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Itatodon tatarinovi (Tegotheriidae, Mammalia), a Docodont from the Middle Jurassic of Western Siberia and Phylogenetic Analysis of Docodonta

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Abstract—*Itatodon tatarinovi* Lopatin et Averianov, 2005 is represented by two lower molars and a lower molar fragment from the upper part of the Itat Formation (Bathonian Stage) of the Berezovskii quarry (southern Krasnoyarsk Region). Based on the presence of a pseudotalonid, bordered by the crests *a–b, b–e, e–g*, and *a–g*, *Itatodon* is assigned to the endemic Asian family Tegotheriidae. In this genus, the crest *a–b* is reduced and the thick lingual cingulid is better developed than that of other docodonts. Phylogenetic analysis of Docodonta shows paraphyly of Morganucodonta relative to docodonts and independent development of the pseudotalonid in the Tegotheriidae and the clade comprising *Krusatodon, Castorocauda, Cyrtlatherium*, and *Dsungarodon*.

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Key words: Docodonta, Middle Jurassic, Western Siberia, phylogenetic analysis.

INTRODUCTION

The first Asian docodont, *Tegotherium gubini* Tatarinov, 1994, was described 12 years ago from the Late Jurassic of Mongolia (Tatarinov, 1994). For a long time, it was the only docodont known from this part of the world. However, during the last years, the knowledge of docodonts from Asia was substantially expanded by the description of *Sibirotherium rossicus* Maschenko et al., 2003 from the Early Cretaceous of Siberia, *Tashkumyrodon desideratus* Martin et Averianov, 2004 from the Middle Jurassic of Kyrgyzstan, *Dsungarodon zuoi* Pfretzschner et Martin, 2005 from the Late Jurassic of Dzungaria, and *Castorocauda lutrasimilis* Ji et al., 2006 from the Middle Jurassic of Inner Mongolia (Maschenko et al., 2003; Martin and Averianov, 2004; Pfretzschner et al., 2005; Ji et al., 2006). These data suggest that docodonts were a rather common and diverse mammal group in the Mesozoic of Asia. This conclusion is corroborated by the study of the Middle Jurassic vertebrate fauna of Western Siberia. The Itat Formation of the Bathonian Stage of the Berezovskii quarry near the village of Nikol'skoe in the southern Krasnoyarsk Region has yielded at least two docodont species (Averianov et al., 2005; Lopatin and Averianov, 2005). The smaller species, Docodonta indet., was represented by dentary fragments without teeth, while the larger species, *Itatodon tatarinovi* Lopatin et Averianov, 2005 was described based on an isolated lower molar.

In the present study, the interpretation of the holotype of *I. tatarinovi* is improved, an additional lower molar from the Berezovskii quarry that probably belongs to the same taxon is described, and the results of phylogenetic analysis of Docodonta based on 29 dental characters are discussed.

The material described and discussed in this study is housed in the Paleontological Museum of Tomsk State University, Tomsk, Russia (PM TGU), and in the Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia (PIN).

SYSTEMATIC PALEONTOLOGY

Order Docodonta

Family Tegotheriidae Tatarinov, 1994

Genus *Itatodon* Lopatin et Averianov, 2005

Itatodon: Lopatin and Averianov, 2005, p. 277.

Type species. *I. tatarinovi* Lopatin et Averianov, 2005, Middle Jurassic of Western Siberia.

Diagnosis. The genus is characterized by the following unique combination of (–) primitive and (+) derived characters: (1) pseudotalonid present, its basin bordered by distinct crests *a–b, b–e, e–g*, and *a–g* (+); (2) additional cuspule *ee* absent (–); (3) crests *a–b* and *a–g* diverging at base of cuspule *a* (+); (4) posterior part of tooth crown reduced (+); (5) cusp *c* reduced, absent from ultimate lower molar (+); (6) complete lingual cingulid present (+); (7) incomplete labial cingulid

reaching anteriorly notch between cusps *a* and *b* (+); and (8) enamel lacking crenulations (–).

Species composition. Type species.

Comparison. *Itatodon* differs from *Tegotherium* Tatarinov, 1994 in characters 2, 3, 5, and 7, from *Tashkumyrodon* Martin et Averianov, 2004, in characters 2–7 and in the absence of a labial rudiment of the crest *b–g*; and from *Sibirotherium* Maschenko, Lopatin et Voronkevich, 2003, in characters 2–8 and in the better developed crest *e–g*.

Remarks. In the original description of *I. tatarinovi*, the reduction of the distolingual cusp *c*, which is located posterior to the cusp *a*, was indicated as a prominent distinctive feature of this taxon (Lopatin and Averianov, 2005). This feature was tentatively proposed to be connected with the posterior position of the tooth in the tooth row. However, the authors thought that the holotype of *I. tatarinovi* should not be regarded as the most posterior molar because of its long crown. Subsequent finds of an additional, more anterior lower molar of *I. tatarinovi* and a complete lower molar row of *Castorocauda* (Ji et al., 2006) are evidence that the holotype is actually the ultimate lower molar, while more anterior molars have a normally developed cusp *c*, which is positioned distolingual to the cusp *a*.

There are certain difficulties in the interpretation of the posterior cusps of the holotype of *I. tatarinovi.* In the previous paper (Lopatin and Averianov, 2005), a strongly reduced denticle-like cuspule at the base of the posterior crest of the cusp *a* was interpreted as a rudiment of the main cusp *c*, while a small ridgelike cuspule located distolabially was taken for cusp *d*. This interpretation was based on topographic relationships between the cusp *c* and the crest extending posteriorly from the apex of the cusp *a*. However, the denticle located at the base of the posterior crest of the cusp *a* is connected to the posterior cingulid and, consequently, corresponds to the cusp *f*. On the ultimate molar of *I. tatarinovi*, cusp *c* is most likely completely reduced, as in *Dsungarodon* (Pfretzschner et al., 2005) and, probably, in *Castorocauda* (Ji et al., 2006). In this case, the cusp at the posterior edge of the crown of the holotype is homologous to the cusp *f*, while the distolabial cingular cusp is cusp *d*.

Unique features of *Itatodon* are the reduced crest *a–b*, so that the crest terminates distally at the base of the cusp *a* or *g*, and a thick lingual cingulid which is developed to a greater extent than in other docodonts.

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

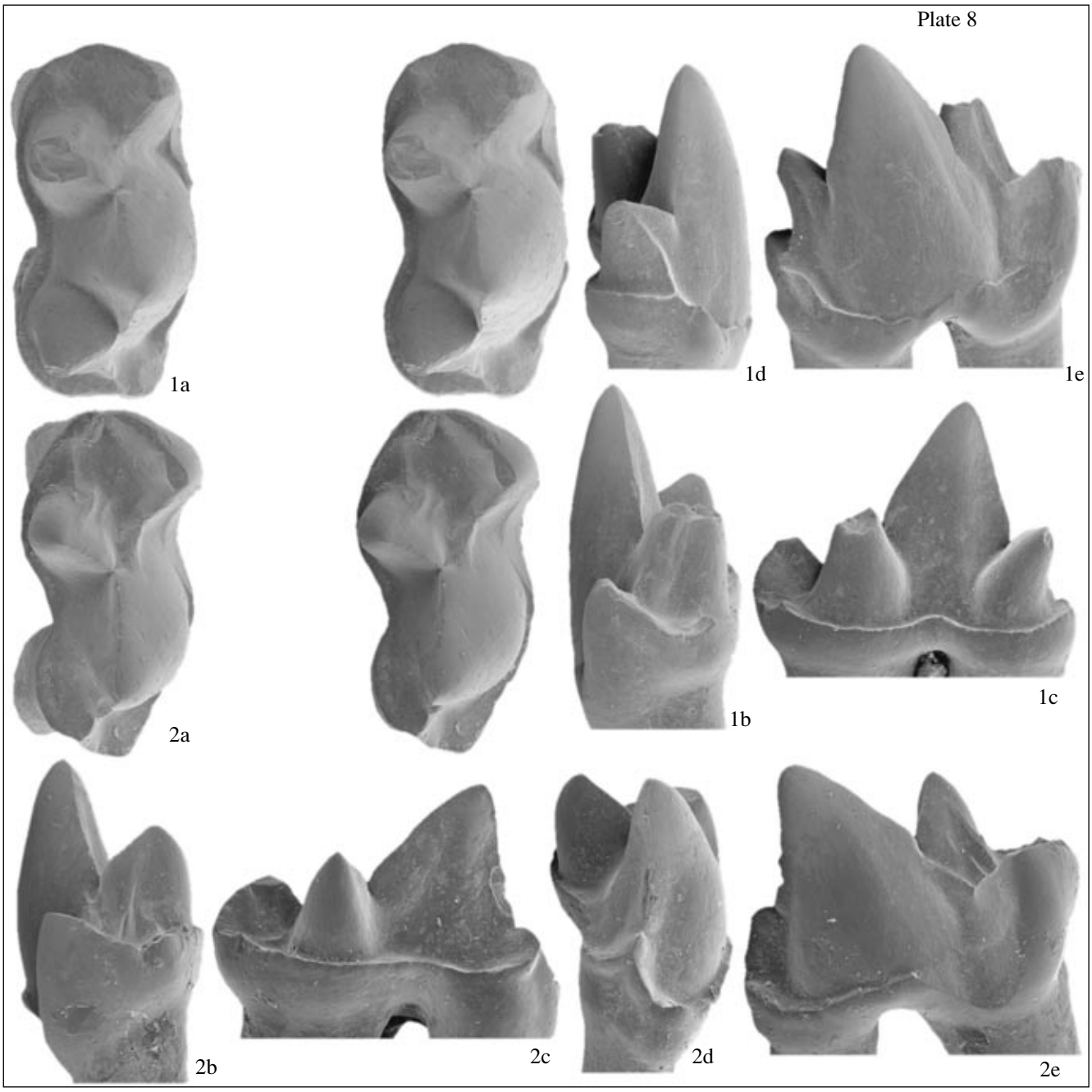
Plate 8, figs. 1 and 2

Itatodon tatarinovi: Lopatin and Averianov, 2005, p. 278, text-fig. 1.

Holotype. PIN, no. 5087/2, isolated right ultimate lower molar; Russia, Krasnoyarsk Region, Sharypovskii District, 500 m south of the village of Nikol'skoe, Berezovskii quarry; Middle Jurassic, Bathonian Stage, upper part of the Itat Formation.

Description (Fig. 1). The crown length of the lower molar of specimen PM TGU, no. 200/3-BR-7 (Figs. 1a–1e) is approximately 1.9 times greater than its maximum width. The cusp *a* is the largest and highest cusp; its base is displaced to the posterior part of the crown. A sharp crest *a–g* descends anteriorly from the apex of the cusp *a*. A relatively low ridge that is probably a rudimentary crest *a–b* extends anterolabially from the base of the cusp *g* to the apex of the cusp *b*. The cusp *g* is located anterolingual to the cusp *a* and is approximately half as high as this cusp. The cusp *b* is lower than the cusp *g* and is located in the mesiolabial corner of the crown. The anterior part of the crown forms a pseudotalonid with an extensive basin bordered by the crests *a–b, b–e, e–g*, and *a–g*. The crest *b–e* has a small notch at the base of the cusp *e*. The cusp *e* is small and very low, but clearly outlined. The crest *e–g* is hardly discernible. The crest *a–c* is directed distolingually. The cusp *c* is relatively large, but lower than the cusp *g*; its apex has a characteristic posterior curvature. The crest *c–f* descends abruptly distolabially. The cusp *f* is very small, located at the point of contact between the crest *c–f* and the posterior cingulid. A rudimentary cusp *d*, which is a small eminence of the posterior cingulid, is located slightly labially relative to the cusp *f*. The crown has a distinct lingual cingulid connecting the bases of the cusps *e* and *f* and a labial cingulid extending anteriorly from the cusp *d* to the base of the cusp *b*. The anterior part of the labial cingulid has an extensive lateral wear facet similar to that of the holotype (see below), but somewhat smaller in size. This facet is probably connected with the strong development of the cusp *C* on the occluding upper molar. The posterior part of the labial cingulid has a smaller additional facet, which is produced by the occlusion of the cusp *A*. The enamel of the crown is smooth, lacking crenulations. The tooth has two relatively narrow and long roots, which are equal in height and slightly widened at the base. The anterior root is slightly longer (in the anteroposterior diameter) than the posterior root. As in the holotype, the posterior side of the anterior root and the anterior side of the posterior root have a longitudinal groove, which is probably developed due to the vertical expansion on the interalveolar bony wall. A similar supplementary articulation of the tooth root and the dentary was noted by A. Averianov in Late Jurassic *Docodon* from North America; it is probably characteristic of other docodonts.

The ultimate lower molar (holotype, Figs. 1h–1l) is elongated, so that the length to width ratio is 1.75. The cusp *a* is large, with its base in the posterior part of the crown; the apex is inclined somewhat posteriorly. A sharp convex crest descends anteriorly from the apex of the cusp *a* and branches at the base of this cusp into the crests *a–b* and *a–g*. The crest *a–g* is higher than the crest *a–b* and forms a notch between the bases of the cusps *a* and *g*. The cusp *g* is pointed, approximately half as high as the cusp *a*, located anterolingual to the cusp *a*. The cusp *b* is lower than the cusp *g*, has a



Explanation of Plate 8

Figs. 1 and 2. *Itatodon tatarinovi* Lopatin et Averianov, 2005: (1) specimen PM TGU, no. 200/3-BR-7, right lower molar, ×22: (1a) stereophoto, occlusal view; (1b) anterior, (1c), lingual, (1d) posterior, and (1e) labial views; (2) holotype PIN, no. 5087/2, right ultimate lower molar, ×26.5: (2a) stereophoto, occlusal view; (2b) anterior, (2c) lingual, (2d) posterior, and (2e) labial views; Russia, Krasnoyarsk Region, Sharypovskii District, village of Nikol'skoe, Berezovskii quarry; upper part of the Itat Formation, Bathonian Stage, Middle Jurassic.

blunted apex; it is located anterior and slightly labial to the cusp *a*. The anterior part of the crown forms a pseudotalonid with an extensive basin bordered by the crests *a–b, b–e, e–g*, and *a–g*. The mesiolabial slope of the cusp *g* has two short ridges descending into the pseudotalonid basin, which are probably rudiments of the crest *b–g*. The crest *b–e* has a small notch. The cusp *e* is small, but distinct. The crest *e–g* is narrow and low. The posterior crest descends almost vertically from the apex of the cusp *a*. A small cuspule connected by the cingulid crest to the hardly discernible distolabial cusp *d* is located at the base of the posterior part of the cusp *a*, within the posterior cingulid. The crown has a complete lingual cingulid and a labial cingulid extending

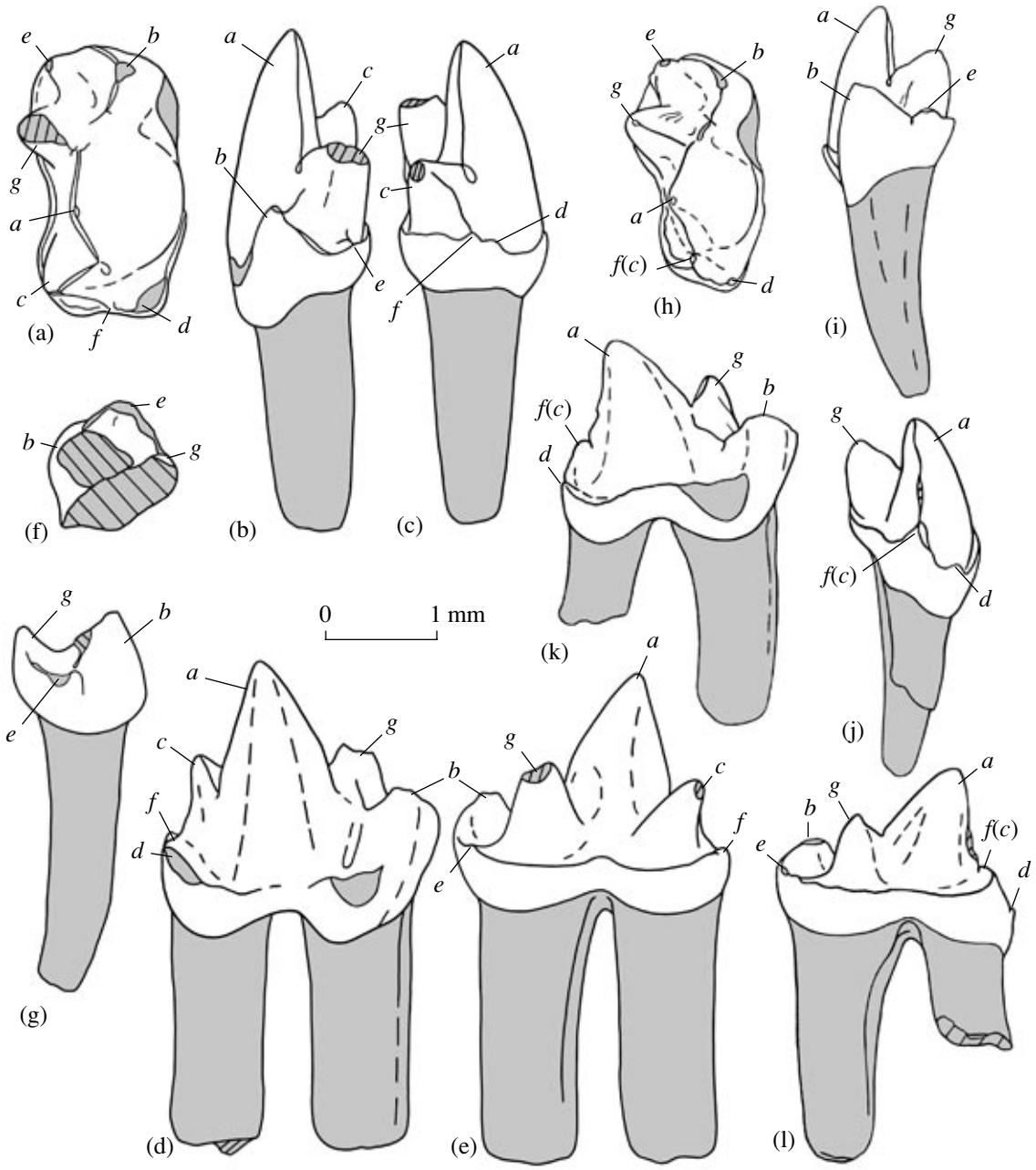


Fig. 1. *Itatodon tatarinovi* Lopatin et Averianov, 2005: (a–e) specimen PM TGU, no. 200/3-BR-7, right lower molar: (a) occlusal, (b) anterior, (c) posterior, (d) labial, and (e) lingual views; (f, g) specimen PM TGU, no. 200/5-BR-1, fragmentary left lower molar: (e) occlusal and (g) anterior views; (h–l) holotype PIN, no. 5087/2, right ultimate lower molar: (h) occlusal, (i) anterior, (j) posterior, (k) labial, and (l) lingual views. Designations: (*a, b, c, d, e, f, g*) cusps, (*f* (*c*)) distal cusp of uncertain homology (*f* or, less probably, *c*).

anteriorly from the cusp *d* to the notch between the cusps *a* and *b*. An extensive wear facet that was probably produced by the strongly developed cusp *C* of the occluding upper molar is located in the anterior part of the labial cingulid. The anterior root is slightly longer (anteroposteriorly) than the posterior root. The crown and roots of the tooth are slightly curved in the frontal plane (convex labially). The crown displays a certain unilateral hypsodonty (so that the labial side of the crown is higher than the lingual side), which is somewhat more pronounced than in specimen PM TGU, no. 200/3-BR-7.

In addition, the material includes an anterior fragment of the left lower molar (PM TGU, no. 200/5-BR-1, Figs. 1f, 1g), with a fragmentary pseudotalonid (in particular, only the base of the cusp *g* is preserved). The cusp *e* and crest *e–g* are worn to a greater extent than in the other specimens described.

M e a s u r e m e n t s, mm. Lower molar (specimen PM TGU, no. 200/3-BR-7): crown length, 2.6; greatest crown width, 1.4; crown height on the labial side of the cusp *a*, 2.25; height of the anterior root on the anterior side, 2.5. Ultimate lower molar (holotype): crown length, 2.1; greatest crown width, 1.2; crown height on the labial side of the cusp *a*, 1.6; height of the anterior root on the anterior side, 2.0.

R e m a r k s. The length of the holotype is 81% of that of specimen PM TGU, no. 200/3-BR-7, whereas in the jaw of *Castorocauda lutrasimilis*, the length of the ultimate lower molar is 95% of the length of the largest lower molar (Ji et al., 2006, text-fig. 2). On the other hand, the length of the isolated ultimate lower molar of *Dsungarodon zoui* is 86% of the length of the isolated more anterior molar referred to this taxon (Pfretzschner et al., 2005). Apparently, docodont taxa varied in the degree of reduction of the posterior lower molar. It is also possible that the range of individual and sex variation was much greater than in extant mammals.

M a t e r i a l. In addition to the holotype, an isolated right lower molar (PM TGU, no. 200/3-BR-7) and a fragment (pseudotalonid) of the left lower molar (PM TGU, no. 200/5-BR-1) from the type locality.

PHYLOGENETIC ANALYSIS

To determine the phylogenetic position of *Itatodon*, we performed phylogenetic analysis of all known docodont genera and the most thoroughly examined representatives of Morganucodonta, including *Morganucodon* Kühne, 1949 from the Rhaetian–Early Jurassic of Eurasia and North America; *Dinnetherium* Jenkins et al., 1983 from the Early Jurassic of Arizona, United States; and *Megazostrodon* Crompton et Jenkins, 1968 from the Early Jurassic of Lesotho and the Republic of South Africa. The analysis is based on the characters of the dental system, including both previously used (Martin and Averianov, 2004; Pfretzschner et al., 2005; Ji et al., 2006) and original characters. The most primitive mammal, *Sinoconodon* Patterson et Olson, 1961 from the Early Jurassic of Yunnan, China, and *Morganucodon* are taken as outgroups. We analyzed the distribution of the following characters:

(1) Posterior upper premolar longer than, or approximately equal in length to M^1 (0); much shorter than M^1 (1).

(2) Ratio of width to labial length of upper molars less than 0.6 (0), 0.6–1.0 (1), or more than 1.0 (2).

(3) Triangular pattern of arrangement of main cusps of upper molars absent (0), present (1).

(4) Upper molars have two (0) or three (1) roots.

(5) Upper molars lacking a constriction in the middle part (0); having a small constriction, 0.7–0.9 of the labial crown length (1), or a considerable constriction, less than 0.7 of the labial crown length (2).

(6) On upper molars, cusp *X* absent (0), or present (1).

(7) On labial side of cusp *X*, wear facet absent (0), or present (1).

(8) On upper molars, cusp *Y* absent (0), or present (1).

The isolated upper molars assigned to *Woutersia* Sigogneau-Russell, 1983 from the Rhaetian of France include teeth that are similar to the molars of *Megazostrodon*, with a weakly pronounced triangular pattern (Sigogneau-Russell and Hahn, 1995, text-figs. 1A, 3B); teeth with a slightly transversely expanded crown and a rudimentary constriction in the middle part (Sigogneau-Russell and Hahn, 1995, text-figs. 5A–5D); and teeth with a much more expanded crown and one or two lingual cusps (*X* and *Y*; Sigogneau-Russell and Hahn, 1995, text-figs. 7, 8). These variations are interpreted here as a morphological gradient from anterior to posterior teeth of the tooth row of one or two closely related taxa. Thus, *Woutersia* is coded by a polymorphic condition of characters 2–5. The data on the upper molars of *Sibirotherium* are based on new undescribed specimens from PM TGU from the Lower Cretaceous of Western Siberia.

(9) On upper molars, cusp *Z* absent (0), or present (1).

(10) On upper molars, crest *A*–*X* absent (0), present, at least partial (1).

(11) Lower canine single-rooted (0), double-rooted (1).

A large double-rooted canine from the Bathonian of England (Sigogneau-Russell, 2003, text-fig. 6B) that was originally referred to as *Peraiocynodon major* Sigogneau-Russell, 2003, is assigned here to *Krusatodon kirtlingtonensis* Sigogneau-Russell, 2003 from the same locality [the synonymy of these taxa was considered by Averianov (2004)]. This tooth was originally determined as an upper canine. However, it is impossible to exclude the possibility that it is a lower canine; in addition, a polymorphism for the number of roots of canines of docodonts has not been recorded; therefore, *Krusatodon* is coded by the derived condition of this character.

(12) Number of lower premolars: two (0), three or four (1), five or six (2).

The exact number of lower premolars in *Borealestes* Waldman et Savage, 1972 from the Bathonian of Scotland is not known (Waldman and Savage, 1972). However, the small size of the first of three available premolars suggests that it is P_1 and this animal had three lower premolars, as *Haldanodon* Kühne et Krusat, 1972 from the Kimmeridgian of Portugal (Krusat, 1980).

(13) Ultimate lower premolar longer than, or approximately equal to, M_1 (0), or much shorter than M_1 (1).

(14) On lower molars, cusp *b* relatively small, positioned close to cusp *a* (0), or large, separated from cusp *a* by wide notch (1).

(15) On lower molars, cusp *c* located posterior to cusp *a* (0), or posterolingual to cusp *a* (1).

(16) On lower molars, cusp *g* absent (0), small (1), or large, almost equal in height to cusp *c* (2).

Table 1. Taxon–character array for Docodonta and some Morganucodonta

Taxa	Characters																												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Sinoconodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0
Morganucodon	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	1	0	?	0	0	0	0	0	0	0	0	0
Dinnetherium	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Megazostrodon	1	0	1	0	0	0	0	0	0	0	0	2	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Woutersia	?	?	1	0	1	?	0	?	0	?	?	?	?	0	1	?	0	1	1	0	0	0	0	0	0	0	0	?	0
Borealestes	?	2	1	1	2	1	1	1	0	1	?	1	1	0	1	1	?	1	1	1	0	?	1	1	?	1	1	?	0
Haldanodon	1	2	1	1	2	1	1	1	0	1	1	1	1	0	1	1	0	?	1	1	0	?	0	1	1	1	2	1	0
Docodon	1	2	1	1	2	1	1	1	0	1	1	1	1	0	1	1	0	1	2	1	0	1	0	1	2	1	2	?	1
Cyrtlatherium	?	?	1	1	?	1	1	1	0	1	?	?	1	1	1	2	?	0	2	0	1	1	1	1	2	0	1	?	1
Dsungarodon	?	2	1	1	2	1	1	1	0	1	?	?	?	1	1	2	0	0	2	0	1	1	1	1	1	0	1	1	0
Krusatodon	?	?	1	1	2	1	1	1	1	1	1	?	?	1	1	2	0	1	1	1	1	1	1	1	2	1	1	?	1
Castorocauda	?	?	?	?	?	?	?	?	?	?	1	2	1	1	1	?	0	1	2	1	1	1	1	1	2	0	0	1	0
Itatodon	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	2	1	1	1	1	2	1	1	0	0	1	1	1	0
Tashkumyrodon	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	2	0	1	1	1	2	1	1	0	1	1	1	?	0
Tegotherium	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	2	1	1	1	1	2	1	1	0	2	0	1	?	0
Sibirotherium	?	2	1	1	2	1	1	1	1	1	1	2	1	1	1	2	?	1	1	1	2	1	1	0	2	0	1	?	0

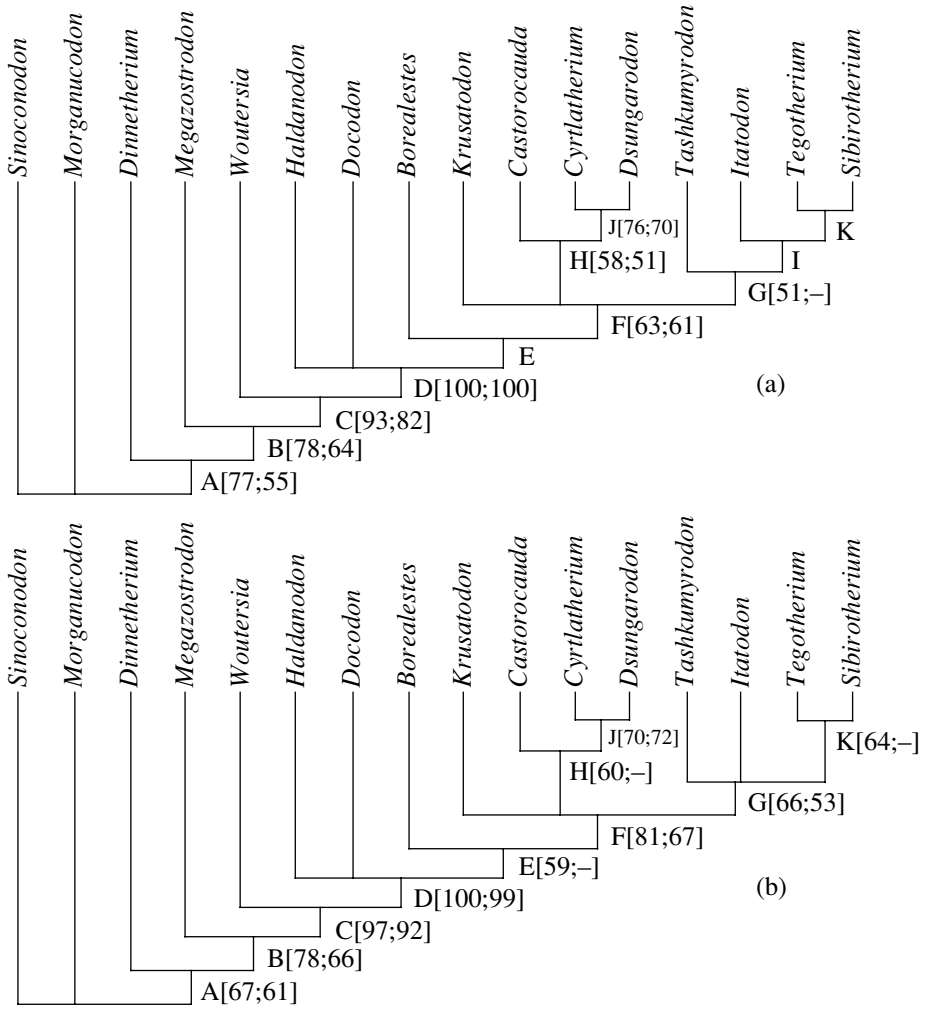


Fig. 2. Hypotheses of phylogenetic relationships of docodonts: (a) strictly consistent tree of three maximum parsimony trees produced by the analysis of the taxon–character matrix (Table 1), with nonordered coding of characters; (b) strictly consistent tree of five maximum parsimony produced by the analysis of the taxon–character matrix, with ordered coding of characters with several conditions; the first figure at nodes shows bootstrap support, %; the second figure is jackknife support, %.

(17) On lower molars, lingual cingulid at base of cusps *g* and *c* absent or *g* is cingulid cusp (0), or lingual cingulid present (1).

(18) On lower molars, cusp *e* absent (0), or present (1).

(19) On lower molars, mesiolingual cingulid directed posteriorly from cusp *e* terminating short of cusp *g* (0), reaching at least base of cusp *g* (1), absent or limited by anterior margin of tooth crown (2).

(20) On lower molars, cusp *f* absent (0), or present (1).

In *Itatodon*, the cusp *f* is clearly reduced, but distinct in specimen PM TGU, no. 200/3-BR-7.

(21) On lower molars, pseudotalonid absent (0); present, with its basin bordered mesiolingually by crest *b–g* (1), or present and bordered mesiolingually by crest *e–g* (2).

(22) On lower molars, crest *a–g* absent (0), or present (1).

(23) On lower molars, crest *b–e* absent (0), or present (1).

(24) On lower molars, crest *b–g* absent (0), or present (1).

In *Itatodon*, specimen PM TGU, no. 200/3-BR-7 has a crest passing from the cusp *b* to the base of the cusp *g* (Fig. 1a). However, the holotype has a posterior extension of this crest that is directed to the base of the cusp *a*; therefore, this crest is probably a rudimentary crest *a–b* rather than the crest *b–g* (which occurs in some docodonts). This homology is also corroborated by the fact that, in *Itatodon*, this crest forms the distolabial rather than mesiolingual wall of the pseudotalonid basin. Therefore, *Itatodon* is coded here by the primitive condition of this character.

(25) On lower molars, crest *a–d* absent (0), incomplete (1), or complete (2).

(26) On lower molars, crest *c–d* absent (0), or present (1).

(27) Interlocking of neighboring lower molars: cusp *d* of more anterior tooth located between cusps *b* and *e* of posterior tooth (0), cusp *e* of posterior tooth located between cusps *d* and *f* of anterior tooth (1), cusp *b* of posterior tooth overlying cusp *d* of anterior tooth (2).

In contrast to the matrix used by Ji et al. (2006), *Megazostrodon* and *Woutersia* are coded here by the primitive condition, while *Tashkumyrodon* and *Dsungarodon* are coded by (1), the derived condition of this character.

(28) On ultimate lower molar, cusp *c* developed to approximately the same extent as in preceding molars (0), or strongly or completely reduced (1).

(29) Plication of enamel (crenulation) on molars is absent or weak (0), is strongly developed (1).

We performed two variants of analysis of the taxon–character matrix (Table 1), using PAUP 4.0b10 software. In the first case, characters with several conditions (characters 2, 5, 12, 16, 19, 21, 25, and 27) were coded as nonordered. Using the *branch and bound* algorithm, three maximum parsimony trees of 50 steps were constructed (*CI* = 0.720, *HI* = 0.280, *RI* = 0.870, *RC* = 0.627). The strictly consistent tree shows a high resolution (Fig. 2a). In this cladogram, bootstrap support of the nodes E, I, and K is less than 50% and jackknife support of the nodes E, G, I, and K is also less than 50%. In the second variant, characters with several conditions were coded as ordered. Using the *branch and bound* algorithm, five maximum parsimony trees of 53 steps were constructed (*CI* = 0.698, *HI* = 0.302, *RI* = 0.871, *RC* = 0.608). The consistent tree is similar in topology to the consistent tree obtained in the previous case; however, *Itatodon* forms a polytomy with *Tashkumyrodon* and the clade *Tegotherium* + *Sibirotherium* in the node G (Fig. 2b). In this analysis, bootstrap support is more than 50% for all nodes, while jackknife support is less than 50% for the nodes E, H, and I. In the first analysis, as the characters are reweighed according to the value of *RC*, the consistent tree retains the same topology.

DISCUSSION

Our analysis shows paraphyly of Morganucodonta in relation to Docodonta, supporting the classical concept of the origin of docodonts from Morganucodonta (Kühne, 1950; Patterson, 1956; Crompton and Jenkins, 1968; Crompton, 1974; Averianov, 2002). Morganucodonts and docodonts share the unique plesiomorphic structure of the lower jaw, with a groove for postdentary bones and pseudoangular process, and the presence of the cusp *g* (kuehneocone) on the lower molars [which is absent from *Dinnetherium*] (Averianov, 2002; Kielan-Jaworowska et al., 2004; Averianov et al., 2005). *Dinnetherium* and *Megazostrodon* along with *Woutersia* and Docodonta belong to the same clade A (Fig. 2a), which is characterized by short ultimate premolars (characters 1 [1] and 13 [1]). The next clade (B, including *Megazostrodon, Woutersia*, and Docodonta) is characterized by triangular arrangement of the main cusps of the upper molars (character 3 [1]).

The clade C (*Woutersia* and Docodonta) is combined based on the transversely expanded upper molars with a constriction in the middle part, the lingual cusps *X* and *Y*, a transverse crest between the labial and lingual cusps (characters 2 [1, 2], 5 [1, 2], 6 [1], 8 [1] and 10 [1]; these characters are clearly pronounced on the presumably posterior molars of *Woutersia*, whereas the anterior teeth of this animal show a typical morganucodont-like pattern), and on the displacement of the cusp *c* to the lingual margin of the crown and the connection of the cusp *g* with the cusp *e* by the mesiolingual cingulid (characters 15 [1] and 19 [1]). *Woutersia* was originally assigned to the family Kuehneotheriidae (Sigogneau-Russell, 1983). Subsequently, it was placed in a monotypic "symmetrodont" family, with the remark that dental characters of this taxon demonstrate "a certain parallelism" with reference to docodonts, while docodonts could have evolved from early Theria sensu lato (= "Holotheria," see Luo et al., 2002 about the undesirability of the use of this term) (Sigogneau-Russell and Hahn, 1995, p. 245). Subsequently, Butler (1997) assigned *Woutersia* to Docodonta and subscribed to the hypothesis of the origin of docodonts from animals with the triangular molar pattern (see also Averianov, 2002; Martin and Averianov, 2004). In a recent report on Mesozoic mammals, *Woutersia* is still placed in "symmetrodonts" (Kielan-Jaworowska et al., 2004). We believe that the similarity between *Woutersia* and *Kuehneotherium* Kermack et al., 1968 from the Late Triassic of Europe and Greenland is convergent and incomplete; in the first taxon, the cusp *b* is located anterior to the central cusp *a*, whereas in *Kuehneotherium*, this cusp is located anterolingual to the central cusp. The main cusps on the lower molars of *Kuehneotherium* are arranged according to the triangular pattern, whereas *Woutersia* shows a semitriangular arrangement. A similar semitriangular pattern of the lower molars is preserved in all docodonts; their cusp *b* is always located anterior to the cusp *a* and never is displaced to the lingual edge of the crown. This character is probably the major synapomorphy of the clade *Woutersia* + Docodonta. Consequently, it is unreasonable to place *Woutersia* in "symmetrodonts," since the lingual displacement of the cusp *c* on the lower molars developed independently in the lineages of Morganucodonta–Docodonta and Theria sensu lato.

True docodonts (order Docodonta) form the clade D, which is characterized by further transverse expansion of crowns of the upper molars combined with distinct constriction in the middle part (characters 2 [2] and 5 [2]); appearance of the third (lingual) root of the upper molars (character 4 [1]); appearance of a wear facet on the labial side of the cusp *X* (character 7 [1]); development of a clear cusp *f* in the posterior part of the crown

of the lower molars (character 20 [1], the cusp *f* is also present in *Morganucodon* and is secondarily reduced in *Dsungarodon* and *Cyrtlatherium*); appearance of additional crests on the lower molars, i.e., *a–g* (character 22 [1], which is poorly developed or absent in *Borealestes* and *Haldanodon*), *b–g* (character 24 [1], which is secondarily reduced in the clade I), and *c–d* (character 26 [1], which secondarily disappeared in the clade G, in *Sibirotherium* and *Tegotherium*). Docodonts also have a double-rooted lower canine (character 11 [1]; the condition of this character in *Woutersia* is not known). Apparently, the cusp *c* of the posterior ultimate molar was reduced in all docodonts (character 28 [1]); however, the distribution of this character remains incompletely known. Docodonts differ sharply from morganucodonts in the pattern of interlocking of the lower molars; in morganucodontids, the cusp *d* projecting posteriorly is located in a notch between the anterior cusps *b* and *e* of the subsequent tooth, whereas, in the majority of docodonts, the anteriorly projecting cusp *e* is located in a notch between the cusps *d* and *f* of the preceding tooth (character 27 [1]; the primitive condition is retained in *Castorocauda*; in *Haldanodon* and *Docodon*, the anterior cusp *b* overlies the cusp *d* of preceding tooth, that is, character 27 [2]).

Docodonts include plesiomorphic taxa, such as *Borealestes, Haldanodon*, and *Docodon* Marsh, 1881 from the Kimmeridgian of the United States and, probably, from the Berriasian of England, which lack a pseudotalonid and have small cusps *b* and *g*, and the clade F, which comprises taxa with a pseudotalonid and large cusps *b* and *g* (characters 21 [1], 14 [1], and 16 [2]). An important synapomorphy of the clade F is probably an increase in the number of lower premolars to five or six (character 12 [2]); however, the number of premolars remains unknown in many taxa. *Borealestes* is slightly more advanced than *Haldanodon* and *Docodon* in the presence of the crest *b–e* (character 23 [1]; clade E).

The clade F is divided into two subclades (G and H). The clade H combines *Castorocauda* Ji et al., 2006 from the Middle Jurassic of Inner Mongolia, *Cyrtlatherium* Freeman, 1979 [= *Simpsonodon* Kermack et al., 1987; for the substantiation of synonymy of these taxa, see Sigogneau-Russell, 2001; Averianov, 2004] from the Bathonian of England, and *Dsungarodon* Pfretzschner et Martin, 2005 from the Bathonian of Dzungaria, in which the mesiolingual cingulid extending from the cusp *e* is reduced (character 19 [2], independently developed in *Docodon*) and the crest *c–d* is also reduced (character 26 [0], this reversion is also characteristic of *Tegotherium* and *Sibirotherium*). The genera *Cyrtlatherium* and *Dsungarodon* are combined (clade J) based on the reduction of cusps *e* and *f* on the lower molars. In this analysis, these characters are regarded as a reversion (18 [0] and 20 [0]). The clade G includes the "asiadocodonts" *Tashkumyrodon, Itatodon*, and *Tegotherium* and *Sibirotherium* (family Tegotheriidae). It is characterized by a special structure of the pseudotalonid, the mesiolingual corner of which is bordered by the crest *e–g* rather than the crest *b–g* (as in other docodonts with the pseudotalonid) (characters 21 [2] and 24 [0]). The fact that the crest *b–g* is secondarily reduced in "asiadocodonts," is corroborated by the presence of its rudiment in *Tashkumyrodon*. The relatively weak statistical support of the clade of "asiadocodonts" (both bootstrap and jackknife) is probably accounted for by a lack of knowledge of these animals.

"Asiadocodonts" include the clades I (*Itatodon, Tegotherium*, and *Sibirotherium*) and K (*Tegotherium* and *Sibirotherium*), which are characterized by the development of a lingual cingulid on lower molars (17 [1]) and reduction of the crest *c–d* (26 [0]), respectively.

The hypothesis proposed in this study for the phylogeny of docodonts allows certain assumptions concerning evolutionary development of this group. It is evident that there was no a basal dichotomy of the order into two stems, "Eudocodonta" (Euramerica) and "Asiadocodonta" (Asia), as was previously supposed (Martin and Averianov, 2004). The clade of "asiadocodonts" evolved from a group of docodonts possessing a pseudotalonid (clade F in Fig. 2). It is evident that the pseudotalonid developed independently in "asiadocodonts" and in the clade H + *Krusatodon*, because their pseudotalonids essentially differ in morphology (characters 21 [2] and 21 [1], respectively). The establishment of the clade F was probably confined to Asia, while its members recorded in the Middle Jurassic of England, such as *Krusatodon* and *Cyrtlatherium*, migrated from Asia; another migrant of this kind was apparently the pseudotribosphenic mammal *Shuotherium* Chow et Rich, 1982, known from the Late Jurassic of Sichuan Province, China, and from the Bathonian of England (see Chow and Rich, 1982; Sigogneau-Russell, 1998; Wang et al., 1998). Thus, progressive development of docodonts may have been restricted to Asia, while Europe and North America were inhabited by relatively plesiomorphic taxa such as *Borealestes, Haldanodon*, and *Docodon*. However, recent finds of docodonts in India (Prasad and Manhas, 2001; Datta, 2005) indicate how little we know about the phylogeny and biogeography of this group.

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REFERENCES

1. A. O. Averianov, "Early Cretaceous 'Symmetrodont' Mammal *Gobiotheriodon* from Mongolia and the Classification of 'Symmetrodonta,'" Acta Palaeontol. Polon. **47** (4), 705–716 (2002).
2. A. O. Averianov, "Interpretation of the Early Cretaceous Mammal *Peraiocynodon* (Docodonta) and Taxonomy of Some British Mesozoic Docodonts," Russ. J. Theriol. **3** (1), 1–4 (2004).
3. A. O. Averianov, A. V. Lopatin, P. P. Skutschas, et al., "Discovery of Middle Jurassic Mammals from Siberia," Acta Palaeontol. Polon. **50** (4), 789–797 (2005).
4. P. M. Butler, "An Alternative Hypothesis on the Origin of Docodont Molar Teeth," J. Vertebr. Paleontol. **17** (2), 435–439 (1997).
5. M.-C. Chow and T. H. V. Rich, "*Shuotherium dongi*, n. gen. and n. sp., a Therian with Pseudo-tribosphenic Molars from the Jurassic of Sichuan, China," Austral. Mammal. **5**, 127–142 (1982).
6. A. W. Crompton, "The Dentitions and Relationships of the Southern African Triassic Mammals *Erythrotherium parringtoni* and *Megazostrodon rudnerae*," Bull. Brit. Mus. Natur. Hist. Geol. **24**, 397–437 (1974).
7. A. W. Crompton and F. A. Jenkins, "Molar Occlusion in Late Triassic Mammals," Biol. Rev. **43** (4), 427–458 (1968).
8. P. M. Datta, "Earliest Mammal with Transversely Expanded Upper Molar from the Late Triassic (Carnian) Tiki Formation, South Rewa Gondwana Basin, India," J. Vertebr. Paleontol. **25** (1), 200–207 (2005).
9. Q. Ji, Z.-X. Luo, C.-X. Yuan, and A. R. Tabrum, "A Swimming Mammaliaform from the Middle Jurassic and Ecomorphological Diversification of Early Mammals," Science **311** (5764), 1123–1127 (2006).
10. Z. Kielan-Jaworowska, R. L. Cifelli, and Z.-X. Luo, *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure* (Columbia Univ. Press, New York, 2004).
11. G. Krusat, "Contribução para o conhecimento da fauna do Kimeridgiano da mina de lignito Guimarota (Leiria, Portugal): Part IV. *Haldanodon exspectatus* Kuhne and Krusat 1972 (Mammalia, Docodonta)," Mem. Serv. Geol. Portugal. **27**, 1–79 (1980).
12. W. G. Kühne, "A Symmetrodont Tooth from the Rhaeto–Liass," Nature **166** (4225), 696–697 (1950).
13. A. V. Lopatin and A. O. Averianov, "A New Docodont (Docodonta, Mammalia) from the Middle Jurassic of Siberia," Dokl. Akad. Nauk. **405** (2), 277–279 (2005).
14. Z.-X. Luo, Z. Kielan-Jaworowska, and R. L. Cifelli, "In Quest for a Phylogeny of Mesozoic Mammals," Acta Palaeontol. Polon. **47** (1), 1–78 (2002).
15. T. Martin and A. O. Averianov, "A New Docodont (Mammalia) from the Middle Jurassic of Kyrgyzstan, Central Asia," J. Vertebr. Paleontol. **24** (1), 195–201 (2004).
16. E. N. Maschenko, A. V. Lopatin, and A. V. Voronkevich, "A New Genus of the Tegotheriid Docodonts (Docodonta, Tegotheriidae) from the Early Cretaceous of West Siberia," Russ. J. Theriol. **1** (2), 75–81 (2003).
17. B. Patterson, "Early Cretaceous Mammals and the Evolution of Mammalian Molar Teeth," Fieldian. Geol. **13** (1), 1–105 (1956).
18. H.-U. Pfretzschner, T. Martin, M. W. Maisch, et al., "A New Docodont Mammal from the Late Jurassic of the Junggar Basin in Northwest China," Acta Palaeontol. Polon. **50** (4), 799–808 (2005).
19. G. V. R. Prasad and B. K. Manhas, "First Docodont Mammals of Laurasian Affinity from India," Curr. Sci. **81** (9), 1235–1238 (2001).
20. D. Sigogneau-Russell, "A New Therian Mammal from the Rhaetic Locality of Saint-Nicolas-de-Port (France)," Zool. J. Linn. Soc. **78**, 175–186 (1983).
21. D. Sigogneau-Russell, "Discovery of a Late Jurassic Chinese Mammal in the Upper Bathonian of England," C. R. Acad. Sci. Terre Planets. **327**, 571–576 (1998).
22. D. Sigogneau-Russell, "Docodont Nature of *Cyrtlatherium*, an Upper Bathonian Mammal from England," Acta Palaeontol. Polon. **46** (3), 427–430 (2001).
23. D. Sigogneau-Russell, "Docodonts from the British Mesozoic," Acta Palaeontol. Polon. **48** (3), 357–374 (2003).
24. D. Sigogneau-Russell and R. Hahn, "Reassessment of the Late Triassic Symmetrodont Mammal *Woutersia*," Acta Palaeontol. Polon. **40** (3), 245–260 (1995).
25. L. P. Tatarinov, "On an Unusual Mammal Tooth from the Jurassic of Mongolia," Paleontol. Zh., No. 2, 97–105 (1994).
26. M. Waldman and R. J. G. Savage, "The First Jurassic Mammal from Scotland," J. Geol. Soc. **128**, 119–125 (1972).
27. Y. Wang, W. A. Clemens, Y.-M. Hu, and C.-K. Li, "A Probable Pseudo-tribosphenic Upper Molar from the Late Jurassic of China and the Early Radiation of the Holotheria," J. Vertebr. Paleontol. **18** (4), 777–787 (1998).