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A new genus of the tegotheriid docodonts (Docodonta, Tegotheriidae) from the Early Cretaceous of West Siberia

Evgeny N. Maschenko, Alexey V. Lopatin & Alexey V. Voronkevich

ABSTRACT. *Sibirotherium rossicus* **gen. et sp. nov.** from the Early Cretaceous Ilek Svita in West Siberia (Shestakovo locality) is described based on lower jaw fragments. The lower molars exhibit the typical docodont pattern with the main cusp *a* connected by transverse crests to the lingual cusps *c* and *g*. By absence of crests *b–g* and *c–d*, and presence of crests *b–e* and *e–g*, as well as by the development of an enlarged anterior basin, *Sibirotherium* **gen. nov.** is similar to *Tegotherium* from the Late Jurassic of Mongolia. These two genera are united in the endemic Asian family Tegotheriidae. The new genus is plesiomorphic in retaining well developed crest *d–f*, and it is more derived than *Tegotherium* in partial reduction of the crest *e–g*. The morphological diversity of the tegotheriids suggests a significant differentiation of the Late Jurassic — Early Cretaceous docodonts in Asia.

KEY WORDS: *Sibirotherium rossicus* **gen. et sp. nov.**, Tegotheriidae, Docodonta, Early Cretaceous, West Siberia.

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Новый род теготериидных докодонтов (Docodonta, Tegotheriidae) из раннего мела Западной Сибири

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РЕЗЮМЕ. На основании фрагментов нижних челюстей из нижнемеловой илекской свиты местонахождения Шестаково в Западной Сибири описан *Sibirotherium rossicus* **gen. et sp. nov.** Его нижние коренные зубы имеют типичный для докодонтов тип строения: главный бугор *a* поперечными гребнями соединен с лингвальными буграми *c* и *g*. По отсутствию гребней *b–g* и *c–d*, наличию гребней *b–e* и *e–g* и увеличенного переднего бассейна *Sibirotherium* **gen. nov.** сходен с *Tegotherium* из верхней юры Монголии. Эти два рода формируют особое семейство азиатских докодонтов — Tegotheriidae. Плезиоморфным признаком нового рода является наличие хорошо развитого гребня *d–f*, а продвинутой по отношению к *Tegotherium* чертой — частичная редукция гребня *e–g*. Известное в настоящее время морфологическое разнообразие теготериид может свидетельствовать о значительной таксономической радиации позднеюрских — раннемеловых докодонтов в Азии.

КЛЮЧЕВЫЕ СЛОВА: *Sibirotherium rossicus* **gen. et sp. nov.**, Tegotheriidae, Docodonta, ранний мел, Западная Сибирь.

Introduction

The Early Cretaceous vertebrate locality near Shestakovo is known since 1953, when two partial skeletons of the ceratopsian dinosaur *Psittacosaurus* were found. The Shestakovo sites, situated in the vicinity of the Shestakovo village in the south-east of the West Siberian plain (the Kiya River Basin, Kemerovo Region, Chebula District), are among the most prominent Mesozoic vertebrate localities in Russia. The Lower Cretaceous fossil-bearing deposits of the Ilek Svita were dated as Neocomian based on invertebrates (Osyko, 1958) or Aptian — Albian based on presence of *Psittacosaurus* (Rozhdestvensky, 1960). Dating of the Shestakovo assemblage is still disputed: different authors estimate its age from the Berriasian-Valanginian to Aptian-Albian (Alifanov *et al.*, 1999; Leshchinskiy *et al.*, 2000, 2001).

First data on Shestakovo Mesozoic mammals were obtained in 1995. Intensive excavations and screen-washing at Shestakovo, carried out since 1995 by a Tomsk University team, with participation of specialists from the Paleontological Institute of the Russian Academy of Sciences, Moscow, and the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, revealed a diverse vertebrate fauna. Most paleontological finds were discovered in mellow meagre chalky crossbedded coarse-grain sands and sandstones. These deposits possibly represent remains of river-spits in lower or middle reaches. Representatives of about 20 genera and 26 species of vertebrates have been recov-

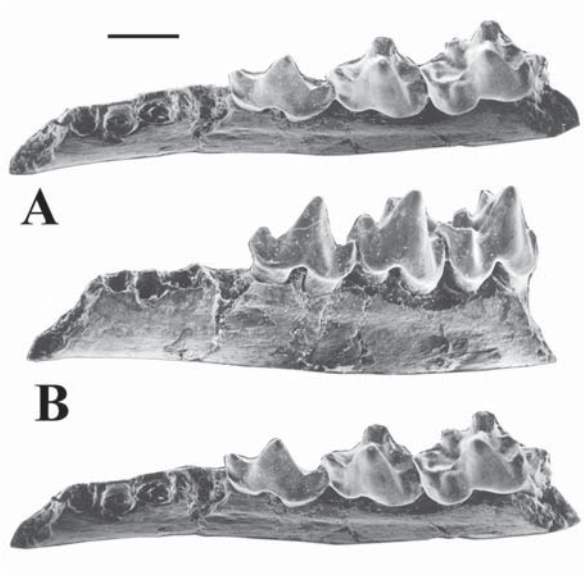

Figure 1. *Sibirotherium rossicus* **gen. et sp. nov.**, PM TSU 16/5-22, holotype, left dentary fragment with dp3(?), dp4(?), and m1. Shestakovo 1, Kemerovo Region, Russia; Ilek Svita, Lower Cretaceous.
A — occlusal and slightly lingual view (stereo pair); B — buccal view. SEM micrographs. Scale bar 1 mm.

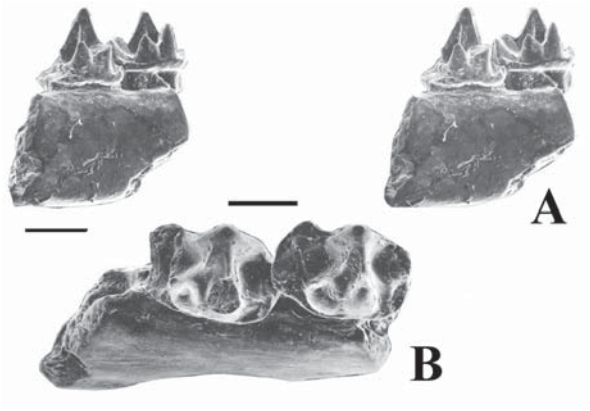

Figure 2. *Sibirotherium rossicus* **gen. et sp. nov.**, PM TSU 16/5-14, right dentary fragment with m2–m3(?). Shestakovo 1, Kemerovo Region, Russia; Ilek Svita, Lower Cretaceous.
A — lingual view (stereo pair); B — occlusal and slightly lingual view. SEM micrographs. Scale bar 1 mm.

ered and identified from Shestakovo: palaeonisciform and sinamiid fishes, amphibians, a "macrobaenid" turtle, lizards, protosuchian and shartegosuchid crocodiles, dinosaurs, pterosaurs, birds, the tritylodontid synapsid *Xenocretosuchus sibiricus*, the amphilestids *Gobiconodon borissiaki, G. hoburensis, Gobiconodon* **sp. nov.** and Amphilestinae indet., the docodont *Sibirotherium rossicus* **gen. et sp. nov.**, and the peramurid "eupantothere" *Kiyatherium cardiodens* (Maschenko & Lopatin, 1998; Tatarinov & Maschenko, 1999; Efimov & Leshchinskiy, 2000; Leshchinskiy *et al.*, 2000, 2001; Averianov *et al.*, 2002; Maschenko *et al.*, 2002).

The new docodont is described below. The specimens were found by L.G. Shikhovtseva, E.N. Maschenko, and A.V. Voronkevich in 2000 at the Shestakovo 1 site (Maschenko *et al.*, 2000, 2001). This site is situated on the right bluff of the Kiya River, 1.5 km downstream from Shestakovo village, N 55°54′12″, E 87°57′28″.

The dental nomenclature and terminology of the Docodonta follows Butler (1997). The lettering of the cusps is coordinated with the descriptive cusp terms used by Kermack *et al.* (1987) and Sigogneau-Russell (2001): cusp *a* — main cusp, cusp *b* — mesiobuccal cusp, cusp *c* — distolingual cusp, cusp *g* — mesiolingual cusp, cusp *e* — lingual anterior cuspule, cusp *ee* — additional anterolingual cingular cuspule, cusp *d* — buccal posterior cusp, cusp *f* — lingual posterior cuspule. The ridges between these cusps, respectively, are crests *a–b*, *a–g*, *a–c*, *a–d*, *b–g*, *b–e*, *e–g*, *c–d*, *d–f*, and *f–c*. The docodont wear facet terminology is after Jenkins (1969).

The material is housed in the collection of the Paleontological Museum of the Tomsk State University (PM TSU) in Tomsk, Russia.

Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Docodonta Kretzoi, 1946

Family Tegotheriidae Tatarinov, 1994

Tegotheriidae: Tatarinov, 1994: 104.

Type genus. *Tegotherium* Tatarinov, 1994, Late Jurassic of Mongolia.

Included genus. *Sibirotherium* **gen. nov.**, Early Cretaceous of West Siberia.

Diagnosis. Docodonts with the following combination of primitive (–) and derived (+) characters of the lower molariform teeth: 1) anterior basin ("pseudotalonid") enlarged (+); 2) cusp *g* enlarged (+); 3) cuspule *e* well developed (–); 4) crest *b–e* well developed (–); 5) crest *b–g* absent (+); 6) crest *e–g* present (+); 7) crest *c–d* absent (+); 8) crest *f–c* present (+); 9) additional cingular cuspule *ee* present (+).

Differential diagnosis. Tegotheriidae differs from Docodontidae Simpson, 1929 by characters 3–6, 8, and 9. Also, the tegotheriids differ from all known docodontids, with the exception of *Simpsonodon* Kermack *et al.*, 1987, by characters 1, 2, and 7. *Simpsonodon* is convergently similar to Tegotheriidae in having enlarged anterior basin, large cusp *g*, and absence of the distal crests. The tegotheriids differ from a new docodont from the Middle Jurassic of Kyrgyzstan (Martin & Averianov, in press) by characters 1, 2, 5 and 7.

Genus *Sibirotherium* **gen. nov.**

Type species. *S. rossicus* **sp. nov.**, Early Cretaceous of West Siberia.

Diagnosis. Differs from *Tegotherium* Tatarinov, 1994, the only other member of Tegotheriidae, by the following combination of primitive (–) and derived (+) characters of the lower molariform teeth: 1) crest *b–e* relatively short (+); 2) crest *e–g* interrupted or reduced, not reached the cusp *g* (+); 3) crest *d–f* well developed (–). The ultimate lower deciduous tooth is partially molariform, but the anterior basin is not

enlarged and cusps *e* and *g* are absent. The lower postcanine dental formula is p1–4? m1–6?.

Etymology. The generic name is after Siberia and θηρι–ον, beast (Greek).

Sibirotherium rossicus **sp. nov.**
Figs. 1–4.

Holotype. PM TSU 16/5-22, a left dentary fragment with dp3, dp4, and m1.

Referred material. PM TSU 16/5-14, a right dentary fragment with m2−m3(?); PM TSU 16/5-2, a left dentary fragment with m4−m5(?) and fragments of m3(?) and m6(?).

Type locality. Shestakovo 1, Chebula District, Kemerovo Region, Russia.

Stratigraphic level. Ilek Svita, Lower Cretaceous.

Diagnosis. As for the genus.

Etymology. The species name is after Russia, the country of provenance.

Description. The holotype is the fragment of a left dentary, with three slightly worn teeth: the penultimate and ultimate deciduous premolars (presumably, dp3 and dp4), and first molar (m1). Anterior to the penultimate deciduous premolar, there are four alveoli for two more anterior deciduous(?) premolars. Judging by the alveoli, the size of the deciduous premolars is dp1 < dp2 < dp3 > dp4. Mental foramina and symphysis region are not preserved in the dentary. The mandible is shallow; the depth of the dentary is approximately equal to height of the molar crown. The deciduous premolars and molar possess two well separated roots of approximately equal size.

The penultimate deciduous premolar has a strong lingual cingulid, and a very small and short anterior buccal cingulid at the level of the mesial cusp. There are three cusps placed in linear arrangement. The highest main cusp is situated in the center of the crown. Mesial and distal accessory cusps are considerably smaller than the main cusp. Longitudinal crests run from the tip of the main cusp to both the mesial and distal cusps. All cusp are slightly worn apically.

The dp4 structure is intermediate between that of dp3 and m1. Dominant main cusp *a* is connected by sharp crests with the mesial cusp *b* and distal cusp *d*. There are a large cusp *c* and prominent transverse crest *a–c*. The anterior transverse crest is very weak, and is connected with the base of cusp *c*. Cusp *g* is absent. The anterior basin is small and shallow. Cusp *e* is absent. The cuspules *d* and *f* are very small, connected by a distinct long crest *d–f*. Crest *f–c* is absent. Lingual cingulid is prominent, but it is interrupted at the level of cusp *c*. The reduced buccal cingulid is weakly developed at the level of cusp *b* only. Wear facets are developed on the tips of cusps *a* (facet *1a*), *b* (facet *4a*), and along the crest *d–f* (facets *11c* and *11d*). The apex of cusp *c* is broken off.

The crown of m1 is rectangular in outline. Large conical cusp *a* has a slightly concave lingual surface and a rounded buccal side. There are four crests running from the tip of cusp *a*: two longitudinal crests (*a–b* and *a–d*), and two transverse crests (*a–g* and *a–c*). Crest *a–g* is directed mesiolingually, and crest *a–c* extends distolingually. The angle between transverse crests is about 40°. Cusp *a* bears a wear facet *1a* at the tip which extends downwards along crest *a–c* (facet *3*). Crests *a–b* and *a–d* are sharp. The crest *a–g* is somewhat rounded, and bears no wear facet.

Cusp *c* is the second highest cusp on m1. It is considerably lower than cusp *a* (apically broken off). Cusp *g* is significantly smaller and lower than cusp *c*. A rather strong apical wear facet (*7a*) is developed on this cusp. Bases of cusps *c* and *g* are not connected, with a distinct space between them. Cusp *b* is considerably smaller than cusp *c,* but somewhat larger and higher than cusp *g*. Cusps *b* and *a* are placed along the buccal border of the crown. There is a distinct side wear facet (*1c*) on the anterior and buccal slopes of cusp *b*, anteriorly from the buccal fold between cusps *b* and *a*. Cusp *b* is connected with crests *a–b* and *b–e*. Crest *b–e* is short and high. Cusp *e* is approximately equal in height to cusp *b*, but is much less stout. Lingually, there is an additional cingular cusp *ee*. Well developed crest *e–g* does not reach cusp *g*. Between the square formed by crests *a–b*, *b–e*, *e–g*, and *a–g*, there is a rather deep anterior basin with slight crenulations on the lingual slope of cusp *b*.

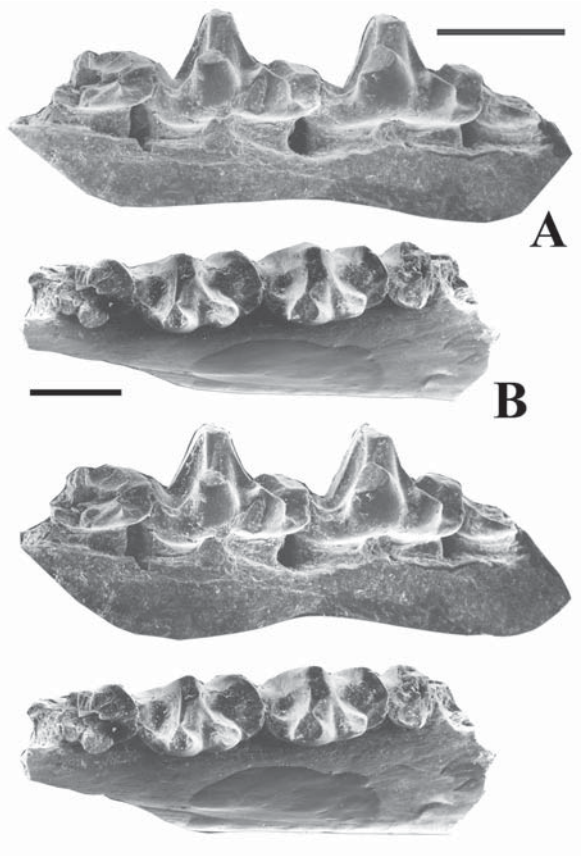

Figure 3. *Sibirotherium rossicus* **gen. et sp. nov.**, PM TSU 16/5-2, left dentary fragment with m4–m5(?) and fragments of m3(?) and m6(?). Shestakovo 1, Kemerovo Region, Russia; Ilek Svita, Lower Cretaceous.
A — lingual and slightly occlusal view. Scale bar 0.3 mm; B — occlusal and slightly lingual view. Scale bar 1 mm. SEM micrographs (stereo pairs).

A small cusp *d* forms the buccal end of the prominent crest *d–f*. At the lingual end of this crest there is a small cusp *f*, which bears a distinct wear facet. Between crests *a–c* and *d–f* there is a rather deep circular posterior basin. It is bounded by crest *a–d* buccally, and by the very thin and short crest *f–c* lingually. Crest *f–c* is connected to the posterior base of cusp *c*, but it does not ascend on the wall of this cusp. There are no prominent cingulids at the base of the crown, with the exception of the anterolingual and posterolingual corners of the tooth. The posterior end of the crown is somewhat oblique.

The second specimen, PM TSU 16/5-14, is a fragment of a right dentary with two unworn molars, probably m2 (ante-

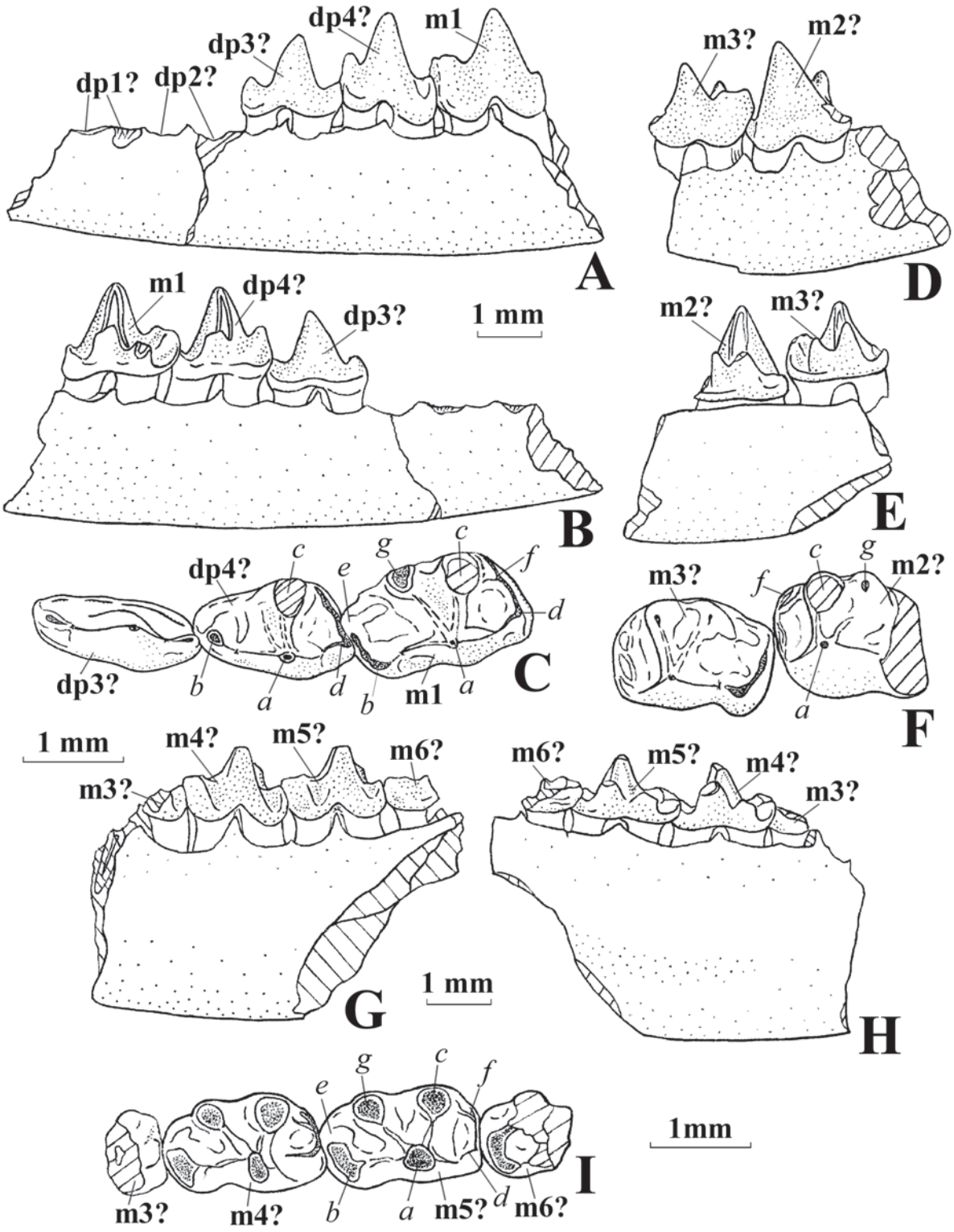

Figure 4. *Sibirotherium rossicus* **gen. et sp. nov.** Shestakovo 1, Kemerovo Region, Russia; Ilek Svita, Lower Cretaceous. A–C — PM TSU 16/5-22, holotype, left dentary fragment with dp3(?), dp4(?), and m1 (A — buccal, B — lingual views, C — occlusal view of teeth); D–F — PM TSU 16/5-14, right dentary fragment with m2–m3(?) (D — buccal, E — lingual views, F — occlusal view of teeth); G–I — PM TSU 16/5-2, left dentary fragment with m4–m5(?) and fragments of m3(?) and m6(?) (G — buccal, H — lingual views, I — occlusal view of teeth). Scale bar 1 mm.

rior lobe is broken off) and m3. The depth of the dentary fragment and size of the teeth suggest that the preserved molars belong to the anterior half of the molar row. However, the structure of the anterior preserved tooth differs from that in m1. Thus, this tooth may be a m2, and the following is a m3. The posterior end of both teeth is straight, not oblique as in m1. Cusp *a* is more robust in m2 than in m3. Cusps *c* and *g* are connected at their bases, but are separated by a wide and deep notch. The posterior basin is wider, and crest *f–c* is more prominent than in m1, highly ascending on the posterior wall of cusp *c*. The anterolingual cingulid is present at the level of cusps *b* and *g*. The crown of m3 is shorter than that of m1 or m2, with a considerably lower main cusp. Principally, the m3 structure does not differ from that of m1 and m2, but crest *a-g* does not reach the base of cusp *g*, crest *e-g* is interrupted in the middle, and crest *f–c* is absent. Cusps *c* and *g* are connected at their bases. The wear facet on cusp *f* is relatively large. There are distinct crenulations between crests *a–c* and *d–f*. The lingual cingulid is well developed, almost complete, but interrupted at the level of cusp *c*. Cusps *a*, *c*, and *g* have strong apical wear facets, *1a*, *9a,* and *7a*, respectively. Distinct short wear facets *3* and *9b* are present along crest *a–c*. They are separated by a deep notch.

The third specimen, PM TSU 15/5-2, is a fragment of the posterior part of a left dentary, containing two strongly worn complete molars, and two molar fragments anteriorly and posteriorly from them. The smallest last molar in this fragment is interpreted as the ultimate molar in the tooth series. Because the molar count of Tegotheriidae is unknown, and other docodont molars differ considerably from that of the specimens described above, we cannot specify the homology of these teeth precisely. However, the shapes of the main cusps of the complete molars suggest that these teeth come from a position posterior to m2. Moreover, the shape of the posterior basin of the most anterior preserved fragmented tooth is similar to that of m3 on specimen PM TSU 15/5-14. Thus, tentatively, we interpret the molars described below as fragmented m3, complete m4 and m5, and fragmented m6.

The preserved part of the mandible is deep, the dentary is approximately twice as deep as the molar crowns. The Meckel's groove is shallow, but relatively wide. It is well developed under m6 and m5, and hardly visible under m4 (Figs. 3B, 4H). The groove is located at the level of one third of the dentary depth.

The preserved fragment of m3 exposes a small posterior basin, cusp *d*, minute cusp *f*, and short crest *d–f*, and a small cingulid in the posterolingual corner of crown.

The crowns of m4 and m5 are equal in length and height. Cusp *a* is not so massive as in m1 or m2, but it is similar to that in m3. The angle between transverse crests *a–g* and *a–c* is about 60°. Strong wear facets descend along crests *a–b* and *a–d*. There is a space between cusps *g* and *c*. Cusp *c* is half as high as cusp *a*, and it bears a strong wear facet *9a+9b*. Cusp *g* is two times smaller and lower than cusp *c*. A strong apical wear facet (*7a*) is developed on this cusp, too. There is a deep buccal fold between cusps *b* and *a*. Cusps *b* and *e* are twinned. They have one undivided wear facet. Crest *e–g* is reduced, very weak and interrupted in the middle. The drop-shaped anterior basin is relatively small and shallow. The anterolingual cingulid is well developed. Cusps *d* and *f* are distinct, and crest *d–f* is short. Cusp *f* is connected to the posterior base of cusp *c* by a short crest *f–c*. The circular posterior basin is small. A lingual cingulid is not present.

Structure of m5 does not differs from that of m4, except in the lower size differentiation between cusps *c* and *g*, and larger posterior basin. Crest *e–g* is more reduced, cusps *e* and *g* are well separated by a wide lingual fold. Cingular cuspule *ee* is well developed. Cusp *d* is relatively large. Crest *f–c* highly ascends on the posterior wall of cusp *c*. Judging by the fragment of the anterior lobe of m6, this tooth was much smaller than m4 or m5, and possibly had a complete crest *e–g*.

Measurements (all in mm). Holotype: dp3: length 1.60, width 0.75, height 1.35; dp4: length 1.50, width 1.10, height 1.75; m1: length 1.90; width 1.20, height 1.75; dentary depth below dp4 2.0, below m1 2.3.

Specimen PM TSU 16/5-14: m2: width 1.30, height 1.70; m3: length 1.65; width 1.10, height 1.30; dentary depth below m2 2.0.

Specimen PM TSU 16/5-2: m4: length 1.60, width 1.10, height 1.25; m5: length 1.60; width 1.05, height 1.20; dentary depth below m4 3.00.

Remarks. The structure of the ultimate deciduous premolar of *Sibirotherium rossicus* **gen. et sp. nov.** is similar to that of *Docodon* ["*Peraiocynodon"*] (Butler, 1939) and *Haldanodon* (Krusat, 1980: figs. 23, 24). However, in comparison to *Docodon*, the penultimate deciduous premolar of *Sibirotherium* **gen. nov.** exhibits the more simplified pattern, without cusp *c* and crest *a–c*. The two anterior deciduous premolars are double-rooted, as dp1 and dp2 of *Docodon*.

Discussion

At present the order Docodonta includes few genera: the Middle Jurassic European *Borealestes* Waldman et Savage, 1972, *Simpsonodon* Kermack *et al.*, 1987, and *Cyrtlatherium* Freeman, 1979 (possible synonym of the latter); *Docodon* Marsh, 1881 from the Late Jurassic of North America and Early Cretaceous of Europe, the Late Jurassic European *Haldanodon* Kühne et Krusat, 1972, a new Middle Jurassic taxon from Kyrgyzstan, and the Late Jurassic *Tegotherium* Tatarinov, 1994 from Mongolia (Simpson, 1929; Kretzoi, 1946; Kühne & Krusat, 1972; Waldman & Savage, 1972; Kron, 1979; Krusat, 1980; Kermack *et al.*, 1987; Lillegraven & Krusat, 1991; Tatarinov, 1994; Martin & Nowotny, 2000; Martin & Averianov, in press). The newly described genus, the Early Cretaceous Asian *Sibirotherium* **gen. nov.**, increases our knowledge on the temporal and geographic distribution of Docodonta, being the first docodont from Siberia and the youngest record for the whole group.

Martin & Averianov (in press) performed a phylogenetic analysis of all known docodont taxa based on lower molar characters. They followed the idea by Butler (1997) that docodonts were derived from a *Woutersia*-like mammal, having a main cusp *a*, a lingually displaced cusp *c*, cusp *b* in a more buccal position, well developed cusps *e*, *g*, and *d*, and three main crests connecting some of the cusps: *a–c*, *a–b*, and *b–e*. They reconstructed the next hypothetical stage in the development of docodont lower molars, with additional four ridges (crests *d–f*, *c–d*, *a–g*, and *b–g*) and one cusp (*f*). Crest *a–g* is present in all known docodonts, but other crests have been secondarily lost in some taxa. Martin & Averianov (in press) suggest that after this stage docodonts split into two main branches: Euroamerican docodonts and Asian docodonts. The discovery of *Sibirotherium* **gen. nov.** confirms Martin's & Averianov's hypothesis.

The Asian branch of the docodonts includes the family Tegotheriidae and one genus outside this family (Martin & Averianov, in press). Mainly, Tegotheriidae are characterized by the following characters in the lower molariform teeth: an enlarged anterior basin ("pseudotalonid"), a large cusp *g*, well developed cuspule *e* and crests *b–e*, *e–g*, *f–c*, and absence of crests *b–g* and *c–d*.

Tegotherium is known by one lower molar from the Late Jurassic Shar-Teg locality in Mongolia (Tatarinov, 1994; Kielan-Jaworowska *et al.*, 2000; Martin & Averianov, in press). *Sibirotherium* **gen. nov.** is similar to *Tegotherium* by absence of crests *b–g* and *c–d*, and presence of crests *b–e* and *e–g*, as well as by the development of an enlarged anterior basin. *Sibirotherium* **gen. nov.** is plesiomorphic in retaining well developed crest *d–f*, and it is more derived than *Tegotherium* in partial reduction of the crest *e–g*. *Sibirotherium rossicus* **gen. et sp. nov.** is much larger than *Tegotherium gubini* Tatarinov, 1994. The molars of *S. rossicus* **gen. et sp. nov.** are 1.6 to 1.9 time longer, than the tooth of *T. gubini*. Representing the most complete and well-preserved tooth row among Asian docodonts, *S. rossicus* **gen. et sp. nov.** considerably increases our knowledge on the morphology of this group.

Thus, *Tegotherium* and *Sibirotherium* **gen. nov.** form the separate Asian docodontan family Tegotheriidae. Newly known morphological diversity of the Asian docodonts suggests a significant differentiation of this branch of the order.

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