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NEW DOCODONTANS FROM THE MIDDLE JURASSIC OF SIBERIA AND REANALYSIS OF DOCODONTA INTERRELATIONSHIPS

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ABSTRACT

Two new docodontans, *Simpsonodon sibiricus* sp. nov. and *Hutegotherium yaomingi* gen. et sp. nov., and a new specimen of *Itatodon tatarinovi* Lopatin et Averianov, 2005 are described from the Middle Jurassic (Bathonian) Itat Formation of Krasnoyarsk Territory in West Siberia, Russia. A new phylogenetic analysis, incorporating 37 dental and mandibular characters and 18 docodontan and outgroup taxa demonstrated that *Itatodon* is the most basal known docodontan. Other docodontans can be classified in Docodontidae (*Docodon* and *Haldanodon*, with *Borealestes* recognized as a stem docodontid), Simpsonodontidae fam. nov. (*Simpsonodon* and *Dsungarodon*), Tegotheriidae (*Krusatodon*, *Hutegotherium* gen. nov., *Tegotherium*, and *Sibirotherium*), and Docodonta incertae sedis (*Castoroconda*, *Tashkumyrodon*, and *Acuoduolodon*). Simpsonodontidae fam. nov. is characterized, in particular, by a strongly developed additional groove dorsal to the Meckelian groove. The Middle Jurassic mammals of Laurasia are now known from three principal assemblages: Forest Marble in England, Balabansai in Kyrgyzstan, and Itat in West Siberia. All these three assemblages are very similar and comprise docodontans, allotherians, eutriconodontans, “symmetrodontans,” dryolestidans, and stem zatherians. The Middle Jurassic radiation of mammals has almost no roots in the known Early Jurassic mammal fauna and the evolutionary events which led to formation of the principal groups of Mesozoic mammals (Docodonta, Multituberculata, Eutriconodonta, Dryolestida, and stem Zatheria) should have occurred sometime between the Sinemurian and Bajocian in Laurasia, most probably in Asia (Siberia?).

Key words: Docodonta, Mammalia, Middle Jurassic, Russia, West Siberia

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НОВЫЕ ДОКОДОНТЫ ИЗ СРЕДНЕЙ ЮРЫ СИБИРИ И НОВЫЙ АНАЛИЗ ФИЛОГЕНЕТИЧЕСКИХ СВЯЗЕЙ ДОКОДОНТОВ

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РЕЗЮМЕ

Два новых докодонта, *Simpsonodon sibiricus* sp. nov. и *Hutegotherium yaomingi* gen. et sp. nov., и новый экземпляр *Itatodon tatarinovi* Lopatin et Averianov, 2005 описаны из среднеюрской (бат) итатской свиты в Красноярском крае, Западная Сибирь, Россия. Согласно новому филогенетическому анализу, включающему 37 признаков зубов и нижней челюсти и 18 таксонов докодонтов и внешней группы, *Itatodon* является наиболее базальным из известных докодонтов. Другие докодонты классифицированы в Docodontidae (*Docodon* и *Haldanodon*); *Borealestes* является стволовым докодонтидом), Simpsonodontidae fam. nov. (*Simpsonodon* и *Dsungarodon*), Tegotheriidae (*Krusatodon*, *Hutegotherium* gen. nov., *Tegotherium* и *Sibirotherium*), и Docodonta incertae sedis (*Castorocauda*, *Tashkumyrodon* и *Acuoduolodon*). Simpsonodontidae fam. nov. характеризуются, в частности, сильно развитой дополнительной бороздой дорсальнее меккелевой борозды. Среднеюрские млекопитающие Евразии теперь известны по трем основным фаунам: Форест-Марбл в Англии, балабансайской в Киргизии и итатской в Западной Сибири. Все эти фауны очень похожи и включают докодонтов, аллотериев, эутриконодонтов, «симметродонтов», дриolestид и стволовых затериев. Среднеюрская радиация млекопитающих практически не имеет корней в известной фауне млекопитающих ранней юры. Эволюционные события, приведшие к формированию основных групп мезозойских млекопитающих (Docodonta, Multituberculata, Eutriconodontia, Dryolestida и стволовые Zatheria), должны были произойти в интервале между синемюрмом и байосом в Лавразии, вероятнее всего в Азии (Сибири?).

Ключевые слова: Docodonta, Mammalia, средняя юра, Россия, Западная Сибирь

INTRODUCTION

For a long time the Middle Jurassic was the poorest known interval of the Mesozoic mammalian history in spite of the fact that the first Mesozoic mammal known to science was found before 1764 at the Middle Jurassic (Bathonian) Stonsfield Slate Quarry near Oxford in England (Simpson 1928; Kermack et al. 1987; Kermack 1988). For about two centuries our knowledge of Jurassic mammals was based almost exclusively on the materials from the Early and Late Jurassic localities in Europe, Asia, Africa, and North America (see Kielan-Jaworowska et al. 2004 for re-

view). Only in the 1970s new Middle Jurassic sites were found in Scotland and England (Waldman and Savage 1972; Freeman 1976a, b, 1979). Now Middle Jurassic mammals are known also from China, Kyrgyzstan, Madagascar, and Russia and Middle to Late Jurassic (Callovian/Oxfordian) mammals were recently found in Argentina (e.g., Flynn et al. 1999; Rauhut et al. 2002; Kielan-Jaworowska et al. 2004; Martin and Averianov 2004, 2007, 2010; Lopatin and Averianov 2005, 2006, 2007; Rougier et al. 2007a, b). The Early and Late Jurassic mammal faunas differ drastically: the former are dominated by stem mammals, like morganucodontans, haramiyid allotheri-

ans, and kuehneotheriid “symmetrodontans”, while the latter show a flourishing of more derived mammal groups: eutriconodontans, multituberculates, tinodontid “symmetrodontans”, dryolestidans, and stem zatherians (Kielan-Jaworowska et al. 2004; Luo 2007a, b). It was obvious that an important faunal turnover occurred sometime within the Middle Jurassic and newly emerging knowledge of the mammal faunas of that age allow us to reconstruct this turnover in some detail.

Here we report the discovery of two new docodontan taxa, *Simpsonodon sibiricus* sp. nov. and *Hutegotherium yaomingi* gen. et sp. nov. from the Middle Jurassic (Bathonian) Itat Formation at Berezovsk Quarry, southern Krasnoyarsk Territory, West Siberia, Russia. *Simpsonodon* was based originally on materials from the Middle Jurassic (Bathonian) Forest Marble Formation at Kirtlington Quarry, England (Kermack et al. 1987; Sigogneau-Russell 2003a). We publish here also a dentary fragment with two teeth of *Itatodon tatarinovi* which was known formerly by two isolated molariform teeth. The previously known mammal assemblage from Berezovsk included the eleutherodontid allotherians, docodontan *Itatodon*, indeterminate docodontans, an eutriconodontan, a dryolestid, and the amphitheriid stem zatherian *Amphibetulimus* (Averianov et al. 2005, 2008; Lopatin and Averianov 2005, 2006, 2007; Averianov and Lopatin 2006).

MATERIAL AND METHODS

The fossil vertebrates, including mammals, were collected by the joint expeditions of the Tomsk and Saint Petersburg universities and Paleontological and Zoological academic institutions in 2005 and 2007 at Berezovsk Quarry utilizing underwater screening technique. The obtained concentrate was broken into two size fractions and the coarser of these fractions was sorted in the field and laboratory. The mammal jaws and tooth described herein were found in this coarse fraction.

The cusp nomenclature for the docodontan molariform teeth employed in this paper is shown in Fig. 1. It follows generally that of Luo and Martin (2007) except for two cases. The cusp distal to cusp c on the lower molariform teeth, called cusp f in Martin and Averianov (2004) or cusp df in Luo and Martin (2007), is designated here as cusp dd following Hu et al. (2007). Maschenko et al. (2002) and Martin and Averianov (2004) recognized for *Sibirotherium* and

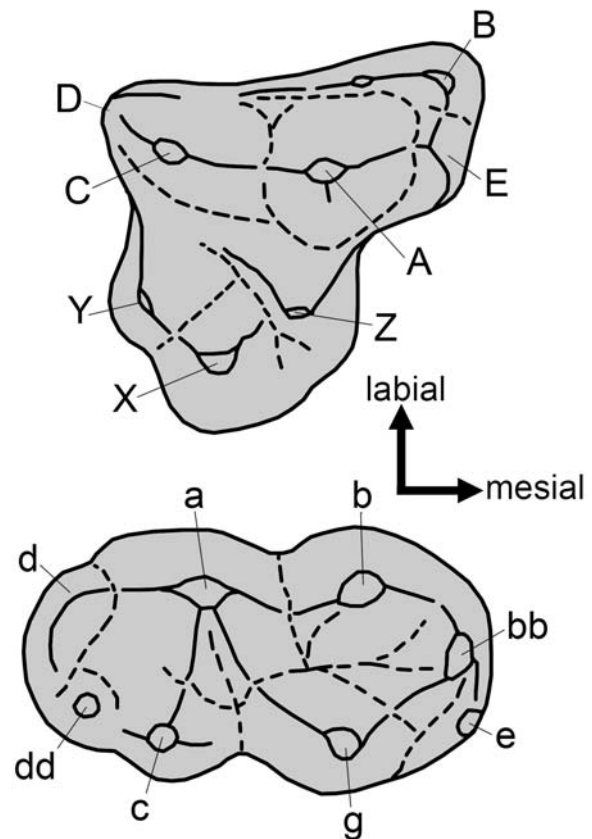


Fig. 1. Cusp nomenclature for Docodonta shown on the right upper molariform tooth of *Krusatodon* and left lower molariform tooth of *Tegotherium* (modified from Luo and Martin 2007).

Tegotherium cusp e on the wall of the pseudotalonid and cusp ee, the mesiolingual cingulid. However, it is now obvious that cusp ee is corresponding to cusp e of other docodontans, while cusp e of *Tegotherium* and *Sibirotherium* is a neomorph. We name the latter cusp as cusp bb (see also Lopatin et al. 2009). Hu et al. (2007) describe this structure as a bicuspidate cusp b, but we think it is more correct to recognize two cusps, b and bb.

Photographs were taken with a Canon PowerShot S60 digital camera mounted on a Leica MZ6 binocular microscope through a Canon conversion lens adapter LA-DC100, or with a MYscope 500M digital camera for microscope. For every image several photographs were taken differing in the focus plane which were combined into a single image manually in Adobe Photoshop or using program CombineZM.

The methods of the phylogenetic analysis are explained in the relevant section.

Institutional abbreviations. BMNH, Natural History Museum, London, Great Britain; MNHN, Muséum national d'Histoire naturelle, Paris, France; PIN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; PM TGU, Paleontological Museum, Tomsk State University, Tomsk, Russia; SGP, Sino-German Project, a collection currently housed at the Institute for Geosciences, University of Tübingen, Germany; USNM, United States National Museum, Washington DC, USA; YPM, Yale Peabody Museum, Yale University, New Haven, USA.

Dental measurements. L, length; W, width. All measurements are in mm.

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758

Docodonta Kretzoi, 1946

Docodonta incertae familiae

Genus *Itatodon* Lopatin et Averianov, 2005

Itatodon Lopatin et Averianov, 2005: 434 [277 of Russian text]

Type species. *Itatodon tatarinovi* Lopatin et Averianov, 2005.

Included species. Type species only.

Comments. Originally *Itatodon* was described as a tegtotheriid docodontan which was confirmed by our previous phylogenetic analysis (Averianov and Lopatin 2006). Luo and Martin (2007) grouped *Itatodon* with *Krusatodon* from the Middle Jurassic of England (Sigogneau-Russell 2003a). Hu et al. (2007) placed *Itatodon* as the sister taxon of the clade ((*Sibiritherium* + *Tegtotherium*) + *Castoroconda*, *Simpsonodon*). According to our current phylogenetic analysis, *Itatodon* is the most basal known docodontan (see below), and subsequently it is excluded here from the Tegtotheriidae (see also Lopatin et al. 2009).

Distribution. Middle Jurassic of Siberia.

***Itatodon tatarinovi* Lopatin et Averianov, 2005**

(Fig. 2)

Itatodon tatarinovi Lopatin and Averianov 2005: 434 [277 of Russian text], fig. 1; Averianov and Lopatin 2006: 669 [82 of Russian text], fig. 1, pl. 8.

Holotype. PIN 5087/2, a right ultimate lower molariform tooth.

Type locality and horizon. Berezovsk Quarry, 2 km south of Nikol'skoe village, Sharypovo District, Krasnoyarsk Territory, West Siberia, Russia. Grey clays of the upper part of Itat Formation, Middle Jurassic, Bathonian (see Averianov et al. 2005 for details).

Included specimens. PIN 5087/7, a left dentary fragment with a premolar, the first lower molariform tooth, and the alveoli for three premolars and m2; PM TGU 200/3-BR-7, a right lower molariform tooth.

Revised diagnosis. *Itatodon* is unique among docodontans in having cusp b reduced to the cingular cusp, crests a-g and a-b diverging at the base of cusp a, no pseudotalonid basin on the first lower molariform tooth (absent also on the highly modified m1 of *Castoroconda*), and having the cingular cusp e incorporated into the wall of the pseudotalonid basin on the more posterior molariform teeth. Additionally, it differs from Docodontidae by having cusp b smaller than cusp c and well separated from cusp a, and a narrow mesiolingual cingulid; from Simpsonodontidae fam. nov. by presence of cusp e, a narrow mesiolingual cingulid, and lack of enamel folding; from Tegtotheriidae by lack of cusp bb. Among docodontans *incertae familiae* it additionally differs from *Castoroconda* by the first lower non-sectorial molariform tooth, a large cusp g which is almost equal to cusp c, absence of crests b-g and a-d, presence of crest c-d, and the presence of cusp c on the lower molariform tooth; from *Castoroconda* and *Tashkumyrodon* by presence of a lingual cingulid and lack of the cusp dd and the crest c-dd.

Description. PIN 5087/7 is an anterior dentary fragment bearing four double-rooted premolar and two molar loci. The alveoli for px and px+1 are similar in size and separated by a diastema. The mesial root is smaller than the distal root on both teeth, but this size difference is more pronounced in px.

px+2 is longer than px+1 but somewhat smaller than px+3. It is a small tooth of oval shape in occlusal view, with the crown almost two times lower than the crown of m1. The main cusp is slightly recurved distally at the top. The mesial carina is slightly convex and joins the lingual cingulid lingually. The distal carina is longer and concave, bearing a small additional cusp at the distal end. The lingual cingulid is well pronounced and complete. There is no labial cingulid. The distal root is slightly longer (mesiodistally) than the mesial root.

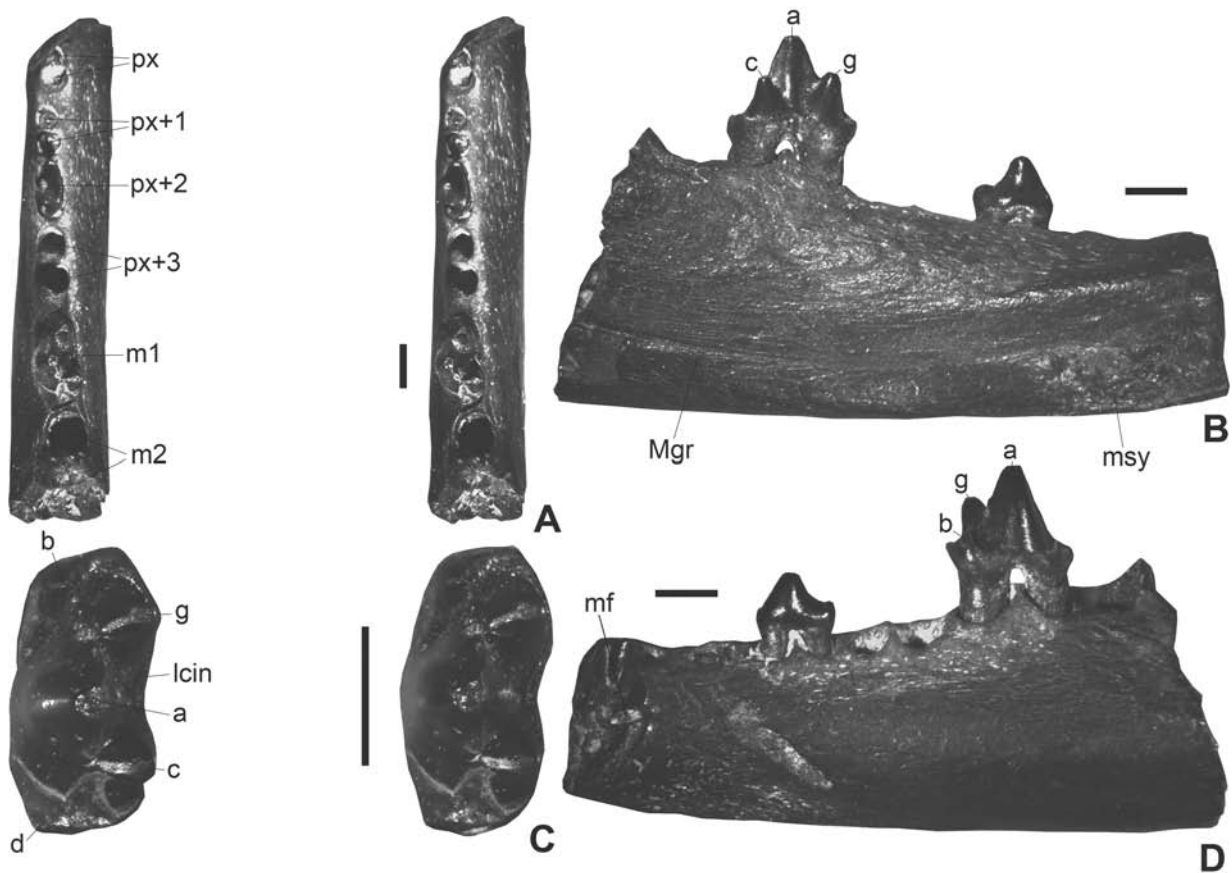


Fig. 2. *Itatodon tatarinovi* Lopatin et Averianov, 2005, PIN 5087/7, a left dentary fragment with a premolar, the first lower molariform tooth, and alveoli for three premolars and the second molariform tooth in occlusal (A and C, stereopairs), lingual (B), and labial (D) views. Berezovsk Quarry, Krasnoyarsk Territory, Russia; Itat Formation, Middle Jurassic (Bathonian).

Abbreviations: a, b, c, d, and g – lower molar cusps; lcin – lingual cingulid; mf – mental foramen; Mgr – Meckelian groove; msy – mandibular symphysis. Scale bars 1 mm.

The first lower molariform tooth (m1) has three main cusps, a, g, and c, arranged in an isosceles triangle. Cusp a is about two times higher than cusp g and cusp c is somewhat lower than cusp g. Crests a-g and a-c are robust. Cusp b is greatly reduced to a cingular cusp on the distolabial end of the mesial cingulid. The mesial cingulid has an anterior projection (cusp e?) and continues lingually into a well developed and complete lingual cingulid. There is a very narrow area between the mesial cingulid and cusp g which is homologous to the pseudotalonid basin in more posterior molariform teeth. The distal cingulid is an oblique crest, connected with the lingual cingulid and with the poorly differentiated cusp d at the labial end. There is a short mesiolabial cingulid connected mesially to the apex of cusp b. There are wear facets

on the mesiolabial slope of cusp b, on the tips of the main cusps, along the crests a-g and a-c, and on the distal slope of the crown. The mesial root is somewhat longer (mesiodistally) than the distal root.

The mandibular body decreases drastically in depth anteriorly, with the preserved posterior end being 1.6 times higher than the anterior end. The alveolar row is oblique in the preserved fragment: px and px+1 are at the labial margin while m2 is at the lingual margin of the mandibular body. The mandibular symphysis is a rough area and covers at maximum half of the dentary height, terminating between px+1 and px+2. The Meckelian groove reaches anteriorly the mandibular symphysis. It is closer to the ventral margin of the mandibular body, narrow posteriorly and becomes filiform anterior to m1. On the labial

side there is a small cleft-like mental foramen at the distal root of px.

m2 was distinctly larger than m1 judging from its alveoli.

For the description of isolated lower molariform teeth see Lopatin and Averianov (2005: 435–436) and Averianov and Lopatin (2006: 669–671).

Comments. PIN 5087/7 is referred to *I. tatarinovi* because of the simple structure and pronounced lingual cingulid of the molariform tooth. Preserved m1 in PIN 5087/7 is identical in size to the holotype (ultimate lower molariform tooth) of *I. tatarinovi* and some 20% shorter than PM TGU 200/3-BR-7, an isolated lower molariform tooth. This indicates that the terminal lower molariform teeth in *Itatodon* were the smallest in the molar series.

In *Docodon* and *Haldanodon* the mandibular symphysis is terminating approximately at the level of the last premolar (Krusat 1980; Lillegraven and Krusat 1991; Kielan-Jaworowska et al. 2004: fig. 5.3A, B₁), while in *Itatodon* there are two more premolars posterior to the end of the mandibular symphysis. We think that this indicates that *Itatodon* had more than four premolars rather than a short mandibular symphysis.

Measurements. PIN 5087/7: px: L=1.3, W=0.7; m1: L=2.1, W=1.1.

Family Docodontidae Simpson, 1929

Docodontidae Simpson 1929: 84.

Type genus. *Docodon* Marsh, 1881.

Included genera. Type genus and *Haldanodon* Kühne et Krusat, 1972.

Revised diagnosis. Docodontans with cusp C reduced and twinned with cusp A, cusp b larger than cusp c and approximated cusp a, and mesiolingual cingulid wide.

Comments. Although we do not describe docodontids in this paper, we think it is necessary to provide a revised diagnosis for the Docodontidae which is equal to Docodonta in the majority of existing classifications. Here the family is restricted to *Docodon* and *Haldanodon*. *Boreolestes* from the Middle Jurassic of Scotland and England (Waldman and Savage 1972; Sigogneau-Russell 2003a) is a stem docodontid sharing with the docodontids 3–4 lower premolars, a weak crest a-g, and an incomplete crest a-d.

Distribution. Late Jurassic and Early Cretaceous of Europe and North America.

Family Simpsonodontidae fam. nov.

Type genus. *Simpsonodon* Kermack, Lee, Lees et Mussett, 1987.

Included genera. Type genus and *Dsungarodon* Pfretzschner et Martin, 2005.

Diagnosis. Docodontans with the pseudotalonid basin large and bordered by crests a-b, a-g, and b-g. Cusp e absent and the mesiolingual cingulid wide. Distal side of the lower molariform crowns with crenulations. There is a continuous additional groove above the Meckelian groove and separated from the more posterior trough for the postdentary bones (see description for details).

Comments. The grouping of *Simpsonodon* and *Dsungarodon* was established in the previous phylogenetic analyses of Docodonta (Pfretzschner et al. 2005; Averianov and Lopatin 2006; but not by Ji et al. 2006; Hu et al. 2007; Luo and Martin 2007) and is confirmed by the analysis present in this paper.

Distribution. Middle Jurassic of Europe and Asia.

Genus *Simpsonodon* Kermack, Lee, Lees et Mussett, 1987

Simpsonodon sibiricus sp. nov.
(Fig. 3)

Etymology. The species name is after Siberia, where the species was found.

Holotype. PIN 5087/5, a left dentary fragment with three last molariform teeth, the alveolus for a more anterior tooth, and the base of the coronoid process.

Type locality and horizon. Berezovsk Quarry, 2 km south of Nikol'skoe village, Sharypovo District, Krasnoyarsk Territory, West Siberia, Russia. Grey clays of the upper part of Itat Formation, Middle Jurassic, Bathonian (see Averianov et al. 2005 for details).

Diagnosis. *Simpsonodon sibiricus* sp. nov. is very similar to *Simpsonodon oxfordensis* Kermack et al., 1987 from the Bathonian of England, the only known previously species of the genus, in size and morphology of the lower molariform teeth. The two species can be nevertheless distinguished by the structure of the mesial cingulid. In *S. sibiricus* sp. nov. it is clearly divided into two portions: a short labial arm directed mesiolingually and a longer lingual arm wrapping around the mesiolingual corner of the crown and extending towards the base of the mesiolingual cusp

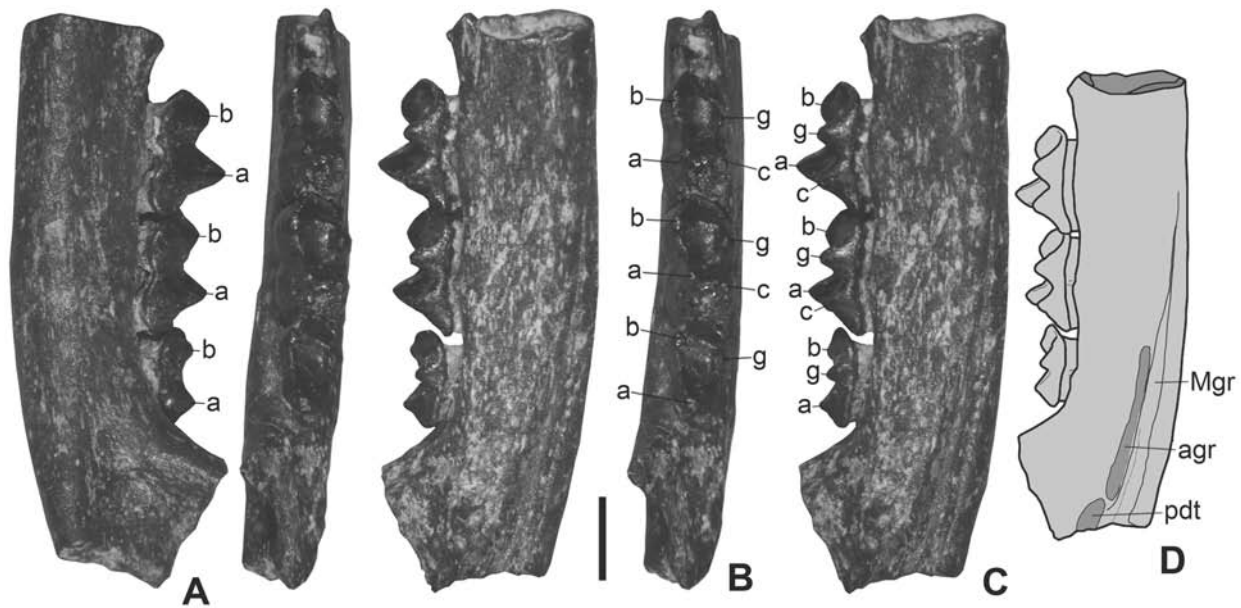


Fig. 3. *Simpsonodon sibiricus* sp. nov., PIN 5087/5, holotype, a left dentary fragment with three last molariform teeth, in labial (A), occlusal (B, stereopair), and lingual (C, stereopair and D, explanatory drawing) views. Berezovsk Quarry, Krasnoyarsk Territory, Russia; Itat Formation, Middle Jurassic (Bathonian).

Abbreviations: a, b, c, and g – lower molar cusps; agr – additional groove above the Meckelian groove; Mgr – Meckelian groove; pdt – postdentary trough. Scale bar 1 mm (the drawing D is reduced in size compared with photographs).

g. In *S. oxfordensis* this division is not clear and a long mesial cingulid is wrapping around the entire mesial end of the crown towards the base of the mesiolingual cusp g.

Description. The antepenultimate and penultimate molariform teeth of the holotype are basically similar in structure, differing slightly in proportions: the former tooth is somewhat longer and narrower. The crown is dominated by the main cusp a which occupies most of its posterior portion. The mesiolabial cusp b is well separated from the latter cusp and about two times lower. The mesiolingual cusp g and the distolingual cusp c are situated at the levels between the cusps a and b and little distally to cusp a respectively. The main cusp is connected with the three other principal cusps by well pronounced ridges a-b, a-g, and a-c. There is also a ridge a-d although the distolabial cusp d is not developed. These longitudinal and transverse crests are accentuated by vertical furrows on cusp a collateral to the ridges a-b and a-d. The transverse ridges a-g and a-c closely approximate each other along cusp a and start to diverge only at the bases of the lingual cusps. The pseudotalonid is rather large and bordered by crests a-b, b-g, and a-g.

The pseudotalonid basin is of triangular shape and deeply concave. The mesial cingulid is clearly divided into two arms: the labial one, directing mesiolingually, and the lingual one, wrapping around the mesiolingual corner of the crown towards the base of cusp g. The adjacent molariform teeth do not interlock but tightly abut by the lingual arm of the mesial cingulid and the whole distal cingulid of the preceding tooth. There is no lingual cingulid. The posterior portion of the crown (distal to the crest a-c) is very short and formed by distal slopes of the cusps a and c. This area is encircled by vertical crests descending from the apices of cusps a and c and the distal cingulid and filled by prominent crenulations. The largest of the latter is a central cuspule connected by a ridge to the apex of cusp c and by a finer ridge to a short transverse ridge parallel to the distal cingulid.

The ultimate molariform tooth is similar to the penultimate tooth, but with cusp a much lower, part of the crown distal to cusp a greatly reduced, and cusp c totally lacking. Cusp a is only little higher than cusp b. In spite of reduction of the posterior part of the crown and cusp c, there are rudimentary crests a-d and a-c descending from the apex of cusp a. There

is also an additional rudimentary crest between the crests a-d and a-c, closer to the latter. The tooth is double rooted, with the distal root more than two times shorter than the mesial root.

The dentary with the Meckelian groove and the most anterior portion of the trough for the post-dentary bones on lingual side is well preserved. The Meckelian groove extends parallel and close to the curved ventral border of the dentary. It is about 5 mm high at the preserved posterior end, but gradually tapers anteriorly into the filiform furrow terminating at the level of the distal root of the antepenultimate molariform tooth. The level of the mandibular foramen is well posterior to the last molariform tooth. The foramen opens into a narrow but deep trough for the postdentary bones. This trough opens mostly ventrally and only little medially. The thin bony layer overhangs the trough dorsally, but a marked median flange, or ridge is not developed in this region. Immediately anterior to the trough and dorsal to the Meckelian groove there is a marked additional sub-horizontal groove, closely aligned to the latter groove but separated by a distinct ridge. This additional groove terminates anteriorly at the mesial end of the ultimate molariform tooth. There is no coronoid facet. No pseudangular process is preserved on the fragment, nor a characteristic curving of the dentary ventral border indicating the presence of such a process in a close proximity. The masseteric fossa is rather deep, bordered anteriorly by the robust masseteric crest. The anterior extremity of the masseteric fossa forms a cleft-like pocket which is overhanging by the masseteric crest and possibly leading into the lateral mandibular foramen.

Measurements. PIN 5087/5: antepenultimate molariform tooth: L=1.6, W=0.8; penultimate molariform tooth: L=1.5, W=0.8; ultimate molariform tooth: L=1.2, W=0.7.

Nomenclatorial note. Sigogneau-Russell (2001) showed that *Cyrtlatherium canei* Freeman, 1979, originally described as a kuehneotheriid “symmetrodontan” from the Kirtlington Quarry (Freeman 1979), is actually based on a milk tooth of a docodontan, most possibly *Simpsonodon oxfordensis* Kermack et al., 1987 from the same locality (see also Sigogneau-Russell 2003a; Kielan-Jaworowska et al. 2004). Averianov (2004; see also Averianov and Lopatin 2006) formally synonymized the genera *Cyrtlatherium* and *Simpsonodon*, with the first name having priority. However, now we think that the stability of

the zoological nomenclature would be better served if the more widely known name *Simpsonodon* would be retained and the name *Cyrtlatherium* would be suppressed, or considered currently as a nomen dubium.

Comments. The structure of the lower molariform teeth of *S. sibiricus* sp. nov. is intermediate in morphology between *S. oxfordensis* and *Dsungarodon zuoi* Pfretzschner et Martin, 2005 from the Oxfordian of Xinjiang-Uygur Autonomous Region, China (Pfretzschner et al. 2005). *S. sibiricus* sp. nov. has crenulations in the posterior region of the crown, like in *S. oxfordensis*, and the mesial cingulid designed exactly as in *Dsungarodon*. The ultimate lower molariform tooth of *S. sibiricus* sp. nov. (unknown for *S. oxfordensis*) is virtually identical with this tooth in *Dsungarodon* (Pfretzschner et al. 2005: fig. 3B). The structure of the Meckelian and an additional horizontal groove (see comments below) is also almost identical in *S. sibiricus* sp. nov. and *Dsungarodon* (Pfretzschner et al. 2005: fig. 3B₃; the posterior portion of the dentary is not known for *S. oxfordensis*). This combination of characters of two genera in one species confirms the close phylogenetic relations between *Simpsonodon* and *Dsungarodon* that have been proposed previously (Pfretzschner et al. 2005; Averianov and Lopatin 2006).

Simpsonodon (as known from *S. sibiricus* sp. nov.) and *Dsungarodon* are unique among other docodontans in strong development of an additional horizontal groove above the Meckelian groove. In the original description of *Dsungarodon* this groove was mistaken for the trough for the postdentary bones (Pfretzschner et al. 2005: 804, fig. 3B₃). The anterior end of the trough, where the mandibular foramen opens, should be more posterior to the preserved posterior end of the discussed dentary fragment of *Dsungarodon*. In *Dsungarodon* the additional groove is somewhat shorter than in *S. sibiricus* sp. nov., terminating at the level of the distal root of the last molariform tooth. A similar but much shorter groove is present in *Morganucodon* and *Haldanodon* (Kermack et al. 1973; Krusat 1980; Lillegraven and Krusat 1991; Kielan-Jaworowska et al. 2004), where it was interpreted as facet for the dorsal flange of the prearticular or the splenial facet respectively. The latter interpretation seems to be incorrect. In Mesozoic mammals the splenial facets are narrow bands of flattened bone dorsal and ventral to the Meckelian groove (e.g., Krebs 1969; Martin 1995).

Family Tegotheriidae Tatarinov, 1994

Tegotheriidae Tatarinov 1994: 104.

Type genus. *Tegotherium* Tatarinov, 1994.

Included genera. Type genus, *Sibirotherium* Maschenko, Lopatin et Voronkevich, 2002, *Krusatodon* Sigogneau-Russell, 2003a, and *Hutegotherium* gen. nov.

Revised diagnosis. Docodontans with cusp Z on upper molariform teeth (except *Tegotherium*), crest A-X absent, cusp bb on the lower molariform teeth, a large pseudotalonid basin bordered by crests a-b, b-bb, bb-g, and a-g, and crest b-g absent.

Comments. Tegotheriidae is recognized as a valid family by the Russian authors only (Maschenko et al. 2002; Lopatin and Averianov 2005; Averianov and Lopatin 2006; Lopatin et al. 2009), although virtually all phylogenetic analyses of Docodonta revealed the clade *Tegotherium* + *Sibirotherium* (Martin and Averianov 2004; Averianov and Lopatin 2006; Ji et al. 2006; Hu et al. 2007; Luo and Martin 2007).

Krusatodon from the Middle Jurassic of England was considered as ancestral to, or possible synonymous with *Tegotherium* from the Late Jurassic of Mongolia (Sigogneau-Russell 2003a: fig. 9). Indeed, the lower molariform teeth of these genera are quite similar. We consider these two genera distinct because *Krusatodon* can be distinguished from *Tegotherium* by widely separated crests a-g and a-c, lack of a cingulid lingual to the cusps g and c, and a more complex posterior region of the crown of lower molariform teeth, with individualized cusps d and dd and the crest c-d well developed. On the cladogram presented by Averianov and Lopatin (2006: fig. 2) *Krusatodon* and *Tegotherium* are widely separated. Now we consider this as an artifact of the miscoding for *Krusatodon*: our coding of its lower molar characters was based on the holotype of *K. kirtlingtonensis*, but this tooth is most likely a m1 with the pseudotalonid reduced because it was occluded with the ultimate upper premolar having a weaker developed talon. An additional, more posterior molariform tooth of *K. kirtlingtonensis* (Sigogneau-Russell 2003a: fig. 3A) shows that the pseudotalonid is enlarged, has a distinct cusp bb, and is bordered mesiolingually by crest bb-g, with the consequence that crest b-g is absent.

Distribution. Middle Jurassic of Europe; Middle Jurassic to Early Cretaceous of Asia.

Genus *Hutegotherium* gen. nov.

Etymology. The new genus and species is named in honor of Dr. Hu Yaoming (1966–2008) in recognition of his work on Mesozoic mammals, and after the genus *Tegotherium* Tatarinov, 1994.

Type species. *Hutegotherium yaomingi* sp. nov.

Included species. Type species only.

Distribution. Middle Jurassic of Siberia.

***Hutegotherium yaomingi* sp. nov.**

(Figs. 4 and 5)

Holotype. PM TGU 200/5-BR-2, a right dentary fragment with the penultimate and antepenultimate molariform teeth and the alveolus for the ultimate tooth.

Type locality and horizon. Berezovsk Quarry, 2 km south of Nikol'skoe village, Sharypovo District, Krasnoyarsk Territory, West Siberia, Russia. Grey clays of the upper part of Itat Formation, Middle Jurassic, Bathonian (see Averianov et al. 2005 for details).

Included specimens. PIN 5087/6, right upper molariform tooth; PIN 5087/8, a right dentary fragment with the penultimate and antepenultimate molariform teeth and the alveolus for the ultimate tooth.

Diagnosis. Referred to Tegotheriidae and differing from all other docodontans by the presence of cusp Z on the upper molariform teeth, absence of crest A-X, presence of cusp bb on the lower molariform teeth, a pseudotalonid that is bordered by crests a-b, b-bb, bb-g, and a-g, and absence of crest b-g. Among tegotheriids it differs from *Tegotherium* Tatarinov, 1994 by the presence of cusp Z, by an incomplete lingual cingulid, and a longer Meckelian groove; from *Krusatodon* Sigogneau-Russell, 2003a it differs by a cusp b that is smaller than cusp c, absence of cusp dd, absence of crest b-e, presence of crest c-dd, and lack of additional crests in the distal portion of the crown of the lower molariform teeth; from *Sibirotherium* Maschenko et al., 2002 it differs by an incomplete lingual cingulid and absence of cusp dd.

Description. The crown of the upper molariform tooth is of triangular shape and dominated by a large mesiolabial cusp A which occupies the mesiocentral third of the crown. The distolabial cusp C is about two times smaller than cusp A and placed somewhat labially to the latter. There are sharp longitudinal crests between cusps A and C and between these cusps and

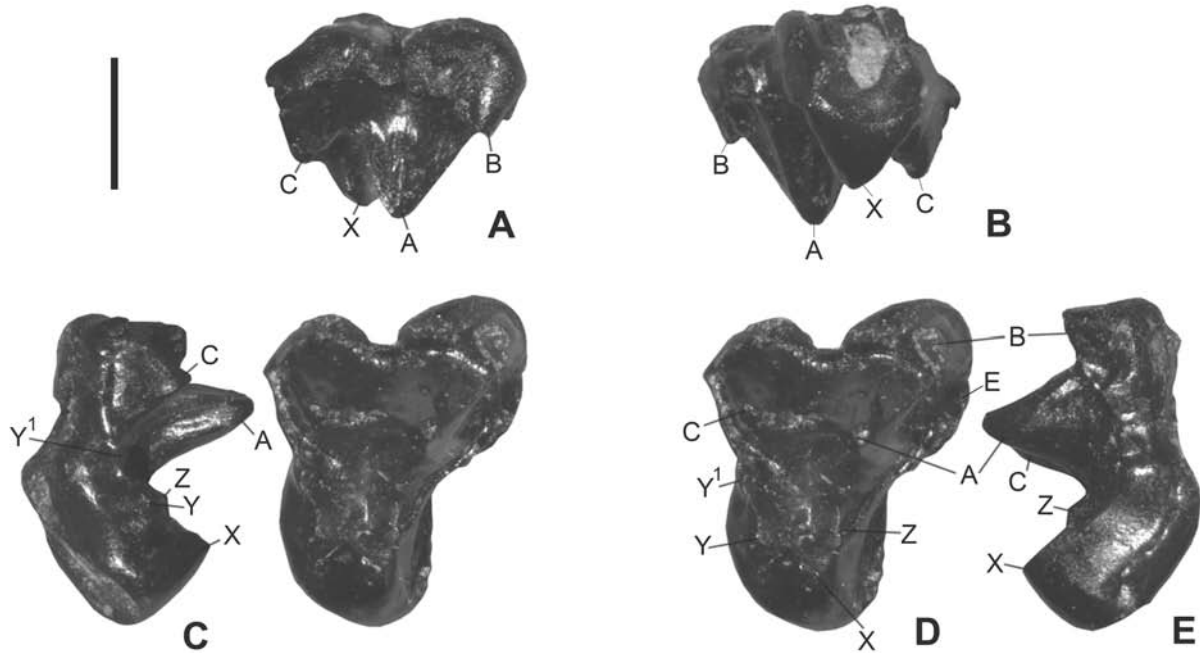


Fig. 4. *Hutegotherium yaomingi* gen. et sp. nov., PIN 5087/6, right upper molariform tooth, in labial (A), lingual (B), distal (C), occlusal (D, stereopair), and mesial (E) views. Berezovsk Quarry, Krasnoyarsk Territory, Russia; Itat Formation, Middle Jurassic (Bathonian).

Abbreviations: A, B, C, E, X, Y, Y¹, and Z – upper molar cusps. Scale bar 1 mm.

the mesial and distal cingula respectively. On cusp A these crests are accentuated by side depressions. There is a prominent ectoflexus, a concavity along the labial border of the crown. The mesial styler cusp B is relatively large and placed exclusively labially to cusps A and C forming a prominent mesiolabial extension of the crown. The cingulum completely surrounds the crown and incorporates cusp B. There is also a minute styler cusp on the ectocingulum, opposite to the center of cusp A. The mesial wall of the crown has a marked socket just lingually to cusp B. Lingual to this socket the mesial cingulum is very wide and its most labial extremity could be considered as an additional mesial styler cusp E. The mesial crest of cusp A extends towards the mesial cingulum halfway between the styler cusps B and E. The mesial cingulum extends lingually towards the lingual cusp X and is analogous to the paracingulum of the tribosphenic dentition. Along the mesial side of the lingual half of the crown, closer to the crown-root junction, there is another mesial cingulum which is analogous of the protocingulum of the tribosphenic dentition. The lingual half of the crown is 64% shorter than the labial half and bears four cusps which fill almost

completely the talon area leaving little space for the talon basin. The largest of these cusps is the mesiolingual cusp X, which is actually placed lingually to the other cusps. It is more than two times higher than the remaining lingual cusps. The distolingual cusps Y and a distinctly smaller more labial additional cusp Y¹ are placed along the distal cingulum (analogue of the postprotocrista of the tribosphenic dentition). An additional mesiolingual cusp Z is located distally to the mesial cingulum and connected to the latter by a short and robust transverse crest. There is also a finer transverse crest extending from cusp Z towards the base of cusp A and meeting the similar opposite crest that extends upwards from the apex of cusp A.

In the holotype dentary fragment the antepenultimate molariform tooth is a little longer and wider and significantly higher than the penultimate molariform tooth. Both preserved molariform teeth have a similar morphology. The crown is dominated by a large main cusp a, occupying the center and distal part of the labial side. The mesiolabial cusp b is two times lower and well separated from cusp a. The distolingual cusp c (broken on the penultimate tooth) is distinctly larger than the mesiolingual cusp g. Cusp c is placed

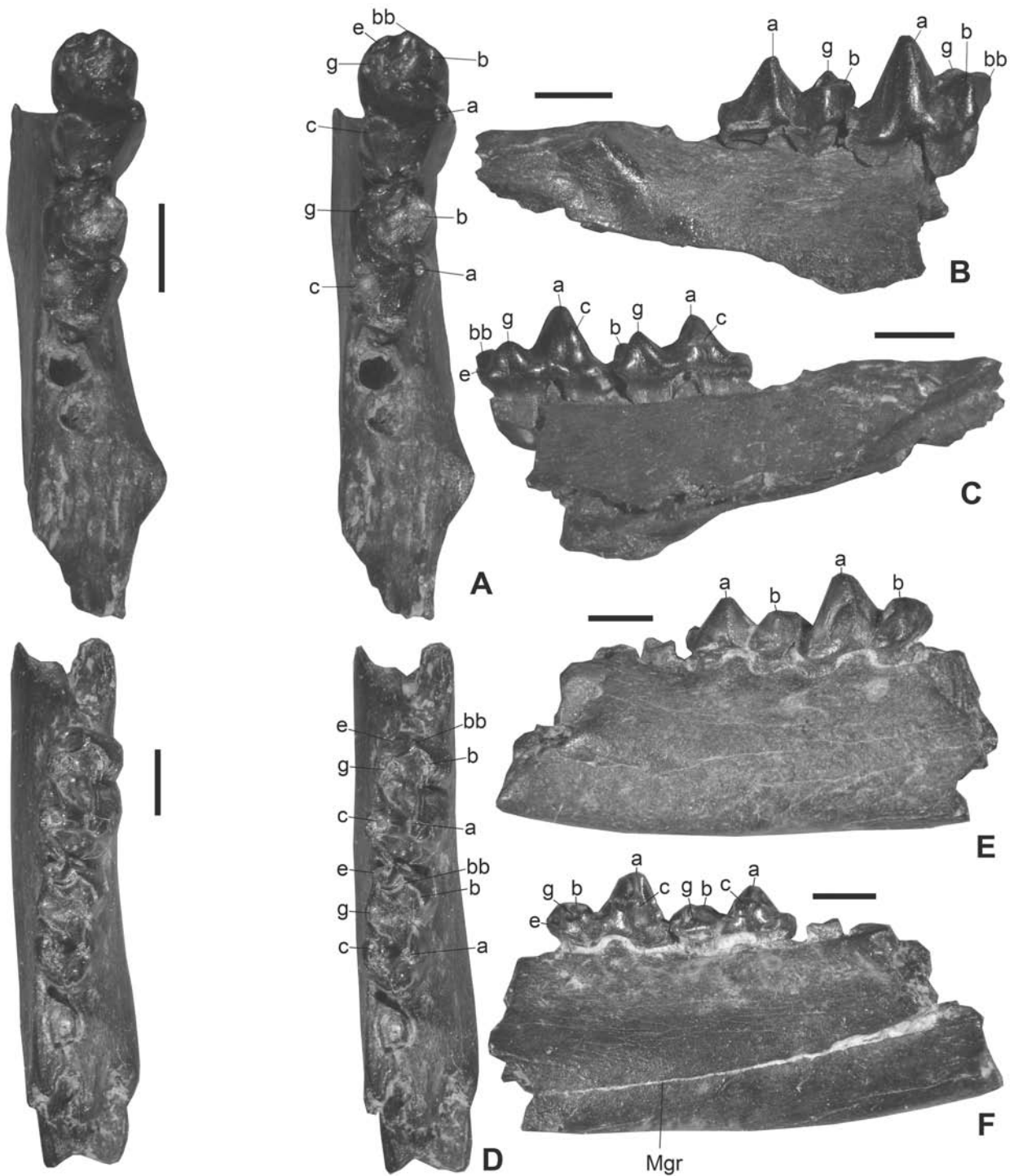


Fig. 5. *Hutegotherium yaomingi* gen. et sp. nov., PM TGU 200/5-BR-2, holotype (A–C) and PIN 5087/8 (D–F), right dentary fragments with antepenultimate and penultimate molariform teeth and alveoli for the ultimate tooth, in occlusal (A and D, stereopairs), labial (B and E), and lingual (C and F) views. Berezovsk Quarry, Krasnoyarsk Territory, Russia; Itat Formation, Middle Jurassic (Bathonian). *Abbreviations:* a, b, bb, c, e, and g – lower molar cusps; Mgr – Meckelian groove. Scale bars 1 mm.

somewhat distal to the level of the main cusp apex. Cusp g is located at the level between cusps b and a on the antepenultimate tooth, or closer to cusp b on the penultimate tooth. There is a short and faint lingual cingulid between the bases of cusps c and g. The pseudotalonid is formed by the crests a-b, b-bb, bb-g, and a-g. The ridge bb-g is characteristically convex towards the pseudotalonid basin. Its external concave side is bordered by a short mesiolingual cingulid (cusp e). The bases of the cusps surrounding the pseudotalonid fill almost all space of the latter. A small pseudotalonid basin is present at the base of cusp a, between the ridges a-b and a-g. It bears two crenulations on the antepenultimate tooth. The longitudinal and transverse crests extending from the apex of the main cusp are robust and accentuated by furrows between them on the lingual side of cusp a. The transverse crests a-g and a-c approximate each other along the lingual side of cusp a. The crest a-c is about two times shorter and directed lingually and somewhat distally towards closely spaced cusp c. The crest a-g is longer because cusp g is more distantly placed. It changes direction from mesiolingual to mesial at the base of cusp a. The distal side of the crown is short and rather simple. It is depressed between a robust vertical crest extending downwards from cusps a and c towards the short but robust distal cingulid. The distal side of cusp c is covered by a deep wear facet on both teeth.

Judging from its alveolus, the ultimate molariform tooth was distinctly shorter than the penultimate tooth. Its alveolus is placed obliquely relative to the tooth row axis and approximates closely the base of the coronoid process.

At the base of the coronoid process on the lingual side, just posterior to the alveolus for the ultimate tooth, there is a marked rugosity apparently representing the facet for the coronoid parodontary bone. Posteroventral to this facet there is an intact dorsal margin of the trough for the postdentary bones. There is no median flange (ridge) present in this region. The cavity of the trough continues gradually into the mandibular canal, which extends anterolaterally labial to the roots of the molariform teeth and without a noticeable tapering anteriorly. Thus the level where the mandibular foramen was situated cannot be established.

The dentition of PIN 5087/8 agrees well with that of the holotype, except that the teeth are more worn. Particularly, cusp g on both teeth is completely worn down while other cusps are still relatively high.

This resembles the wear pattern in the holotype dentary of *Acuodulodon sunae* from the Late Jurassic of China (Hu et al. 2007). PIN 5087/8 preserves the Meckelian groove which is filiform anteriorly and becomes wider below the ultimate molariform tooth. The groove is two times closer to the ventral border of the dentary anteriorly than posteriorly.

Measurements. PIN 5087/6: L=2.0, W=2.5. PM TGU 200/5-BR-2: antepenultimate molariform tooth: L=1.9, W=1.25; penultimate molariform tooth: L=1.8, W=1.1. PIN 5087/8: antepenultimate molariform tooth: L=2.1, W=1.1; penultimate molariform tooth: L=1.7, W=0.9.

PHYLOGENETIC ANALYSIS OF DOCODONTA

Docodontans for long time were considered as a small group of mostly Late Jurassic North American and European mammals (Kron 1979). Recent discoveries of Middle Jurassic and other docodontans in England and Asia demonstrated that it was a much more diverse group with complex interrelationships. These discoveries allowed first cladistic analyses of Docodonta (Sigogneau-Russell 2003a; Martin and Averianov 2004; Pfretzschner et al. 2005; Averianov and Lopatin 2006; Ji et al. 2006). Here we shall concentrate on the critical discussion of the two most recently proposed analyses of Docodonta, by Luo and Martin (2007) and Hu et al. (2007).

Luo and Martin (2007) provided a phylogenetic analysis of Docodonta based on the distribution of 31 characters. Luo and Martin (2007) coded for many upper molar characters *Gondtherium* from the Kota Formation of India, although it is known from a single upper premolar (Prasad and Manhas 2007). *Gondtherium* is excluded from the further consideration here. We think that eight of the 31 characters used in the analyses by Luo and Martin (2007) are uninformative or are incorrectly defined or scored, and we comment on these characters below.

Character 6. All docodontans with known upper dentition were coded as having the posterior transverse crest between cusps C and Y on upper molariform teeth. However, none of the known docodontans have a crest connecting the cusps C and Y. The crest extending distolabially from the cusp Y is continuing into the distal cingulum.

Character 11. *Docodon* and *Dsungarodon* were coded, in contrast to other docodontans, as having

weakly developed or incomplete crest a-c on lower molariform teeth. Many specimens of *Docodon* have a well developed and complete crest a-c (e.g., YPM 10648, 14619, 20992; pers. obs. by AA). On the holotype of *Dsungarodon zuoi* (SGP 2001/21) most of cusp a is broken off, but what is preserved from the crest a-c shows that it is as sharp and prominent as the crest a-g (pers. obs. by AA). Newly collected specimens of *Dsungarodon* (e.g., SGP 2004/24) also have a well developed crest a-c (Martin et al. in press).

Character 16. *Krusatodon*, *Dsungarodon*, and *Tegotherium* were coded as having medially placed cusp d on lower molariform teeth, while in other docodontans and in *Woutersia* this cusp is in labial position. However, on the single previously known non-ultimate lower molariform tooth of *Dsungarodon* (SGP 2001/21) the cusp d is actually missing. On a newly collected specimen it is labial in position (SGP 2004/4; Martin et al. in press). In the holotype of *Krusatodon kirtlingtonensis* (NHM J526) there are two cusps in d position: a smaller labial and a larger medial. In NHM 784 the larger cusp is connected by a crest to the crest a-c (to the peculiar doubled crest a-c on the holotype), not to cusp a where cusp d should be connected. Therefore it is likely that in *Krusatodon* the smaller labial cusp corresponds to cusp d of other docodontans, while the larger median cusp is a neomorph. In NHM 784 there is a rudiment of the real crest a-d directed to the labial corner of the distal portion of the tooth. Cusp d is very small or absent in *Tegotherium*. In *Woutersia* a small cusp d has a similar median position, like in *Tegotherium*.

Character 18. The crest defined in this character (posteromain crest on Fig. 1D in Luo and Martin 2007) is the same crest as the crest a-d defined in the following character 19. Moreover, in scoring of taxa Luo and Martin (2007) confused this crest with the crest a-c: what is angled in *Borealestes*, *Krusatodon*, and *Tashkumyrodon*, is the crest a-c, not a-d. The crest a-d might be complete or incomplete, but it is straight in all docodontans.

Character 22. *Itatodon*, *Borealestes*, *Krusatodon*, *Tashkumyrodon*, and *Haldanodon* were coded as having the mesiolingual cingulid as extending below cusp g, while in *Docodon*, *Castorocauda*, *Simpsonodon*, *Dsungarodon*, *Tegotherium*, and *Sibirotherium* this cingulid is absent or limited to the mesial part of the tooth. However, in *Itatodon*, *Tegotherium*, and *Sibirotherium* there is a well developed lingual cingulid, extending below cusp g and connecting to the mesiolingual

cingulid and these taxa cannot be coded differently for this character. In *Borealestes* and *Krusatodon* the mesiolingual cingulid actually does not extend below cusp b, while it does so in at least some specimens of *Simpsonodon*.

Character 25. The “standart cusplule f” is absent in all docodontans and present in symmetrodontans, *Woutersia*, and *Megazostrodon*. In *Woutersia* it is a prominent ridge rather than a “cusplule,” possibly not homologous to cusp f of symmetrodontans.

Character 28. All dodocontans, *Kuehneotherium*, *Woutersia*, and *Delsatia* were coded as having a cusp triangulation on lower molariform teeth. However, this triangulation is not homologous in these taxa and they may not be coded as representing the same character state. In *Woutersia* and docodontans it is semitriangulation (Averianov and Lopatin 2006), with the crest a-c rotated lingually but the crest a-b preserved in the original longitudinal direction, while in *Kuehneotherium* and *Delsatia*, as well as in other symmetrodontans, it is real triangulation, with both crest a-b and a-c rotated lingually (compare “obtuse triangulation” and “acute triangulation” on fig. 2 in Luo and Martin 2007). *Tikitherium* and *Gondtherium* should be coded by an unknown state for this character because their lower dentition is not known.

Character 29. *Simpsonodon*, *Borealestes*, *Tashkumyrodon*, *Dsungarodon*, *Tegotherium*, and *Sibirotherium* are coded as a having median position of cusp e on the lower molariform teeth, while other docodontans have a lingual position of this cusp. The coding of this character is quite arbitrary. In *Simpsonodon* there is no individualized cusp e but a continuous mesial cingulid that is wrapping around the mesial end of the tooth between the cusps b and g and a mesial and lingual placement of cusp e would be equally possible for this taxon. In *Borealestes* and *Tashkumyrodon* cusp e (=the mesiolingual cingulid) is distinctly lingual to the median axis of the tooth, not median in position. In *Tegotherium* and *Sibirotherium* there are two cusps: cusp e incorporated in the wall of the pseudotalonid and a mesiolingual cingulid ee (terminology after Martin and Averianov 2004). Apparently the cingulid ee is corresponding to cusp e of other docodontans and both these taxa should be coded as having a lingual position of this cusp.

Hu et al. (2007) criticized our previous analysis of Docodonta (Averianov and Lopatin 2006). Some of these critics are accepted in this paper. In particular, we omitted character 3 from Averianov and Lopatin’s

(2006) data matrix. Hu et al. (2007) stated that we should code *Sinoconodon*, *Morganucodon*, *Dinnetherium*, and *Morganucodon* by an unknown state for the wear facet on the labial side of cusp X because they lack the cusp X. Our coding of these taxa by “absent” state was considered to be redundant. However, this procedure contradicts the basic principle of inferring phylogenetic relationships based on synapomorphic characters. Taxa are coded having the plesiomorphic state if they lack the apomorphic state, irrelevant if this is due to the plesiomorphic condition of the morphological structure, or to the lack of this structure.

The main disadvantage of the phylogenetic hypothesis proposed by Hu et al. (2007) is the restriction of the analysis to lower molariform characters only. A phylogenetic reconstruction should be based on all available characters, not on a subset of characters. We cannot agree with Hu et al. (2007: 187) that association of the upper and lower dentition in most docodontan taxa is “ambiguous.” It is absolutely certain for *Docodon* and *Haldanodon* and quite reasonable for other docodontan taxa. It was found erroneous only for *Dsungarodon*, where the supposed upper molariform tooth is now referred to *Tegotherium* (Martin et al. in press). Upper dentitions of docodontans provide a wealth of phylogenetic information and ignoring of this information is not productive.

Hu et al. (2007) provided a number of new characters most of which are incorporated in our phylogenetic analysis, but some of these are problematic and require discussion.

Character 19. Several taxa of docodontans are coded as having the pseudotalonid basin wider “than width at cusp a” (Hu et al. 2007: 192). The definition of this character is not clear. Is this a width of the crown at the cusp a or width of the cusp a? According to our measurements, none of docodontan taxa has the pseudotalonid basin wider than the cusp a.

Character 21. *Docodon*, *Borealestes*, *Dsungarodon* and *Tashkumyrodon* were coded as having the distal basin wider than the mesial (pseudotalonid) basin. The distal (posterior) basin is defined in Hu et al. (2007: fig. 1) as an area between the crests a-d, a-c, and c-d. This area is certainly not wider than the pseudotalonid basin in *Dsungarodon*. The single known lower molariform tooth of *Tashkumyrodon* has a narrow pseudotalonid basin because it is possible m1 (see comments in Appendix under character 23); more distal teeth might have a wider pseudotalonid.

In *Docodon* the distal basin has a distinctly greater area than the pseudotalonid basin, but the width of both basins is approximately the same. The same is true for *Haldanodon* which was coded as having the plesiomorphic state of this character.

Character 22. All taxa analyzed except *Morganucodon* were coded as having the distal cingulid. However, a distal cingulid is actually present in *Morganucodon*.

Character 23. *Borealestes*, *Krusatodon*, and *Dsungarodon* are coded as having a protruding mesiolingual corner, while in other docodontans it is not protruding. However, what is protruding in *Dsungarodon* is rather the mesiolabial corner, not the mesiolingual. This character is better described in the terms of the lower molariform teeth interlock (our character 31, see Appendix).

Character 24. *Borealestes* and *Itatodon*, in contrast to other docodontans, have no broadening of the lower molariform teeth (crown width less than half of maximal crown length). This might be a potentially important character if we knew the tooth position within the tooth row. In docodontans m1 is usually relatively longer and narrower than other molariforms and the width to length ratio increases towards the distal end of the dental series. Comparison of taxa known from isolated teeth by this parameter is problematical because it cannot be excluded that anterior teeth are compared with the posterior ones.

The new analysis was based on the data matrix incorporating 18 taxa and 37 characters (Table 1; see Appendix for explanation and discussion of characters) and conducted using PAUP, version 4.0b10 (Swofford 2002). A branch and bound search algorithm produced eight trees (tree length = 75, CI = 0.67, and RI = 0.84). Support for branches was estimated by Bremer indices calculated with TreeRot (Sorenson 1999). Analysis of character distributions, drawing, and editing of the trees were conducted using Winclada version 1.00.08 (Nixon 1999). The strict consensus tree is shown in Fig. 6.

HOMOGENITY OF THE MIDDLE JURASSIC LAURASIAN MAMMAL FAUNAS

The Middle Jurassic Laurasian mammals are known from three principal assemblages in England, Kyrgyzstan, and West Siberia (Table 2). Also there is a less diverse mammal assemblage from the Middle Jurassic beds at Daohugou in Inner Mongolia,

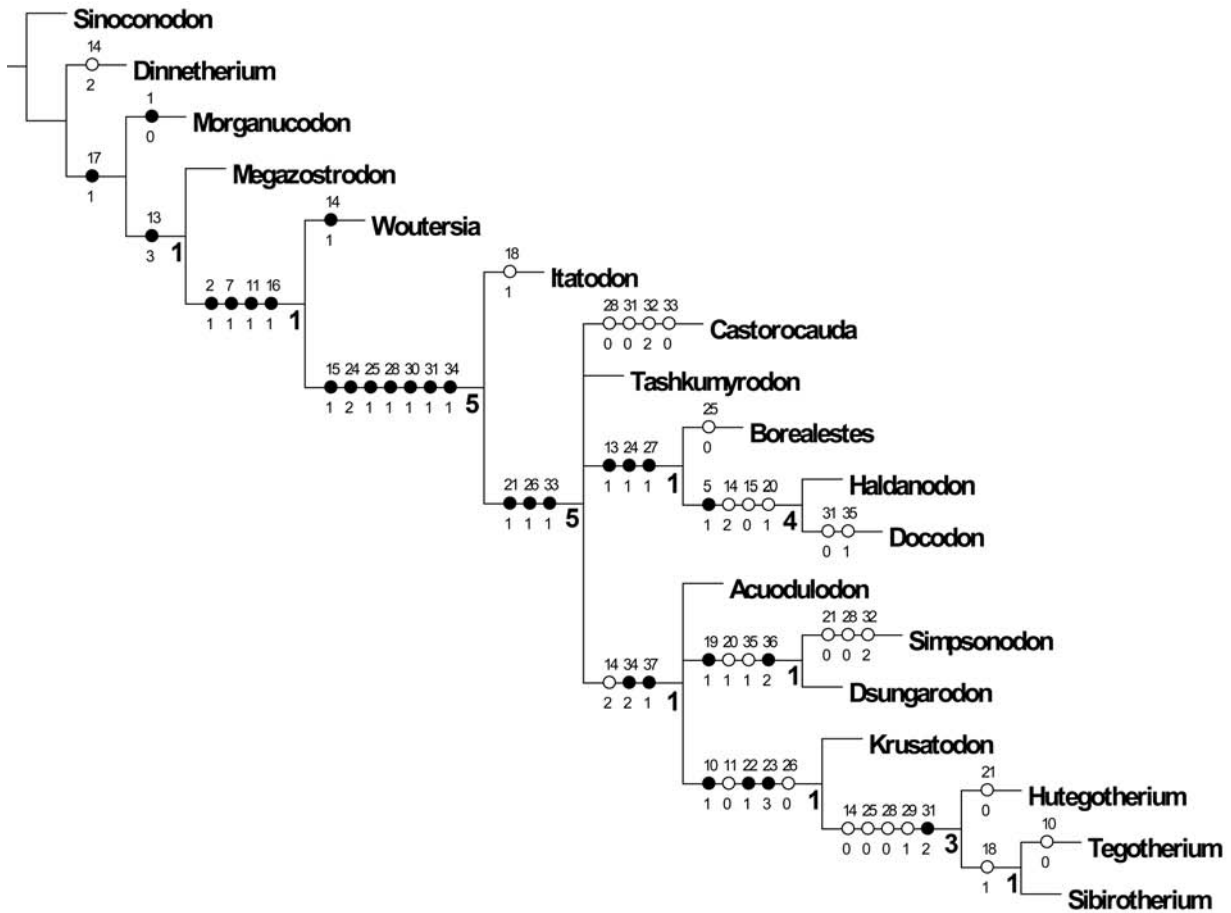


Fig. 6. Strict consensus tree of eight most parsimonious trees produced by branch and bound search algorithm of PAUP 4.0b10 used a dataset present in Table 1. Only unambiguous characters are shown (black circles are nonhomoplasies and white circles are homoplasies). The numbers at the circles are characters (above) and states (below). Bremer support values for clades are listed below the branches.

fauna allotherians are represented by two unidentified eleutherodontids.

Eutriconodontans are an infrequent component of the Middle Jurassic assemblages. Amphilestids are present in all three assemblages, while Triconodontidae have their first appearance in the Balabansai assemblage. The latter assemblage is the most diverse in eutriconodontans: this group is here also represented by the klameliid *Ferganodon*, possible endemics of Central Asia (Martin and Averianov 2007; Martin et al. 2007).

“Symmetrodontans” are apparently the rarest element of the Middle Jurassic assemblages. In Forest Marble they are known from few teeth of *Shuotherium*, described also from the Late Jurassic of China (Chow and Rich 1982; Sigogneau-Russell 1998; Wang et al.

1998). In the Balabansai assemblage “symmetrodontans” are present by a single tooth of Tinodontidae, the oldest record for the family (Martin et al. 2007; Martin and Averianov 2010). “Symmetrodontans” are currently not known in the Itat fauna.

Dryolestidans are also very rare in the Middle Jurassic. In the Forest Marble they are represented by two lower molars of Dryolestidae indet. (Freeman 1979). Few isolated teeth from the Balabansai fauna are attributable to Paurodontidae indet. (Martin et al. 2007; Martin and Averianov 2010). A single edentulous jaw fragment from the Itat fauna was determined as Dryolestidae indet. (Lopatin and Averianov 2006).

Stem zatherians are quite abundant in the Forest Marble and known there by two genera of amphitheriids (Freeman 1976b, 1979; Sigogneau-Russell

Table 2. Comparison of the three principal Middle Jurassic Laurasian mammal faunas at the family level (compiled after Freeman 1976, 1979; Kermack et al. 1987, 1998; Sigogneau-Russell 1998, 2003a, b; Kielan-Jaworowska et al. 2004; Butler and Hooker 2005; Lopatin and Averianov 2006, 2007, 2009; Martin and Averianov 2007, 2010; Martin et al. 2007; Averianov et al. 2008, and original data). *Simpsonodon* (marked by boldface) is common for all three faunas.

Family	Formation / Age / Country		
	Forest Marble Formation / Bathonian / Great Britain	Balabansai Formation / Callovian / Kyrgyzstan	Itat Formation / Bathonian / Russia
Morganucodonta			
Morganucodontidae	<i>Wareolestes</i> *		
Docodonta			
stem Docodontidae	<i>Boreolestes</i>		
Simpsonodontidae	<i>Simpsonodon</i>	cf. <i>Simpsonodon</i>	<i>Simpsonodon</i>
Tegotheriidae	<i>Krusatodon</i>	Tegotheriidae indet.	<i>Hutegotherium</i>
Docodonta indet.	<i>“Shuotherium” kermacki</i>	<i>Tashkumyrodon</i>	<i>Itatodon</i>
Allotheria			
Eleutherodontidae	<i>Eleutherodon</i>		Two forms of Eleutherodontidae indet.
Kermackodontidae	<i>Kermackodon</i>		
Hahnotheriidae	<i>Hahnotherium</i>		
Allotheria indet.	<i>Millsodon, Kirtlingtonia</i>		
Eutriconodonta			
Amphilestidae	<i>Amphilestes</i>	Amphilestidae indet.	Amphilestid-grade Eutriconodonta indet.
Klameliidae		<i>Ferganodon</i>	
Triconodontidae		Triconodontidae indet.	
“Symmetrodonata”			
Shuotheriidae	<i>Shuotherium</i>		
Tinodontidae		Tinodontidae indet.	
Dryolestida			
Dryolestidae	Dryolestidae indet.		Dryolestidae indet.
Paurodontidae		Paurodontidae indet.	
stem Zatheria			
Amphitheriidae	<i>Palaeoxonodon, Kennetheredium</i>	Amphitheriidae indet.	<i>Amphibetulimus</i>

*Possible based on a docodontan premolar, see the text.

2003b). In the Balabansai Svita they are known by a single tooth of Amphitheriidae indet. (Martin et al. 2007; Martin and Averianov 2010). In the Itat assemblage, amphitheriids are represented by a distinct genus (Lopatin and Averianov 2007).

Three factors may contribute to the marked uniformity of the Middle Jurassic mammal faunas of Laurasia:

1) Unity of a huge Laurasian landmass and lack of geographic barriers, like mountain ridges and very big rivers in that time (see paleogeographic maps in e.g., Golonka et al. 1996).

2) Uniform climate and paleoenvironments across the large territory. The paleoenvironmental reconstructions were done for the English and Kyrgyz sites (Kaznyshkin 1988; Kaznyshkin et al. 1990; Metcalf 1995, 1996) but yet have to be produced for the Siberian site.

3) Recency of major diversification events when members of diverging lineages are still very close to each other. This phenomenon is most obvious for docodontans with a number of very similar genera. The Middle Jurassic radiation of mammals has almost no roots in the Early Jurassic (Kielan-Jaworowska et al. 2004; Luo 2007a, b). The most obvious predecessors of this radiation in the Late Triassic and Early Jurassic are the “predocodontan” *Woutersia* and haramiyidan allotherians. The ancestry of the Triassic – Early Jurassic “holotherian” *Kuehneotherium* for the later “symmetrodontans” is highly debated (Luo et al. 2002; Kielan-Jaworowska et al. 2004). The ancestors of eutriconodontans, dryolestidans, and stem zatherians are not found in the Early Jurassic. This suggests that sometime between the Sinemurian and Bajocian a major radiation, which led to the origin of Docodonta, Multituberculata, Eutriconodonta, Dryolestida, and stem Zatheria took place somewhere on the vast Eurasian landmass, most probably in Asia (Siberia?). Exploration of these radiations is one of the major tasks of the Mesozoic paleomammalogy.

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APPENDIX. LIST OF CHARACTERS

Character 1: Length of the ultimate upper pre-molar relative to M1 length (Averianov and Lopatin 2006: character 1, modified):

(0) More than 90%: *Morganucodon* [P4/M1: 103–111%; BMNH M23408, M24626, U224, U516, and others].

(1) Less than 90%: *Sinoconodon* [P2r/M1: 67%; Zhang et al. 1998: fig. 1], *Dinnetherium* [P4/M1: 86%;

Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [P5/M1: 79%, Crompton 1974: fig. 6], *Haldanodon* [P3/M1: 72–78%, Gui Mam 41/75 (6721) and 12/74], *Docodon* [P4/M1: 56%, YPM 13769].

(?) Unknown: *Woutersia*, *Borealestes*, *Simpsonodon*, *Dsungarodon*, *Acuodulodon*, *Krusatodon*, *Castorocauda*, *Itatodon*, *Tashkumyrodon*, *Hutegotherium*, *Tegotherium*, *Sibirotherium*.

Character 2: Ratio of width to labial length for the upper non-ultimate molariform teeth (Sigogneau-Russell 2003a: character 1, modified; Averianov and Lopatin 2006: character 2, modified; Ji et al. 2006: character 1, modified; Luo and Martin 2007: character 1, modified):

(0) Less than 60%: *Sinoconodon* [42–52%: Crompton and Luo 1993: fig. 4.10], *Morganucodon* [49–55%: BMNH M23408, M24626, U224, U516, and others], *Dinnetherium* [52–55%: Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [47–52%: Crompton 1974: fig. 6B].

(1) More than 60%: *Woutersia* [56–89%: MNHN SNP 52W, 426W, 719 and 720], *Borealestes* [incomplete tooth BMNH J871], *Haldanodon*, *Docodon*, *Simpsonodon* [117%: BMNH J249], *Krusatodon* [106%, BMNH J222], *Hutegotherium* [125%, PIN 5987/6], *Tegotherium* [incomplete teeth SGP 2001/23 and 2005/7], *Sibirotherium* [112–143%: PM TGU 120/7-SH1-3 and 120/5-SH1-5].

(?) Unknown: *Dsungarodon*, *Acuodulodon*, *Castorocauda*, *Itatodon*, *Tashkumyrodon*.

Character 3: Number of roots on the upper molariform teeth (Averianov and Lopatin 2006: character 4; Luo and Martin 2007: character 30):

(0) Two: *Sinoconodon*, *Morganucodon* [BMNH M23273, 24626, and others], *Dinnetherium*, *Megazostrodon* [BMNH M26407], *Woutersia* [MNHN SNP 52W, 426W, and others].

(1) Three: *Borealestes* [BMNH J396, J580, and J871], *Simpsonodon* [BMNH J249 and others], *Haldanodon* [GuiMam 16/78/6724, 41/75/6721 and others], *Docodon* [YPM 10647, 13769 and others], *Dsungarodon* [incomplete tooth SGP 2005/15], *Krusatodon* [BMNH J222 and J437], *Hutegotherium* [PIN 5987/6], *Tegotherium* [SGP 2001/23 and 2005/7], *Sibirotherium* [PM TGU 120/7-SH1-3 and 120/5-SH1-5].

(?) Unknown: *Acuodulodon*, *Castorocauda*, *Itatodon*, *Tashkumyrodon*.

Character 4: Constriction of the upper molariform teeth at the centre (Averianov and Lopatin 2006: character 5, modified; Luo and Martin 2007: character 8, modified):

(0) No constriction: *Sinoconodon* [Crompton and Luo 1993: fig. 4.10], *Morganucodon* [BMNH M23408, M24626, U224, U516, and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26407].

(1) Slight constriction (minimal length of constriction 80–95% from labial length): *Woutersia* [87–95%; MNHN SNP 88, 719, and 720].

(2) Strong constriction (minimal length of constriction less than 80% from labial length): *Borealestes* [incomplete teeth BMNH J396, J580, and J871], *Haldanodon* [52–57%; Gui Mam 16/78 (6724)], *Docodon* [45–53%; YPM 10647], *Simpsonodon* [74%; BMNH J249], *Dsungarodon* [incomplete tooth SGP 2005/15], *Krusatodon* [55–61%; BMNH J222 and J437], *Hutegotherium* [61%, PIN 5987/6], *Tegotherium* [incomplete teeth SGP 2001/23 and 2005/7], *Sibirotherium* [47–63%; PM TGU 120/7-SH1-3 and 120/5-SH1-5].

(?) Unknown: *Acuodulodon*, *Castorocauda*, *Itatodon*, *Tashkumyrodon*.

Character 5: The cusp C on the upper molariform teeth (Luo and Martin 2007: character 5, modified):

(0) Large and separated from the cusp A: *Sinoconodon* [Crompton and Luo 1993: fig. 4.1], *Morganucodon* [BMNH M24626 and M24633], *Dinnetherium* [Crompton and Luo 1993: fig. 4.15], *Megazostrodon* [BMNH M26407], *Woutersia* [MNHN SNP 719 and 720], *Borealestes* [BMNH J396, J 580, and J871], *Simpsonodon* [BMNH J249], *Krusatodon* [BMNH J222 and J667], *Hutegotherium* [PIN 5987/6], *Tegotherium* [SGP 2001/23 and 2005/7], *Sibirotherium* [PM TGU 120/7-Sh1-3 and 120/5-Sh1-5].

(1) Reduced and twinned with the cusp A: *Haldanodon* [GuiMam VJ1008-155 and VJ1009-155], *Docodon* [USNM 2715].

(?) Unknown: *Dsungarodon*, *Acuodulodon*, *Castorocauda*, *Itatodon*, *Tashkumyrodon*.

Comments: In *Woutersia* the cusp C approximated to the cusp A but not reduced in size. This taxon is coded here by plesiomorphic state for this character, contra coding in Martin and Luo (2007).

Character 6: The cusp E lingual to the cusp B on the upper molariform teeth (Luo and Martin 2007: character 7, modified):

(0) Present: *Morganucodon* [BMNH M24633], *Dinnetherium* [Crompton and Luo 1993: fig. 4.15], *Megazostrodon* [BMNH M26407], *Woutersia* [MNHN SNP 52W and 719], *Simpsonodon* [BMNH J249 and J783], *Krusatodon* [BMNH J222 and J437],

Hutegotherium [PIN 5987/6], *Tegotherium* [SGP 2004/23], *Sibirotherium* [PM TGU 120/7-SH1-3].

(1) Absent: *Haldanodon* [GuiMam VJ1008-155 and VJ1009-155], *Docodon* [USNM 2715].

(?) Unknown: *Sinoconodon*, *Borealestes*, *Dsungarodon*, *Acuodulodon*, *Castorocauda*, *Itatodon*, *Tashkumyrodon*.

Comments: Luo and Martin (2007) coded *Borealestes* and *Dsungarodon* as having no cusp E. However, none of the figured upper molariform teeth attributable to *Borealestes* have preserved the mesiolabial corner of the tooth (Sigogneau-Russell 2003a and pers. obs. by AA). Similarly, the only upper molariform tooth referred to *Dsungarodon* (SGP 2001/23; Pfreundschner et al. 2005: fig. 2A) lacks the mesiolabial corner of the tooth where the cusp E should be placed. Now this specimen is referred to *Tegotherium* (Martin et al. in press). Both *Borealestes* and *Dsungarodon* are coded here by unknown state for this character.

Character 7: The cusp X on the upper molariform teeth (Averianov and Lopatin 2006: character 6):

(0) Absent: *Sinoconodon* [Crompton and Luo 1993: fig. 4.10], *Morganucodon* [BMNH M23408, M24626, U224, U516, and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26407].

(1) Present: *Woutersia* [MNHN SNP 719; absent in other, possibly anterior teeth], *Borealestes* [BMNH J396, J580, and J871], *Haldanodon* [Gui Mam 16/78 (6724)], *Docodon* [YPM 10647], *Simpsonodon* [BMNH J249], *Dsungarodon* [SGP 2005/15], *Krusatodon* [BMNH J222 and J437], *Hutegotherium* [PIN 5987/6], *Tegotherium* [SGP 2001/23 and 2005/7], *Sibirotherium* [PM TGU 120/7-SH1-3 and 120/5-SH1-5].

(?) Unknown: *Acuodulodon*, *Castorocauda*, *Itatodon*, *Tashkumyrodon*.

Character 8: Wear facets on the labial side of cusp X (Averianov and Lopatin 2006: character 7; Ji et al. 2006: character 2, modified; Luo and Martin 2007: character 2, modified):

(0) Absent, or cusp X absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon* [these four taxa have not cusp X], *Woutersia* [MNHN SNP 719].

(1) Present: *Haldanodon* [VJ 1008-155], *Docodon* [YPM 10647], *Borealestes* [BMNH J580], *Simpsonodon* [BMNH J249], *Dsungarodon* [SGP 2005/15], *Krusatodon* [BMNH J667], *Hutegotherium* [PIN 5987/6], *Tegotherium* [SGP 2001/23 and

2005/7], *Sibirotherium* [PM TGU 120/7-SH1-3 and 120/5-SH1-5].

(?) Unknown: *Acuodulodon*, *Castorocauda*, *Itatodon*, *Tashkumyrodon*.

Character 9: Cusp Y (Averianov and Lopatin 2006: character 8; Ji et al. 2006: character 3; Luo and Martin 2007: character 4, modified):

(0) Absent: *Sinoconodon* [Crompton and Luo 1993: fig. 4.10], *Morganucodon* [BMNH M23408, M24626, U224, U516, and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26407], *Woutersia* [absent in all known teeth except possibly MNHN SNP 719].

(1) Present: *Borealestes* [BMNH J396, J580, and J871], *Haldanodon* [Gui Mam 16/78 (6724)], *Docodon* [YPM 10647], *Simpsonodon* [BMNH J249], *Dsungarodon* [SGP 2005/15], *Krusatodon* [BMNH J222 and J437], *Hutegotherium* [PIN 5987/6], *Tegotherium* [SGP 2001/23 and 2005/7], *Sibirotherium* [PM TGU 120/7-SH1-3 and 120/5-SH1-5].

(?) Unknown: *Acuodulodon*, *Castorocauda*, *Itatodon*, *Tashkumyrodon*.

Character 10: Cusp Z (Averianov and Lopatin 2006: character 9):

(0) Absent: *Sinoconodon* [Crompton and Luo 1993: fig. 4.10], *Morganucodon* [BMNH M23408, M24626, U224, U516, and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26407], *Woutersia* [MNHN SNP 719, 720], *Borealestes* [BMNH J396 and J580], *Haldanodon* [Gui Mam 16/78 (6724)], *Docodon* [YPM 10647], *Simpsonodon* [BMNH J249], *Dsungarodon* [SGP 2005/15], *Tegotherium* [SGP 2001/23 and 2005/7].

(1) Present: *Krusatodon* [BMNH J222, J437 and J667], *Hutegotherium* [PIN 5987/6], *Sibirotherium* [PM TGU 120/7-SH1-3 and 120/5-SH1-5].

(?) Unknown: *Acuodulodon*, *Castorocauda*, *Itatodon*, *Tashkumyrodon*.

Comments: Cusp Z is present in a lingual tooth fragment BMNH J404 attributed to *Borealestes* (Sigogneau-Russell 2003a: fig. 4B), but absent in other, more complete specimens. BMNH J404 may belong to a tegotheriid-like docodontan currently recognized in the Forest Marble fauna (Martin et al. in press).

Character 11: Crest A-X (Averianov and Lopatin 2006: character 10; Luo and Martin 2007: character 3, modified):

(0) Absent, or cusp X absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon* [these four

taxa have not cusp X], *Krusatodon* [BMNH J222, J437 and J667], *Hutegotherium* [PIN 5987/6], *Tegotherium* [SGP 2001/23 and 2005/7], *Sibirotherium* [PM TGU 120/7-SH1-3 and 120/5-SH1-5].

(1) Present at least partially: *Woutersia* [MNHN SNP 719], *Borealestes* [BMNH J396, J580, and J871], *Haldanodon* [Gui Mam 16/78 (6724)], *Docodon* [YPM 10647], *Simpsonodon* [BMNH J249], *Dsungarodon* [SGP 2005/15].

(?) Unknown: *Acuodulodon*, *Castorocauda*, *Itatodon*, *Tashkumyrodon*.

Character 12: Lower canine (Averianov and Lopatin 2006: character 11; Luo and Martin 2007: character 31):

(0) One-rooted: *Sinoconodon* [Crompton and Luo 1993: fig. 4.2], *Morganucodon* [BMNH U22a/1], *Dinnetherium* [Crompton and Luo 1993: fig. 4.4], *Megazostrodon* [Gow 1986: fig. 7].

(1) Two-rooted: *Haldanodon* [VJ 1001-155], *Docodon* [YPM 11826], *Dsungarodon* [SGP 2004/18], *Acuodulodon* [Hu et al. 2007: fig. 2], *Castorocauda* [Ji et al. 2006: fig. 2F], *Sibirotherium* [PM TGU 120/9-34].

(?) Unknown: *Woutersia*, *Borealestes*, *Simpsonodon*, *Krusatodon*, *Itatodon*, *Tashkumyrodon*, *Hutegotherium*, *Tegotherium*.

Character 13: Number of lower premolars (Averianov and Lopatin 2006: character 12, modified):

(0) Two: *Sinoconodon* [two, Zhang et al. 1998: fig. 2].

(1) Three-four: *Borealestes* [three based on a small size of the most mesial premolar in the anteriorly incomplete dentary, Waldman and Savage 1972: fig. 2], *Haldanodon* [three, Martin and Nowotny 2000: 94], *Docodon* [three-four, Simpson 1929: fig. 38].

(2) Four-five: *Dinnetherium* [four, Kielan-Jaworowska et al. 2004: 180], *Morganucodon* [four-five, Kielan-Jaworowska et al. 2004: 174].

(3) Five-six: *Megazostrodon* [five, Kielan-Jaworowska et al. 2004: 179], *Castorocauda* [five, Ji et al. 2006: fig. 2F], *Sibirotherium* [six, PM TGU 120/9-34].

(?) Unknown: *Woutersia*, *Simpsonodon*, *Dsungarodon*, *Acuodulodon*, *Krusatodon*, *Itatodon*, *Tashkumyrodon*, *Hutegotherium*, *Tegotherium*.

Character 14: Cusp b (Martin and Averianov 2004: character 1, modified; Pfretzschner et al. 2005: character 1, modified; Averianov and Lopatin 2006: character 14, modified; Hu et al. 2007: character 3, modified):

(0) Smaller than cusp c: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Megazostrodon* [BMNH M26507], *Borealestes* [Waldman and Savage 1972: fig. 2], *Castorocauda* [Ji et al. 2006: fig. 2B], *Itatodon* [PM TGU 200/3-BR-7], *Tashkumyrodon* [ZIN 85279], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167], *Sibirotherium* [PM TGU 16/5-22 and others].

(1) Approximately equal to cusp c: *Woutersia* [MNHN SNP 101, 517, 975 and others].

(2) Larger than cusp c: *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Haldanodon* [VJ 1001-155 and others], *Docodon* [YPM 11826 and others], *Simpsonodon* [BMNH J100, 251 and others], *Dsungarodon* [SGP 2001/21], *Acuodulodon* [Hu et al. 2007: fig. 4], *Krusatodon* [BMNH J526 and J784].

Character 15: Cusp b (Martin and Averianov 2004: character 1, modified; Pfretzschner et al. 2005: character 1, modified; Averianov and Lopatin 2006: character 14, modified; Ji et al. 2006: character 16, modified; Hu et al. 2007: character 2; Luo and Martin 2007: character 23, modified):

(0) Approximated to cusp a: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Megazostrodon* [BMNH M26507], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Woutersia* [MNHN SNP 101, 517 and others], *Haldanodon* [Gui Mam 141/76 and others], *Docodon* [YPM 11826 and others].

(1) Well separated from cusp a by a notch: *Borealestes* [Waldman and Savage 1972: fig. 2], *Simpsonodon* [BMNH J100, 251 and others], *Dsungarodon* [SGP 2001/21], *Acuodulodon* [Hu et al. 2007: fig. 4], *Krusatodon* [BMNH J526 and J784], *Castorocauda* [Ji et al. 2006: fig. 2B], *Itatodon* [PM TGU 200/3-BR-7], *Tashkumyrodon* [ZIN 85279], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167], *Sibirotherium* [PM TGU 16/5-22 and others].

Character 16: Position of cusp c relative to cusp a (Averianov and Lopatin 2006: character 15; Hu et al. 2007: characters 1 and 9, modified; Luo and Martin 2007: character 9, modified):

(0) Distal to cusp a: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Megazostrodon* [BMNH M26507], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5].

(1) Distolingual to cusp a: *Woutersia* [MNHN SNP 101, 517 and others], *Borealestes* [Waldman and

Savage 1972: fig. 2], *Haldanodon* [Gui Mam 141/76 and others], *Docodon* [YPM 11826 and others], *Simpsonodon* [BMNH J100, 251 and others], *Dsungarodon* [SGP 2001/21], *Acuodulodon* [Hu et al. 2007: fig. 4], *Krusatodon* [BMNH J526 and J784], *Castorocauda* [Ji et al., 2006: fig. 2B], *Itatodon* [PM TGU 200/3-BR-7], *Tashkumyrodon* [ZIN 85279], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167], *Sibirotherium* [PM TGU 16/5-22 and others].

Character 17: Cusp g (Sigogneau-Russell 2003a: character 5, modified; Martin and Averianov 2004: character 2, modified; Pfretzschner et al. 2005: character 2, modified; Averianov and Lopatin 2006: character 16; Ji et al. 2006: character 7, modified; Hu et al. 2007: characters 5 and 6, modified; Luo and Martin 2007: characters 10 and 12, modified):

(0) absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5].

(1) small: *Morganucodon* [BMNH M16536 and others], *Megazostrodon* [BMNH M26507], *Borealestes* [Waldman and Savage 1972: fig. 2], *Haldanodon* [Gui Mam 141/76 and others], *Docodon* [YPM 11826 and others], *Castorocauda* [Ji et al. 2006: fig. 2B].

(2) large, almost equal to cusp c: *Woutersia* [MNHN SNP 101, 975 and others], *Simpsonodon* [BMNH J100, 251 and others], *Dsungarodon* [SGP 2001/21], *Acuodulodon*, *Krusatodon* [BMNH J526 and J784], *Itatodon* [PM TGU 200/3-BR-7], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167], *Sibirotherium* [PM TGU 16/5-22 and others].

(?) Unknown: *Tashkumyrodon*.

Character 18: Development of lingual cingulid (Averianov and Lopatin 2006: character 17):

(0) Cingulid lingual to cusps g and c absent, g might be cingulid cusp: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 975 and others], *Borealestes* [Waldman and Savage 1972: fig. 2; might be present in some specimens of *B. mussettae*], *Haldanodon* [Gui Mam 141/76 and others], *Docodon* [YPM 11826 and others], *Simpsonodon* [BMNH J100, 251 and others], *Dsungarodon* [SGP 2001/21], *Acuodulodon*, *Krusatodon* [BMNH J526 and J784], *Castorocauda* [Ji et al. 2006: fig. 2B], *Tashkumyrodon* [ZIN 85279], *Hutegotherium* [PIN 5987/5].

(1) Present: *Itatodon* [PM TGU 200/3-BR-7], *Tegotherium* [PIN 4174/167], *Sibirotherium* [PM TGU 16/5-22 and others].

Character 19: Cusp e (Martin and Averianov 2004: character 3; Pfretzschner et al. 2005: character 3; Averianov and Lopatin 2006: character 18, modified; Ji et al. 2006: character 14, modified; Hu et al. 2007: character 8; Luo and Martin 2007: character 21, modified):

(0) Present: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 975 and others], *Borealestes* [Waldman and Savage 1972: fig. 2], *Haldanodon* [Gui Mam 141/76 and others], *Docodon* [YPM 11826 and others], *Krusatodon* [BMNH J526 and J784], *Castorocauda* [Ji et al. 2006: fig. 2B], *Tashkumyrodon* [ZIN 85279], *Itatodon* [PM TGU 200/3-BR-7], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167], *Sibirotherium* [PM TGU 16/5-22 and others].

(1) Absent: *Simpsonodon* [BMNH J100, 251 and others], *Dsungarodon* [SGP 2001/21].

(?) Unknown: *Acuodulodon*.

Comments: According to Hu et al. (2007), the cusp e in *Acuodulodon* is vestigial or absent. However, in the single known non-ultimate lower molariform tooth the mesial area is heavily worn and it could be gone by wear. *Acuodulodon* is coded here by unknown state for this character.

Character 20: Mesiolingual cingulid (Hu et al. 2007: character 17):

(0) Narrow or vestigial: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 975 and others], *Borealestes* [BMNH J239, J495, and J610], *Krusatodon* [BMNH J526 and J784], *Castorocauda* [Ji et al. 2006: fig. 2B], *Tashkumyrodon* [ZIN 85279], *Itatodon* [PIN 5087/2 and PM TGU 200/3-BR-7], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-22 and others].

(1) Wide: *Simpsonodon* [BMNH J100, 251 and others], *Dsungarodon* [SGP 2001/21], *Haldanodon* [Gui Mam 141/76, VJ 1001-155 and others], *Docodon* [USNM 2710 and others].

(?): Unknown: *Acuodulodon*.

Character 21: Additional cusp dd distal to cusp c and lingual to cusp d (Martin and Averianov 2004: character 4, modified; Pfretzschner et al. 2005: character 4, modified; Averianov and Lopatin 2006: character 20, modified; Ji et al. 2006: character 17; Hu et al. 2007: character 7; Luo and Martin 2007: character 24, modified):

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975], *Simpsonodon* [BMNH J100, J251, and J761], *Itatodon* [PM TGU 200/3-BR-7], *Hutegotherium* [PIN 5987/5].

(1) Present: *Borealestes* [Waldman and Savage 1972: fig. 2], *Haldanodon* [Gui Mam 141/76 and VJ 1001/155], *Docodon* [YPM 13767 and others], *Krusatodon* [BMNH J526 and J784], *Dsungarodon* [SGP 2004/24], *Acuodulodon* [Hu et al., 2007: fig. 4], *Castorocauda* [Ji et al. 2006: fig. 2B], *Tashkumyrodon* [ZIN 85279], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-14 and others].

Comments: Ji et al. (2006) coded *Dsungarodon* as lacking the cusp dd (=cusp f), apparently following incorrect description of the distally incomplete holotype tooth in Pfretzschner et al. (2005). A newly collected specimen SGP 2004/24 has a well developed cusp dd (Martin et al. in press).

Character 22: A neomorph cusp bb mesiolingual to the cusp b (Hu et al. 2007: character 4, modified).

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975], *Borealestes* [Waldman and Savage 1972: fig. 2], *Haldanodon* [Gui Mam 141/76 and VJ 1001/155], *Docodon* [USNM 2710, YPM 13767 and others], *Simpsonodon* [BMNH J100, J251, and J761], *Dsungarodon* [SGP 2001/21], *Acuodulodon* [Hu et al., 2007: fig. 4], *Castorocauda* [Ji et al. 2006: fig. 2C], *Itatodon* [PIN 5087/2 and PM TGU 200/3-BR-7], *Tashkumyrodon* [ZIN 85279].

(1) Present: *Krusatodon* [BMNH J784], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-22 and others].

Character 23: Pseudotalonid in molariform teeth distal to m1 (Sigogneau-Russell 2003a: character 2, modified; Martin and Averianov 2004: character 5, modified; Pfretzschner et al. 2005: character 5; Averianov and Lopatin 2006: character 21, modified; Ji et al. 2006: character 6, modified; Hu et al. 2007: character 18, modified; Luo and Martin 2007: character 13, modified):

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975].

(1) Present and bordered mesiolingually by crest b-g: *Borealestes* [Waldman and Savage 1972: fig. 2], *Haldanodon* [Gui Mam 141/76 and VJ 1001/155], *Docodon* [USNM 2710, YPM 13767 and others], *Simpsonodon* [BMNH J100, J251, and J761], *Dsungarodon* [SGP 2001/21], *Acuodulodon* [Hu et al. 2007: fig. 4], *Castorocauda* [Ji et al. 2006: fig. 2C].

(2) Present and bordered mesiolingually by crest e-g: *Itatodon* [PIN 5087/2 and PM TGU 200/3-BR-7].

(3) Present and bordered mesiolingually by crest bb-g: *Krusatodon* [BMNH J784], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-22 and others].

(?) Unknown: *Tashkumyrodon*.

Comments: In the holotypes of *Krusatodon kirtlingtonensis* (BMNH J526) and *Tashkumyrodon desideratus* (ZIN 85279) the pseudotalonid is relatively small and narrow, bordered by crests a-b, b-g, and a-g, and technically should be coded by state 1 of this character. However, we consider these teeth as the first molariform teeth which have reduced pseudotalonid because of a presumably little developed lingual cusp on the ultimate upper premolar. In a referred specimen of *Krusatodon* (BMNH J784; Sigogneau-Russell 2003a: fig. 3A) the pseudotalonid is larger and bordered by crests a-b, b-bb, bb-g, and a-g and thus *Krusatodon* is coded here by the state 3 of this character. For *Tashkumyrodon* the lower molariform teeth distal to m1 are not known and it is coded here by unknown state.

Character 24: Crest a-g (Averianov and Lopatin 2006: character 22, modified; Ji et al. 2006: character 8, modified; Hu et al. 2007: characters 10 and 11, modified; Luo and Martin 2007: character 14, modified):

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975].

(1) Weak ridge: *Borealestes* [Waldman and Savage 1972: fig. 2], *Haldanodon* [Gui Mam 141/76 and VJ 1001/155], *Docodon* [USNM 2710 and others].

(2) Raised ridge: *Simpsonodon* [BMNH J100, J251, and J761], *Dsungarodon* [SGP 2001/21], *Krusatodon* [BMNH J526 and J784], *Castorocauda* [Ji et al. 2006: fig. 2C], *Itatodon* [PIN 5087/2 and PM TGU 200/3-BR-7], *Tashkumyrodon* [ZIN 85279], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-22 and others].

(?) Unknown: *Acuodulodon*.

Comments: According to Hu et al. (2007), the crest a-g is absent in *Acuodulodon*. However, in the single known non-ultimate lower molariform tooth the mesial area is heavily worn and it could be gone by wear (a remnant of this crest can be seen in Hu et al. 2007: fig. 4). *Acuodulodon* is coded here by unknown state for this character.

Character 25: Crest b-e (Martin and Averianov 2004: character 6, modified; Pfretzschner et al. 2005: character 6; Averianov and Lopatin 2006: character 23; Ji et al. 2006: character 18, modified; Hu et al. 2007: character 16; Luo and Martin 2007: character 26, modified):

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975], *Borealestes* [Waldman and Savage 1972: fig. 2], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-22 and others].

(1) Present: *Haldanodon* [Gui Mam 141/76], *Docodon* [YPM 11826 and 13767], *Simpsonodon* [BMNH J100, J251, and J761], *Dsungarodon* [SGP 2001/21], *Krusatodon* [BMNH J526 and J784], *Castorocauda* [Ji et al. 2006: fig. 2C], *Itatodon* [PIN 5087/2 and PM TGU 200/3-BR-7], *Tashkumyrodon* [ZIN 85279].

(?) Unknown: *Acuodulodon*.

Comments: According to Hu et al. (2007), the crest b-e in is absent in *Acuodulodon*. However, the in the single known non-ultimate lower molariform tooth the mesial area is heavily worn and it could be gone by wear. *Acuodulodon* is coded here by unknown state for this character.

Character 26: Crest b-g (Martin and Averianov 2004: character 7; Pfretzschner et al. 2005: character 7; Averianov and Lopatin 2006: character 24; Ji et al.

2006: character 13, modified; Hu et al. 2007: character 12; Luo and Martin 2007: character 20, modified):

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975].

(1) Present: *Borealestes* [Waldman and Savage 1972: fig. 2], *Haldanodon* [Gui Mam 141/76], *Docodon* [USNM 2710 and YPM 13767], *Simpsonodon* [BMNH J100, J251, and J761], *Dsungarodon* [SGP 2001/21], *Acuodulodon* [Hu et al. 2007: fig. 4], *Krusatodon* [BMNH J784], *Castorocauda* [Ji et al. 2006: fig. 2C], *Itatodon* [PIN 5087/2 and PM TGU 200/3-BR-7], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-22 and others].

(?) Unknown: *Tashkumyrodon*.

Comments: In the holotypes of *Krusatodon kirtlingtonensis* (BMNH J526) and *Tashkumyrodon desideratus* (ZIN 85279) there is crest b-g, while in an additional, more distal tooth of *Krusatodon* BMNH J784 (see comments to the character 20), the crest is b-e-g. Reduction of the cusp e on the first lower molariform teeth in these taxa is connected with the small size of the pseudotalonid and apparently not characteristic for the more distal molariform teeth.

Character 27: Crest a-d (Averianov and Lopatin 2006: character 25; Ji et al. 2006: character 11, modified; Hu et al. 2007: character 14, modified; Luo and Martin 2007: character 19, modified):

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al., 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975], *Itatodon* [PIN 5087/2 and PM TGU 200/3-BR-7], *Tashkumyrodon* [ZIN 85279].

(1) Incomplete: *Borealestes* [BMNH J239 and J495], *Haldanodon* [Gui Mam 141/76], *Docodon* [YPM 13767].

(2) Complete: *Simpsonodon* [BMNH J100 and J251], *Dsungarodon* [SGP 2004/24], *Acuodulodon* [Hu et al. 2007: fig. 4], *Krusatodon* [BMNH J526 and J784], *Castorocauda* [Ji et al. 2006: fig. 2C], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-22 and others].

Comments: Ji et al. (2006) coded *Dsungarodon* as having incomplete crest a-d. At that time only single

lower non-ultimate molar was known for *Dsungarodon* (holotype SGP 2001/21) which has distal portion of the crown housing the cusp d broken off (contra description in Pfreundschuh et al. 2005). In a newly collected specimen SGP 2004/24 the cusp d is preserved and connects by a continuous crest with the cusp a (Martin et al. in press).

Character 28: Crest c-d (Averianov and Lopatin 2006: character 26; Ji et al. 2006: character 9, modified; Hu et al. 2007: character 13; Luo and Martin 2007: character 15, modified):

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975], *Castorocauda* [Ji et al. 2006: fig. 2C], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-22 and others].

(1) Present: *Borealestes* [BMNH J610 and J836], *Haldanodon* [Gui Mam 141/76 and VJ 1001/155], *Docodon* [YPM 13767], *Simpsonodon* [BMNH J100 and J251], *Dsungarodon* [SGP 2004/24], *Acuodulodon* [Hu et al. 2007: fig. 4], *Krusatodon* [BMNH J526 and J784], *Itatodon* [PM TGU 200/3-BR-7], *Tashkumyrodon* [ZIN 85279].

Character 29: Crest c-dd (Hu et al. 2007: character 15):

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975], *Borealestes* [Waldman and Savage 1972: fig. 2], *Simpsonodon* [BMNH J100, J251, and J761], *Dsungarodon* [SGP 2004/24], *Acuodulodon* [Hu et al. 2007: fig. 4], *Krusatodon* [BMNH J526 and J784], *Itatodon* [PM TGU 200/3-BR-7].

(1) Present: *Haldanodon* [Gui Mam 141/76 and VJ 1001/155], *Docodon* [YPM 13767 and others], *Castorocauda* [Ji et al. 2006: fig. 2], *Tashkumyrodon* [ZIN 85279], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-14 and others].

Comments: In *Hutegotherium* the crest c-dd is present and well developed, although there is no cusp dd.

Character 30: Distal basin on lower molariform teeth (Hu et al. 2007: character 20):

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A], *Morganucodon* [BMNH M16536

and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975].

(1) Present: *Borealestes* [Waldman and Savage 1972: fig. 2], *Haldanodon* [GuiMam 141/76 and 1001/155], *Docodon* [YPM 13767 and others], *Simpsonodon* [BMNH J100, J251, and J761], *Dsungarodon* [SGP 2004/24], *Acuodulodon* [Hu et al. 2007: fig. 4], *Krusatodon* [BMNH J526 and J784], *Castorocauda* [Ji et al. 2006: fig. 2], *Itatodon* [PM TGU 200/3-BR-7], *Tashkumyrodon* [ZIN 85279], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-14 and others].

Character 31: Lower molar interlock (Ji et al. 2006: character 19, modified; Averianov and Lopatin 2006: character 27, modified; Ji et al. 2006: character 19, modified; Luo and Martin 2007: character 27, modified):

(0) b-d-e: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975], *Docodon* [USNM 2710], *Castorocauda* [Ji et al. 2006: fig. 2C].

(1) d-e-dd: *Borealestes* [BMNH J610, J836, and others], *Haldanodon* [Gui Mam 141/76], *Simpsonodon* [BMNH J100], *Dsungarodon* [SGP 2001/21], *Krusatodon* [BMNH J526], *Itatodon* [PM TGU 200/3-BR-7], *Tashkumyrodon* [ZIN 85279].

(2) d-bb-dd: *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-22 and others].

(?) Unknown: *Acuodulodon*.

Character 32: Cusp c on ultimate lower molariform tooth (Averianov and Lopatin 2006: character 28, modified):

(0) Developed as in previous molariform teeth: *Sinoconodon* [Crompton and Luo 1993: fig. 4.2], *Morganucodon* [BMNH M24560 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507].

(1) Greatly reduced: *Haldanodon* [m5, Gui Mam 141/76 and VJ 1017/155], *Dsungarodon* [SGP 2001/22], *Acuodulodon* [Hu et al. 2007: fig. 4], *Itatodon* [PIN 5087/2], *Tegotherium* [SGP 2004/5].

(2) Absent: *Simpsonodon* [PIN 5087/5], *Castorocauda* [Ji et al. 2006: fig. 2B].

(?) Unknown: *Woutersia*, *Borealestes*, *Docodon*, *Krusatodon*, *Tashkumyrodon*, *Sibirotherium*, *Hutegotherium*.

Character 33: Pseudotalonid basin on m1 (new character):

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Castorocauda* [Ji et al. 2006: fig. 2A, B], *Itatodon* [PIN 5087/7].

(1) Present: *Borealestes* [Waldman and Savage 1972: fig. 2], *Haldanodon* [Gui Mam 141/76 and VJ 1017/155], *Docodon* [USNM 2707 and others], *Simpsonodon* [BMNH J100], *Krusatodon* [BMNH J526], *Tashkumyrodon* [ZIN 85279], *Sibirotherium* [PM TGU 16/5-22 and 120/9-34].

(?) Unknown: *Woutersia*, *Dsungarodon*, *Acuodulodon*, *Hutegotherium*.

Comments: About assessing of this character to *Krusatodon* and *Tashkumyrodon* see comments to the character 20.

Character 34: Pseudotalonid basin on ultimate lower molariform tooth (new character):

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975].

(1) Less than 50% from the crown length: *Haldanodon* [28%, Gui Mam 141/76], *Castorocauda* [36%, Ji et al. 2006: fig. 2C], *Itatodon* [32%, PIN 5087/2].

(2) More than 50% from the crown length: *Simpsonodon* [52%, PIN 5087/5], *Dsungarodon* [47–51%, SGP 2001/22 and 2004/7], *Acuodulodon* [Hu et al. 2007: fig. 4], *Tegotherium* [64%, SGP 2004/5].

(?) Unknown: *Borealestes*, *Docodon*, *Krusatodon*, *Tashkumyrodon*, *Hutegotherium*, *Sibirotherium*.

Character 35: Enamel folding (Sigogneau-Russell 2003a: character 6, modified; Ji et al. 2006: character 10; Averianov and Lopatin 2006: character 29; Ji et al. 2006: character 10; Luo and Martin 2007: character 17, modified):

(0) Absent or weakly developed: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3A, B], *Morganucodon* [BMNH M16536 and others], *Dinnetherium* [Crompton and Luo 1993: fig. 4.5], *Megazostrodon* [BMNH M26507], *Woutersia* [MNHN SNP 101, 517, and 975], *Borealestes* [Waldman and Savage 1972: fig. 2], *Haldanodon* [Gui Mam 141/76 and VJ

1001/155], *Acuodulodon* [Hu et al. 2007: fig. 4], *Krusatodon* [BMNH J526 and J584], *Castorocauda* [Ji et al. 2006: fig. 2C], *Itatodon* [PIN 5087/2 and PM TGU 200/3-BR-7], *Tashkumyrodon* [ZIN 85279], *Hutegotherium* [PIN 5987/5], *Tegotherium* [PIN 4174/167 and SGP 2004/3], *Sibirotherium* [PM TGU 16/5-22 and others].

(1) Present: *Docodon* [USNM 2710, YPM 11826, 13767, and others], *Simpsonodon* [BMNH J100, J251, and J761], *Dsungarodon* [SGP 2001/22].

Comments: Ji et al. (2006) erroneously coded *Krusatodon* as having folding enamel.

Character 36: An additional groove above the Meckelian groove and anterior to the mandibular foramen (new character):

(0) Absent: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3D], *Morganucodon* [Kermack et al. 1973: fig. 7], *Megazostrodon* [BMNH M26507], *Hutegotherium* [PM TGU 200/5-BR-2], *Tegotherium* [SGP 2004/20].

(1) Short, little longer than the ultimate molariform tooth: *Haldanodon* [VJ 1003/155 and others], *Docodon* [YPM 11823].

(2) Long, about twice longer than ultimate molariform tooth: *Simpsonodon* [PIN 5087/5], *Dsungarodon* [SGP 2001/22].

(?) Unknown: *Dinnetherium*, *Woutersia*, *Borealestes*, *Acuodulodon*, *Krusatodon*, *Castorocauda*, *Itatodon*, *Tashkumyrodon*, *Sibirotherium*.

Character 37: The Meckelian groove (new character):

(0) Reaches the mandibular symphysis anteriorly: *Sinoconodon* [Kielan-Jaworowska et al. 2004: fig. 4.3D], *Morganucodon* [Kermack et al. 1973: fig. 7], *Megazostrodon* [Kielan-Jaworowska et al. 2004: fig. 4.8B], *Haldanodon* [VJ 1003/155 and others], *Docodon* [YPM 11823], *Itatodon* [PIN 5087/7].

(1) Restricted to the posterior portion of the dentary horizontal ramus: *Simpsonodon* [PIN 5087/5], *Dsungarodon* [SGP 2004/18], *Acuodulodon* [Hu et al. 2007: 178], *Tegotherium* [SGP 2004/20], *Sibirotherium* [PM TGU 120/9-34].

(?) Unknown: *Dinnetherium*, *Woutersia*, *Borealestes*, *Krusatodon*, *Castorocauda*, *Tashkumyrodon*, *Hutegotherium*.

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