

辽宁早白垩世义县组一新的三尖齿兽类¹⁾

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摘要: 描述了戈壁锥齿兽科 (*Gobiconodontidae*) 一个新的属种——陆家屯弥曼齿兽 (*Meemannodon lujiatunensis* gen. et sp. nov.)。标本产于辽宁西部朝阳市上园镇陆家屯下白垩统义县组一段的凝灰质砂岩层中,为一具完整齿列的左下颌骨。新属与戈壁锥齿兽 (*Gobiconodon*) 共有以下区别于其他三尖齿兽类的特征: 2 颗下门齿, *i*₁ 增大, 后部门齿、犬齿和前部前臼齿尖锥形, 前臼齿具有高的中央尖和小的附尖, *i* ~ *p*₁ 向前平伏。因此, 新属被归入戈壁锥齿兽科。弥曼齿兽与戈壁锥齿兽及其相近属的区别在于: 下门齿和下犬齿更加平伏, *i*₁ 在比例上更大, 而 *i*₂ 则更小; 最后一枚下前臼齿与第一枚下臼齿之间没有齿隙; 前臼齿退化; 下臼齿长度大于高度, 主尖向后倾斜, 与 *b* 尖和 *c* 尖相比, *a* 尖较低, *m*₁ 显著小于 *m*₂ ~ 4。新属下臼齿没有齿带, 与爬兽 (*Repenomamus*) 相似, 而与戈壁锥齿兽不同。

基于与爬兽齿列的对比, 讨论了戈壁锥齿兽类的齿式, 认为其应具有两颗门齿, 而不是以前认为的 1 颗门齿, 从而将戈壁锥齿兽类下齿列齿式修订为: 2·1·2 ~ 3·5。

关键词: 辽宁西部, 早白垩世, 义县组, 戈壁锥齿兽类

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A NEW TRICONODONT (MAMMALIA) FROM THE EARLY CRETACEOUS YIXIAN FORMATION OF LIAONING, CHINA

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Abstract A new genus and species of gobiconodontid, *Meemannodon lujiatunensis*, from the basal member of the Early Cretaceous Yixian Formation at Lujiatun locality, Liaoning, northeast China is described. The new genus, *Meemannodon*, differs from other triconodonts but is similar to *Gobiconodon* in having enlarged *i*₁, lower incisors reduced to 2, conical and pointed posterior incisors, canines and anterior premolariforms, premolariforms with a tall central cusp but no accessory cusp, and procumbent *i* ~ *p*₁. It differs from *Gobiconodon* and its close relatives in having more procumbent lower incisors and canines, proportionally larger *i*₁ and smaller *i*₂, lack of diastema between *p*₂ (the last premolariform) and *m*₁, main cusps of molariforms inclined posteriorly, molariform length greater than height, cusp *a* relatively low compared to distinct cusps *b* and *c*, premolariforms reduced, and *m*₁ significantly smaller than *m*₂ ~ *m*₄. It is similar to *Repenomamus* but further differs from *Gobiconodon* in lacking the cingulid on lower molariforms.

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Key words Western Liaoning, Early Cretaceous, Yixian Formation, gobiconodontid

1 Introduction

The Early Cretaceous is a critical period of time in mammalian evolution, during which diverse groups of non-tribosphenic and basal tribosphenic mammals were found in Asia, Europe, North America, and Australia (Fox, 1975; Butler, 1978, 1992; Rougier et al., 2001). These include several groups, such as triconodonts, symmetrodonts, multituberculates, and basal tribosphenic mammals. Triconodonts, which may well be a paraphyletic group (Rougier et al., 1996a; Cifelli et al., 1998; Kielan-Jaworowska and Dashzeveg, 1998; Ji et al., 1999), were carnivorous and/or insectivorous, judging from their tooth pattern, body size and stomach content, that lived from the Jurassic to Late Cretaceous (Owen, 1871; Simpson, 1928, 1929; Kermack, 1963; Patterson, 1956; Slaughter, 1969; Fox, 1969; Bonaparte, 1986, 1992; Rasmussen and Callison, 1981; Krusat, 1989; Zhou et al., 1991; Sigogneau-Russell, 1995; Cifelli et al., 1998; Cifelli and Madsen, 1998; Engelman and Callison, 1998; Heinrich, 1998; Godefroit and Guo, 1999; Ji et al., 1999; Li et al., 2000; Rougier et al., 2001; Hu et al., in press). Similar to other Mesozoic mammals, most triconodonts were small-sized creatures. The largest triconodont species are among gobiconodontids (Trofimov, 1978; Jenkins and Schaff, 1988; Maschenko and Lopatin, 1998; Kielan-Jaworowska and Dashzeveg, 1998), particularly those in the genus *Gobiconodon* (Jenkins and Schaff, 1988; Rougier et al., 2001) and among repenomamids (Li et al., 2000; Wang et al., 2001; Hu et al., in press). Triconodont mammals are represented primarily by dental and fragmentary jaw materials but more complete specimens of cranial and postcranial skeletons have been known of *Gobiconodon ostromi* from North America (Jenkins and Schaff, 1988) and *G. zofiae* (Li et al., 2003), *Jeholodens jenkinsi* (Ji et al., 1999) and *Repenomamus* (Li et al., 2000; Wang et al., 2001; Hu et al., in press) from China.

Here we report yet another new genus and species of triconodonts, *Meemannodon lujiatunensis*, from the Early Cretaceous Yixian Formation at Lujiatun locality, Liaoning. Known from the same site are three species of mammals, *Gobiconodon zofiae* (Li et al., 2003), *Repenomamus robustus* (Li et al., 2000) and a new species of *Repenomamus* (Hu et al., in press). The discovery of the new species increases the diversity of the mammal fauna of the Yixian Formation. Given that several recent studies have provided thorough reviews on the research history, taxonomy, distribution and phylogeny of triconodonts, particularly gobiconodontids (Kielan-Jaworowska and Dashzeveg, 1998; Rougier et al., 2001; Cuenca-Bescós and Canudo, 2003; Li et al., 2003), our report focuses on description of the new taxon and does not attempt a phylogenetic analysis.

2 Methods

We follow Rowe (1987, 1988) for the crown-group concept of Mammalia. Triconodonts, which are taxa traditionally included in the Triconodonta, are used informally because this group of mammals is probably paraphyletic (Rougier et al., 1996a, 1999; Kielan-Jaworowska and Dashzeveg, 1998; Ji et al., 1999). Among triconodonts, Triconodontidae probably is a monophyletic group (Crompton and Jenkins, 1968; Hopson and Crompton, 1969; Jenkins and Crompton, 1979; Rougier et al., 1996a, b; Cifelli et al., 1998; Ji et al., 1999). The nature of other triconodont groups, such as amphilestids, remains uncertain. Amphilestidae (Simpson, 1928; Mills, 1971; Jenkins and Crompton, 1979) was treated as a family that contains the subfamily Gobiconodontinae (Kielan-Jaworowska and Dashzeveg, 1998), but that family was considered to be paraphyletic (Rougier et al., 2001). We here adopt the family Gobiconodontidae as used by Rougier et al. (2001), in which the new genus is included. For terminology of tooth structure we follow previous work (Crompton and Jenkins, 1968; Jenkins and Schaff, 1988; Kielan-Jaworowska

and Dashzeveg, 1998; Rougier et al., 2001). The tooth denotation used in the study does not necessarily imply homology; it only follows the convention and provides convenience for the purpose of description.

3 Systematic paleontology

Class Mammalia

Order Triconodonta Osborn, 1888

Family Gobiconodontidae Chow et Rich, 1984

Genus and species *Meemannodon lujiatunensis* gen. and sp. nov.

(Figs. 1, 2)

Holotype IVPP V 13102, a left lower mandible with complete dentition.

Etymology The generic name is in honor of Dr. Meemann Chang, who has been persistently conducting and promoting researches on the Jehol Biota. The trivial name is after that of the locality, Lujiatun.

Locality and age Lujiatun Village, Beipiao, Liaoning; the basal member of the Yixian Formation; early Cretaceous.

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Diagnosis A large triconodont with similar size of *Gobiconodon rostromi* and *Repenomamus robustus*; differing from other triconodonts but similar to *Gobiconodon* in having enlarged i1, reduction of number of lower incisors to 2, conical and pointed incisors, canines and anterior premolariforms, premolariforms with tall central cusp but no accessory cusp, and procumbent $i \sim p1$; differing from *Gobiconodon* in having more procumbent lower incisors and canines, proportionally larger i1 and smaller i2, lack of diastema between p2 (the last premolariform) and m1, main cusps of molariforms inclined posteriorly, molariform length greater than height, cusp a relatively low compared to distinct cusps b and c, cheek teeth bearing no cingulid, premolariforms reduced, and m1 significantly smaller than $m2 \sim m4$.

Description The specimen represents a young adult in having all teeth fully erupted except for p1 and m5. The dentary was broken anterior to p2; small bone chips were missing at this region so that the two portions of the dentary cannot be fitted together precisely. The dentary is estimated as 92 mm long, 12.4 mm deep and 7.6 mm thick at m3. The anterior portion of the dentary is robust that accommodates an enlarged i1. On the medial side of the mandible the symphysis is large and oblique. Below the molariforms is the large internal groove or meckelian groove. This groove gradually narrows anteriorly and ends below m2; it opens posteriorly to confluent with the pterygoid fossa. The groove is ventrally bounded by a strong ridge that extends posteriorly to the mandibular condyle; thus this ridge also bounds the pterygoid fossa ventrally. The coronoid process is broken. On the lateral side of the mandible, there are at least two mental foramina, one below p2 and the other below m2. The masseteric is broad and deep and is ventrally delimited by a strong ridge that also extends to the condyle. In ventral view, the bottom of the mandible broadens posteriorly and reaches its maximum at the mandibular condyle. The condyle does not have a distinct boundary with the rest part of the mandible. The articular surface of the condyle is restricted and rough. The most part of the condyle is positioned lateral to the plane of the coronoid process and the horizontal ramus. In posterior view, the condyle is oblique, with its medial end being higher than the lateral one. There is no angular process.

The dental formula is $i2 \ c1 \ p2 \ m5$. All teeth show no wear except for slightly polished facets on the lateral surfaces of cusps b and f on m3. The incisors, canine and premolariforms are single rooted. The enlarged i1 is a strong tooth with sharp-pointed tip (see Table 1 for measurements of

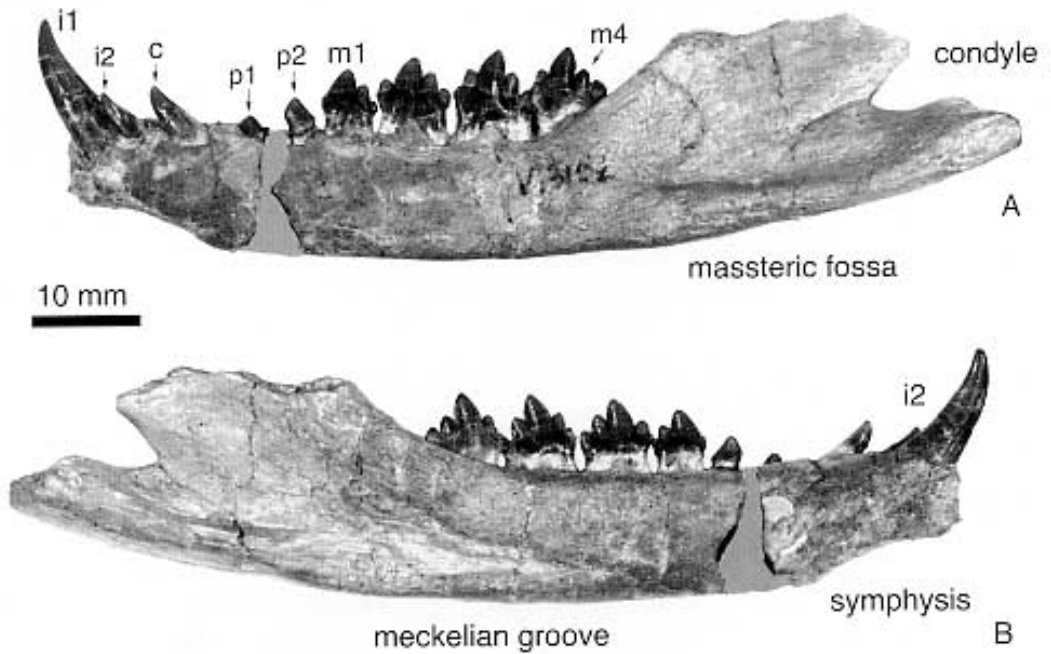


Fig.1 Lateral (A) and medial (B) views of the mandible of *Meemannodon lujiatunensis* gen. et sp. nov. (holotype, IVPP V 13102)
Broken area of the dentary is photographically filled in gray

teeth). It is procumbent and curved. On the medial and lateral surfaces there are weak ridges extending along the tooth from the base to the tip. The small, procumbent tooth on the posterolateral side of i1, separated from the latter by a small gap, is identified as i2 (see below). The tooth crown is ridge-shaped on its anteromedial and posterolateral sides.

The canine is similar to i2 in morphology and orientation but is larger. In contrast to the robust symphysis, the i2 and canine are small and marginally positioned on the jawbone. The diastema between the canine and p1 is the largest on the lower dentition.

Table 1 Measurements of tooth crown

(mm)

| | Length | Width | Height |
|----|----------|-------|--------|
| i1 | 5.53 | 3.78 | 11.66 |
| i2 | 2.39 | 2.06 | 5.22 |
| c | 2.94 | 2.44 | 6.35 |
| p1 | erupting | | |
| p2 | 2.82 | 2.44 | 4.26 |
| m1 | 5.33 | 2.90 | 4.78 |
| m2 | 6.95 | 3.30 | 6.08 |
| m3 | 7.62 | 3.56 | 6.98 |
| m4 | 7.43 | 3.69 | 7.28 |

There are two premolariforms. The p1 is partially erupted. This tooth may also be a successive tooth younger than the erupted p2. The p1 is simple, similar to the canine in shape and size but less procumbent. The p2 is also simple and is the smallest tooth in the lower dentition. It is more vertically positioned and is transversely narrow. In lateral view, p2 is asymmetric in having a short

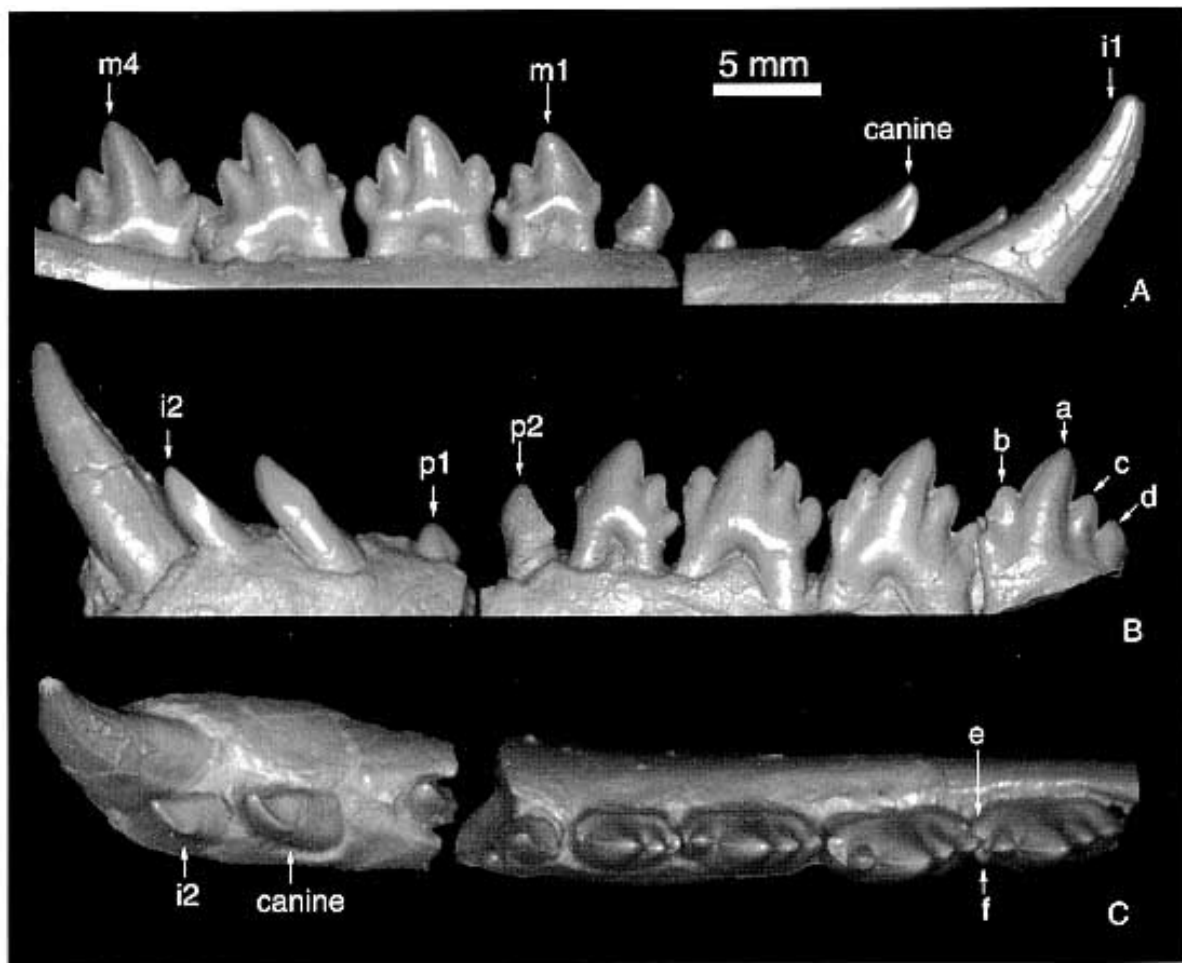


Fig. 2 Medial (A), lateral (B) and occlusal (C) views of the dentition of *Meemannodon lujiatunensis* gen. et sp. nov. (holotype, IVPP V 13102)
Tooth cusps are denoted as a ~ f

anterior crown edge and long posterior edge; the tip of the tooth is more anteriorly positioned. The lateral surface of p2 is convex and the posteromedial surface shows some gentle concavity. There is no accessory cusp.

All molariforms are double-rooted with the posterior root stronger than the anterior one, bear no cingulid, and have the tooth length being greater than the height. Because of the relatively greater length, all cusps appear broad in lateral or medial view. Cusps show a tendency of posterior inclination. Cusp a is the largest of tooth cusps and its tip is slightly anterior to the mid-axis of the tooth in lateral view. On all molariforms, cusps b, c and d are well-developed with cusps c and d being larger than cusp b. In dorsal view, the tooth cusps are aligned in line anteroposteriorly. The edges of the cusps are sharp. For each tooth, the lateral surface is more convex than the medial surface so that the tooth is not bilaterally symmetric in occlusal view. The groove separating any pair of adjacent cusps on a tooth is slightly deeper and longer on the medial side than on the lateral side.

The m1 is significantly smaller than other molariforms. It differs from other molariforms in having only a rudimentary cusp b and no cusps e and f. Cusp d is also proportionally less developed than in other molariforms. The m2 differs from m3 ~ 4 in having poorly developed cusps e and f, although the anterior margin of the tooth is indented for reception of cusp d of m1. In addition, cusp

b is lower than cusp c on m2, whereas the opposite is true for m3 ~ 4. The m3 and m4 are similar in general morphology except that cusps e and f are better developed and preserved on m4. On the anterior end of the tooth these accessory cusps confine a vertical trough that accommodates cusp d of m3. The m4 is located at the anterior base of the coronoid process and its posterior root is not fully exposed. The m5 is within the jaw bone at the anterior base of the coronoid process, cusp a of which is visible in occlusal view. As observed in other triconodonts, the relationship of the last molariform with the coronoid process reflects to some degree the age of the individuals (Rougier et al., 2001). In adult individual, there is usually a space between the anterior base of the coronoid and the last molariform. In young individual, there is no such space and, as in the case of V 13102, the last molariform can be within the base of process.

4 Discussion

Identification of anterior teeth Because only lower dentition is available for *Meemannodon lujiatunensis*, the tooth count is uncertain and has to be based on comparison with those of other taxa, such as *Gobiconodon* and *Repenomamus*. The lower dentition of *Gobiconodon ostromi* was denoted as $1 \cdot 1 \cdot 3 \sim 4 \cdot 5$ (Jenkins and Schaff, 1988), and this dental formula was considered to be common for the genus (Li et al., 2003; note the formula was erroneously printed as $2 \cdot 1 \cdot 3 \sim 4 \cdot 5$ in the English version on page 1132). In extant mammals designations of teeth are based on morphology, ontogeny, and position (Clemens and Lillegraven, 1986; Butler and Clemens, 2001). The benchmark for positional characters is the upper canine, which is defined as the tooth whose alveolus is at or immediately behind the premaxillary-maxillary suture (Butler and Clemens, 2001). The corresponding lower tooth is usually half tooth anterior to its upper counterpart. Because of incomplete preservation of specimens in known species of *Gobiconodon*, the designations of these teeth for published specimens are not conclusive (Trofimov, 1978; Jenkins and Schaff, 1988; Kielan-Jaworowska and Dashzeveg, 1998; Rougier et al., 2001; Li et al., 2003). Although skull material is preserved in *G. zofiae*, the premaxillary-maxillary suture is unclear in the holotype. Therefore, the designations of the non-molariform teeth in *G. zofiae* were tentative and the tooth formula $1 \cdot 1 \cdot 3 \sim 4 \cdot 5$ was adopted. However, the tooth identified as the lower canine appears too anterior in the tooth row of *G. ostromi* and *G. zofiae*.

Better-preserved specimens of *Repenomamus* (Li et al., 2000; Wang et al., 2001; Meng et al., 2003; Hu et al., in press), a genus that is similar to *Gobiconodon*, show clearly the premaxillary-maxillary suture in several well-preserved skulls, which helps to determine the upper canine and thus other non-molariform teeth. In *Repenomamus*, the tooth formula is $3 \cdot 1 \cdot 2 - 3 \cdot 4/2 \cdot 1 \cdot 2 - 3 \cdot 4$ (Hu et al., in press; unpublished material). The i2 of *Repenomamus* is similar to the tooth designated as the lower canine in *G. ostromi* and *G. zofiae*, although in the former the i1 is not enlarged. In light of the dental formula of *Repenomamus*, it is probable that the tooth designated as the lower canine in gobiconodontids is actually the second lower incisor. Therefore, the alternative tooth formula for lower dentition could be $2 \cdot 1 \cdot 2 - 3 \cdot 5$ for gobiconodontids. This emended designation is used here in describing *Meemannodon*. This dental formula is shared by *Gobiconodon*, *Repenomamus* and *Meemannodon*.

Comparison The primary content of Gobiconodontidae is the genus *Gobiconodon*, which contains at least five species, including *G. hoburensis*, *G. borissiaki*, and *G. hopsoni* from Mongolia (Trofimov, 1978; Kielan-Jaworowska and Dashzeveg, 1998; Rougier et al., 2001), *G. zofiae* from Liaoning, China (Li et al., 2003) and *G. ostromi* from North America (Jenkins and Schaff, 1988). Some of the features characterizing *Gobiconodon* in the emended diagnosis for the genus furnished by Rougier et al. (2001: 6) include "large procumbent i1 and correspondingly enlarged I1; reduction of number of incisors to 1 or 2; conic and pointed posterior incisors, canines and anterior premolariforms. Anterior premolariforms (p1 ~ p3) with tall central cusp and crown

height greater than mesiodistal measurement. Accessory cusp on these premolariforms very small to absent. Procumbent $i \sim p1$." All these features are present in V 13102 except for those unknown, such as the I1 condition. In an earlier study, Kielan-Jaworowska and Dashzeveg (1998) included the interlocking mechanism of lower molariforms as another generic diagnostic feature for *Gobiconodon*, in which cusp d of a tooth fits into the embayment between cusps e and f of the succeeding tooth. Because this feature is of "*Kuehneotherium* type", it is probably plesiomorphic. *Meemannodon* has the interlocking structure. Rougier et al. (2001; see also Kielan-Jaworowska and Dashzeveg, 1998; Godefroit and Guo, 1999) also considered replacement of anterior molariform teeth, as seen in *Gobiconodon ostromi*, as another feature for the genus, although they cautioned that this feature may be plesiomorphic and thus not diagnostic. Radiography we did for V 13102 does not provide convincing evidence of molariform replacement. Nonetheless, replacement is not present in known specimens of at least two species of *Gobiconodon*, *G. borissiaki* and *G. hoburensis* (Kielan-Jaworowska and Dashzeveg, 1998).

In addition to morphology, body size of *Meemannodon* is also similar to some species of *Gobiconodon*. The largest known gobiconodontid is *Gobiconodon hopsoni* (Rougier et al., 2001). Because measurements of *G. hopsoni* are known only from M3 ~ 4 (These teeth were originally identified as M4 ~ 5, but we consider them as M3 ~ 4. See Li et al. [2003] for discussion on cheek tooth count in gobiconodontids.), direct size comparison with V 13102 is not possible. *G. hopsoni* is unique in that the estimated length of M4 is greater than that of M3. In other species of the genus, such as *G. zofiae*, *G. borissiaki*, and *G. hoburensis*, the last molariform (M4) is usually shorter than M3. As shown in *G. zofiae*, in which articulated upper and lower dentitions of the same individual are known, M3 is longer than either m3 or m4 that are in occlusion with M3. The M3 of *G. hopsoni* is 5.2 mm long. In contrast, the lengths of m3 ~ 4 of *Meemannodon* are measured 7.43 and 7.62, respectively, which indicate that the new species is probably larger than *G. hopsoni*. This is supported by the fact that the dentary (PSS-MAE139) referred to *G. hopsoni* (Rougier et al., 2001; fig. 2) is shallower than that of the new species. Estimated lengths of the alveolus for m1 of PSS-MAE139 is 3.25 mm, whereas the length is 4.67 for m1 of the new species. The fragmentary specimens of *G. hopsoni* and lack of the upper dentition of the new species prevent further comparison of the two species. *Gobiconodon ostromi* comes second in size to compare with *Meemannodon*. *G. ostromi* is apparently smaller than the new taxon in all teeth, including i1 (Jenkins and Schaff, 1988; table 1). Given the similarities in morphology and size between *Gobiconodon* and *Meemannodon*, we consider the two genera are related more closely than either of them to any other known taxon of triconodonts and therefore place the new genus in the family Gobiconodontidae.

Meemannodon differs from *Gobiconodon* in several aspects. The incisors and canine of *Meemannodon* are more procumbent than those of *Gobiconodon*. More notable is the proportionally larger i1 and smaller i2 in the new taxon. *Meemannodon* has two premolariforms that are proportionally more reduced than those of *Gobiconodon*. Using our assignment of cheek teeth, many specimens of *Gobiconodon* have three premolariforms (Jenkins and Schaff, 1988; Kielan-Jaworowska and Dashzeveg, 1998; Li et al., 2003); some, however, lost p3 (Jenkins and Schaff, 1988). The p3 in *Gobiconodon* is an unusual tooth — it is the smallest tooth, usually has two packed roots, and display more complex crown pattern than premolariforms. The known p3 of *Gobiconodon* is distinctively different from the last premolariform of *Meemannodon*, which we denoted as p2. In fact, the p2 of *Meemannodon* is similar to p2 of *Gobiconodon*. Lost of p3 in *Gobiconodon* usually creates a considerable gap between p2 and m1. In *Meemannodon*, however, p2 and m1 are closely placed. If tooth reduction represents a derived condition in gobiconodontids, then the condition in *Meemannodon* is more derived in that not only p3 is lost, the space between p2 and m1 also disappears. An alternative interpretation is that the last premolariform of *Meemannodon* occupies the homologous locus of p3 of gobiconodontids and that p1 or p2 was lost in *Meemannodon*. If this is the

case, one may expect that the last premolariform in *Meemannodon* and p3 in other gobiconodontids belong to different generation because of their distinctive difference in morphology. In such a case, the last premolariform in *Meemannodon* is more likely from a generation younger than the known p3 in gobiconodontids because p3 in gobiconodontids is more molariform and deeply worn than the molariforms, whereas the last premolariform of *Meemannodon* is simple and bear no wear. However, because p3 lost is a common phenomenon in gobiconodontids and *Repenomamus*, the last premolariform of *Meemannodon* is similar to p2 in gobiconodontids, and there is no evidence of p3 replacement in known specimens of gobiconodontids, we favor the designation of the last premolariform of *Meemannodon* as p2.

Molariform teeth of *Meemannodon* also show significant differences from those of *Gobiconodon*. Cusps of molariforms notably incline posteriorly, in contrasting to more vertically pointed molariforms of *Gobiconodon*. The molariforms of *Meemannodon* are long and relatively low; thus the tooth length is greater than the height. This condition may be attributable to inflation of cusps b, c and d, which are more conspicuous than those of other gobiconodontids. In *Gobiconodon*, however, the molariform is relatively higher and short and cusp a is more dominant. The molariforms of *Meemannodon* bear no cingulid. Development of the cingulid on lower molariforms varies in *Gobiconodon*, but it usually exists. Moreover, m1 of *Meemannodon* is remarkably smaller than m2 ~ m4. Because of these differences we consider V 13102 should not be placed in *Gobiconodon*.

Hangjinia chowi from Nei Mongol (Inner Mongolia) (Godefroit and Guo, 1999) was considered another gobiconodontid characterized by having fewer postcanine teeth but more incisors than *Gobiconodon* (Godefroit and Guo, 1999). As pointed out by Rougier et al. (2001), the tooth counting of *Hangjinia* is questionable and the type specimen may represent a juvenile individual, a view we fully agree with. In addition to the interpretation entertained for *Hangjinia* by Rougier et al. (2001), the dentition of *Hangjinia* could also be interpreted as having two incisors, following the tooth assignment that we use here. The i3 originally identified in *Hangjinia* may well be a canine and the canine is a premolariform, and possibly the only premolariform. The p1 and ?p2 originally identified in *Hangjinia* could be m1 and m2. There are several reasons to believe so. First, in all known specimens of *Gobiconodon* the premolariforms have either a single root or two closely packed roots. The two strong and well-separated roots of "p1" and "?p2" in the mandible of *Hangjinia* are more similar to those of molariforms. Second, in *Gobiconodon* there is usually a space between premolariforms and, in contrast, the molariforms are usually closely packed and separated from the premolariforms by a gap. In the mandible of *Hangjinia*, the "p1", "?p2" and the last two molariforms form a tightly packed tooth row unit, separated from what we think to be the premolariform by a diastema. Thirdly, the premolariforms in *Gobiconodon*, particularly the last one, are small and certainly smaller than the molariforms. As indicated by the alveoli and partial tooth preserved in the mandible of *Hangjinia*, the "p1" and "p2" are as large as, if not larger than, the last two molariforms. Finally, although cusps b, c and d are small on the "p1", as originally described, they do exist. Presence of these accessory cusps makes the tooth more molariform than premolariform. In fact, Rougier et al. (2001) considered this tooth to be molariform and is somewhat similar to the m1 of *G. borissiakii*. Nonetheless, even counting the teeth the way we suggest, the dentition of *Hangjinia* still remains peculiar. This is again because the type specimen of *Hangjinia* is from a juvenile individual. Although the only known specimen of *Hangjinia* clearly differs from those of *Meemannodon*, a meaningful comparison between these forms has to wait for discovery of more complete material of the former.

Klamelia zhaopengi (Chow and Rich, 1984), originally assigned to gobiconodontids, was considered to be *Mammaliaformes incertae sedis* (Rougier et al., 2001). Because of the fragmentary nature of the holotype of *Klamelia*, the tooth assignment remains controversial (Rougier et al., 2001). Broken teeth of *Klamelia* also hamper precise comparison with those of *Meemannodon*. However, the double-rooted premolariform and the distinct cingulid on cheek teeth clearly set the

two genera apart. The sizes of the two genera are beyond comparison.

Amphilestidae (Simpson, 1928; Mills, 1971; Jenkins and Crompton, 1979) was treated as a family that contains the subfamily Gobiconodontinae (Kielan-Jaworowska and Dashzeveg, 1998), but that family was considered to be paraphyletic (Rougier et al., 2001). Taxa typical of the subfamily Amphilestinae, such as *Amphilestes* and *Phascalotherium* (Simpson, 1928), are significantly smaller than *Meemannodon* and are different from the latter in many aspects, such as having more incisors, larger canine, lower cheek teeth that are somewhat symmetric in lateral view, distinct cingulid on molariforms, and smaller tooth cusps.

Repenomamus robustus (Li et al., 2000) is a triconodont that comes from the same locality as does *Meemannodon*. Although *Repenomamus* is undoubtedly a distinctive taxon, its diagnosis in the original description was not precise. This is largely because preparation of the skull was not fully completed when the taxon was proposed. For instance, the lower jaws were not separated from the skull at the time, which prohibited examination of the crown pattern of teeth. Further preparation of the holotype (V 12549) and discovery of additional specimens (e.g., V 12613, Wang et al., 2001) enabled more accurate observations of the dentition of *Repenomamus*. In lower dentition, *Repenomamus* differs from *Gobiconodon* and *Meemannodon* in having i1 not enlarged and molariforms higher and more piecing; cusp a is more inflated. Similar to *Meemannodon* but differing from other *Gobiconodon*, the lower molariforms of *Repenomamus* lack cingulid. Some other features that differ *Meemannodon* from *Gobiconodon* also applicable to distinguish *Meemannodon* from *Repenomamus*, such as posterior inclination of cusps, tooth length being greater than the height and m1 being considerably smaller than m2 ~ m4.

In summary, *Meemannodon* is more similar to *Gobiconodon* than to any other known triconodonts and is therefore placed in the family Gobiconodontidae. However, *Meemannodon* differs from *Gobiconodon* and other related triconodonts in several dental structures, which provides the basis for the proposal of the new genus and species.

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References

- Bonaparte J F, 1986. Sobre *Mesungulatum houssayi* nuevos mamíferos Cretácicos de Patagonia, Argentina. Actas IV Congr Argent Paleont Bioestratigr, 2: 48 ~ 61
- Bonaparte J F, 1992. Una nueva especie de Triconodonta (Mammalia), de la Formación Los Alamitos, provincia de Rio Negro y comentarios sobre su fauna de mamíferos. Ameghiniana, 29: 99 ~ 110
- Butler P M, 1978. A new interpretation of the mammalian teeth of tribosphenic pattern from the Albian of Texas. Breviora, 446: 1 ~ 27
- Butler P M, 1992. Tribosphenic molars in the Cretaceous. In: Smith P, Tchernov E eds. Structure, Function and Evolution of Teeth. Tel Aviv: Freund Publishing House Ltd. 125 ~ 138
- Butler P M, Clemens W A, 2001. Dental morphology of the Jurassic holotherian mammal *Amphitherium*, with a discussion of the evolution of mammalian postcanine dental formulae. Palaeontology, 44: 1 ~ 20
- Chow M, Rich T H V, 1984. A new triconodontan (Mammalia) from the Jurassic of China. J Vert Paleont, 3: 226 ~ 231
- Cifelli R L, Madsen S K, 1998. Triconodont mammals from the medial Cretaceous of Utah. J Vert Paleont, 18: 403 ~ 411
- Cifelli R L, Wible J R, Jenkins F A Jr, 1998. Triconodont mammals from the Cloverly Formation (Lower Cretaceous), Montana and Wyoming. J Vert Paleont, 18: 237 ~ 241

- Clemens W A, Lillegraven J A, 1986. New Late Cretaceous, North American advanced therian mammals that fit neither the marsupial nor eutherian molds. *Contrib Geol Univ Wyo*, **3**: 55 ~ 85
- Crompton A W, Jenkins F A Jr, 1968. Molar occlusion of Late Triassic Mammals. *Biol Rev*, **43**: 427 ~ 458
- Cuenca-Bescós G, Canudo J I, 2003. A new gobiconodontid mammal from the Early Cretaceous of Spain and its palaeogeographic implications. *Acta Palaeont Pol*, **48**: 575 ~ 582
- Engelmann G, Callison G, 1998. Mammalian faunas of the Morrison Formation. *Modern Geol*, **23**: 343 ~ 379
- Fox R C, 1969. Studies of Late Cretaceous vertebrates. III. A triconodont mammal from Alberta. *Can J Zool*, **47**: 1253 ~ 1256
- Fox R C, 1975. Molar structure and function in the Early Cretaceous Mammal *Pappotherium*: Evolutionary implications for Mesozoic Theria. *Can J Earth Sci*, **12**: 412 ~ 442
- Godefroit P, Guo D Y, 1999. A new amphilestid from the Early Cretaceous of Inner Mongolia (P. R. China). *Bull Inst R Sci Nat Belg Sci Terre*, **69**(suppl B): 7 ~ 16
- Heinrich W-D, 1998. Late Jurassic mammals from Tendaguru, Tanzania, East Africa. *J Mamm Evol*, **5**: 269 ~ 290
- Hopson J A, Crompton A W, 1969. Origin of mammals. In: Dobzhansky T, Hecht M K, Steere W C eds. *Evol Biol*, **3**: 16 ~ 72
- Hu Y M, Meng J, Wang Y Q et al. (in press). Large Mesozoic mammals fed on young dinosaurs. *Nature*.
- Jenkins F A Jr, Crompton A W, 1979. Triconodonta. In: Lillegraven J A, Kielan-Jaworowska Z, Clemens W A eds. *Mesozoic Mammals: the First Two-thirds of Mammalian History*. Berkeley: Univ California Press. 74 ~ 90
- Jenkins F A Jr, Schaff C R, 1988. The Early Cretaceous mammal *Gobiconodon* from the Cloverly Formation in Montana. *J Vert Paleont*, **8**: 1 ~ 24
- Ji Q, Luo Z, Ji S A, 1999. A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. *Nature*, **398**: 326 ~ 330
- Kermack K A, 1963. The cranial structure of the triconodonts. *Philos Trans R Soc London, Ser B*, **246**: 83 ~ 103
- Kielan-Jaworowska Z, Dashzeveg D, 1998. Early Cretaceous amphilestid ('triconodont') mammals from Mongolia. *Acta Palaeont Pol*, **43**: 413 ~ 438
- Krusat G, 1989. Isolated molars of a triconodont and a symmetroid (Mammalia) from the uppermost Jurassic of Portugal. *Berl Geowiss Abh, Reihe A*, **106**: 277 ~ 289
- Li C K (李传夔), Wang Y Q (王元青), Hu Y M (胡耀明) et al., 2003. A new species of *Gobiconodon* from the Jehol Biota and its implication to the age of the fauna. *Chinese Sci Bull (科学通报)*, **48**(2): 177 ~ 182 (in Chinese)
- Li J L (李锦玲), Wang Y (王原), Wang Y Q (王元青) et al., 2000. A new family of primitive mammal from the Mesozoic of western Liaoning, China. *Chinese Sci Bull (科学通报)*, **45**(23): 2545 ~ 2549 (in Chinese)
- Maschenko E N, Lopatin A V, 1998. First record of an Early Cretaceous triconodont mammal in Siberia. *Bull Inst R Sci Nat Belg Sci Terre*, **68**: 233 ~ 236
- Meng J, Hu Y M, Wang Y Q et al., 2003. The ossified Meckel's cartilage and internal groove in Mesozoic mammaliaformes: implications to origin of the definitive mammalian middle ear. *Zool J Linn Soc*, **138**: 431 ~ 448
- Mills J R E, 1971. The dentition of *Morganucodon*. In: Kermack D M, Kermack K A eds. *Early mammals*. *Zool J Linn Soc*, **50** (suppl 1): 29 ~ 63
- Owen F R S, 1871. Fossil Mammalia of the Mesozoic Formations. *Palaeontogr Soc Monogr*, **24**: 1 ~ 115
- Patterson B, 1956. Early Cretaceous mammals and the evolution of mammalian molar teeth. *Fieldiana (Geol)*, **13**(1): 1 ~ 105
- Rasmussen T E, Callison G, 1981. A new species of triconodont mammal from the Upper Jurassic of Colorado. *J Paleont*, **55**: 628 ~ 634
- Rougier G W, Isaji S, Manabe M, 1999. An Early Cretaceous Japanese triconodont and a revision of triconodont phylogeny. *J Vert Paleont*, **19**(suppl 3): 72A
- Rougier G W, Novacek M J, McKenna M C et al., 2001. Gobiconodonts from the Early Cretaceous of Oshih (Ashile), Mongolia. *Am Mus Novit*, (3348): 1 ~ 30
- Rougier G W, Wible J R, Hopson J A, 1996a. Basicranial anatomy of *Priacodon fruitaensis* (Triconodontidae, Mammalia) from the Late Jurassic of Colorado, and a reappraisal of mammaliaform interrelationships. *Am Mus Novit*, (3183): 1 ~ 38
- Rougier G W, Wible J R, Novacek M J, 1996b. Middle-ear ossicles of the multituberculate *Kryptobaatar* from the Mongolian Late Cretaceous: implications for mammalian relationships and the evolution of the auditory apparatus. *Am Mus Novit*, (3187): 1 ~ 43
- Rowe T, 1987. Definition and diagnosis in the phylogenetic system. *Syst Zool*, **36**: 208 ~ 211
- Rowe T, 1988. Definition, diagnosis and origin of Mammalia. *J Vert Paleont*, **8**: 241 ~ 264
- Sigogneau-Russell D, 1995. Two possibly aquatic triconodont mammals from the Early Cretaceous of Morocco. *Acta Palaeont Pol*, **40**: 149 ~ 162
- Simpson G G, 1928. A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. London: Trustees of the British Museum. 1 ~ 215
- Simpson G G, 1929. American Mesozoic Mammalia. *Mem Peabody Mus Yale Univ*, **3**: 1 ~ 171
- Slaughter R H, 1969. *Astroconodon*, the Cretaceous triconodont. *J Mamm*, **50**: 102 ~ 117
- Trofimov B A, 1978. The first triconodonts (Mammalia, Triconodonta) from Mongolia. *Dokl Akad Nauk SSSR*, **243**(1): 213 ~ 216 (in Russian)
- Wang Y Q, Hu Y M, Meng J et al., 2001. An ossified Meckel's cartilage in two Cretaceous mammals and origin of the mammalian middle ear. *Science*, **294**: 357 ~ 361
- Zhou M Z (周明镇), Cheng Z W (程政武), Wang Y Q (王元青), 1991. A mammalian lower jaw from the Jurassic of Lingyuan, Liaoning. *Vert Palasiat (古脊椎动物学报)*, **29**(3): 165 ~ 175 (in Chinese with English summary)