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新疆东北部晚侏罗世一新的柱齿兽

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摘要：描述了哺乳纲柱齿兽目柱齿兽科（Docodontidae，Docodonta，Mammalia）一新属种——孙氏尖钝齿兽（*Acuodulodon sunae* gen. et sp. nov.）。标本产于新疆东北部准噶尔盆地五彩湾地区上侏罗统牛津阶石树沟组上部（159～161 Ma），为一不完整左下颌骨及齿列。新属下臼齿具柱齿兽类典型特征：齿尖 b 位于齿尖 a 前方；齿尖 c 位于齿尖 a 后舌侧；齿尖 a 前舌侧发育有齿尖 g。不同于其他柱齿兽，新属下臼齿无齿尖 e 和齿脊 b－e。齿尖 g 和齿脊 b－g 很快被磨蚀掉而齿尖 a 和 c 却能保持尖锐状态，表明该动物的臼齿在生活中具备并保持切割和碾压双重功能。基于下臼齿性状特征的系统发育分析表明，柱齿兽目作为一单系类群具有显著的鉴定特征。其中尖钝齿兽和 *Itatodon* +（*Simpsonodon*，*Castorocauda* +（*Tegotherium* + *Sibirotherium*））形成一单系子类群；但 tegotheriids 各分子未形成独立于柱齿兽科的单系类群。尖钝齿兽的下颌齿骨亦为典型的柱齿兽类型。齿骨内侧下部近腹缘有浅的齿后骨槽和宽大的内侧脊，但两者未延伸到下颌关节髁的基柄部。这表明尖钝齿兽的齿后骨与齿骨的连接比摩根齿兽类更为松散，其中耳在进化上更接近真正意义上的哺乳动物中耳。

关键词：新疆，晚侏罗世，柱齿兽目，尖钝齿兽，系统发育

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A NEW LATE JURASSIC DOCODONT (MAMMALIA) FROM NORTHEASTERN XINJIANG, CHINA

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Abstract A new genus and species of docodontid (Docodonta, Mammalia), *Acuodulodon sunae*, represented by a partial left lower jaw and dentition, is described. It is from the upper part of the Shishugou Formation in the Wucaiwan area of the Junggar Basin in northeastern Xinjiang, China, with an estimated age of 159～161 Ma (Oxfordian, early Late Jurassic). The new mammal is typical of docodonts in having a cusp b in front of cusp a, a cusp c distolingual to cusp a and a cusp g mesiolingual to cusp a on lower molariforms. Differing from other docodonts, it has no cusp e or crest b-e developed on lower molariforms. Unique among docodonts, cusps a and c of the new animal maintained their sharpness while cusp g and crest b-g wore away fast, indicating that both shearing and crushing/grinding occurred in the chewing cycle and probably last for most of the life span of the animal. Phylogenetic analysis of a data matrix with 24 lower molariform characters across 15 taxa recovers a

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monophyletic Docodonta, which has distinct diagnostic characters in lower molariforms. Within docodonts, *Docodon* and *Borealestes* are successively basal to other docodonts; *Acuodulodon* and *Itatodon* + (*Simpsonodon*, *Castorocauda* + (*Tegotherium* + *Sibirotherium*)) form a monophyletic clade. Tegotheriid genera are nested within Docodontidae, but a monophyletic tegotheriid clade composed of *Tegotherium*, *Sibirotherium*, *Itatodon*, and *Tashkumyrodon* is not recovered. The dentary of *Acuodulodon* is typical of docodonts. It has a shallow postdentary trough and a wide and sharp medial ridge, both of which do not extend onto the medial side of the condylar peduncle, indicating looser contact between postdentary bones and the dentary than in morganucodontids, a more derived condition in the evolution toward the definitive mammalian middle ear.

Key words Xinjiang, Late Jurassic, Docodonta, *Acuodulodon*, phylogeny

1 Introduction

Docodonts are a group of Mesozoic mammals with a dentition that superficially resembles tribosphenic mammals (Kron, 1979). Docodont molariforms partially retain the cusp-in-line dental pattern of stem mammals, such as morganucodontids and sinoconodontids, but are also transversely expanded to allow a crown-to-crown occlusion. In particular, the upper molariform of docodonts lacks cusp B but develops lingual cusp X and, in some genera, cusp Y, whereas the lower molariform is characterized by a lingually shifted cusp c, a neomorphic cusp g on the mesiolingual side of the tooth, and various crests connecting tooth cusps (Sigogneau-Russell, 2003). Similar to morganucodontids and sinoconodontids, docodonts are plesiomorphic among mammals in retaining the postdentary bones attached to the lower jaws.

While recognizing the mammalian family Docodontidae, Simpson (1929) regarded these mammals as part of the pantothere radiation. Docodonta as a mammalian order was proposed by Kretzoi (1946), but the ordinal diagnosis for the group was first furnished by Patterson (1956: 76) and has become widely accepted since. Patterson also placed *Morganucodon* in the same order, a view not accepted by later authors (Kermack and Mussett, 1958; Simpson, 1961; Hopson and Crompton, 1969; Hopson, 1970; Kron, 1979). Kielan-Jaworowska et al. (2004) proposed docodontans as a conventional name for the high-rank group of docodont mammals. They defined docodontans as a monophyletic group that consists of "the common ancestor of *Docodon*, *Simpsonodon*, and all other Mesozoic mammal taxa more closely related to *Docodon* and *Simpsonodon* than to morganucodontans, *Shuotherium*, and cladotherians". Under this stem-group definition, docodontans are phylogenetically recognizable, but morphologically un-diagnosable. Potentially, there are some or even many docodontan taxa which only partially acquiring the suite of features characterizing the docodonts in traditional usage. In this study, we use both conventional terms docodonts and docodontans, but for different purposes (see below).

The first discovered docodont was *Docodon* from the Upper Jurassic of North America (Marsh, 1881; Simpson, 1929). Since the description of *Docodon*, a handful species of docodonts have been reported from the Middle and Upper Jurassic of Europe and North America (Simpson, 1928, 1929; Kühne and Krusat, 1972; Waldman and Savage, 1972; Freeman, 1979; Kron, 1979; Krusat, 1980). Our knowledge on the morphology, diversity, distribution and biology of docodonts has increased dramatically during the last two decades (Kermack et al., 1987; Lillegraven and Krusat, 1991; Tatarinov, 1994; Martin and Nowotny, 2000; Maschenko et al., 2002; Sigogneau-Russell, 2003; Martin and Averianov, 2004; Lopatin and Averianov, 2005; Martin, 2005; Pfretzschner et al., 2005; Averianov and Lopatin, 2006; Ji et al., 2006). Most of the docodonts described recently are from Asia, where they represent the most diverse mammalian group during the Middle to Late Jurassic. Adding to the list of Asian docodonts we report here another new genus and species from the Upper Jurassic Shishugou Formation in Wucaiwan area of Junggar Basin, Xinjiang, northwestern China.

2 Methods and terminology

We follow Kielan-Jaworowska et al. (2004) in defining Mammalia as a monophyletic taxon containing the latest common ancestor of *Sinoconodon*, *Morganucodon* and extant mammals, and all its descendants. Docodonta, as a mammalian order, is defined as a group containing the latest common ancestor of *Docodon*, *Haldanodon*, *Simpsonodon*, and *Tegotherium* and all of its descendants. We use "docodonts" as the conventional name of Docodonta. We follow Kielan-Jaworowska et al. (2004) in defining docodontans as the stem-group clade (but not a formal taxon) based on Docodonta, including but not necessarily equal to the latter. Two families have been erected for docodont mammals, Docodontidae Simpson, 1929, and Tegotheriidae Tatarinov, 1994. Since most phylogenetic analyses (see below) do not reveal two separate clades corresponding to these two families, we follow Kielan-Jaworowska et al. (2004) to regard Tegotheriidae as the junior synonym of Docodontidae.

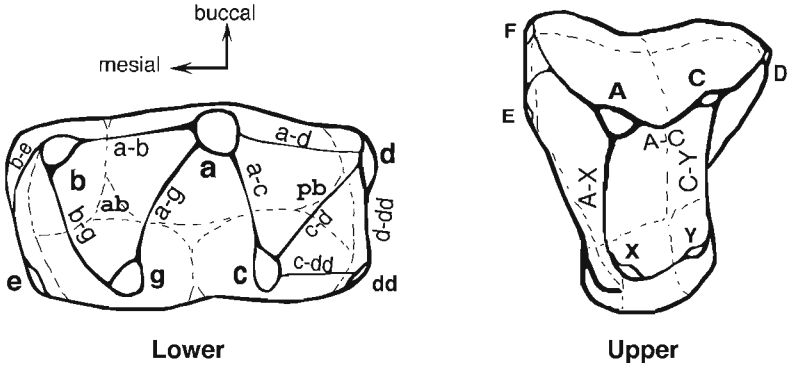

Fig. 1　Terminology for crown structures of docodont molariforms
a, b, c, d, e, g, and dd. cusps of lower tooth; a–b, a–c, c–d, a–g, b–g, a–d, b–e, d–dd, and c–dd. crests of lower tooth; ab and pb. anterior and posterior basin of lower tooth; A, C, D, E, F, X, and Y. cusps of upper tooth; A–C, A–X, and C–Y. crests of upper tooth

Although many authors have attempted to establish homologous relationships of dental structures between docodonts and other mammals (Patterson, 1956; Crompton and Jenkins, 1968; Jenkins, 1969; Krusat, 1973, 1980; Kron, 1979; Butler, 1997), a universally accepted scheme for the dental structures of docodonts is not in place (see Butler, 1997). Some authors therefore prefer a purely descriptive terminology for the dental structures of docodonts in order to avoiding any implied homology with those of other mammals (Kermack et al., 1987; Sigogneau-Russell, 2001, 2003; Kielan-Jaworowska et al., 2004). In this study, we follow Butler (1997) for the terminology of the docodont dental morphology with some modification (Fig. 1). Under such a terminology system, the implied homology between the dental structures of docodonts and other Mesozoic mammals can be further tested with the homology criteria (Patterson, 1982). Such homologization allows comparative study among different groups and can be further incorporated into the phylogenetic analysis (Schuh, 2000). Most recent studies on docodonts indeed followed Butler's terminology. One exception is cusp "f", which Butler (1997) designated the distolingual cingular cusp of lower docodont molariform teeth. However, as Sigogneau-Russell (2003) pointed out, cusp f is the name given to the mesiobuccal cingular cuspule of triconodont and other mammal teeth. Here we designate cusp dd as the distolingual cuspule on the lower molariforms of docodonts and use cusp f to refer to the mesiobuccal cuspule. Maschenko et al. (2002) listed the coordination between Butler's system and descriptive ter-

minology. They also designated cusp ee for what they recognized as a mesiolingual cuspule lingual to cusp e; however cusp e that they recognized on the teeth of those docodonts with "cusp ee" is not a cingular cusp, but a crown cuspule. Since cusp e seen in all other docodonts is a cingular cuspule, here we follow Kielan-Jaworowska et al. (2004) to accept the crown cuspule in these docodonts as one of two cuspules of the bi-cuspidate cusp b, and the cingular cuspule (cusp ee of Maschenko et al.) as cusp e. Below is an modified coordination:

Lower molariform: cusp a = main cusp; cusp b = mesiobuccal cusp (or twin cuspules); cusp c = distolingual cusp; cusp d = distobuccal cingular cuspule; cusp dd = distolingual cingular cuspule; cusp e = mesiolingual cingular cuspule; cusp g = mesiolingual cusp; crests are named after the cusps they connect, such as crests a-b, a-c, c-d, a-g, b-g, a-d, b-e, d-dd, and c-dd, etc.; ab = anterior basin enclosed by cusps a, b and g; sometimes cusp e and/or c also participate in enclosing the anterior basin; pb = posterior basin enclosed by cusps a, c and d; sometimes cusp dd also participates in the basin.

Upper molariform: cusp A = main cusp; cusp C = distobuccal cusp; cusp X = mesiolingual cusp; cusp Y = distolingual cusp; cusp D = distobuccal cingular cuspule; cusp E = mesiolingual cingular cuspule; cusp F = mesiobuccal cingular cuspule; crests are named after the cusps they connect, such as crests A-C, A-X, C-Y, etc.

The phylogenetic analysis of docodontan mammals was performed using PAUP 4.0b10 for Mac (Swofford, 2002) with the parsimony principle assumed. All characters are unordered and equally weighted. The dataset is constructed using Mesquite v. 1.12 (Maddison and Maddison, 2006), and further converted into the final data matrix using MacClade 4.08 for Mac OS X (Maddison and Maddison, 2005).

Photographs of the specimen were taken using a RT SPOT digital camera mounted on a Nikon SMZ-U microscope. The SEM image was taken using a Hitachi S4700 Field Emission Scanning Electron Microscope (FE-SEM) with the specimen uncoated. Linear measurements (Table 1) were taken with a Microcode II digital measuring microscope. Angles of teeth were measured in crown view images using the Measure Tool in Adobe® Photoshop® CS V 8.0 for Mac.

3 Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Docodonta Kretzoi, 1946
Family Docodontidae Simpson, 1929
Acuodulodon gen. nov.

Type species *Acuodulodon sunae* sp. nov.

Etymology *Acuo-* is from *acuere* (Latin): to sharpen; *dulo-* is from *dul* (Middle English): to dull; *-odon* is from *odous* (Greek), tooth. The genus name indicates cusps a and c on lower molariforms of the new taxon maintaining sharpness despite considerable wear while cusp g and crest b-g are deeply worn.

Diagnosis Dental formula as i2 + ?, c1, p3(4), m5(4), similar to other docodonts in that cusp b is in front of cusp a, cusp c distolingual to cusp a and cusp g mesiolingual to cusp a on lower molariforms; cusps a and c trenchant; cusp e vestigial or absent; cusp g similar to c in size; crests a-b and a-c deeply notched, crest a-g absent; anterior basin broad, enclosed by cusps a, b, c and g and crests connecting them; cusps d, dd, and crests c-d, c-dd present; posterior part of the lower molariform relatively short; similar to *Docodon* but differing from all other docodonts in lack of crest b-e; differing from *Tegotherium*, *Sibirotherium*, *Itatodon*, and *Castorocauda* in lack of cusp e and crests a-g and c-dd; differing from *Simpsonodon* in having a small cusp b, a vestigial mesiolingual cingulid, and no crest a-g.

Distribution and age　Junggar Basin in northeastern Xinjiang, China; Oxfordian, Late Jurassic (159 ~ 161 Ma, Clark et al., 2006; Eberth et al., 2001, 2006).

Acuodulodon sunae sp. nov.

(Figs. 2-4; Table 1)

Holotype　A fragmentary left dentary with three premolariforms, roots of the canine, two posterior molariforms, and fragments of two anterior molariforms preserved in situ, which is the only known specimen of the species (Institute of Vertebrate Paleontology and Paleoanthropology catalog number: IVPP V 15332).

Repository　Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing.

Etymology　The trivial name "sunae" honors Professor Ailin Sun from the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China, to recognize her contribution to the study on Chinese Mesozoic mammals.

Diagnosis　As for the genus.

Locality and horizon　Wucaiwan area of Junggar Basin in northeastern Xinjiang, China; the upper part of the Shishugou Formation; Oxfordian, Late Jurassic (159 ~ 161 Ma, Clark et al., 2006; Eberth et al., 2001, 2006).

4　Description

Dentary　The dentary was severely damaged; only its anterior and posterior portions are

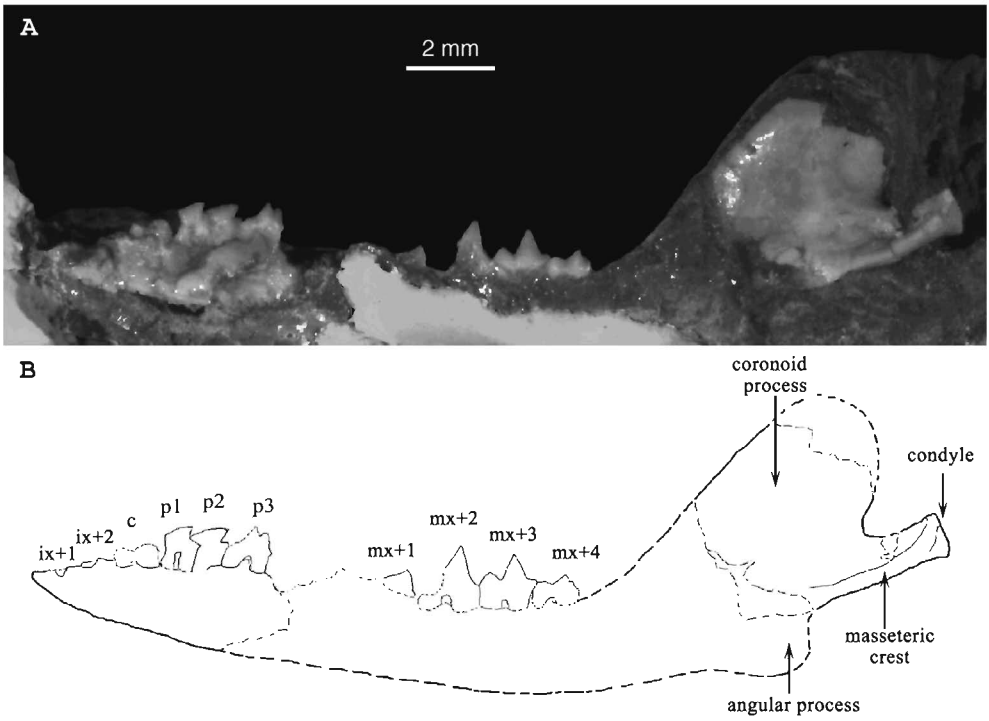

Fig. 2　Buccal view of left dentary and dentition of *Acuodulodon sunae* (holotype, IVPP V 15332)
A. photo; B. line drawing with the shape of the dentary outlined; c. lower canine; ix + 1 and ix + 2, last two lower incisors; mx + 1 to mx + 4, last four lower molariforms; p1 to p3, anterior three lower premolariforms

preserved (Fig. 2). The preserved fragments are likely in their original relationship and allow an estimate of the shape and size of the bone. The dentary is slender and shallow. Its anterior end tapers mesially, and its anterior tip is broken. On the medial surface the symphyseal facet of the dentary has a rough contour near the mesioventral border of the bone, and is slightly medially protruded (the medial view is not figured, but visible in the specimen). This rough surface is shallow and extends distally to underneath the first premolariform. The rest of this area is smooth, suggesting that the meckelian groove, if present, does not extend to the symphyseal region mesially. Due to the severe breakage, there is no mental foramen recognized on the buccal side of the preserved portion.

The coronoid process, although broken, is large and thin (Fig. 3: 1). Its anterior edge is slightly thickened but lacks a distinct external flaring. This edge is obliquely oriented, forming an obtuse angle (about 130°) with the tooth row. The coronoid notch (Fig. 3: 2) between the coronoid process and mandibular condyle is moderately deep.

The mandibular condyle and its peduncle (Fig. 3: 3 and 4) were well preserved, but the peduncle was damaged during preparation so that a sizable breakage was created (Fig. 3). The condyle is supported by the stout peduncle and is well above the level of the tooth row. It expands both laterally and medially beyond the edges of the peduncle (Fig. 3: 7 and 8). The articular facet of the condyle is convex and directed posterodorsally; the arc of the facet is small. A masseteric crest (Fig. 3: 5) begins on the lateral side of the condyle, extends mesioventrally along the peduncle and reduces its thickness mesially. A shallow concavity is above the masseteric crest. The ventral surface of the peduncle is smooth and flat, with its medial border being concave due to the medial expansion of the condyle. The curvature of the ventral border of the dentary changes anterior to the masseteric crest, suggesting the presence of the angular process (Fig. 3: 6).

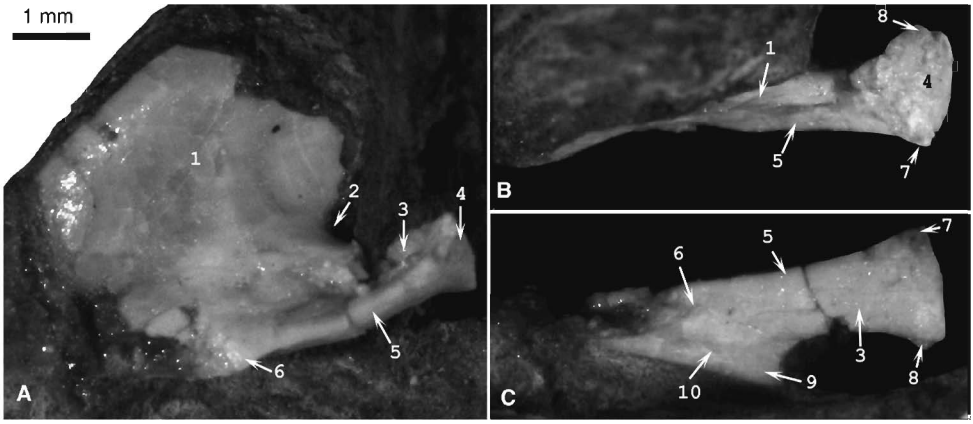

Fig. 3 Posterior part of left dentary of *Acuodulodon sunae*, holotype, IVPP V 15332
A. lateral, B. dorsal, and C. ventral views; 1. coronoid process; 2. coronoid notch; 3. peduncle of condyle; 4. condyle; 5. masseteric crest; 6. base of broken angular process; 7. lateral protruding of condyle; 8. medial protruding of condyle; 9. medial ridge; 10. postdentary trough

A sharp bony ridge projects medially anterior to the condylar peduncle and slightly dorsal to the ventral surface of the dentary (Fig. 3: 9, medial ridge). This ridge starts at a place ventral to the coronoid notch and extends mesially with decreasing height; its mesial extension is unknown. A shallow, concave, and smooth space (Fig. 3: 10) separates the ridge and the ventral border of the dentary and widens anteriorly. This is probably the posterior portion of the postdentary trough.

Table 1　Measurements of *Acuodulodon sunae*, holotype, IVPP V 15332　(mm)

Length of dentary	20.0*
Length of canine	1.0*
Length of p1	0.7
Length of p2	0.8
Length of p3	1.0*
Width of mx+2 at a-c	0.9
Width of mx+3 at pb	0.5
Length of mx+3	1.3
Width of mx+3 at ab	0.7
Width of mx+3 at a-c	0.8
Width of mx+3 at pb	0.5
Length of mx+4	0.8
Width of mx+4 at ab	0.7
Width of mx+4 at a-c	0.5
Width of mx+4 at pb	0.3

* estimated.

Dentition The lower dental formula of *Acuodulodon* is tentatively designated as i2+.c1.p3.m5 or i2+.c1.p4.m4 (Figs. 2 and 4). The anterior portion of the left dentary has two sockets on the alveolar edge of the bone. The sockets are similar in size and slightly procumbent. We interpret these as the alveoli of two posterior, single-rooted incisors. Posterior to the incisor alveoli are roots and a partial crown of a double-rooted tooth that is larger than the one posterior to it. This double-rooted tooth is identified as the lower canine. Three double-rooted premolariforms are preserved and increase in size posteriorly. Four molariform teeth can be recognized. The posterior two molariforms are in good condition whereas the anterior ones are broken. A gap is present between the preserved last premolariform and the anterior molariform. Assuming absence of a diastema between premolariforms and molariforms in *Acuodulodon*, as in other docodonts, the size of the gap indicates that either a premolariform or a molariform is present. Tooth formulae of known docodonts could not lead to an unambiguous conclusion because species of docodonts have either three or four premolariforms. The middle molariforms of docodonts are normally larger than the more anterior or posterior teeth, but the largest one could be either the second or third tooth. Therefore, the lower cheek tooth formula of *Acuodulodon* is either p3m5 or p4m4.

No incisor is preserved. The alveoli of two posterior incisors indicate that the teeth are small, single-rooted, and slightly inclined anteriorly. The broken anterior tip makes it unclear whether any additional incisors were present.

Only a small, posterior portion of the crown of the double-rooted canine is preserved. Judging from the size of the roots, the canine is much larger than its neighboring teeth. The preserved part of the crown shows a crest that probably extends from the main cusp to a posterior cuspule. A fine lingual cingulid extends anteriorly from the cuspule, but there is no buccal cingulid.

Three premolariforms (p1-3) are preserved, but are slightly crushed so that p3 and the bone supporting it are slightly shifted buccally. The p2, the best preserved premolariform, is double-rooted, anteroposteriorly elongated and transversely compressed. The main cusp is primarily supported by the anterior root and posterodorsally inclined; it bears an oblique anterior crest and a nearly steep posterior crest. The anterior crest terminates as a small swelling at the cingular level, whereas the posterior crest ends at a notch that separates the posterior cusp from the main cusp. The posterior cusp also has an anterior and a posterior crest, both of which are oblique. Its posterior crest terminates at a swelling at the end of the tooth on the cingular level. The buccal flanks of both cusps are slightly convex while lingual flanks slightly concave. A fine

lingual cingulid extends from the anterior swelling to the posterior one. The buccal cingulid is absent. The p1 is similar to, but smaller than, p2. The main cusp of p3 is broken; it is also similar to p2 except being larger and having a better developed lingual cingulid.

Only tooth crowns of four molariforms are preserved, in various conditions (Fig. 4). Given the uncertain status of the missing tooth, we designate these molariforms as mx + 1, mx + 2, mx + 3 (penultimate), and mx + 4 (ultimate) (x = 0 or 1), respectively. The mx + 1 preserves only cusp c, while mx + 2 has cusp b broken. The mx + 3 and mx + 4 are complete except that the apex of cusp c was broken on mx + 3. Given their similar morphology and preservation condition, our description focuses on mx + 3 and mx + 4.

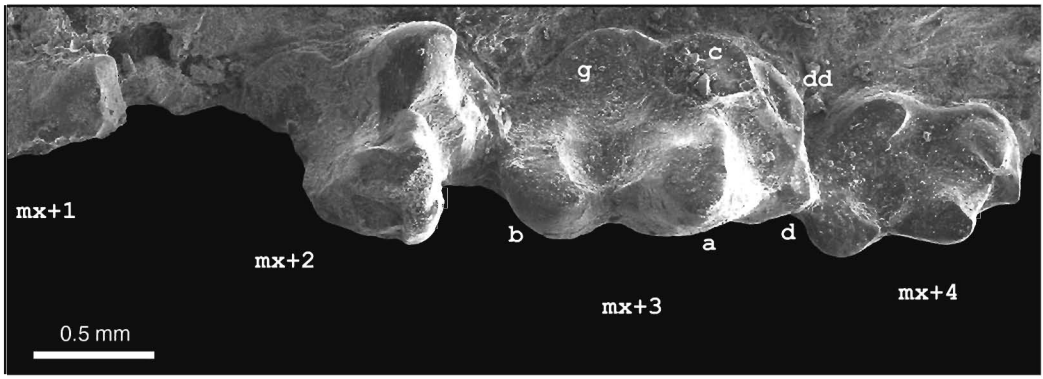

Fig. 4 Crown view of last four left lower molariforms of *Acuodulodon sunae*, holotype, IVPP V 15332 (SEM image) Cusps on the penultimate tooth (mx + 3) are labeled

The crown of mx + 3 is roughly rectangular in crown view, with the anterior part wider than the posterior part. Cusp a is the largest and highest cusp. It is trenchant, with a steep flank. The buccal side of the cusp is convex, while the lingual side is slightly concave. Cusp b is anterior to cusp a in position, and much lower and less trenchant than the latter. Crest a-b has a sharp edge and is deeply notched. Cusp c of mx + 3 is broken at the base, but the cusp is perfectly preserved on the other three molariforms, which allows us to reconstruct its morphology on mx + 3. The cusp is lingual and slightly distal to cusp a in position. It is probably higher than cusp b but lower than cusp a. Assuming that the morphology of cusp c is similar on mx + 2 and mx + 3, cusp c on mx + 3 is probably also trenchant like cusp a and has a steep flank. Crest a–c has sharp edge but is deeply notched. The angle between crest a–b and a–c is about 90°. A stout and steep crest c–d extends distobuccally from cusp c toward cusp d; but it only reaches the flank of cusp d where crest d–dd begins, rather than reaching the apex of cusp d. Cusp g is worn away to the base. Judged by the size of its base, it is probably slightly larger than cusp c on this tooth (but not necessarily higher than the latter). There was probably a stout crest b–g originally, which has been completely worn away leaving a wide wear facet extending from the apex of cusp b to the base of cusp g. A tiny swelling is detectable mesiobuccal to cusp g and lingual to cusp b, which is also worn to its base. The swelling probably represents a vestigial cusp e, but a distinct cusp e is not recognizable, neither is crest b–e. There is no crest g–e, nor crest a–g. The anterior basin (ab) is large, enclosed by cusps a, b, g, and c and crests a–b, b–g, and a–c. The tooth crown posterior to cusp a is much shorter than the part anterior to it. Cusp d is well developed and distal to and much lower than cusp a. It is a small cusp protruding distally. Crest a–d is a fine structure, low and deeply notch. A ridge extends from cusp d and diverges lingually into two crests, of which the first is crest c–d (which has been described above) and the second is the distolingual cingulid, or crest d–dd, that con-

tains cusp dd. Cusp dd is less distally protruding than cusp d. Crest c-d divides the posterior basin (pb, enclosed by cusp a, c, d, and dd, and crest a-c, a-d and d-dd) into a larger buccal and a smaller lingual concavity.

The tooth (mx +3) is worn considerably. The apex of cusp a has a wear facet that extends onto the mesiolingual side of its flank, between crests a-b and a-c, and is steeply oriented. The anterior basin is heavily worn so that only the bases of cusp g and crest b-g remain. The wear facet is continuous, extending to the apex of cusp b, but part of the bottom adjacent to crest a-b bears no wear. On the posterior part of the crown, a wear facet is on the low (posterior) part of crest c-d, the apex of cusp d and crest d-dd; the facet is obliquely oriented and faces distodorsally.

The ultimate molariform (mx +4) is much smaller than the penultimate one. Its morphology is generally similar to the latter, but its posterior part is more reduced than its anterior part. Cusp a is the highest cusp and trenchant. It sends two crests, a-b and a-c; the latter is obliquely oriented (in a mesiobuccal-to-distolingual direction) and at an angle of about 120° to crest a-b. Cusp c is distolingual, rather than nearly lingual, to cusp a, and relatively smaller than that on the penultimate tooth. The posterior flank of cusp c reaches the posterior wall of the tooth. The cusp also sends a fine crest (c-d) toward the distobuccal extremity of the tooth. Cusp d is diminished as the terminal point of crest c-d. There is no recognizable cusp dd. A vestigial distolingual cingulid is visible distal to crest c-d. A lingual cingulid is present on the lingual side of cusp c. It almost goes around the distolingual corner of the tooth, but does not connect the distolingual cingulid mentioned above. Mesially, the lingual cingulid extends to the base of cusp g. Cusp g is worn to the base and the outline of the cusp is still visible. The cusp appears to be obliquely positioned, and longer (in a mesiobuccal-to-distolingual direction) than wide. Cusp b is smaller than cusp a but is relatively larger than the corresponding cusp on the penultimate tooth. The anterior edge of the tooth is smooth. There is no swelling representing a vestigial cusp e. The tooth is also worn to some degree. Cusp a presents a wear facet extending from its apex onto its mesiolingual flank. Cusp g and crest b-g are largely worn away, but to a degree less severe than on the penultimate tooth. The facet extends on to the lingual side of cusp b, but does not reach the very apex of the cusp.

The mx +2 is larger than the penultimate tooth (mx +3). It is probably the largest tooth of the lower dentition. Cusp b, crest b-g and much of the anterior basin of the tooth are missing. The remaining part shows similar morphology to the penultimate tooth, but with some differences in the proportions of corresponding structures. Its anterior part is probably not much wider than the posterior part as cusp g does not protrude more lingually than cusp c. The crown posterior to cusps a and c is relatively narrower (compared to the width at cusp a and c) than the corresponding structure on the penultimate tooth. Cusp c is relatively high, probably higher than cusp b; and cusp a is more buccally protruding than that on penultimate tooth. The tooth is more severely worn than the penultimate tooth. Nevertheless, cusps a and c maintain their sharpness despite considerable wear. Cusp g is completely worn away, and the wear facet covers the entire floor of the anterior basin. Cusp d is also worn and the wear facet on crest c-d approaches the apex of cusp c.

Only cusp c of mx +1 is preserved, which shows that the tooth is probably smaller than mx +2 and is subequal to the penultimate tooth. The wear facet on crest c-d reaches the apex of cusp c, indicating that the tooth is even more severely worn than mx +2.

5 Comparison and discussion

Most docodont mammals are known only from their teeth or dentitions. Their dentitions are unique among mammals and easily recognizable. Diagnostic dental characters of docodonts in-

clude upper molariforms transversely expanded, cusps A and C being mesiodistally aligned and buccally positioned, development of cusp X (and an additional cusp Y in some genera) on lingual side of tooth, a transverse crest connecting the buccal and lingual cusps, lower molariforms having cusp b anterior to cusp a, cusp c shifted to a more lingual position, and development of a mesiolingual cusp g. In addition, the upper and lower teeth are engaged in crown-to-crown occlusion with shearing and, in many genera, crushing functions (Simpson, 1928, 1929; Patterson, 1956; Crompton and Jenkins, 1968; Jenkins, 1969; Gingerich, 1973; Krusat, 1973, 1980; Kron, 1979; Kielan-Jaworowska et al., 2004; Pfretzschner et al., 2005). The dentary of docodonts also retains the postdentary trough and medial ridge. However, differing from more basal mammals such as morganucodontids and sinoconodontids, both structures of docodonts do not extend posteriorly onto the medial side of the mandibular condyle (Simpson, 1929; Krusat, 1973, 1980; Kielan-Jaworowska et al., 2004). *Acuodulodon* so far is only known from one dentary and the associated partial lower dentition. Both show the diagnostic features of docodonts, which justify the assignment of the genus to the order. On the other hand, the lower dentition of *Acuodulodon* displays features different from known docodonts, as discussed below.

The first described docodont was *Docodon* Marsh, 1881 from the upper Jurassic of North America. It has several species that are represented by multiple upper and lower jaws and dentitions (Marsh, 1881; Simpson, 1929). The premolariforms of *Docodon*, similar to those of *Acuodulodon*, are relatively long and narrow and have a posterior cusp and a continuous lingual cingulid. However, the posterior cusp on premolariforms of *Docodon* is small and located on the flank of the main cusp; the cingulid also extends to the buccal side of the tooth; and the main cusp is less compressed than in *Acuodulodon*. On the posterior premolariforms of *Docodon* there is a distinct accessory cusp anterior to the main cusp. Species of *Docodon* have seven or eight lower molariforms, much more than *Acuodulodon* does. The lower molariforms of *Docodon* have characteristic vertical crenelations (ribs or furrows, Jenkins, 1969), which is not seen in other docodonts, including *Acuodulodon*. Molariforms of *Docodon* have high and sharp cusps and crests when erupted, these structures inevitably become blunt in use (Simpson, 1929; Jenkins, 1969; Gingerich, 1973). In addition to their different dental formulae, *Acuodulodon* differs from *Docodon* in that cusps a and c maintain their sharpness after considerable wear while cusp g and crest b–g are easily worn away. In *Docodon*, cusp b is a small cusp located in the anterior flank of cusp a; cusp g is a minor cusp much smaller than cusp c; cusp e, although tiny, is distinct even in posterior teeth; the anterior basin forms a small concavity below the mesiolingual flank of cusp a; the posterior basin is longer and wider than the anterior one, forming a distally opened concavity below the flank of cusps a and c as the distolingual cingulid (crest d–dd) is deeply notched in the middle; there is no crest c–d dividing the posterior basin into two concavities; cusp c sends a crest to cusp dd. In all these aspects the molariforms of *Acuodulodon* are different from those of *Docodon*. One similarity of the two genera is absence of crest a–g on lower molariforms.

Haldanodon has a single species, *H. exspectatus* Kühne & Krusat, 1972, represented by numerous jaws and teeth, some skulls, a partial skeleton, and many isolated skeletal elements from the upper Jurassic Guimarota beds near Leiria, Portugal (Kühne and Krusat, 1972; Krusat, 1973, 1980; Lillegraven and Krusat, 1991; Martin and Nowotny, 2000; Martin, 2005). Its dentition was thoroughly studied by Krusat (1973, 1980). The lower premolariforms of *Haldanodon* are quite similar to those of *Docodon*, and unlike those of *Acuodulodon*, in the roundness of the main cusps, presence of an anterior accessory cusp (on posterior teeth), and development of the buccal cingulid. The cingulid on some premolariforms of *Haldanodon* is wider than those seen in *Docodon* and *Acuodulodon*; the anterior portion of the cingulid on lower premolariforms of *Haldanodon* is particularly wide. The wider cingulid gives the premolariforms of *Hal-*

danodon a more molariform (rectangular) look in crown view than those of *Acuodulodon* and *Docodon*. On the other hand, the premolariforms of *Haldanodon* are similar to those of *Acuodulodon*, and therefore different from those of *Docodon*, in the more posterior location of the posterior cusp. The size of the posterior cusp in *Haldanodon* is between that of *Docodon* and *Acuodulodon*. The lower molariforms of *Haldanodon* are similar to those of *Acuodulodon* in the arrangement of cusps (except cusp e), the separation and relative sizes of cusps b and a, the large size (width and length) of the anterior basin relative to the posterior basin, and the development of crests c-d, a-d and d-dd. But the lower molariforms of *Haldanodon* also have a distinct cusp e, a broad mesiolingual cingulid and a crest a-g; the lower molariforms of *Acuodulodon* do not have these structures. On the lower molariforms of *Haldanodon*, cusps b and c are subequal in height, cusp g is a minor cusp, much smaller than cusps b and c, and crest c-d extends to the apex, rather than the flank, of cusp d. The lower molariforms of *Acuodulodon* are distinctively different from those of *Haldanodon* in these aspects. Cusps a and c on the lower molariforms of *Haldanodon* are also less trenchant than those on the lower molariforms of *Acuodulodon*.

Borealestes has two species, *B. serendipitus* Waldman & Savage, 1972 and *B. mussetti* Sigogneau-Russell, 2003, both from Middle Jurassic Bathonian of Great Britain (Waldman and Savage, 1972; Sigogneau-Russell, 2003). The lower molariforms of *Borealestes* are relatively longer and narrower with a more distally protruding cusp d than those of *Acuodulodon*, as well as those of *Haldanodon* and *Docodon*. The genotype, *B. serendipitus*, has a lower jaw (with most cheek teeth) and several isolated teeth preserved (Waldman and Savage, 1972, Sigogneau-Russell, 2003). Its premolariforms are similar to those of *Docodon* (Sigogneau-Russell, 2003; contrary to Krusat [1980: 51] who suggested great similarity between premolariforms of *Borealestes* and *Haldanodon* but did not indicate it in detail) in their length and narrowness in crown view, which is similar to *Acuodulodon* and different from *Haldanodon*, and in the presence of an anterior accessory cusp on posterior premolariforms, which is different from both *Acuodulodon* and *Haldanodon*. Its lower molariforms are very similar to those of *Haldanodon* in many features (Krusat, 1980; Sigogneau-Russell, 2003), which are either similar to or different from those of *Acuodulodon* as described for *Haldanodon* in the above paragraph. Among the major differences of its lower molariforms from those of *Haldanodon* are the absence of crest a-g and cusp b lower than cusp c. In both of these aspects, *B. serendipitus* is similar to *Acuodulodon*. Sigogneau-Russell (2003) established a second species, *B. mussetti* of the genus based on isolated teeth and tooth fragments. Among the difference of the latter species and the genotype is the presence of crest a-g, which makes the species further different from *Acuodulodon* and more similar to *Haldanodon* than the genotype.

Sigogneau-Russell (2003) also recognized a new genus, *Krusatodon*, with one species, *K. kirtlingtonensis* Sigogneau-Russell, 2003, based on isolated teeth from the upper Bathonian Kirtlington mammal bed in the Forest Marble, England. The lower molariforms of the genus are similar to those of *Acuodulodon* in having a large cusp b well separated from cusp a; subequal and sizable cusps c and g, with the latter more lingually protruding; and a large anterior basin wider and longer than the posterior basin. Cusp b on the lower molariforms of *Krusatodon* is actually larger than cusps c and g; cusp e and crest a-g are well-developed; there are three cuspules (cusps dd, d and a cuspule buccal to d) on the posterior edge of teeth, with cusp d in the middle; and crest c-d connects to the middle of crest a-c rather than the apex of cusp c. In all these aspects, *Krusatodon* is different from *Acuodulodon*.

Another docodont genus from the Kirtlington bed is *Simpsonodon*, having one species, *S. oxfordensis* Kermack et al., 1987, represented by a partial left dentary with three cheek teeth and several isolated molariforms (Kermack et al., 1987). The last lower premolariform of the genus is quite similar to those of *Docodon* and *Borealestes* and therefore different from that of

Acuodulodon in having a distinct anterior accessory cusp and a smaller posterior accessory cusp. The anterior part of its lower molariforms are very similar to, if not identical to, that of the molariforms of *Krusatodon* in the relative position and size of cusps a, b, c, and g, and the development of crests connecting them; and therefore similarly distinguishable from the teeth of *Acuodulodon*. There is no distinct cusp e on the lower molariforms of *Simpsonodon*, but a sizable mesiolingual cingulid is well developed (Kermack et al., 1987). The posterior basin of lower molariforms of *Simpsonodon* is unique among docodonts in having complicated ornamentation with pits and grooves, delimited by a posterior cingulid with cusp d as its terminal end. In this aspect, *Simpsonodon* is distinctly different from all other docodonts, including *Acuodulodon*.

Tegotherium gubini Tatarinov, 1994 is the first docodont from Asia (Tatarinov, 1994, Kielan-Jaworowska et al., 2000), represented by a single lower molariform from the Upper Jurassic of Trans-Altai Gobi, Mongolia. Tatarinov (1994) erected a new mammalian family, Tegotheriidae, for the genus. *Tegotherium* is similar to *Acuodulodon* in having a high cusp a, a large cusp g, presence of crests a–b, b–g, a–c and a–d, and a large anterior basin relative to the posterior basin. However, it is distinctively different from *Acuodulodon* in having a bi-cuspidate cusp b, cusp g higher than cusp b, distinctive cusp e, mesiolingual cingulid and crest a–g, but lacking crest c–d. The bi-cuspidate cusp b is a distinctive feature of *Tegotherium* (Kielan-Jaworowska et al., 2004). Another Asian docodont with this feature is *Sibirotherium* Maschenko et al., 2002 from the Lower Cretaceous of West Siberia (Maschenko et al., 2002). It is very similar to *Tegotherium* and therefore distinctively different from *Acuodulodon*. Maschenko et al. also assigned the genus to the family Tegotheriidae. They distinguished the twin cuspules anterior to cusp a in *Sibirotherium* and *Tegotherium* as cusp b and e, respectively, and further named the mesiolingual cingular cusp as cusp ee. Given that the designated cusp e in all other docodonts and other mammals is a cingular cusp, we choose to follow Kielan-Jaworowska et al. (2004) and identify the twin crown cuspules as a bi-cuspidate cusp and the cingular cusp (cusp ee of Maschenko et al.) as cusp e.

Two additional Asian docodont genera, *Tashkumyrodon* and *Itatodon*, were recently assigned to Tegotheriidae. *Tashkumyrodon* has one species, *T. desideratus* Martin & Averianov, 2004, represented by one left lower molariform from Sarykamyshsai near Tashkumyr in Osh Province, Kyrgyzstan (Martin and Averianov, 2004). This tooth does not have the bi-cuspidate cusp b characterizing abovementioned two "tegotheriid" genera. It resembles that of *Acuodulodon* in having a short posterior basin with cusp d and dd, crest a–d, d–dd and c–d. Crest c–d also extends obliquely as in *Acuodulodon*, but this crest does not extend to the flank of cusp d. There is a crest c–dd on the lower molariform of *T. desideratus*, a feature that is absent in *Acuodulodon*. The tooth of *Tashkumyrodon* has an anterior basin that is narrower than the posterior basin, a small cusp g, well-developed cusp e and crests b–e and e–g, and a crest a–g. In all these aspects, *Tashkumyrodon* is distinctively different from *Acuodulodon*.

Itatodon has one species, *I. tatarinovi* Lopatin & Averianov, 2005, represented by isolated right lower molariforms from the Bathonian Itat Formation at Krasnoyarsk Krai, Sharypovskii raion in Siberia of Russia (Lopatin and Averianov, 2005; Averianov and Lopatin, 2006). Its lower molariforms do not have a bi-cuspidate cusp b. It is similar to *Acuodulodon* in having an anterior basin that is larger than the posterior one. In *Itatodon*, however, cusp g is larger than cusp b; and crest a–g is well-developed. *Itatodon* also has a distinct cusp e and crest e–g. These differentiate *Itatodon* from *Acuodulodon*.

Pfretzschner et al. (2005) reported a new docodont, *Dsungarodon* Pfretzschner & Martin, 2005, with one species, *D. zuoi*, represented by isolated teeth from Oxfordian Qigu Formation of Liuhuanggou near Urumqi, Xinjiang, China, which is the first docodont found from China (Martin and Pfretzschner, 2003). The only known lower premolariform of the taxon is most similar to the posterior premolariforms of *Docodon* and *Borealestes* and therefore different from

those of *Acuodulodon* in the small size of the posterior cusp and presence of the buccal cingulid. The holotype of the genotype (SGP 21) is a lower molariform. It is similar to those of *Acuodulodon* in having a short posterior basin with cusps d and dd, and crests a–c, c–d and a–d. The difference between the two genera in this part of the lower molariforms is that the tooth of *Dsungarodon* has a second crest from cusp a toward but not reaching the base of cusp c, unique in docodonts, *Acuodulodon* included. Cusp dd in *Dsungarodon* is also much smaller than that in *Acuodulodon*. The anterior part of that lower molariform of *Dsungarodon* has a long but relatively narrow anterior basin; cusp g is smaller than c; and crest a–g is well developed. The tooth also has a crest b–e, which defines a straight valley anterior to crest b–g. In these aspects *Dsungarodon* is different from *Acuodulodon*; and its oblique crest b–e without cusp e and the straight valley between crest b–g and b–e are unique among docodonts. A second lower tooth (SGP 22) is attributed to *D. zuoi* as a right ultimate lower molariform. It is similar to the ultimate tooth of *Acuodulodon* and other docodonts in having the distal part of the crown reduced.

The second Chinese docodont is *Castorocauda lutrasimilis* Ji et al., 2006, known from an incomplete skeleton from Daohugou beds in Ningcheng County, Nei Mongol, northeastern China (Ji et al., 2006). The age of the beds is in dispute, which ranges from the Middle Jurassic to Early Cretaceous (Wang et al., 2005). Among six preserved check teeth of the holotype (JZMP05–117), two anteriormost teeth were originally recognized as the first two molariforms, but their blade-like shape with cusps mesiodistally aligned makes them more like premolariforms than molariforms of other docodonts. Nevertheless, even if these teeth are indeed premolariforms, they are unique among premolariforms of docodonts in having two accessory cusps anterior and posterior to the main cusp, respectively. The molariforms (m3–6 in original description) are similar to those of *Acuodulodon* in having the anterior basin larger than the posterior one, cusp b well separated from cusp a, and cusp c much higher than cusp b. They are different from those of *Acuodulodon* in having cusp e, crests a–g and b–e, and lacking crest c–d. In addition, *Castorocauda* is much larger than *Acuodulodon*.

Several other Mesozoic mammals acquire some docodont-like dental features. *Cyrtlatherium canei* Freeman, 1979 and *Peraiocynodon major* Sigogneau-Russell, 2003 are from Kirtlington mammal bed in Oxfordshire, England (Simpson, 1928; Freeman, 1979; Sigogneau-Russell, 2001, 2003). The genotype of the latter genus, *P. inexpectatus* Simpson, 1928, is from Berriasian Purbeck Limestone in England (Simpson, 1928; Sigogneau-Russell, 2003). Prasad and Manhas (2001) reported an unnamed lower tooth from Lower/Middle Jurassic Kota Formation of India. The status and/or affinity of these mammals are still controversial (Butler, 1939; Freeman, 1979; Krusat, 1980; Sigogneau-Russell, 2003; Kielan-Jaworowska et al., 2004). They are all different from all docodonts, including *Acuodulodon*, in lacking cusp g and anterior basin. If the order Docodonta is defined as the monophyletic group mentioned above, presence of cusp g should be one of the synapomorphies and diagnostic features for the group. Therefore, these mammals are not docodonts *sensu stricto*. Some, if not all, of them probably represent non-docodont docodontans that have developed only partial docodont features; these shared features might suggest that they are phylogenetically closer to docodonts than to other mammals.

To sum up, *Acuodulodon* possesses diagnostic features of the dentary and lower teeth of Docodonta and bears features distinct from other docodonts; therefore, we recognize it as a new docodont genus. A unique feature of the new genus is that cusps a and c maintained their sharpness as only one side of their flanks contacted the upper teeth while cusp g was considerably worn and probably wore away fast in life. This wear pattern indicates that both shearing and crushing/grinding occurred in the chewing cycle and probably persisted for most of the life span of the animal. The progression of wear on the teeth of *Acuodulodon* seems different from two other docodonts in which the wear pattern has been well studied. Teeth of *Docodon* had multiple wear facets, which largely kept their individuality as wear proceeded (Jenkins, 1969; Gingerich,

1973). Oblique orientations of these wear facets and well-developed ribs and furrows on the tooth crown indicate that sharing between ridges of upper and lower teeth is the main function of molariforms. On the other hand, teeth of *Haldanodon* showed both shearing and crushing components because obliquely and horizontally oriented wear facets coexist, but in old individual, all cusps and ridges were worn away and the shearing component was probably lost (Krusat, 1980).

Phylogenetic analyses of docodonts based on dental characters were performed in several previous studies. Sigogneau-Russell (2003) presented a manual phylogenetic analysis for eight docodont genera, whereas Martin and Averianov (2004) conducted the first computer assisted phylogenetic analysis, for seven genera based on seven lower molariform characters (using *Woutersia* as outgroup). They recovered two clades of docodonts, an Asian clade and a Euroamerican clade. In a follow-up study with a similar dataset, which includes two additional genera and one additional state for one character, Pfretzschner et al. (2005) presented a significantly different tree topology in which the geographical clusters of docodonts in the previous study failed to hold. However, Pfretzschner et al. repeatedly assigned two synapomorphic characters (reduction of crest c–d, cusps c and g of equal size) to two successive internodes and omitted one character (reduction of crest c–d) in their data matrix, which may significantly altered the tree topology given that only a few characters are involved in the analysis.

Ji et al. (2006) performed another phylogenetic analysis on the interrelationships of docodonts. Interestingly, the authors presented only one cladogram (tree length = 49 steps; methods: Branch-and-bound search with 'MulTrees' option not in effect) displaying a dichotomous topology of docodonts in their study. Our reanalysis of their original data matrix showed that this cladogram is but one of 23 equally most parsimonious trees (tree length = 49 steps; methods: Branch-and-bound search with 'MulTrees' option in effect) generated from the dataset using PAUP (Ji et al., 2006: supporting online material); the strict consensus of these trees displays a much poorer resolution of the docodont relationship than the one presented in the paper.

Averianov and Lopatin (2006) presented the latest phylogenetic analysis of docodonts, employing 29 upper and lower dental characters across 16 taxa. The analysis generated three equally most parsimonious trees. Their strict consensus is a well-resolved cladogram in which *Haldanodon* and *Docodon* were basal within the monophyletic docodont clade and a monophyletic tegotheriid clade, composed of *Tashkumyrodon*, *Itatodon*, *Tegotherium*, and *Sibirotherium*, was recovered. However, there are also some problems in character designation and coding of this study. For instance, character 3 (absence [0] vs. presence [1] in triangular arrangement of main cusps of upper molars) was designed for relative positions of cusps on upper molariforms; "presence" was coded for docodont taxa that have upper molars preserved, *Woutersia* and *Megazostrodon*, while "absence" was coded for *Sinoconodon*, *Morganucodon* and *Dinnetherium*. However, the triangular pattern of docodont taxa is due to the development of neomorphic lingual cusps (X, Y), and the absence vs. presence of these cusps, which implied the triangular pattern of upper tooth cusps (ch. 3), were dealt with in other characters (6 and 8). The coding of character 7 (absence vs. presence of the wear facet on the labial side of cusp X) is also problematic. It was coded as "absence" for *Woutersia*, but character 6 (absence vs. presence of the cusp) was coded as "uncertain" for the same taxon. The wear facet character (ch. 7) was coded as "absent" rather than unknown for *Sinoconodon*, *Morganucodon*, *Dinnetherium*, and *Megazostrodon*, which is redundant because in character 6 these taxa were coded as lacking this cusp. Several other characters (character 22: absence vs. presence of crest a–g; character 24: absence vs. presence of crest b–g) have similar problem. Codings of several other characters (1, 3, 4, 11, 13, 18, 26, and 29) for some taxa are also disputable. These potential problematic character codings cast doubt on the resultant cladogram of docodont relationships.

In this study a new phylogenetic analysis of docodonts is performed. Only lower molariform characters are employed because the new specimen has only the lower teeth preserved, as in most docodont taxa known to date. Isolated upper molariforms have been referred to several docodonts (*Borealestes serendipitus*, *B. mussetti*, *Dsungarodon*, *Krusatodon*, and *Simpsonodon*). However, all theses referrals are tentative, and most of them are ambiguous. Without further confirmation, we prefer not to include upper tooth characters in the phylogenetic analysis. The data matrix is composed of 24 characters across 15 taxa (14 docodontans plus *Morganucodon* as the outgroup; see Table 2 for the data matrix and Appendix I for the character list). The status of *Peraiocynodon* Simpson, 1928 is still in controversy. Some authors (Butler, 1939; Averianov, 2004) believed that the dental specimens the genus based on may represent deciduous teeth and the genus is invalid. However, other students (Krusat, 1980; Sigogneau-Russell, 2003) interpreted that the specimens contain permanent cheek teeth and the genus represents a valid taxon. Here we tentatively accept the latter opinion and regard it as a valid docodontan genus. Phylogenetic analysis of the data matrix using PAUP generates seven most parsimonious trees (tree length = 48 steps; CI = 0.542; HI = 0.607). The strict consensus tree (tree length = 53 steps; CI = 0.491; HI = 0.518) is illustrated in Fig. 5; and the apomorphic characters for each internode and changes of each character on the strict consensus tress are listed in Appendix II.

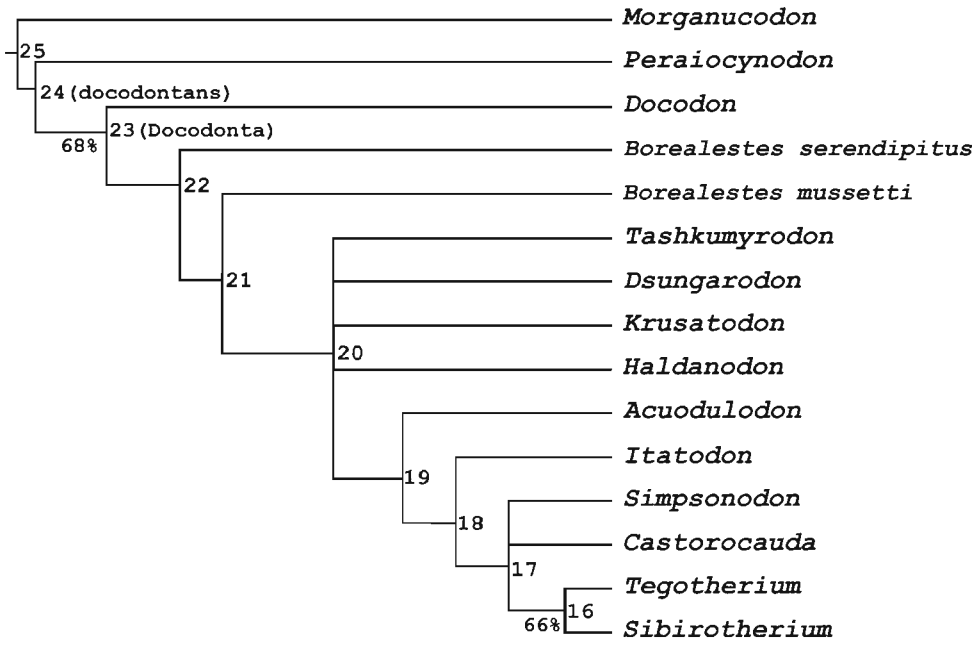

Fig. 5　Phylogenetic relationships of docodont mammals

The cladogram is the strict consensus tree (length = 53; consistency index [CI] = 0.491; homoplasy index [HI] = 0.518) of seven most parsimonious trees (tree length = 48; consistency index [CI] = 0.542; homoplasy index [HI] = 0.607) from the dataset with 24 characters cross 15 taxa (Table 2 and Appendix I); all characters are unordered and equally weighted; the strict consensus tree is rooted; heuristic search with 1000 replicates and branch-and-bound search recover identical most parsimonious trees; bootstrap values higher than 50% are indicated; the apomorphies for internodes and changes of each character are listed in Appendix II

Table 2 Data matrix

Character										1	1	1	1	1	1	1	1	1	1	2	2	2	2	2
Taxon	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4
Morganucodon	0	0	0	0	0	?	0	0	0	?	?	?	0	0	0	0	0	0	?	0	?	0	0	0
Peraiocynodon	1	0	0	0	0	?	1	0	1	?	?	?	0	1	1	0	0	0	?	1	1	1	0	0
Docodon	1	0	0	0	1	0	1	0	2	0	?	1	0	1	1	1	0	1	0	1	1	1	1	1
Borealestes serendipitus	1	1	1	0	1	0	1	0	2	0	?	1	0	0	0	0	1	1	0	1	1	1	0	0
Borealestes mussetti	1	1	0	0	1	0	1	0	2	1	0	1	0	1	0	0	1	1	0	1	1	1	0	0
Haldanodon	1	1	0	0	1	0	1	0	2	1	0	1	0	1	0	0	1	1	1	1	0	1	1	1
Krusatodon	1	1	1	0	1	1	1	0	2	1	1	1	0	1	0	0	1	2	1	1	0	1	0	1
Simpsonodon	1	1	1	0	1	1	1	1	2	1	1	1	1	1	1	0	1	2	1	1	0	1	1	1
Tegotherium	1	1	0	1	1	1	1	0	2	1	1	1	1	1	1	0	0	2	1	1	0	1	1	1
Sibirotherium	1	1	0	1	1	1	1	0	2	1	1	1	1	1	1	0	0	2	1	1	0	1	1	1
Itatodon	1	1	0	0	1	1	1	0	1	1	1	0	0	0	1	0	0	2	1	1	0	1	1	0
Tashkumyrodon	1	1	0	0	1	?	1	0	2	1	1	1	0	1	1	0	1	2	0	1	1	1	0	1
Castorocauda	1	1	0	0	1	0	1	0	2	1	1	1	1	1	1	0	0	2	1	1	0	1	1	1
Dsungarodon	1	1	0	0	1	1	1	1	2	1	1	1	0	1	0	0	0	2	0	1	1	1	0	1
Acuodulodon	1	1	0	0	1	1	1	1	2	0	?	1	0	1	0	1	0	2	1	1	0	1	1	1

A monophyletic Docodonta (node 23) is recovered. Its unambiguous synapomorphies include development of cusp g, present of the anterior basin as a concavity or pseudotalonid, and a more transversely than anteroposteriorly oriented crest c. A non-docodont docodontan taxon, *Peraiocynodon*, forms the sister group of Docodonta. It lacks diagnostic features of Docodonta mentioned above. Among shared features of *Peraiocynodon* and Docodonta are the lingual shift of cusp c and presence of cusp dd, distal basin and distal cingulid. Within Docodonta, *Docodon* and *Borealestes* are basal to other taxa. *Docodon* is the sister group to the rest of docodonts; it lacks the deep notch separating cusp b from cusp a. Despite its basal position within Docodonta, *Docodon* has its own autapomophies (not included in the data matrix), such as very sharp transverse crests connecting lingual and buccal cusps, steep slopes of main cusps, and unique crenelations (ribs and furrows) on the occlusal surface of molariforms. Two *Borealestes* species form the next successive outgroups of a monophyletic clade composed of other docodonts (node 20). A monophyletic tegotheriid clade as recognized by previous authors is not recovered, only two of them, *Tegotherium* and *Sibirotherium*, are close to each other, sharing a bi-cuspidate cusp b. *Simpsonodon* and *Castorocauda* are closer to *Tegotherium* + *Sibirotherium* than another tegotheriid, *Itatodon*. *Acuodulodon* is the sister of the monophyletic group composed of these five genera. The apomorphies of the clade are a narrow mesiolingual cingulid and a non-protruding mesiolingual corner on lower molariforms. The fourth tegotheriid, *Tashkumyrodon*, forms a cluster with *Haldanodon*, *Krusatodon*, *Dsungarodon*, and *Acuodulodon* + (*Itatodon*, *Simpsonodon*, *Castorocauda*, *Tegotherium*, and *Sibirotherium*).

Overall, the interrelationships of docodonts are only partially resolved using the lower tooth characters. As listed in Appendix II, the characters at most internodes within the docodont clade have a low consistency index, which indicates pervasive homoplasy in the dentition of docodonts. Our analysis also reveals that there are numerous suboptimal trees (branch-and-bound search recovers 329 trees with 49 steps, 5095 trees with 50 steps, 53538 trees with 51 steps). The bootstrap value is low for most groups; only two nodes (16 and 23) have the value higher than 50%. These suggest that the interrelationships among docodonts as revealed by lower tooth characters are far from being stable.

The distribution of wear facets on the dentition of IVPP V 15332 also indicates the eruption sequence of different teeth. The molariforms are moderately worn but the premolariforms are only slightly worn and have no distinct wear facet. The obvious discrepancy of the wear between the premolariform and molariform regions indicates that on this specimen the preserved premo-

lariforms most likely erupted later than the molariforms. In extant therian mammals, the premolar teeth erupt earlier than the molar teeth of the same generation during the ontogeny (Luckett, 1993). If the same principle can be applied to docodonts, the premolariforms on IVPP V 15332 must be replacement teeth and one generation younger than the molariforms regardless of whether the molariforms have been replaced. Among molariforms, the degree of wear decreases from front to back, which is best demonstrated on cusp c. Such a pattern is consistent with the position of the teeth, the anterior molariforms are in the middle of the dentary and play a more important role in chewing and suffer more wear. The wear pattern also suggests that the molariforms were added in a mesial-to-distal order, as seen in extant therians.

The wear facets on the lower molariforms also provide some clue about the morphology of the upper molariforms. The wear facets on the posterior basin are continuous from the distal flank of cusp c, through the ridge of crest c-d, and to crest c-dd. All these facets are in the same plane, which is more vertically than horizontally oriented. These facets are most likely the result of sequential contact with the same structure on the upper tooth, a strong crest A-X, which forms the anterior edge of the upper tooth. The major wear facet in the anterior basin extends lingually from the apex of cusp b, through crest b-g, and onto cusp g. This is probably resulted from occlusion with a well-developed cusp X. The third facet is on the mesiolingual flank of cusp a, which resulted from contact with the distal margin of the upper tooth. It is unclear whether there is an additional lingual cusp, cusp Y, distal to cusp X. If the cusp does exist, it is probably a small cusp and there is no wear on the anterior flank of cusp c of any preserved lower molariform.

The dentary of *Acuodulodon* is typical of docodonts. The mandibular condyle of the dentary expands medially; the postdentary trough and associated medial ridge do not extend onto the peduncle of the condyle; and the medial ridge is large, as in *Docodon* and *Haldanodon* in which this part of mandible is known (Simpson, 1929; Krusat, 1973, 1980; Lillegraven and Krusat, 1991). The morphology of the medial aspect of the dentary in these docodonts indicates that the articular complex, if it is indeed still attached to the dentary, must have its posterior part separated from the dentary. This differs from the condition in *Morganucodon*, in which the articular complex attaches to the dentary, including the condyle (Kermack et al., 1973). Lillegraven and Krusat (1991) reconstructed the articular complex of *Haldanodon* as medioventral to the condyle. Ji et al. (2006) suggested that in *Castorocauda* the angular is located in the concavity on the posterior aspect of the angular process of the dentary. Whether these reconstructions prove to be correct, it is certain that the postdentary bones are more loosely attached to the dentary in docodonts than in morganucodontids, which represents a more derived condition toward the definitive mammalian middle ear.

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Appendix I　Character list

1. Cusp c: (0) distal to cusp a; (1) distolingual to a.
2. Cusp b, position: (0) close to cusp a; (1) well-separated from cusp a by a deep notch.
3. Cusp b, size: (0) small; (1) large.
4. Cusp b, shape: (0) single, (1) bi-cuspidate.
5. Presence of cusp g: (0) absent; (1) present.
6. Size of cusp g: (0) as small cusp; (1) enlarged, subequal to cusp c.
7. Cusp dd: (0) absent; (1) present.
8. Cusp e: (0) present; (1) absent.

9. Orientation of crest a–c: (0) anteroposterior; (1) oblique, more anteroposterior than transverse; (2) oblique, nearly transverse.
10. Crest a–g: (0) absent; (1) present.
11. Development of crest a–g: (0) weak ridge; (1) raised ridge.
12. Crest b–g: (0) absent; (1) present.
13. Crest c–d: (0) present; (1) absent.
14. Crest a–d: (0) absent; (1) present.
15. Crest c–dd: (0) absent; (1) present.
16. Crest b–e: (0) present; (1) absent.
17. Mesiolingual cingulid: (0) narrow or vestigial; (1) wide.
18. Anterior basin: (0) no delimited basin formed; (1) small concavity; (2) pseudotalonid basin.
19. Width of anterior basin: (0) narrower than width at cusp a; (1) wider.
20. Distal basin: (0) absent; (1) present.
21. Size of distal basin: (0) narrower than anterior basin (or anterior part of the tooth); (1) wider.
22. Distal cingulid: (0) absent; (1) present.
23. Mesiolingual corner: (0) protruding; (1) not protruding.
24. Broadening of lower molariforms: (0) absent, width less than half of maximal length; (1) present, width more than half of maximal length.

Appendix II Apomorphy and character change lists for the cladogram in Fig. 5

Apomorphy list:

Branch	Character	Steps	CI	Change
node 25 – – > node 24	1 (cusp c)	1	1.000	0 – – > 1
	7 (cusp dd)	1	1.000	0 – – > 1
	9 (orientation of crest a – c)	1	0.667	0 – – > 1
	14 (crest a – d)	1	0.333	0 – – > 1
	15 (crest c – dd)	1	0.250	0 – – > 1
	20 (distal basin)	1	1.000	0 – – > 1
	22 (distal cingulid)	1	1.000	0 – – > 1
node 24 – – > node 23	5 (presence of cusp g)	1	1.000	0 = = > 1
	9 (orientation of crest a – c)	1	0.667	1 – – > 2
	18 (anterior basin)	1	0.667	0 = = > 1
node 23 – – > *Docodon*	16 (crest b – e)	1	0.500	0 = = > 1
	23 (mesiolingual corner)	1	0.333	0 = = > 1
	24 (broadening of lower molar)	1	0.333	0 = = > 1
node 23 – – > node 22	2 (cusp b, position)	1	1.000	0 = = > 1
	15 (crest c – dd)	1	0.250	1 – – > 0
	17 (mesiolingual cingulid)	1	0.250	0 = = > 1
node 22 – – > node 21	10 (crest a – g)	1	0.500	0 = = > 1
node 21 – – > node 20	6 (size of cusp g)	1	0.333	0 = = > 1
	11 (development of crest a – g)	1	0.500	0 – – > 1
	18 (anterior basin)	1	0.667	1 = = > 2
	19 (width of anterior basin)	1	0.333	0 – – > 1
	24 (broadening of lower molar)	1	0.333	0 = = > 1
node 20 – – > *Haldanodon*	6 (size of cusp g)	1	0.333	1 = = > 0

continued

Branch	Character	Steps	CI	Change
	11 (development of crest a – g)	1	0.500	1 = = > 0
	18 (anterior basin)	1	0.667	2 = = > 1
	23 (mesiolingual corner)	1	0.333	0 = = > 1
node 20 – – > *Krusatodon*	3 (cusp b, size)	1	0.333	0 = = > 1
node 20 – – > node 19	17 (mesiolingual cingulid)	1	0.250	1 = = > 0
	23 (mesiolingual corner)	1	0.333	0 = = > 1
node 19 – – > node 18	15 (crest c – dd)	1	0.250	0 = = > 1
node 18 – – > node 17	13 (crest c – d)	1	1.000	0 = = > 1
node 17 – – > *Simpsonodon*	3 (cusp b, size)	1	0.333	0 = = > 1
	8 (cusp e)	1	0.333	0 = = > 1
	17 (mesiolingual cingulid)	1	0.250	0 = = > 1
node 17 – – > node 16	4 (cusp b, shape)	1	1.000	0 = = > 1
node 17 – – > *Castorocauda*	6 (size of cusp g)	1	0.333	1 = = > 0
node 18 – – > *Itatodon*	9 (orientation of crest a – c)	1	0.667	2 = = > 1
	12 (crest b – g)	1	1.000	1 = = > 0
	14 (crest a – d)	1	0.333	1 = = > 0
	24 (broadening of lower molar)	1	0.333	1 = = > 0
node 19 – – > *Acuodulodon*	8 (cusp e)	1	0.333	0 = = > 1
	10 (crest a – g)	1	0.500	1 = = > 0
	16 (crest b – e)	1	0.500	0 = = > 1
node 20 – – > *Tashkumyrodon*	15 (crest c – dd)	1	0.250	0 = = > 1
	19 (width of anterior basin)	1	0.333	1 – – > 0
	21 (size of distal basin)	1	0.333	0 – – > 1
node 20 – – > *Dsungarodon*	8 (cusp e)	1	0.333	0 = = > 1
	17 (mesiolingual cingulid)	1	0.250	1 = = > 0
	19 (width of anterior basin)	1	0.333	1 – – > 0
	21 (size of distal basin)	1	0.333	0 – – > 1
node 22 – – > *B. serendipitus*	3 (cusp b, size)	1	0.333	0 = = > 1
	14 (crest a – d)	1	0.333	1 = = > 0

Character change list:

Character	CI	Steps	Changes
1 (cusp c)	1.000	1	node 25 0 – – >1 node 24
2 (cusp b, position)	1.000	1	node 23 0 = = >1 node 22
3 (cusp b, size)	0.333	1	node 20 0 = = > 1 *Krusatodon*
		1	node 17 0 = = > 1 *Simpsonodon*
		1	node 22 0 = = > 1 *B. serendipitus*
4 (cusp b, shape)	1.000	1	node 17 0 = = > 1 node 16
5 (presence of cusp g)	1.000	1	node 24 0 = = > 1 node 23
6 (size of cusp g)	0.333	1	node 21 0 = = > 1 node 20
		1	node 20 1 = = > 0 *Haldanodon*
		1	node 17 1 = = > 0 *Castorocauda*

continued

Character	CI	Steps	Changes						
7 (cusp dd)	1.000	1	node	25	0	- - >	1	node	24
8 (cusp e)	0.333	1	node	17	0	= = >	1	*Simpsonodon*	
		1	node	19	0	= = >	1	*Acuodulodon*	
		1	node	20	0	= = >	1	*Dsungarodon*	
9 (orientation of crest a - c)	0.667	1	node	25	0	- - >	1	node	24
		1	node	24	1	- - >	2	node	23
		1	node	18	2	= = >	1	*Itatodon*	
10 (crest a - g)	0.500	1	node	22	0	= = >	1	node	21
		1	node	19	1	= = >	0	*Acuodulodon*	
11 (development of crest a - g)	0.500	1	node	21	0	- - >	1	node	20
		1	node	20	1	= = >	0	*Haldanodon*	
12 (crest b - g)	1.000	1	node	18	1	= = >	0	*Itatodon*	
13 (crest c - d)	1.000	1	node	18	0	= = >	1	node	17
14 (crest a - d)	0.333	1	node	25	0	- - >	1	node	24
		1	node	18	1	= = >	0	*Itatodon*	
		1	node	22	1	= = >	0	*B. serendipitus*	
15 (crest c - dd)	0.250	1	node	25	0	- - >	1	node	24
		1	node	23	1	- - >	0	node	22
		1	node	19	0	= = >	1	node	18
		1	node	20	0	= = >	1	*Tashkumyrodon*	
16 (crest b - e)	0.500	1	node	23	0	= = >	1	*Docodon*	
		1	node	19	0	= = >	1	*Acuodulodon*	
17 (mesiolingual cingulid)	0.250	1	node	23	0	= = >	1	node	22
		1	node	20	1	= = >	0	node	19
		1	node	17	0	= = >	1	*Simpsonodon*	
		1	node	20	1	= = >	0	*Dsungarodon*	
18 (anterior basin)	0.667	1	node	24	0	= = >	1	node	23
		1	node	21	1	= = >	2	node	20
		1	node	20	2	= = >	1	*Haldanodon*	
19 (width of anterior basin)	0.333	1	node	21	0	- - >	1	node	20
		1	node	20	1	- - >	0	*Tashkumyrodon*	
		1	node	20	1	- - >	0	*Dsungarodon*	
20 (distal basin)	1.000	1	node	25	0	- - >	1	node	24
21 (size of distal basin)	0.333	1	node	21	1	- - >	0	node	20
		1	node	20	0	- - >	1	*Tashkumyrodon*	
		1	node	20	0	- - >	1	*Dsungarodon*	
22 (distal cingulid)	1.000	1	node	25	0	- - >	1	node	24
23 (mesiolingual corner)	0.333	1	node	23	0	= = >	1	*Docodon*	
		1	node	20	0	= = >	1	*Haldanodon*	
		1	node	20	0	= = >	1	node	19
24 (broadening of lower molariform)	0.333	1	node	23	0	= = >	1	*Docodon*	
		1	node	21	0	= = >	1	node	20
		1	node	18	1	= = >	0	*Itatodon*	