; Sues 1986c; Watabe et al. 2007), the premaxilla and palatine of IVPP V15335 contact each other on the palate and the maxilla is highly reduced. IVPP V15335 further shows that the premaxilla ventrally overlapped the reduced maxilla, although the latter is not completely excluded from the secondary plate by the expanded premaxilla. The condition is unclear in the other taxa with reduced maxillae.

IVPP V15335 displays the typical tooth morphology of tritylodontids and unquestionably belongs to the family. *Yuanotherium minor* is one of the smallest tritylodontids. Its PC2 is comparable in size to that of *Oligokyphus minor* Kühne, 1956 and smaller than all other tritylodontids except for *Lufengia* and *Yunnanodon*. The presence of closely packed posterior cusps in the median row of PC2–3 (and probably in more distal teeth as well) is unique among tritylodontids. Judging from moderate tooth wear and small size gradient of teeth, the specimen was probably from a young adult and thus the packed posterior cusps on the median row are not juvenile features. These morphological differences warrant establishment of the new genus and species within Tritylodontidae.

The early Jurassic *Oligokyphus* has a wide distribution and is known by abundant fossil remains (Simpson 1928; Kühne 1956; Sues 1985b; Luo and Sun 1993). Given its basal position in tritylodontid phylogeny (Clark and Hopson 1985; Sues 1986b; Setoguchi et al. 1999; Watabe et al. 2007), *Oligokyphus* may be regarded as approximating the ancestral morphotype of tritylodontids. Overall, the upper postcanine of *Oligokyphus* is longer than wide, which is different from all other tritylodontids. *Oligokyphus* differs from *Yuanotherium* in many aspects. In *Oligokyphus*, the cusp formula of a typical upper postcanine (PC2–5) is 3:4:4; the mesial and distal edges of the tooth are convex instead of being truncated; the median cusp row is longer than other two; the buccal row is placed mesially relative to the lingual row; the posterior median cusp projects posteriorly well beyond the margin of the tooth crown; the cusps are low, with minor differences in height between neighboring cusps, and are not linguobuccally compressed; the crests of most cusps (except for the anterior cusps) embrace the bases of their respective preceding cusps. The anterior cusp on the median row is crescentic. A similarity between PCs of *Oligokyphus* and those of *Yuanotherium* is that their buccal and lingual margins are somewhat convex rather than straight.

The early Jurassic *Tritylodon* from Africa (Owen 1884; Simpson 1928) has the same PC cusp formula (2:4:3) as in *Yuanotherium*, but as in *Oligokyphus* the dental morphology of *Tritylodon* differs from *Yuanotherium* in having similar cusp shape, small height difference between cusps, crescentic shape of the anteromedian cusp, and anterior shifting of the buccal cusp row. *Tritylodon* resembles *Yuanotherium* in having straight anterior and posterior margins and convex lingual margins on upper postcanines. In addition, the posterior median cusp does not project posteriorly beyond the tooth margin.

A PC cusp formula of 2:3:3 exists in several tritylodontid genera, including *Bienotherium, Dianzhongia, Lufengia, Kayentatherium,* and *Bienotheroides*, of which *Bienotherium*, *Dianzhongia* and *Lufengia* are from the early Jurassic of Yunnan, China (Young 1940, 1947, 1974; Chow and Hu 1959; Chow 1962; Hopson 1965; Cui 1981; Luo and Wu 1994). In *Bienotherium* a small cuspule is present in front of each cusp row (Hopson 1965; Sun 1984; Luo and Wu 1994) so that the total cusp number of a typical PC can be as many as eleven (Sun 1984). As in *Oligokyphus* the upper tooth of *Bienotherium* is square-shaped and has low cusps and a short buccal cusp row that is more anterior than the lingual row. As in *Yuanotherium* the upper tooth cusps of *Bienotherium* have weak crests.

Dianzhongia and *Lufengia* are similar to each other in upper postcanine morphology but differ from each other in size. *Lufengia* is by far the smallest known tritylodontid, with a skull length only about 40 mm (Chow and Hu 1959; Cui 1981; Cui and Sun 1987; Luo and Wu 1994; see also Fig. 3). The buccal cusp row in these two genera is short but is not shifted anteriorly relative to the lingual row. In the two genera, the anterior edge of the tooth is transversely straight but the posterior edge is convex, due to the protruding of the posterior median cusp, and most cusps have well-developed crests. The two genera are similar to *Yuanotherium* in having a reduced posterolingual cusp but in *Lufengia* the reduced posterolingual cusp extends more anteriorly to its preceding cusp, a condition absent in *Dianzhongia* and *Yuanotherium*.

Kayentatherium Kermack, 1982 (including *Nearctylodon* Lewis, 1986, as a junior synonym; Sues 1986a, c; Sues and Jenkins 2006), is from the Lower Jurassic Kayenta Formation of southwestern North America, whereas *Bienotheroides*, with four named species, comes from the middle to late Jurassic of eastern and central Asia (Young 1982, Sun 1984, 1986; Sun and Li 1985; Sun and Cui 1989; Maisch et al. 2004; Watabe et al. 2007). Both genera have postcanine tooth cusps buccolingually compressed and trenchant with steep flanks, resembling the condition of *Yuanotherium*, but crests on the cusps are more conspicuous than in *Yuanotherium*. The tooth crowns of the two taxa are somewhat oval in occlusal view due to the rounded tooth corners, in contrast to a more angular appearance in *Yuanotherium*. The anterior and posterior edges

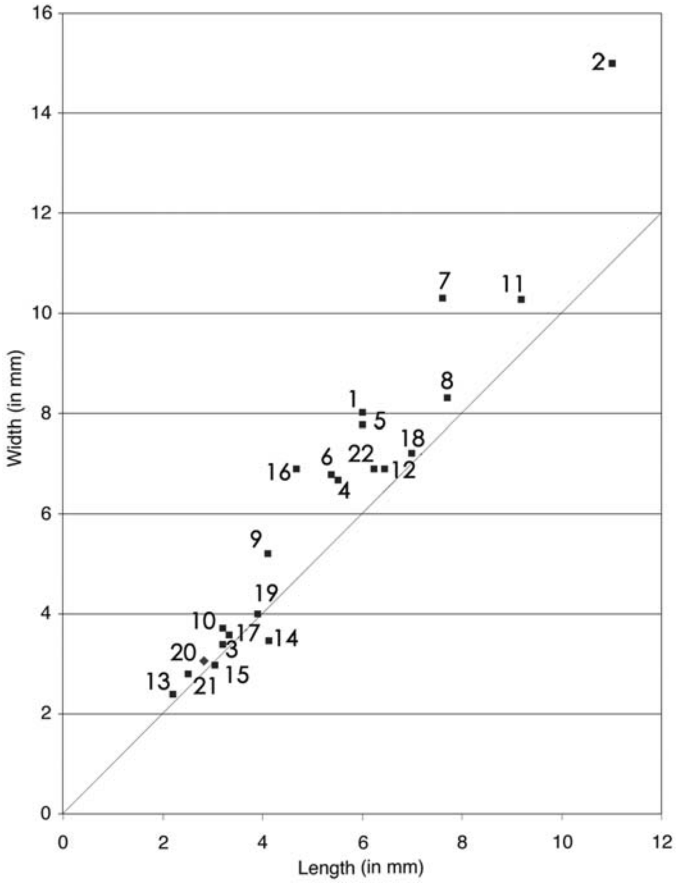

Fig. 3. Size distribution of upper postcanines in tritylodontids. Line indicates where length and width are equal. Unless indicated, all teeth are second upper postcanines. Data source: 1, *Bienotherium yunnanense*: Young (1947); Chow (1962); 2, *Bienotherium magnum*: Chow (1962); 3, *Bienotherium minor*: Young (1947); Chow (1962); 4, *Bienotherium elegans*: Young (1947); 5, *Bienotheroides wansienensis*: Sun (1984); 6, *Bienotheroides zigongensis*: PC3 measured from Sun (1986); 7, *Bienotheroides shartegensis*: Watabe et al. (2007); 8, *Bienotheroides ultimus*: isolated tooth, Maisch et al. (2004); 9, *Bocatherium mexicanum*: Clark and Hopson (1985); 10, *Dianzhongia longirostrata*: Cui (1981); 11, *Dinnebitodon amarali*: Sues (1986c); 12, *Kayentatherium wellesi*: MCZ8811, Sues (1986a); 13, *Lufengia delicata*: PC3, Chow and Hu (1959); 14, *Oligokyphus major*: R7030, Kühne (1956); 15, *Oligokyphus minor*: R7025, Kühne (1956); 16, *Polistodon chuannanensis*: He and Cai (1984); 17, *Stereognathus ooliticus*: a middle tooth, Simpsom (1928); Savage (1971); 18, *Tritylodon longaevus*: Butler (1939); 19, *Xenocretasuchus sibiricus*: isolated upper tooth, Tatarinov and Matchenko (1999); 20, *Yuanotherium minor* gen. et sp. nov.: this study (holotype, IVPP V15335); 21, *Yunnanodon brevirostre*: Cui (1976); 22, Unnamed Japanese specimen (a right upper tooth): measured from Setoguchi et al. (1999: fig. 1-1).

of the postcanines are straight in *Bienotheroides*, except for *B. ultimus*, but are convex in *Kayentatherium*. *Kayentatherium* is more comparable to *Yuanotherium* in tooth crown shape, whereas those of *Bienotheroides* are much wider than long. *Kayentatherium* is further similar to *Yuanotherium* in having a cuspule in front of the anterobuccal cusp and in the presence of a distinct posterior crest (“posteromedial crest” of Sues 1986) attached to the posterobuccal cusp, although the crest appears shorter and steeper than that in *Yuanotherium*. However, the buccal cusp row is the shortest cusp row in *Kayentatherium*, differing from both *Bienotheroides* and *Yuanotherium*. In *Bienotheroides*, a vestigial cuspule is developed in front of the anterobuccal cusp only in the genotype (*Bienotheroides wansiensis*), and the posterior crest from the posterobuccal cusp is not developed (Watabe et al. 2007: fig. 7).

Two early Jurassic genera, *Yunnanodon* from Yunnan, China (Cui 1981) and *Dinnebitodon* from the Kayenta Formation, western North America (Sues 1986c), share an upper cusp formula of 2:3:2. In addition to the difference in the cusp formula, their upper postcanines further differ from those of *Yuanotherium* in having a quadrangular outline, cusps with more distinct crests that embrace the bases of preceding cusps, and cusps less transversely compressed. They are similar to *Yuanotherium* in having a reduced anteromedian cusp. *Dinnebitodon* is further similar to *Yuanotherium* in having a posterior crest extending posteromedially from the posterobuccal cusp, but the cusp is more posteriorly situated and the crest is shorter. *Dinnebitodon* also has a crest extending posterobuccally from the posterolingual cusp, in contrast to *Yuanotherium* in which a small third lingual cusp is developed at the posterolingual corner of the tooth. In contrast, the posterolingual and posterobuccal cusps in *Yunnanodon* have rounded posterior flanks (Cui 1976: fig. 4; Luo and Wu 1994: fig. 14.4D).

Stereognathus from the Middle Jurassic of England has a cusp formula of 2:2:2 on upper postcanines (Charlesworth 1854; Simpson 1928; Evans and Milner 1994). It further differs from *Yuanotherium* in having quadrangular upper postcanines, cusps with distinct and long crests extending from apices and extending to the lingual/buccal flanks of the preceding cusps, and any cusp on the lingual or buccal row having only a single crest.

Xenocretosuchus from the Lower Cretaceous of Siberia is similar to *Stereognathus* in upper tooth cusp formula and morphology of lingual and buccal cusps (Tatarinov and Matchenko 1999). However, it has small cuspules in front of the principal cusps, which are absent in *Stereognathus*. An unnamed tritylodontid from the Lower Cretaceous of Japan has upper postcanines similar to those of *Stereognathus*, although they probably differ in the development of cuspules along the anterior edges of the teeth (Setoguchi et al. 1999: figs. 1, 3). *Polistodon* from the Middle Jurassic of Sichuan, China (He and Cai 1984) and *Bocatherium* from the Lower Jurassic of Mexico (Clark and Hopson 1985; Clark et al. 1994; Fastovsky et al. 2005) have the same cusp formula as *Stereognathus*, on upper postcanines, but they also have a small cuspule in front of each cusp row, which is a condition more similar to *Yuanotherium* than to *Stereognathus*. *Polistodon* is unique among tritylodontids in having thirteen upper postcanines, with each tooth being relatively wide and short compared to those of other tritylodontids, *Yuanotherium* included. *Bocatherium* is similar to *Yuanotherium* in having an oval coronal shape of the upper postcanine.

To sum up, the new specimen differs from those of previously known tritylodontids and represents a new genus and

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species within Tritylodontidae. The interrelationships among tritylodontid genera have been explored in several studies (Clark and Hopson 1985; Sues 1986b; Setoguchi et al. 1999; Watabe et al. 2007). Based primarily on dental and cranial characters, these studies concluded that *Oligokyphus* was probably the most basal member of the tritylodontid clade and that more derived members of the clade evolved a relatively short and broad snout with a highly reduced maxilla and upper postcanines bearing fewer cusps in each row. Though uncertainties remain on several aspects of the tritylodontid morphology, such as the cusp homologies (Setoguchi et al. 1999; Watabe et al. 2007), it is notable that tritylodontid postcanines are highly conservative and variations among different taxa are small, if not trivial.

In IVPP V15335 the first upper postcanine has a rounded anterior margin decorated with minor cuspules, in contrast to more posterior teeth whose anterior margin is truncated. Evidence suggests that in tritylodontids the postcanines were not replaced and that new teeth were added sequentially at the posterior end of the tooth row, while anterior ones were shed after severe wear (Crompton 1955; Kühne 1956; Sues 1986a; Matsuoka and Setoguchi 2000). The morphology and the degree of wear of the first preserved tooth (PC1) of IVPP V15335 suggests that there has not been a tooth shed anterior to PC1, and that PC1 is probably the first upper postcanine this individual ever developed in life. PC1 of V15335 is only slightly smaller than more posterior teeth, suggesting that the animal probably grew to a substantial size before the first cheek tooth erupted. This appears also the case for several other tritylodontids with well-preserved upper dentitions, such as *Bocatherium*, *Bienotherium*, *Bienotheroides*, *Dianzhongia*, *Lufengia*, *Oligokyphus*, *Tritylodon*, and *Yunnanodon*. Timing of the first tooth eruption could be demonstrated with fossils from earlier ontogenetic stages, which would shed light on tritylodontid biology, such as parental care of neonates.

Tritylodontids have been inferred to have been herbivorous (Kühne 1956; Kemp 1982, 2005; Sues 1986a). The opposing crescent cusps of upper and lower postcanines are considered to be efficient for cutting vegetable fibers (Kühne 1956), and the cranial morphology is also consistent with an herbivorous masticatory apparatus (Sues 1986a). However, the postcanine morphology of *Yuanotherium* suggests some deviation from a purely herbivorous diet. The cusps in *Yuanotherium* are slender, with relatively weak crests, and the posterolingual cusp being high and blade-like. These features indicate more trenchant and probably more fragile postcanines in *Yuanotherium* than in other tritylodontids. The postcanines of *Yuanotherium* appear not well adapted for processing tough plants but suitable for puncturing, tearing and slicing soft food items, suggesting that this tritylodontid may have been omnivorous rather than herbivorous. This is consistent with the observation that some rodents and other extant mammals with teeth seemingly adapted to plant eating are actually omnivorous (Landry 1970; Nowak 1999 and references therein).

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