

记中国首次发现的“真古兽类” (eupantotherian)化石¹⁾

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摘要:记述了在中国首次发现的采自辽宁黑山县八道壕矿区早白垩世晚期沙海组的一件“eupantotherian”(“真古兽类”)下颌骨化石。标本保存了最后两个前臼齿和4个臼齿,它以抬高的下颌角突,半臼齿化的最后一枚前臼齿,臼齿上面积增大但未发育成完整盆形的跟座,尚未形成的facet-5,及加长的最后臼齿等特点有别于所有已知的“eupantotherian”和具有锥形磨楔式臼齿的*Kielantherium*,被命名为一新属新种,*Mozomus shikamai* gen. et sp. nov. (鹿间明镇古兽),并由它而创建了一新科,*Mozomuridae* fam. nov.

“Eupantotherian”是早期哺乳动物演化中的一个重要环节,是从无跟座的对齿兽(symmetrodont)到具有磨楔式(tribosphenic)臼齿兽类的中间类型。早期兽类进化的成功模式是发育成具有磨楔式的臼齿,即在上臼齿上发育出原尖,而下臼齿的跟座形成由3个齿尖围成的盆状。这种结构扩大了牙齿的面积,使咀嚼切割能力更趋完善,今天的有袋类和真兽类均是如此。但在哺乳动物系统发育史上,“eupantotherian”类的化石发现不多,这给探讨具有磨楔式臼齿构造的两大门类(后兽类和真兽类)的起源带来不少困难和疑惑。而传统上的真古兽类形态分异又很大,并不是一个单系类群。其中有跟座发育较好者,如peramurans有可能更接近具有磨楔式臼齿兽类的基部位置,本文记述的*Mozomus shikamai*也应属于这一类型。具有锥形的被认为处于基干上的磨楔式臼齿类化石,迄今只有两种,即发现在英国早白垩世地层中的滨齿兽(*Aegialodon*)和蒙古早白垩世晚期Höbör层的*Kielantherium*,前者仅有一颗下臼齿,后者由一枚下臼齿和一具有4颗臼齿的下牙床为代表。两种化石在分类上被归入单一的滨齿兽目(Order Aegialodontia Butler, 1978),视为Boreosphenidans的基干(stem)。本文记述的*Mozomus*,其时代与*Kielantherium*的大体相当,在大小、齿式及臼齿形态上与后者也多有相近之处,但前者以其臼齿的facet-5尚未出现和跟盆发育不全等特点表明它较*Kielantherium*更为原始,不具备磨楔式臼齿的模式,因之不能归入Aegialodontia,而只能纳入“eupantotherians”。但在后一类的组合中,*Mozomus*以它半臼齿化的最后前臼齿和面积增大但未发育成盆形的跟座等特点,又是组合中相当进步的类型。无论如何*Mozomus*的发现是在为数极少的向磨楔式臼齿模式进化的中间环节上增添了一件重要的化石标本,也增加了不少新的信息。它必会引起学者对这一进化过程的更加深入的反思和新的启示。

关键词: 辽宁黑山,早白垩世,沙海组,真古兽类,磨楔式

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THE FIRST RECORD OF “EUPANTOTHERIAN” (THERIA, MAMMALIA) FROM THE LATE EARLY CRETACEOUS OF WESTERN LIAONING, CHINA

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Abstract A mammalian lower jaw with the last two premolars and four molars was discovered from the late Early Cretaceous (Aptian-Albian) Shahai Formation in Heishan County, Liaoning Province, China. It represents the first record of “eupantotherian” in China. It is characterized by submolarized last premolar, relatively large but unbasined talonid and lacking facet 5 on molars, enlarged m4 and elevated angular process. A new genus and species, *Mozomus shikamai* gen. et sp. nov., is named based on the specimen. Morphologically, the new taxon is similar to the Mongolian *Kielantherium* of ? Aptian or ? Albian in general (Dashzeveg and Kielan-Jaworowska, 1984), but differs from the latter, probably primitively, in lacking facet 5 on molars. Kielantheriids were regarded as “plesiomorphic in molar structure among mammals with tribosphenic pattern” and possess “a putative phylogenetic position as a stem boreosphenidan” (Luo et al., 2002:11). Reexamination of the specimen of *Kielantherium gobiensis* (GI PST 10-16) brings into question of the shearing facet, and a comparison between *Kielantherium* and *Mozomus* is given in the present paper.

Key words Heishan, Liaoning, Aptian-Albian, Shahai Formation, “eupantotherian”, tribosphenic

In 1947, Tokio Shikama described an Early Cretaceous Eutheria, *Endotherium niinomii*, from Fuxin (formerly as Husin) coal-field, Liaoning, China. Since then, half a century has passed by, and until recently no fieldwork collecting vertebrae fossils was done and no more fossil was collected from that area, even though the *Endotherium* aroused a wide range of interest and controversy among paleomammalists. Since 1994, a team from IVPP has continuously worked in the field of Fuxin area, mainly concentrated on the local coal mines. Since 1998, a group of scientists from Kyoto University visited the sites and joined IVPP colleagues in searching for Cretaceous mammal fossils. A Chinese-Japanese collaborative project was initiated in 2002. As the result of research during the last decade, a lot of important mammalian remains of late Early Cretaceous were collected from two formations: the Shahai Fm (mainly in Badaobao, Heishan county) and the overlying Fuxin Fm (Wang et al., 1995). The material described herein is from the Shahai Formation.

In western Liaoning, there is another well-known vertebrate assemblage, so-called Jehol Biota, which mainly distributed on the southwest side of Fuxin (Fig. 1). Fossils of Jehol Biota come from two formations and can be divided into five vertebrate assemblages (Wang et al., 1998; Zhou et al., 2003). The stratigraphical sequence of early Cretaceous in western Liaoning could be summarized as following (in descending order):

Fuxin Formation; *Endotherium-Teihardosaurus* assemblage

Shahai Formation; *Heishanlestes-Mozomus* (Hu et al., 2005 and this paper)

—— disconformity ——

Jehol Biota (s. s.):

Jiufotang Formation

1. *Cathayornis-Chaoyangia-Lycopteria* assemblage

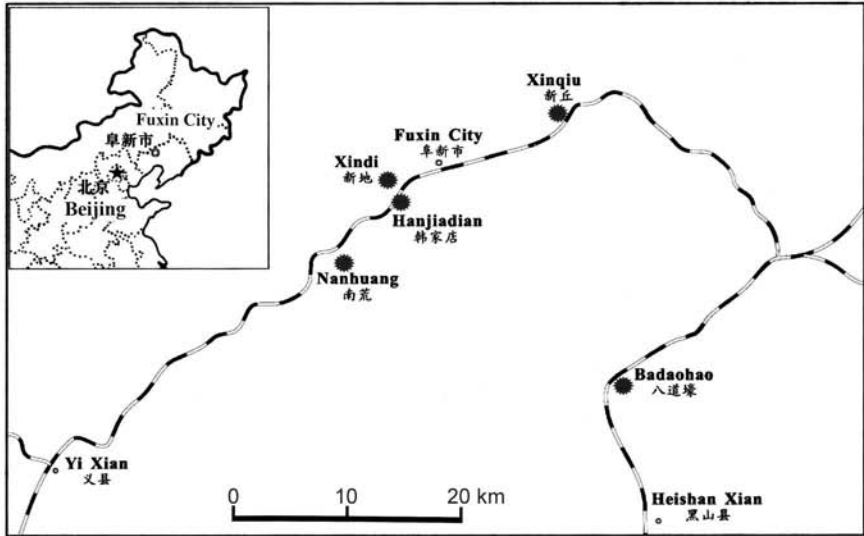


Fig. 1 Main mammalian fossil localities in Fuxin-Heishan area

—— conformity ——

Yixian Formation:

2. Jingangshan beds; *Lycoptera muroii*-*Manchurochelys* assemblage
3. Dawangzhangzi beds; *Lycoptera divide*-*Sinobaatar* assemblage
4. Jianshangou beds; *Sinosauroptryx*-*Zhangheotherium* assemblage
5. Lujiatun beds; *Jeholosaurus*-*Repenomamus* Assemblage

The radiometric date of Jianshangou beds is 125.0 ± 0.19 Ma (Swisher et al., 2002), roughly middle Barremian of Early Cretaceous in age. While the date of Jiufotang Formation is tentatively given as 120.3 ± 0.7 Ma, equal to Aptian age (He et al., 2004). Based on these measurements given above, it would be possible to deduce the Shahai Formation, which yields the specimen described in this paper, as late Aptian-early Albian in age. It might be correlated roughly the Shahai Formation, even including Fuxin Formation, to the Höövör beds of Mongolia. Of course, some different opinions about the age of Shahai and Fuxin formations, mainly considering them as to be earlier than Aptian, were among invertebrate paleontologists and paleobotanists.

1 Systematic paleontology

Class Mammalia

Legion Cladotheria McKenna, 1975

Sublegion Zatheria McKenna, 1975

Family Mozomuridae fam. nov.

Genus *Mozomus* gen. nov.

Type species *Mozomus shikamai* sp. nov.

Included species The type species only.

Diagnosis As for the type species.

Etymology The genus name is derived from the abbreviation of the first name of late

Prof. Ming-zhen Zhou (formerly known as Minchen Chow), in honor of his great contribution to the study of Mesozoic mammals in China.

Mozomus shikamai sp. nov.

(Figs. 2, 3)

Holotype A left lower jaw, with last two premolars and four molars, collected in May, 1994 (IVPP V 7479).

Hypodigm The type specimen only.

Horizon and locality Shapai Formation. Hongshi (red stone) pit of Badaohao coal mine, Heishan County, Liaoning Province, China.

Diagnosis An advanced "eupantotherian" mammal. Dental formula: $?.?.3 + ?.4$. The jaw is deeper than in *Kielantherium*. The angular process elevated near to the level of the dental alveolar line. Last premolar submolarized. Talonids of molars are relatively large, but without a distinct basin. No anterior lingual cuspule appears on the molars. Protoconid is the largest. Paraconid is taller than metaconid and the height increases from m1 to m4. Crista obliqua extends to the metaconid. The shearing facet 1 occupied the most part of metaconid but no facet 5. The m4 is the largest among the cheek teeth series.

Etymology The species name is after late Prof. Tokio Shikama who described *Endotherium niinomii* (the first Mesozoic mammal known in the region).

Description The specimen was preserved in the matrix of coal. Because the bone is too fragile and soft, it is impossible to prepare it completely, especially the talonid of midst molars.

Mandible: The lower jaw originally preserves six cheek teeth *in situ*, with the anterior part and both condylar and coronoid processes missing. The horizontal ramus is deeper than that of *Kielantherium* (2.14 mm height under the posterior root of m1, 2.28 mm below the anterior root of m4). The lower margin of the jaw curved gently at the anterior end and much strongly concaved upward beneath the ascending ramus. On the labial side, a small hole (0.5 mm in diameter) under the anterior part of p3, represents the only preserved mental foramen. On the lingual side of the jaw, the surface of the bone was peeled off, so that all roots of cheek teeth are visible clearly. Each cheek tooth possesses two equal sized roots. A groove inlaid into the lower margin of the jaw appearing from posterior part of m4 and ending anteriorly beneath the talonid of m1 with 4 mm in length, may represents the groove for the Meckel's cartilage as in *Kielantherium* (Dashzeveg and Kielan-Jaworowska, 1984). It is not certain whether there exists the coronoid in our specimen, but a fragmentary bone attached on the jaw at the same place as shown in *Kielantherium* (*ibid*, fig. 1D) suggests such a possibility. The ascending ramus is very large and extends upwards at an almost right angle with the horizontal one. The massesteric fossa is deep and forms an inclined acute triangle shape. The bottom line of the fossa runs posterodorsally along a ridge leading to the mandibular condyle. The anterior line of the fossa projects laterally as a thickened rim and widens down to the base of the fossa. The antero-inferior corner of the fossa forms a deep depression. Unfortunately, due to the poor preservation we could not identify whether or not a labial mandibular foramen, as in *Kielantherium* (Dashzeveg and Kielan-Jaworowska, 1984), is present in our specimen. Judging from the shape of the massesteric fossa, the process of coronoid, although not preserved, may be very high and with a relatively long distance to the condylar process. The condylar process, not preserved either, should be located far backward and at least 4 mm above the occlusal plane of the cheek teeth. A distinctly curved notch leading from the posterior side of the condyle runs down to the angular process. The angular process elevated in a much higher position, which is different from that in Boreosphenidan (Luo et al., 2001, fig. 5). The tip of the angle is missing.

Premolars: As we mentioned in 1995 (Wang et al., 1995, p. 224) the jaw "preserved seven cheek teeth. Because the specimen is very fragile, the anteriormost tooth was damaged

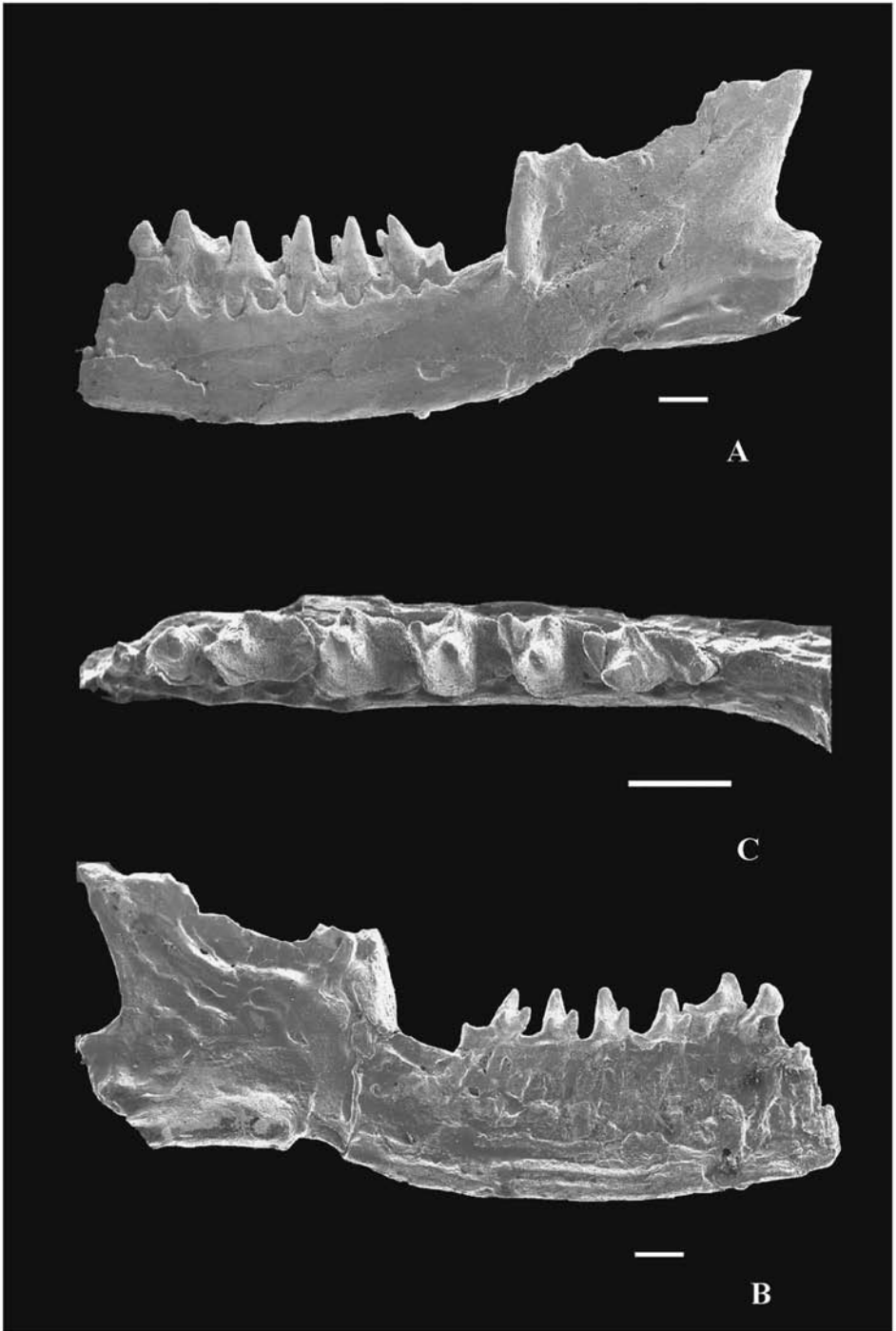


Fig.2 Lateral (A), medial (B) and occlusal (C) views of cheek teeth of *Mozomus shikamai* gen. et sp. nov. (holotype, IVPP V 7479), scale bar = 1 mm

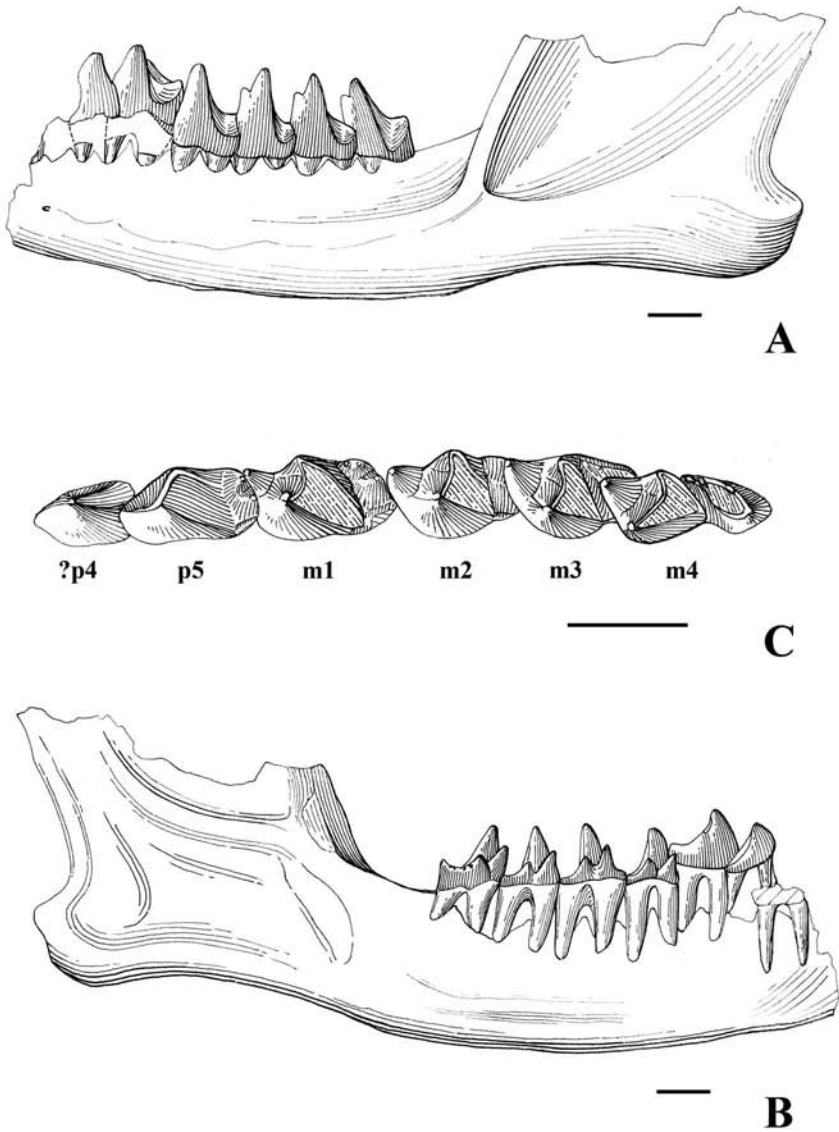


Fig. 3 Diagram (camera drawing): Lateral (A), medial (B) and occlusal (C) views of cheek teeth of *Mozomus shikamai* gen. et sp. nov. (holotype, IVPP V 7479), scale bar = 1 mm

during preparation. It is identical to the following tooth in crown structure but smaller". It means that *Mozomus* possesses at least three premolars. The anteriormost premolar (? p3), although the crown is lost, has two roots still preserved in the jaw bone. The roots are very long and extend straightly downwards to the lower margin of the dentary. In occlusal view, the anterior root is smaller than the posterior one. The tooth is not greatly reduced in size, based on the comparison of its root surface length with that of the subsequent premolar (0.6 mm/0.7 mm). Such a less reduction in size and straightly downward extension of the anterior root, suggest that it has another one (or two) premolar in front of the anteriormost preserved tooth. Having five

premolars is a common situation in *Kielantherium*, *Arguitherium*, etc. The penultimate premolar (? p4) is larger than p3 by the larger distance between their roots. It has a conical main cusp with a prominent ridge projected anteriorly down to the base of the tooth. The main cusp widened downward at its posterior side and derived into two tiny crests. The last premolar (? p5) is the largest one in the premolar series and even larger than m1. It consists of two parts: an incipient trigonid and a heel with twin cusps. The protoconid dominates the trigonid. A very low and unseparated metaconid located on its postero-lingual side of the trigonid. There is no paraconid but a sharp keel extends anteriorly from protoconid to anterior margin of the tooth. Two twin-like cusps budded on the linguo-posterior part of the tooth. A tiny cingulid, lower than the twined cusps, exists on the postero-labial side of the tooth.

Molars: The m1 has a fully developed trigonid and a narrow talonid. The protoconid is the tallest and largest cuspid, inclining lingually and its apex cross the midline of the tooth. The paraconid, interlocked by the heel of p5 on the buccal side, is slightly higher than the metaconid and more lingually placed compared with that of *Kielantherium*. It is separated from the metaconid at the base by a wide furrow, the opening of the trigonid basin. The paracristid, connecting the protoconid and paraconid, intersects with the longitudinal axis of the tooth at an acute angle and has a deep carnassial notch in its middle part as in that of *Deltatheridium*. The metaconid fused with the protoconid at the base and the posterior wall of trigonid forms a steep slope. No mesial cuspid and mesial ridge exist on the anterior side of trigonid as seen in *Aegialodon* (Kermack et al., 1965) and *Kielantherium*. A large facet 1 (Crompton, 1971), located at the posterior surface of protoconid, extends downward to the base of the trigonid and along the upper margin of the cristid obliqua. A quite large continuous surface of facet 1 and no facet 5 probably mean that the paracone of upper tooth has a wider transversal movement when it occludes with the protoconid and also indicate that there is no space for a large protocone, even no protocone developed on the upper molar. The talonid of m1, though damaged, is comparatively large, but narrow and much lower than the trigonid. It is placed slightly oblique to the longitudinal axis of the jaw and with a rhomboid shape. The cusps of the talonid are difficult to identify due to the poor preservation. A short ridge extending antero-lingually to the middle of metacristid indicates the existence of a crista obliqua. The linguo-posterior side of talonid is surrounded by a cluster of three small cusps. The m2 and m3 are same in size and structure. The trigonid of the m2 is similar to that of m1, except the paraconid is higher than the metaconid and is placed slightly buccally. The outline of the m2 talonid is also in rhomboid shape and with a quite large area. There is a longitudinal low crest with two tiny cusps enveloped the lingual side of the talonid. Since no normal cusps appeared, the talonid is not basined and has a plane surface that inclines buccally because the lingual side is higher than the buccal one. In contrast to *Kielantherium*, in which m3 is smaller than m1 and m2, the third molar of *Mozomus* has the same size of m2. The paraconid is distinctly higher than the metaconid. The carnassial notch is wide and the trigonid basin is more opened. The cristid obliqua extends more lingually to the inner side of the tooth, so that there is no space for a true basin and the hypoflexid is deeper than in m2. The m4 is the best preserved molar. Unlike that of *Kielantherium*, the m4 of *Mozomus* is the largest of the cheek teeth. The paraconid, gradually increased in height from m1 to m4, is relatively taller and larger than in the preceding molars, while the metaconid is reduced in size and almost fused with the protoconid in posterior view. The shearing facet 1 on the posterior wall of trigonid is clearer and larger than that on the preceding molars. There is no facet 5 on the posterior wall of the metaconid. The talonid is spindle-shaped and its longitudinal axis is in an acute angle with the tooth axis. The cristid obliqua runs almost to the lingual side of the tooth and the hypoflexid is the deepest and widest. A distinct cusp (probably the hypoconulid) locates at the postero-buccal side of the talonid, and three tiny cusps enveloped the lingual side. So, a small and inclined basin is surrounded by the cristid obliqua, the hypoconulid and lingual cusps.

Measurements See Table 1.

Table 1 Measurements of tooth crown

(mm)

	p3	p4	p5	m1	m2	m3	m4	m1 ~4
Length		0.90	1.30	1.25	1.15	1.15	1.30	4.45
Width	—	0.60	0.80	0.80	0.90	0.90	0.80	—

2 Comparison and discussion

2.1 The characters of *Mozomus*

Based on the description above, we could tentatively analyze the characters of *Mozomus* as following:

- A) Pleisiomorphies; a. the paraconid taller than metaconid;
 - b. talonid of the molars unbasined;
 - c. lacking normal cusps on the talonid;
 - d. lacking shearing facet 5;
- B) Apomorphies; a. the last premolar tends to be molarized;
 - b. the talonid of molars relatively large;
- C) Autapomorphies; a. the last molar enlarged;
 - b. elevated angular process of lower jaw.

Both B) and C) show the nature of the new taxon, which distinguishes it from all known “eupantotherians” and aegialodonts. It probably represents a form primitive than aegialodonts, but more advanced than other “eupantotherians”.

2.2 The systematic position of *Mozomus*

In general, the early mammal evolutionary trend of the molar occlusion leads into the tribosphenic pattern which means extending the lingual space of molar, namely developed a protocone on the upper molar and a complete talonid basin on the lower one, and strengthening the moving of the lower jaw upwards and medially during active occlusion (Crompton, 1971). A typical tribosphenic molar possesses at least six matching shearing surfaces (facet 1 ~ 6) as shown in Metatheria and Eutheria. Among those shearing facets, the existence of facet 5, located at the back wall of the metaconid of the lower molar, indicates the development of a protocone on the upper molar. If a protocone is present on the upper molar, it means that a tribosphenic pattern is developed. Fossil evidence linking non-tribosphenic therians and tribosphenic mammals is very rare. It has been widely accepted that *Aegialodon* and *Keilanthorium* are the most primitive Mesozoic mammals, whose lower molars possess facet 5 and in which the existence of a definitive protocone can be inferred (Kermack et al., 1965; Dashzeveg and Kielan-Jaworowska, 1984). As to *Mozomus*, a quite large talonid on the lower molar, even larger than that of *Aegialodon* and all other non-tribosphenic therians, led us to consider that it should be referred to a taxon that is comparable to the grade of *Aegialodon* and *Kielanthorium*. However, no distinct normal cusps can be identified on the talonid, its more inclined cristid obliqua (deep hypoflexid) giving no space for a large talonid basin and no shearing facet 5 indicate that *Mozomus* is out of the tribe possessing a primitive or basal tribosphenic molars. Consequently, it could be roughly referred to the “eupantotherians”. “Eupantotherians”, as Kielan-Jaworowska et al. (2004, p. 371) pointed out, “represent a very important assemblage of Mesozoic mammal clades that are placed between the plesiomorphic symmetrodontans and the more advanced boreosphenidan mammals with tribosphenic molars. The three main groups, traditionally assigned to ‘eupantotherians’ are peramurids and their kin, amphitheriids, and dryolestoids, in-

cluding paurodontids and dryolestids.” Among these three main groups, both dryolestoids and amphitheriids, characterized by having a very tiny talonid, are obviously different from *Mozomus*. Peramurids was referred to a new Infraclass Permura by McKenna in 1975, together with another new Infraclass Tribosphenida consist of a new Sublegion Zatheria. In 2001, Luo et al. created a new taxon, Boreosphenida, including the Tribosphenida McKenna 1975, for the therian origins on the northern continents during the Mesozoic with tribosphenic molars and split up the Zatheria property into two taxa. In 2004, Kielan-Jaworowska, Cifelli and Luo classified the “eupantotherians” as following:

- Subclass and order *incertae sedis* (“eupantotherians”)
 - Superorder Dryolestoides Butler, 1939
 - Order Dryolestida Prothero, 1981
 - Order Amphitheriida Prothero, 1981
 - Superorder Zatheria McKenna, 1975
 - Stem-lineage Zatheria Martin, 2002
 - “Peramurans” (formerly the order Permura McKenna, 1975)
- Subclass Boreosphenida Luo, Kielan-Jaworowska et Cifelli, 2001

Since this classification is too complicated, we simply follow the classification of McKenna and Bell (1997).

According to Kielan-Jaworowska et al. (2004, p.402), the “peramurans” differ from all other “eupantotherians” by having lower molars with at least incipiently basined talonid, one or two cusps; . . . and in having dental formula of the postcanine teeth P5/5, M3/3. . . Obviously, *Mozomus* differs from “peramurans” (including *Peramus* and its relatives, e. g. *Palaeoxonodon*, *Tendagurutherium*, *Abelodon*, and *Afriquiamus*) not only in having a different dental formula, but also in the talonid structure and the dentary morphology. Three genera, *Arguimus*, *Arguitherium* and *Nanolestes*, and a family, Vincelestidae, were included in the stem-lineage Zatheria Martin, 2002 (Kielan-Jaworowska et al., 2004). *Vincelestes*, the only genus of Vincelestidae, was discovered in Early Cretaceous of Argentina. It is much larger in size and possesses the dental formula as /1.1.2.3, which is quite different from *Mozomus*. *Nanolestes*, collected from the late Jurassic of Portugal, could be distinguished from *Mozomus* by having five molars and a special mesoconid on the cristid obliqua. *Arguitherium* and *Arguimus* were referred to their own families respectively by Dashzeveg (1994). Each of the taxa was represented by only one partial lower jaw, discovered from Höövör Beds of Mongolia. *Arguitherium* preserved three teeth and was identified as p4, p5, and m1 by the author. However Sigogneau-Russell (1999) and Martin (2002) interpreted the monotype as p3, p4, and p5. If they were correct, *Arguitherium* is represented by only premolars and its last premolar (p5) is also molarized. *Mozomus* shares the same size and the molarization of the last premolar with *Arguitherium*, but is quite different on the tooth structure. In *Arguitherium* there is a distinct paraconid on the trigonid and a single cusp (hypoconulid) on the incipient talonid basin (we are not sure that three shearing facets, 1, 3, and 4 appeared on the talonid as shown on fig.4 by Dashzeveg exist or not). Anyway, based on the different structure of p5, it can be concluded that *Arguitherium* represents another lineage and is not closely related to *Mozomus*. The monotype of *Arguimus khosbajari* possesses five teeth, identified by Dashzeveg (1994) as three last premolars and two molars. They were reasonably reinterpreted as two last premolars and three molars by Butler and Clemens (2001). *Arguimus* resembles *Mozomus* in having similar size and possessing a relatively large talonid on molars. However it differs from the latter in the following aspects: 1) the last premolar is smaller and not molarized; 2) three main cusps on the trigonid form an obtuse angle, shaping the trigonid much elongated, and a mesial cuspule exists at the front base of paraconid; 3) hypoflexids is much wide and runs through the anterior part of talonid; and 4) a

large hypoconulid and a tiny entoconid appear on midst lower molars.

To sum up, *Mozomus* is different from all known zathoids obviously. Among these taxa, the Mongolian *Arguimus* may have a shorter disparity to our new taxon. With more materials discovered, the “eupantotherians” of Central Asia might be referred into an independent higher taxa.

2.3 To inquire the feature of *Kielantherium gobiensis* (GI PST 10-16)

In 1975, Dashzeveg erected the new genus and species, *Kielantherium gobiensis*, based only on one lower molar (PST 10-14). The author assigned *Kielantherium* in the Aegialodontidae on the basis of the strong similarity to the lower molar of *Aegialodon* in that “the trigonid (should be talonid. corrected by the present authors) is small and narrow; shearing surfaces 5 and 3 are small; . . .”. As we discussed above, presence of the shearing facet 5 is so important to imply the presence of protocone on the upper molar and thus possesses a tribosphenic structure. However in 1984, another lower jaw of *Kielantherium gobiensis* with four molars *in situ* (PST 10-16) was described by Dashzeveg and Kielan-Jaworowska, in which they did not mention the facet 5, but emphasized that the talonid is basined. Reexamination of the jaw shows no facet 5 preserved. We are not sure whether the facet 5 appears in the type specimen only or absent in both specimens. Nonetheless, a basined talonid developed in *Kielantherium* indicates that it is more derived than our new taxon and it may have an incipient, nonfunctional protocone and with an ambryonic tribosphenic pattern.

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