

A NEW DOCODONT (MAMMALIA) FROM THE MIDDLE JURASSIC OF KYRGYZSTAN, CENTRAL ASIA

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ABSTRACT—*Tashkumyrodon desideratus*, gen. et sp. nov. from the Middle Jurassic (Callovian) Balabansai Formation near Tashkumyr in Kyrgyzstan is described from a single lower molar. The tooth exhibits the typical structure of a docodont lower molar with the main cusp a connected by crests to the lingual cusps (c and g) and to the mesial cusp b. *Tashkumyrodon* is plesiomorphic in retaining well developed crests c-d and d-f, and derived in reduction of crest b-g. By formation of crests b-e and e-g (derived), *Tashkumyrodon* resembles *Tegotherium* from the Late Jurassic of Mongolia and *Sibirotherium* from the Early Cretaceous of West Siberia, Russia. *Tegotherium* is more derived than *Tashkumyrodon* by the more prominent anterior basin (“pseudotalonid”) and the reduction of the crests distal to cusp c. The Asian docodonts probably represent the sister group of all remaining docodonts, an Euramerican clade characterized by retention of crest b-g and reduction of cusp e as well as crest b-e. *Simpsonodon* from the Middle Jurassic of England is convergently similar to *Tegotherium* in development of a “pseudotalonid” and reduction of distal crests.

INTRODUCTION

The record of Jurassic mammals in Asia is poor and mainly restricted to the eastern part of the continent. Several skulls and postcranial remains of *Sinoconodon* and *Morganucodon* have been described from the Lower Jurassic Lufeng Formation in southern China (Patterson and Olson, 1961; Crompton and Sun, 1985; Crompton and Luo, 1993; Zhang et al., 1998). The Lower Jurassic Kota Formation in India has yielded isolated teeth of “symmetrodonts” and morganucodontid “triconodonts” which have been attributed to several genera (Datta, 1981; Yadagiri, 1984, 1985; Prasad and Manhas, 1997, 2002; Datta and Das, 2001). Chow and Rich (1984) described the “triconodont” *Klamelia zhaopengi* based on a mandibular fragment from the Middle or Late Jurassic of the Junggar Basin in northwestern China. *Shuotherium*, represented by a mandible and an upper molar from the Late Jurassic of Sichuan Province (China), is a highly specialized “symmetrodont” with a pseudotalonid at the anterior part of the lower molars (Chow and Rich, 1982; Wang et al., 1998). *Tegotherium*, based on an isolated lower molar, is a docodont from the (?) Upper Jurassic Shar Teg Beds of Mongolia (Tatarinov, 1994; Kielan-Jaworowska et al., 2000).

The record of Middle Jurassic mammals in Asia is even more scarce, only two fragmentary specimens of uncertain systematic position have been reported so far. One edentulous mandible from the Haifanggou Formation in the Liaoning Province in northeastern China has been interpreted as amphilestid triconodont (*Liaotherium*) by Zhou et al. (1991). From Central Asia, one badly damaged upper mammalian molar, tentatively assigned to the Docodonta, has been reported from red beds of the Balabansai Formation near Kalmakerchin, Kyrgyzstan (Nessov et al., 1994). Here we describe a much better preserved mammalian tooth from the grey part of the Balabansai Formation near Tashkumyr in the north-western Fergana Valley, Kyrgyzstan, which we attribute to a new genus of Docodonta.

In summer 2000, a joint project of the Institut für Geologische Wissenschaften of the Freie Universität in Berlin (Germany), the Zoological Institute of the Russian Academy of Sciences in St. Petersburg (Russia), and the Institute of Geology of the National Academy of Science in Bishkek (Kyrgyzstan)

began field work in Kyrgyzstan with the aim to recover Jurassic mammals. One of the localities worked was Sarykamyshtsai 1 (FTA-30 site) in the northern Fergana Valley, Osh Province, which was discovered by N. N. Verzhilin in 1965 (Verzhilin et al., 1970). The locality is situated on the right bank of Sarykamyshtsai Creek about 3–4 km east of the town of Tashkumyr (Fig. 1) and has produced a rich non-mammalian vertebrate fauna of sharks, holostean and teleostean fishes, a dipnoan, a brachyopoid labyrinthodont, a xinjiangchelyid turtle, a possible eosuchian, lizards, pterosaurs, the goniopholidid *Sunosuchus*, a possible thalattosuchian crocodyliform, and dinosaurs (Averianov, 2000). The fossiliferous sediments are grey claystones and marls exposed as badlands with scarce vegetation. Screen-washing of matrix yielded, besides numerous non-mammalian bones and teeth, a docodont lower molar which is described in this paper.

MATERIALS AND METHODS

Weathered claystones were taken from the surface and transported to the nearby Sarykamyshtsai Creek and screen-washed with the Henkel process (Henkel, 1966). The fraction above 2 mm was picked in the field and the fine fraction between 2 and 0.5 mm was taken to the laboratory for further treatment. About two metric tons of sediment yielded about 15 kilograms of fine fraction. In the laboratory, this fraction was reduced by using 10% acetic acid and heavy liquid treatment. The residue, which contained less than 10% of non-phosphatic particles was picked under a stereomicroscope.

For SEM study, the molar was mounted with acetone soluble SEM mount and sputtered with gold. A camera lucida was used for the ink drawings. The measurements were taken with a Reflex-Microscope (Reflex Measurement LTD), theoretical measuring accuracy, 2 μm.

Although the cusp homology of docodont molar teeth with that of other mammals has not been established with any certainty, we follow the terminology proposed by Butler (1997) for practical reasons and because we think this homology is correct (see below). The purely descriptive cusp terminology used by Kermack et al. (1987) and Sigogneau-Russell (2001)



FIGURE 1. Diagrammatic map of Kyrgyzstan and neighboring countries in Central Asia. The Sarykamysai 1 locality (FTA-30 site) where the docodont molar comes from is situated 3–4 km east of the town of Tashkumyr.

is more unbiased, but has proven rather cumbersome for morphological description. Docodont wear facet terminology is after Jenkins (1969). We follow the stem-based definition of Mammalia as proposed by Luo et al. (2002), which is equivalent to the Mammaliaformes of Rowe (1988) and McKenna and Bell (1997). The holotype is housed in the collection of the Zoological Institute, Russian Academy of Sciences in St. Petersburg, Russia (ZIN).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
 Order DOCODONTA Kretzoi, 1946
 Family TEGOTHERIIDAE Tatarinov, 1994
 Genus *TASHKUMYRODON*, gen. nov.

Etymology—Named after the town of Tashkumyr and *odont*, stem of *ὄδους* (Greek), tooth. *Tashkumyrodon* (masculine), tooth from Tashkumyr.

Type and Only Known Species—*Tashkumyrodon desideratus*, sp. nov.

Diagnosis—The new taxon can be diagnosed by the following combination of primitive (–) and derived (+) characters: 1) crest c-d well developed (–); 2) crest f-d well developed (–); 3) crest b-e well developed (–); 4) crest e-g present (+); 5) crest b-g partially reduced (+); 6) small mesial portion of crest b-g still present (–); 7) anterior basin (“pseudotalonid”) not enlarged (–); 8) cusp g not enlarged [reconstructed] (–).

Differential Diagnosis—Differs from *Borealestes* Waldman and Savage, 1972 by characters 4 and 5; from *Haldanodon* Kühne and Krusat, 1972 and *Docodon* Marsh, 1881 by characters 3 and 5; from *Simpsonodon* Kermack et al., 1987 by characters 1–5, 7, and 8; from *Tegotherium* Tatarinov, 1994 by characters 1, 2, 6–8; and from *Sibirotherium* Maschenko et al., 2003 by characters 6 and 7.

Remarks—*Delsatia* Sigogneau-Russell and Godefroit, 1997 from the Late Triassic of France, originally described as a docodont, is a “symmetrodont” (Butler, 1997:439; Averianov, 2002:711) and not considered here. *Reigitherium* Bonaparte, 1990 from the Late Cretaceous of Argentina, recently reinterpreted as a docodont (Pascual et al., 2000), is obviously different from *Tashkumyrodon*, gen. nov., although the taxa cannot be directly compared because of the highly modified molar structure in the former. The relationship of *Tashkumyrodon* to a previously reported upper molar from the Balabansai Formation at Kalmakerchin, Kyrgyzstan (Nessov et al., 1994), which was tentatively identified as a docodont, can not be determined due to the poor preservation of the latter specimen.

The closest relatives of *Tashkumyrodon* are *Tegotherium* from the Late Jurassic of Mongolia and *Sibirotherium* from the Early Cretaceous of West Siberia, Russia, the only docodonts described so far from Asia (see Discussion).

TASHKUMYRODON DESIDERATUS, sp. nov.

Diagnosis—As for the genus.

Etymology—*desideratus* (Latin), desired.

Holotype—ZIN 85279, left lower molar with the tip of cusp g and roots broken off.

Type Locality—Sarykamysai 1 (FTA-30 site), right bank of Sarykamysai Creek, 3–4 km east of the town of Tashkumyr, Osh Province, Kyrgyzstan.

Stratigraphic Level—The lower part of the Balabansai Formation. Middle Jurassic, Callovian (Aliev et al., 1981).

DESCRIPTION

The holotype tooth (Figs. 2–3) was broken into two parts which were found independently when picking the concentrate from FTA-30 and subsequently glued together. Minor crown fragments between these parts, including the tip of cusp g, were lost. The crown is dominated by cusp a, which is situated in the center of the tooth (Fig. 3). It is a blunt conical cusp with almost flat or slightly concave lingual and smoothly rounded labial sides. There are four differently expressed crests radiating from the tip of cusp a: two longitudinal ones, a-b and a-d, directed mesially and distally, respectively, and two small more transverse crests, a-g and a-c directed mesiolingually and distolingually, respectively. The angle between crests a-g and a-c is about 70°. Between crests a-g and a-c is one rather large vertical enamel fold (crenulation). Cusp a bears a strong, somewhat distally oriented wear facet at the tip (facet 1a), which extends distolingually and downwards along the crest a-c (facet 3). The crests a-b, a-g, and a-d are not sharp but somewhat rounded, and bear no wear facets. Crest a-b is the strongest, crest a-d is the weakest. The latter fades before reaching cusp d. Second highest cusp is cusp c (Fig. 3B). Although the tip of cusp g is broken off, it was definitively smaller and lower than cusp c judging by the extent of its preserved base. Cusp c is considerably lower than cusp a and reaches about half of its height. It is slightly bent distolingually and like cusp a it bears a strong apical wear facet (9a). A distinct short wear facet 9b is present along the crest a-c; it is separated from the wear facet 3 by a deep notch. Both facets are of equal length. The strong and broad wear facet 11b is present along crest c-d; it becomes broader distobuccally. This wear facet is not polished but appears rough and slightly pitted. Some irregular scratches on the buccal portion of the wear facet are oriented in longitudinal direction of the worn surface. Between crests a-d and c-d is a rather deep V-shaped valley narrowing distobuccally. Cusp d is broken off, but it was apparently present because of the rising of the crest d-f immediately before the broken area. Cusp d possibly formed one end of the prominent ridge-like crest d-f; the other (lingual) end of this crest is the cusp f. Crest d-f is somewhat obliquely oriented and bears along its lingual half an undivided wear facet 11d. Between crests c-d and d-f is a rather deep basin which narrows distobuccally and which does not exhibit any wear facet. Cusp b is significantly smaller than cusp c. It is in the same buccolingual position as cusp a and separated by a wide V-shaped valley from the latter. Cusp b (apex is broken) is connected with three ridges: crests b-a, b-g, and b-e. Crest b-a is rounded and not worn. Crest b-g is robust and worn (facet 6), but very short, fading shortly after having left the tip of cusp b. Crest b-e is much longer, connecting with the tip of cusp e, and is also worn (this and the following structures are reduced in *Docodon* and therefore the nomenclature for their wear facets is not worked out). Cusp e is half as high as

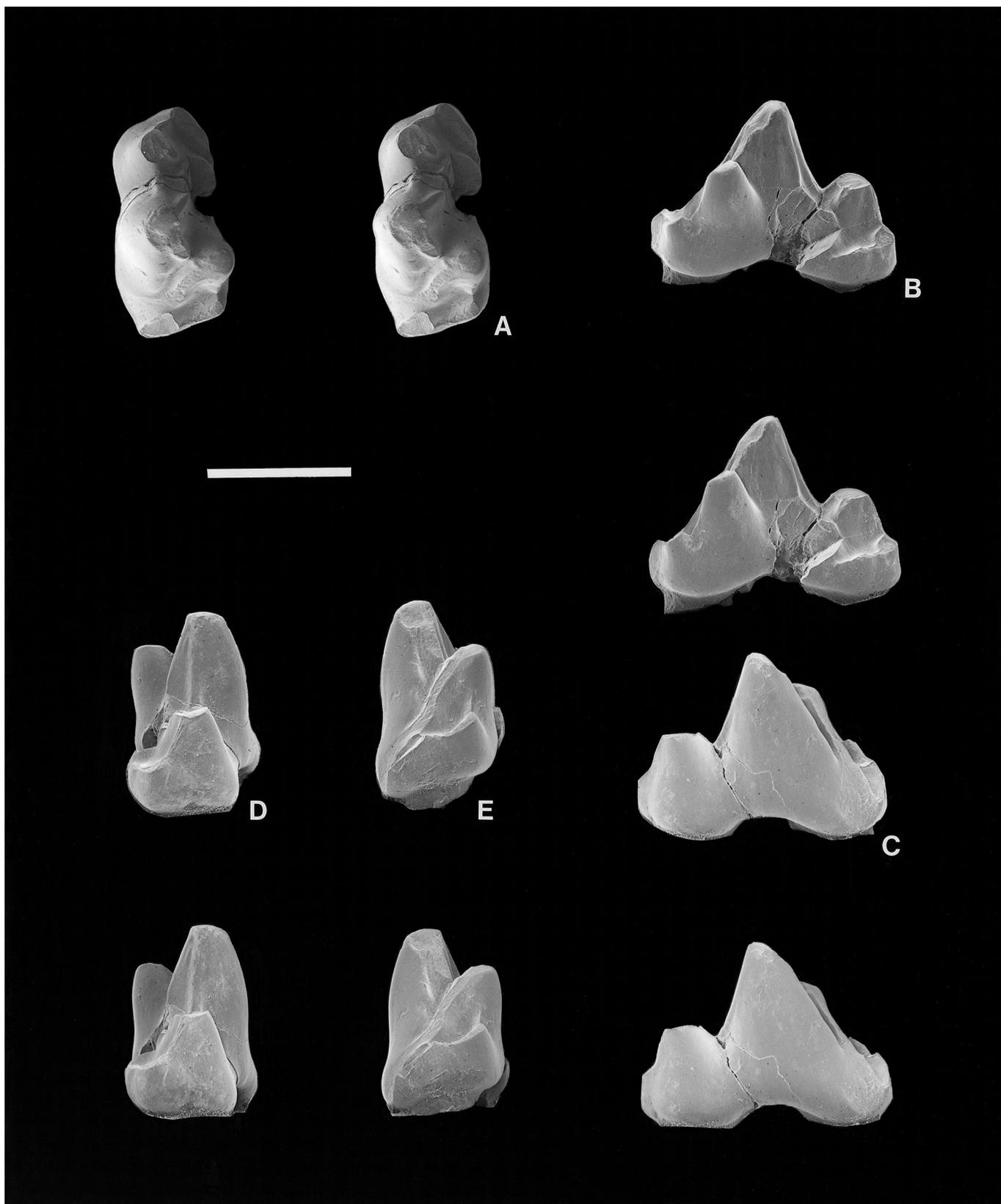


FIGURE 2. *Tashkumyrodon desideratus*, gen. et sp. nov., ZIN 85279, holotype, left lower molar. Sarykamyshtsai 1 (FTA-30), Kyrgyzstan; Balabansai Formation, Middle Jurassic (Callovian). SEM micrographs (stereo pairs) in **A**, occlusal view (mesial to the top); **B**, lingual view (mesial to the right); **C**, buccal view (mesial to the left); **D**, mesial view; **E**, distal view. For stereoscopic observation, turn B-E 90° to the right. Scale bar is 1 mm.

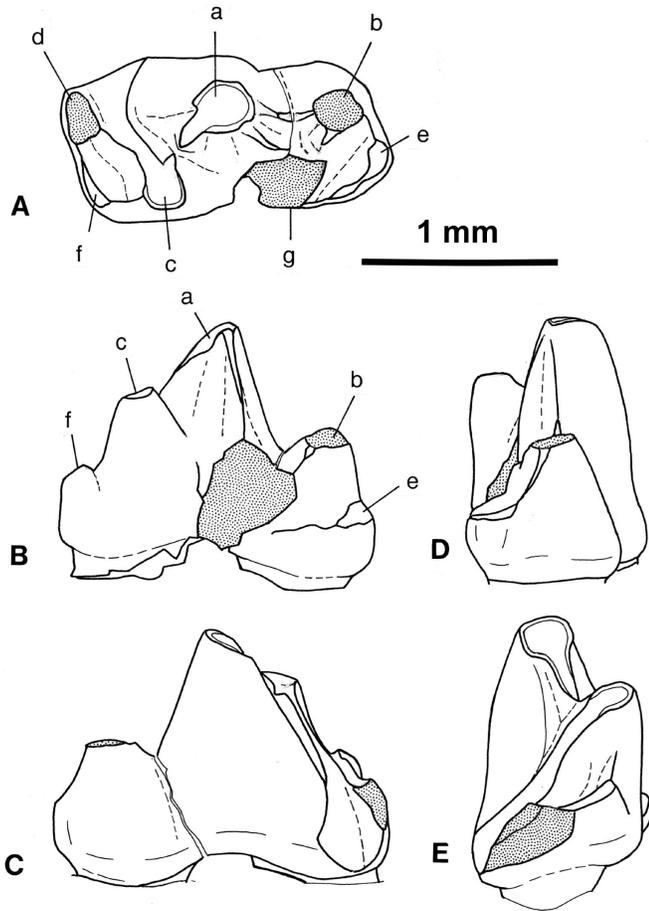


FIGURE 3. *Tashkumyrodon desideratus*, gen. et sp. nov., ZIN 85279, holotype, left lower molar. Sarykamyshtsai 1 (FTA-30), Kyrgyzstan; Balabansai Formation, Middle Jurassic (Callovian). Line drawings in A, occlusal view (mesial to the right); B, lingual view (mesial to the right); C, buccal view (mesial to the left); D, mesial view; E, distal view. A and B with designation of cusps. Broken areas are stippled.

cusps b and g bears a small wear facet on its apex. It is connected by a well developed worn crest e-g, bearing an additional cusp, with the lingual surface of cusp g. A rather deep basin (“pseudotalonid”) is located between the triangle formed by crests b-g, b-e, and e-g. No lingual or other cingulid is present at the base of the tooth crown.

The molar possessed two roots of which only the bases are preserved. Judging by their shape and the symmetrical appearance of the base of the tooth crown in labial aspect, both roots were approximately of equal size and were separated by a comparatively wide, U-shaped notch, like in the majority of other docodonts.

Measurements—Length = 1.70 mm; width = 0.85 mm; height = 1.25 mm.

DISCUSSION

The “peculiar and highly modified” (Simpson, 1929:84) morphology of docodont molars was recognized and acknowledged long ago. This may be the main reason for the lack of an explicit diagnosis of the group in the scientific literature. Simpson (1929) did not cite diagnostic characters when describing the new family Docodontidae. The original concept of the order Docodonta by Kretzoi (1946) included *Docodon* [= *Peraiocynodon* Simpson, 1928] and *Peramus* Owen, 1871 and is

thus misleading: the latter is now considered a pretribosphenic zatherian, not a docodont (e.g., Clemens and Mills, 1971). The Docodonta have not been included in most formal phylogenetic (cladistic) analyses of early mammals (e.g., Lillegraven and Krusat, 1991; Luo, 1994; Wible et al., 1995; Rougier et al., 1996), and, if included, are usually represented only by one taxon, *Haldanodon*, known by numerous dentaries, some skulls, and a partial skeleton (Krusat, 1980; Lillegraven and Krusat, 1991; Martin and Nowotny, 2000). These studies did not point out dental synapomorphies for Docodonta. “A broad expansion of the internal cingula in upper and lower teeth accompanied by inflation of the internal cusps and the development of transverse ridges connecting the cusps” (Kron, 1979:92) is most often cited as the distinguishing feature of the docodont dentition. *Tashkumyrodon* has at least one “inflated” internal cusp (cusp c) and transverse ridges connecting the main cusp a with the internal cusps c and g, and thus is referred to the Docodonta.

For many years, Docodonta remained a small group with a single genus (*Docodon*, possibly including *Peraiocynodon*) from the Late Jurassic of North America and Early Cretaceous of Europe. Subsequent discovery of *Haldanodon* and *Borealestes* in the Late and Middle Jurassic of Europe raised the question of phylogenetic relationships within the group, solved at that time by assumed linear (ancestor-descendant) relationships between *Haldanodon* and *Docodon* (Hopson and Crompton, 1969) or between *Borealestes* and *Haldanodon* (Waldman and Savage, 1972). The discoveries of *Simpsonodon* from the Middle Jurassic of Europe (Kermack et al., 1987) and *Tegotherium* from the Late Jurassic of Mongolia (Tatarinov, 1994) complicated the picture. Hopson (1995) proposed that the last two genera, possessing an enlarged anterior basin (“pseudotalonid”), “form, with *Borealestes*, a distinct clade of docodontids,” but details of this analysis have not been published. The last few years have witnessed a considerable improvement of knowledge about the diversity and distribution of Docodonta and this group was far more successful than previously thought (Kron, 1979:97). A possible docodont molar was described from the Middle Jurassic of Kyrgyzstan (Nessov et al., 1994), a definitive docodont molar was reported but not described from the Early Cretaceous of Mongolia (Agadjanian, 1999), and a new docodont *Sibirotherium* with a “pseudotalonid,” represented by rather complete lower dentitions and jaw fragments, was discovered in the Early Cretaceous of Western Siberia (Leshchinskiy et al., 2001; Maschenko et al., 2003). Discovery of *Tashkumyrodon* in the Middle Jurassic of Kyrgyzstan confirms that docodonts were abundant and diverse in the Mesozoic of Asia. Indeed, in the Mongolian and Kyrgyz Jurassic localities Shar Teg, Sarykamyshtsai, and Kalmakerchin, docodonts were the first (and currently only known) mammals to be found.

To assess the phylogenetic relationships of *Tashkumyrodon* with other docodonts, we performed a phylogenetic analysis of lower molar characters for all known docodont taxa, except *Reigitherium*, of which the attribution to Docodonta is not well established (Table 1; Fig. 4). We restrict our analysis to lower molar characters because they are known for all docodonts, whereas the upper dentition is known only for three docodont taxa. The skull and postcranium are known only for *Haldanodon* (a partial skeleton was reported for *Borealestes* by Kron (1979:96), but it remains undescribed). A PAUP 3.1.1 analysis (exhaustive search) of seven characters (multistate character 5 was treated as unordered) and eight taxa produced seven most parsimonious trees (MPT; TL = 11, CI = 0.812, RI = 0.833, RC = 0.682). In the 50% Majority Rule tree docodonts fall into two clades, one formed by Euramerican taxa, and the other by Asian taxa. The Euramerican clade is better supported (71% of MPTs; with the *Haldanodon-Docodon* clade revealed by all MPTs). The relationships within the Asian taxa currently remain unresolved. We consider this phylogenetic analysis pre-

TABLE 1. Data matrix for a cladistic analysis of Docodonta, based on lower molar characters: 1—cusp b small, approximated to cusp a (0), larger, well separated from cusp a by notch (1); 2—cusp g small (0), large, almost equal to cusp c in size (1); 3—cusp e present, unreduced (0), reduced, or lost (1); 4—cusp f absent (0); present (1); 5—pseudotalonid absent (0), present (1), enlarged and bordered mesiolingually by crest b-g (2), enlarged and bordered mesiolingually by crest e-g (3); 6—crest b-e present (0), absent (1); 7—crest b-g absent (0), present (1).

| Taxon | Characters | | | | | | |
|----------------------------------|------------|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| <i>Woutersia</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Borealestes</i> | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| <i>Haldanodon</i> | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>Docodon</i> | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>Simpsonodon</i> | 1 | 1 | 1 | 1 | 2 | 0 | 1 |
| <i>Tashkumyrodon</i> , gen. nov. | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| <i>Sibirotherium</i> | 1 | 0 | 0 | 1 | 3 | 0 | 0 |
| <i>Tegotherium</i> | 1 | 1 | 0 | 1 | 3 | 0 | 0 |

liminary, as current knowledge of most of the taxa remains limited. However, these results are consistent with our interpretation of the morphological evolution of lower molars in Docodonta (see below).

The homology of the docodont lower molar cusps is a matter of long debate, and it is not our intention to review this question. The purely descriptive cusp nomenclature proposed by Kermack et al. (1987) and recently completed by Sigogneau-Russell (2001) is the most unbiased system, as it does not imply any homology with the cusps of other mammals. However, this terminology is very cumbersome, particularly when crests and ridges between cusps are described. We here follow the nomenclature proposed by Butler (1997) because we agree with him that docodonts were derived from a *Woutersia*-like mammal having main cusp a, lingually displaced cusp c, cusp b in a more buccal position, and well developed cusps e, g, and d (Fig. 5). Four main crests connect some of the cusps: a-c, a-b, and b-e. The next stage in the development of a docodont lower molar is not known from the fossil record and thus is hypothetically reconstructed here (Fig. 5). We suggest that four ridges (crests d-f, c-d, a-g, and g-b) and one cusp (f) were added at this stage. Crest a-g is present in all known docodonts, but other crests probably have been secondarily lost in some taxa. We propose the presence of the former character as a lower molar synapomorphy for Docodonta. *Woutersia*, lacking this crest, is not formally included in Docodonta here. *Woutersia* comes from the Late Triassic and the oldest known docodont (*Borealestes*) is of Middle Jurassic (middle Bathonian) age. Some 40 myr between these taxa is a sufficient time to achieve the reconstructed hypothetical primitive condition for all docodonts. This condition unites all common lower molar characters that should be present, at least initially, in all subsequent docodont lineages. Furthermore, we suggest that after this stage docodonts split into two main branches: Euramerican docodonts and Asian docodonts (Martin and Averianov, 2001). Separation of these two clades could be related to the formation of the Turgai Strait, which separated land areas of Europe and Asia at various times between the Bathonian and Oxfordian (Golonka et al., 1996). All Euramerican docodonts, including *Simpsonodon*, are characterized by reduction or loss of cusp e and strong reduction of crest b-e. *Borealestes*-*Haldanodon*-*Docodon* is a conservative lineage, mainly retaining the primitive construction achieved at the hypothetical stage. These taxa differ in minor details. Particularly, *Docodon* is distinct in its relatively wider lower molars complicated by secondary structures. Principally, however, *Docodon* has the same construction of lower molars as *Borealestes* and *Haldanodon*. The Middle Jurassic

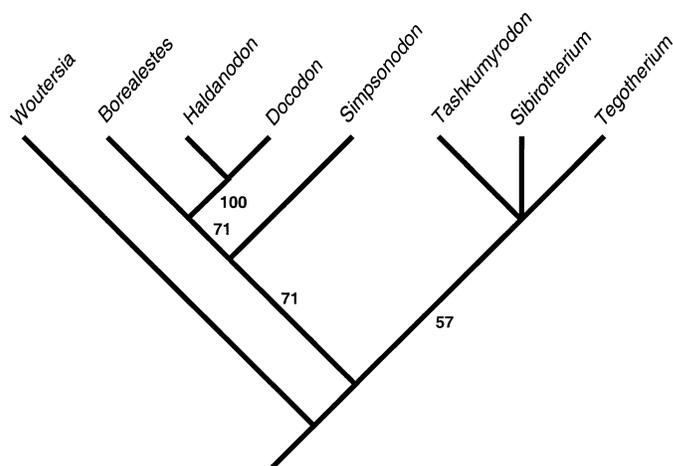


FIGURE 4. Cladogram showing the relationships within Docodonta based on lower molar characters. 50% Majority Rule consensus tree resulting from seven most parsimonious trees produced by analysis of data matrix (Table 1). Values indicate percentage of the seven trees supporting that node.

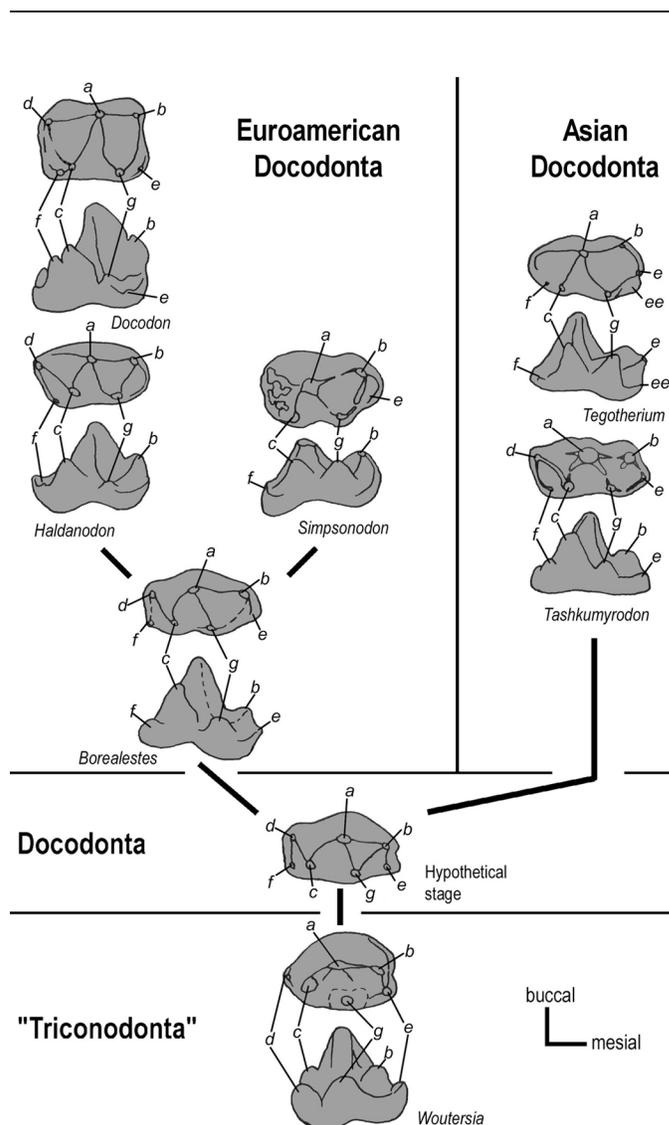


FIGURE 5. Lower molar evolution of Docodonta. Left molars in lingual and occlusal views.

(Late Bathonian) *Simpsonodon* represents a side branch of Euramerican docodonts, possibly deriving from a *Borealestes*-like ancestor (Fig. 5). In the lineage leading to *Simpsonodon*, the anterior basin was considerably enlarged and formed a “pseudotalonid.” This “pseudotalonid,” however, is not fully homologous with the “pseudotalonid” in tegotheriids (see below). In *Simpsonodon* crests in the posterior part of the lower molar (c-d and d-f) together with cusps d and f were lost and this flattened area was filled by a complex system of enamel foldings (crenulations). Cusp g was enlarged and became similar to cusp c in size and height.

The Asian docodonts differ markedly from Euramerican docodonts by retention of unreduced cusp e, formation of crests b-e and e-g (which are not present in any known Euramerican docodont), and by subsequent reduction of crest b-g (Fig. 5). In *Tashkumyrodon* there is a remnant of the latter crest at cusp b, whereas it is completely lost in *Tegotherium* and *Sibirotherium*. *Tashkumyrodon*, gen. nov., *Tegotherium*, and *Sibirotherium* are also similar in presence of a well developed although not complete crest a-d, which is longitudinally oriented, like the crest a-b (“lateral flanges” of Tatarinov, 1994:99). In all three Asiatic docodont taxa, cusps a and b are well separated; in Euramerican docodonts, except *Simpsonodon*, these cusps are closer, cusp b being sometimes placed on the mesial slope of cusp a. *Tegotherium* is advanced beyond *Tashkumyrodon* in enlargement of the anterior basin (“pseudotalonid”), development of an additional cusp or cingulid lingual to crest e-g, reduction of crests c-d and d-f, and enlargement of cusp g. Only a small mesial portion of crest c-d seems to be present, and a possible remnant of cusp f. *Sibirotherium*, although geologically youngest among these three taxa, is more primitive than *Tegotherium* with a more weakly developed “pseudotalonid,” a less reduced posterior “talonid,” and a cusp g that is distinctly smaller than cusp c. Morphologically, *Sibirotherium* is intermediate between *Tashkumyrodon* and *Tegotherium*. By development of an enlarged “pseudotalonid” and reduction of the distal crown structures, *Tegotherium* is strikingly convergent with *Simpsonodon*. We interpret this similarity as homoplasy (convergence) rather than homology, because *Simpsonodon* has no cusp e and strongly reduced crest b-e. In contrast, cusp e is unreduced and crest b-e is well developed in *Tegotherium* and *Sibirotherium*. As a result, the “pseudotalonid” of *Simpsonodon* is delimited by crests a-b, b-g, and a-g, whereas in tegotheriids by crests a-b, b-e, e-g, and a-g. Therefore, we consider the “pseudotalonid” structures in *Simpsonodon* and tegotheriids as not fully homologous and independently acquired.

The taxon Tegotheriida Tatarinov, 1994 was originally proposed as an order within the superorder Symmetrodonta. This concept is no longer valid because *Tegotherium* is a docodont rather than a “symmetrodont” (Hopson, 1995; Kielan-Jaworowska et al., 2000). The family Tegotheriidae Tatarinov, 1994 is considered here as a valid name for a docodontan group of Asian origin, uniting taxa with a well developed “pseudotalonid” (*Tegotherium* and *Sibirotherium*), or taxa developing in this direction (*Tashkumyrodon*, gen. nov.). Maschenko et al. (2003) recently presented a revised diagnosis of Tegotheriidae.

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Note added in proof: After this paper had been accepted for publication new docodont teeth from the Middle Jurassic of Great Britain were published (Sigogneau-Russell, 2003). One of the new taxa, *Krusatodon*, was described as being similar, or even “possibly synonymous” with *Tegtotherium*, and on this basis it was suggested to revise the concept of “Asiadocodonta” proposed by Martin and Averianov (2001). We have no space here to discuss the taxonomy and relationships of the new British docodonts in detail, but wish to point out that *Krusatodon* is similar to *Simpsonodon* and differs from *Tegtotherium* and *Tashkumyrodon* gen. nov. by retention of a complete crest b-g and therefore belongs to the Euroamerican clade of Docodonta.

Sigogneau-Russell, D. 2003. Docodonts from the British Mesozoic. *Acta Palaeontologica Polonica* 48:357–374.