Discovery of Middle Jurassic mammals from Siberia

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Mammal remains from the Middle Jurassic (Bathonian) Berezovsk Quarry on the south of Krasnoyarsk Territory, West Siberia, Russia are referred to Docodonta indet. (two edentulous fragmentary dentaries) and Mammalia indet. (a single-rooted tooth). The dentaries exemplify a unique combination of plesiomorphic characters found among stem mammals only in Docodonta and *Morganucodon*: well developed Meckel's groove, trough for postdentary bones with overhanging medial ridge and a diagonal ridge on the floor separating the "adductor fossa" and angular facet, and well developed and posteroventrally directed pseudangular process with facet for the reflected lamina of angular. Both specimens share with Docodonta the prearticular facet placed ventral to the angular facet and extending posteriorly to the mandibular foramen. This facet is not present in *Morganucodon*, where the prearticular lies medial to the angular. Medial position of the prearticular in *Morganucodon* is connected with the compound jaw articulation in this genus, in which a rudimentary articular-quadrate mandibular joint is present medially to the dentary-squamosal joint. In Docodonta indet. from Berezovsk Quarry, *Haldanodon* and *Docodon* the position of the prearticular ventral to the angular is connected with the position of the articular complex ventral to the dentary condyle. Such articular complex could not function as a mandibular joint and postdentary bones in Docodonta were used solely for sound transmission. One specimen from Berezovsk Quarry shares with *Morganucodon* a groove for replacement dental lamina, which was not reported previously for Docodonta. Mammal remains from Berezovsk Quarry are among the oldest occurrences for Docodonta, the first record of Jurassic mammals for Siberia, and only second such record for the whole of Russia.

Key words: Docodonta, *Morganucodon*, dentary, anatomy, Bathonian, Jurassic, Siberia.

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Introduction

During the past decade our knowledge on the Mesozoic vertebrate life of Siberia greatly increased. Remarkable were findings of Early Cretaceous mammals in Siberia (Maschenko and Lopatin 1998; Leshchinskiy et al. 2003; Maschenko et al. 2002, 2003). But probably the most exciting was discovery of a Middle Jurassic microvertebrate locality Berezovsk Quarry in the south of the Krasnoyarsk Territory, made by S.A. Krasnolutskii in 2000 (Alifanov et al. 2001). This locality produced numerous disarticulated, but nicely preserved bones of fishes, turtles, crocodiles, dinosaurs, and less common the remains of salamanders, pterosaurs, lizards, tritylodontids, and mammals (Table 1). Notably, all vertebrates in the assemblage are fresh-water or terrestrial, no shark teeth have been found. The rocks yielding the fossils were formed in an inland area of the ancient Asiatic landmass, far from the nearest sea in the Middle Jurassic, and thus represent a rarely sampled Middle Jurassic continental biota.

The primitive mammals from the Berezovsk Quarry are represented by two edentulous dentary fragments of Docodonta indet. and a tooth of Mammalia indet. These remains

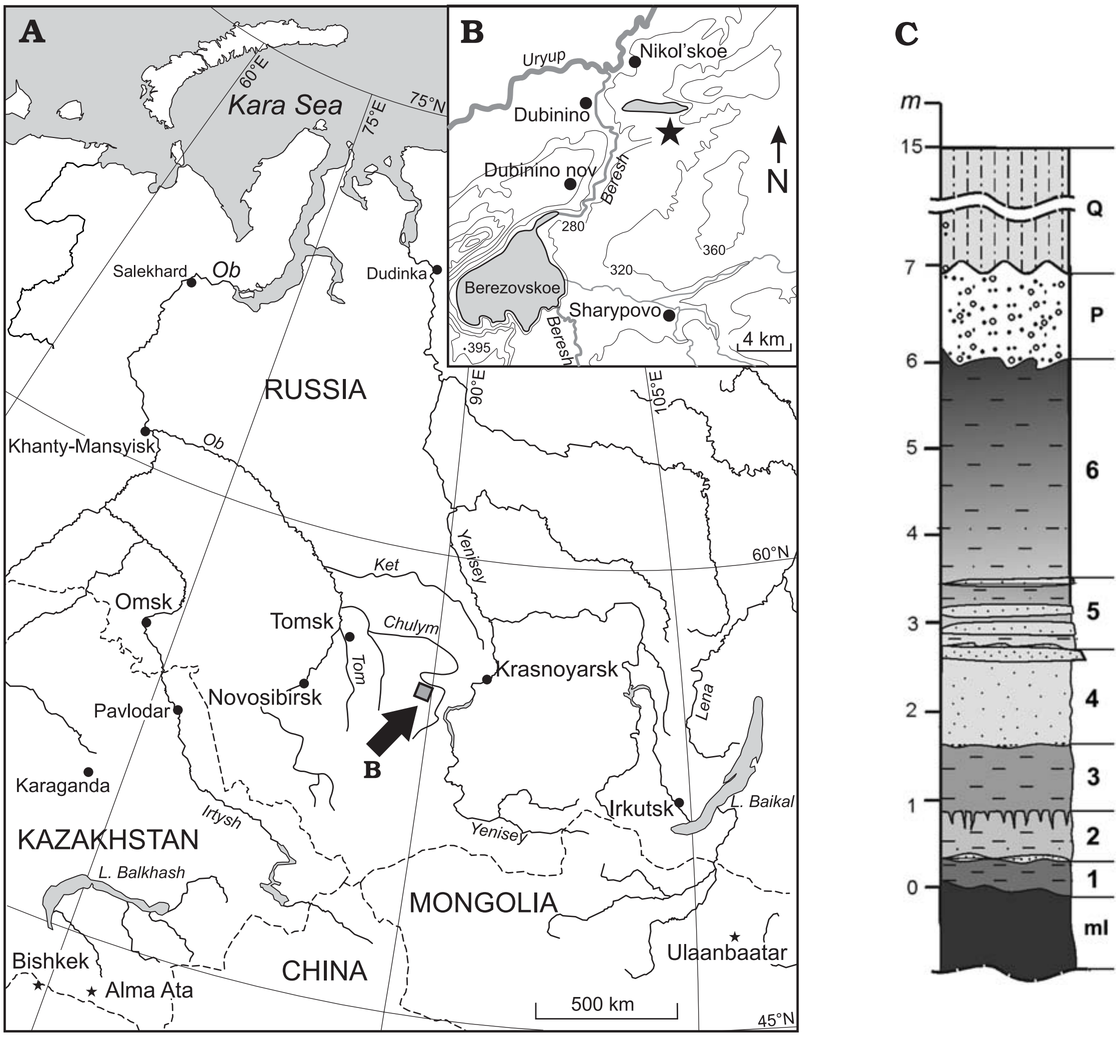

Fig. 1. **A**. Geographic position of Berezovsk Quarry in West Siberia. **B**. Vicinity of Nikol'skoe village with the Berezovsk Quarry indicated by asterisk. **C**. Local geologic section consisting of coal of the Middle Member of Itat Formation (mI), layers 1–6 of the Upper Member of Itat Formation (see text for description), Palaeogene sands (P) and Quaternary loess (Q). Vertebrate remains come from the layers 3, 4, and 5.

are the first record of Jurassic mammals for Siberia and only the second such record for the whole Russia (a femur of Morganucodontidae indet. was reported from the Bajocian–Bathonian locality Peski nearby Moscow: Gambaryan and Averianov 2001). The first jaw from the Berezovsk Quarry (PIN 5087/1) was found by N.V. Martynovich in 2001. The second jaw (PM TGU 200/3-BR-1) was found by the joint expedition from Saint Petersburg and Tomsk universities in 2003. Finally, a tooth (PM TGU 200/3-BR-2) was found by P.P. Skutschas in 2004 in Saint Petersburg during sorting of washed concentrate obtained by the 2003 expedition.

In classification of Mesozoic mammals we follow Averianov (2002) and Kielan-Jaworowska et al. (2004). The latter book is also followed in the anatomical terminology, except that we designate the process on the dentary in morganucodontans and docodontans pseudangular rather than angular.

Institutional abbreviations.—PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; PM TGU, Paleontological Museum, Tomsk State University, Tomsk.

Geographic and geological setting

The Berezovsk Quarry is situated 500 m south of Nikol'skoe village, Sharypovo District, Krasnoyarsk Territory, Russia (Fig. 1A, B). The quarry exposes Jurassic, Paleogene and Quaternary deposits. The Jurassic consists of Middle and Upper Members of the Itat Formation. The Middle Member is a productive brown coal layer of some 40 m thickness. It is dated as Bajocian based on the pollen complex including *Cyathidites minor*, *Dicksonia densa*, and *Neoraistrickia rotundiforma* (Raevskaya et al. 1993). Above there are deposits of the Upper Member of Itat Formation divided into six layers (Fig. 1C):

Layer 1: Deep-brown or black clay with inclusion of coalicified plant remains. Thickness ~0.4 m.

Layer 2: Light green-grey plastic clay with lenses up to 5 cm in thickness and 15–20 cm in size of fine to medium-grained sand. Thickness ~0.5 m.

Layer 3: Dark green-grey solid clay with vertebrate remains, concentrated at the top of the layer. Thickness 0.75 m.

Table 1. List of vertebrates from the Berezovsk Coal Quarry, Krasnoyarsk Territory, Russia; Upper Member of Itat Formation, Bathonian, Middle Jurassic.

- Pisces
  - Dipnoi indet.[1]
  - Palaeonisciformes indet.[2]
- Amphibia
  - Caudata indet. (cf. Karauridae)[3]
- Reptilia
  - Testudinata
    - Cryptodira
      - Xinjiangchelyidae
        - *Xinjiangchelys* sp.[4]
  - Squamata
    - Scincomorpha indet. (cf. Paramacellodidae)[5]
  - Crocodylomorpha
    - Goniopholididae indet. (cf. *Sunosuchus* sp.)[6]
  - Dinosauria
    - Theropoda
      - Theropoda indet. (cf. Dromaeosauridae)[7]
    - Sauropoda
      - Titanosauriformes indet.[7]
    - Stegosauria
      - Stegosauria indet.[7]
    - Ornithopoda
      - Heterodontosauridae indet.[7]
  - Pterosauria
    - Pterodactyloidea indet.[8]
- Cynodontia
  - Tritylodontidae indet.[9]
- Mammalia
  - Docodonta indet.
  - Mammalia indet.

1, one tooth plate; 2, numerous scales, vertebrae, and skull bones; 3, dentary fragment with sculptured outer surface and short robust femur; 4, numerous cranial and limb bones, vertebrae, and shell plates; 5, dentary fragment and postcranial elements; 6, isolated teeth and osteoderms; 7, isolated teeth; 8, isolated teeth and wing metacarpal fragment; 9, fragmentary upper molariform tooth.

Layer 4: Green-grey medium grained sand and cemented sandstone at the top with coalicified plant remains at the bottom and vertebrate remains and sulphide concretions throughout the layer. Thickness ~1.1 m.

Layer 5: Interbedded light green-grey sand, grey siltstone, and dark green clay. Vertebrate remains are confined to sandy interlayers. Thickness 0.9 m.

Layer 6: Dark green siltstone and clay, brown to black (with plant detritus) toward the top. Thickness ~2.5 m.

Above the Jurassic section there is sand and gravel of supposedly Toilok Bed of Upper Paleogene (1–2 m) and Quaternary loess (up to 7 m).

The age of the Upper Member of Itat Formation is Bathonian according the pollen complex including *Cyathidites minor*, Piceapollenites indet., *Eboracia torosa*, *Quadraeculina limbata*, and *Classopollis* sp. (Raevskaya et al. 1993; Alifanov et al. 2001). The vertebrates do not indicate unequivocally the Middle Jurassic age (*contra* Alifanov et al. 2001), although the assemblage is similar in composition to the Bathonian–Callovian vertebrate faunas of Fergana Depression in Kyrgyzstan and Junggar Basin in Xinjiang, China (Averianov 2000; Maisch and Matzke 2003; Maisch, Matzke and Stöhr, 2003; Maisch, Matzke et al. 2003; Martin and Averianov 2004a, b; Matzke et al. 2004; Averianov et al. 2005). One of the main differences is the presence of a pterodactyloid pterosaur instead of a rhamphorhynchoid. Only three elements of the Berezovsk assemblage are of essentially Jurassic age: a dipnoan fish, which are not known in Asia after Jurassic, a salamander cf. Karauridae, and a turtle *Xinjiangchelys*. Other taxa (cf. Paramacellodidae, cf. *Sunosuchus*, cf. Dromaeosauridae, Titanosauriformes indet., Stegosauria indet., Tritylodontidae indet., and Docodonta indet.) could occur in the Jurassic, as well as in the Early Cretaceous. The age assessing for the Berezovsk Quarry is further complicated by the fact that in Siberia some Jurassic taxa may have persisted in the Early Cretaceous much longer than in other areas (Leshchinskiy et al. 2001). The best examples are tritylodontids and docodontans found in Aptian–Albian (Tatarinov and Maschenko 1999; Maschenko et al. 2003).

Systematic paleontology

Mammalia Linnaeus, 1758

Docodonta Kretzoi, 1946

Docodonta indet.

Figs. 2–4.

Locality and horizon: Berezovsk Quarry, Krasnoyarsk Territory, Russia; Upper Member of Itat Formation, Bathonian, Middle Jurassic.

Material.—PIN 5087/1, posterior fragment of a right dentary with alveoli for the ultimate molar, posterior alveolus for the penultimate molar and partially preserved coronoid and pseudangular processes. PM TGU 200/3-BR-1, posterior fragment of a right dentary with alveoli for the two last molars and partially preserved coronoid process.

Description.—PIN 5087/1 (Figs. 2A, 3). The alveolus for the ultimate molar is 1.5 mm long. The alveolus for the posterior root is smaller than that for the anterior root. Only posterior alveolus from the penultimate molar is preserved, with remnant of the posterior root. It seems that the penultimate molar does not differ much in size from the ultimate molar. Breakage of the anterior side of the fragment reveals a relatively large mandibular canal. Along the medial side and just adjacent to the alveoli there is a groove for the replacement dental lamina that posteriorly deviates ventrally and terminates in the coronoid area. It is possible that eruption of molars was not completed at death of the individual and at least one more posterior molar could be added later in the ontogenesis. But there is no replacement pit at the end of the replacement groove. On the medial side closer to the ventral border there is a continuous Meckel's groove. On the fragment preserved the Meckel's groove is remarkably straight, without any ten-

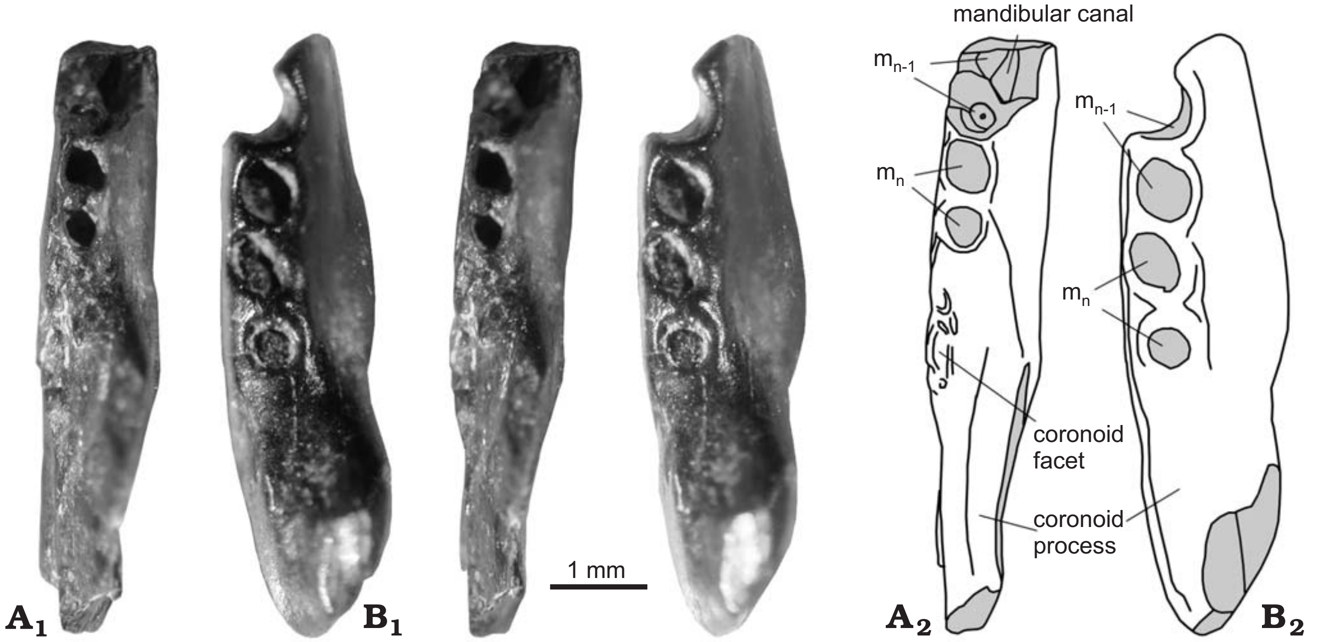

Fig. 2. Docodonta indet., Berezovsk Quarry, Krasnoyarsk Territory, Russia; Itat Formation, Middle Jurassic. Damaged bone is shown in grey. **A**. PIN 5087/1, right dentary fragment, occlusal view (A_1, stereopair) and outline drawing (A_2). **B**. PM TGU 200/3-BR-1, right dentary fragment, occlusal view (B_1, stereopair) and outline drawing (B_2). Anterior is to the top.

dency to converge upon the ventral border of the dentary. It is quite deep and terminates near the mandibular foramen. There is a distinct ridge just anterior to the mandibular foramen that overhangs the Meckel's groove dorsally. A narrow area ventral to this ridge is interpreted here as a facet for the dorsal flange of the prearticular. If this is correct, at least the portion of the Meckel's groove ventral and posterior to this ridge was housing the prearticular. The Meckel's groove continues posteriorly into a shallow facet, tapering posteriorly and reaching the anterior end of the pseudangular process. This facet is most probably for the prearticular. It is adjacent and just ventrally to the angular facet. The mandibular foramen is placed deeply at the anterior border of the postdentary trough at the level of the posterior root of the ultimate molar. The foramen is facing posteriorly. Posteriorly to the mandibular foramen the postdentary groove markedly widens dorsoventrally. The trough is deepest anteriorly, where it is partly overhanging by the thin bony lamina, and becomes shallower posteriorly. The trough is separated into two unequal parts by a longitudinal diagonal ridge. The deeper but smaller dorsal part of the trough is analogous to the structure in *Morganucodon* interpreted as adductor fossa by Kermack et al. (1973). However, according to Luo (personal communication, 2005), this interpretation is wrong as adductor muscle could not have inserted into this space because it is block off by the coronoid. As we do not know for sure the function of this depression and there is no other available name for this structure, it is referred here to as "adductor fossa" in quotation marks. The shallower but larger ventral part of the trough is the angular facet. The latter is not clearly subdivided, so it is not clear if the surangular facet is present on this fragment. Dorsally to the "adductor fossa" there is quite a weak medial ridge overhanging the postdentary trough. The pseudangular process (= angular process of other authors, see discussion in Kielan-Jaworowska et al. 2004) is prominent and directed posteroventrally. It lacks a minor part of the ventral margin but its posterior margin is intact and very thin. From the medial side the pseudangular process is subdivided by a strong vertical ridge. Area posterior to this ridge is deeply concave and continuous with the angular facet. It is interpreted here as the facet for reflected lamina of angular. On the medial side dorsal to the postdentary trough and posterior to the last tooth there is a marked rugosity, which is interpreted as an attachment area for the coronoid. This facet does not extend on to the coronoid process. On the lateral side there is an extensive but shallow masseteric fossa reaching anteriorly the posterior end of the ultimate molar. The coronoid crest is quite robust.

PM TGU 200/3-BR-1 (Figs. 2B, 4). This specimen is more water-worn compared with PIN 5087/1. It is similar in size to the latter specimen, having alveoli for the ultimate and penultimate molars, 1.5 and ~1.8 mm in diameter respectively. The ultimate molar is slightly smaller than the penultimate molar and its long axis is set somewhat obliquely to the axis of the latter. On the medial side the dorsal border of the postdentary trough is partially destroyed, but a weak medial ridge overhanging the trough is visible. Meckel's groove is straight and deep anteriorly (as in PIN 5087/1) and continuous to the shallower prearticular facet posteriorly without any tapering. Moreover, the floor of the prearticular facet rotates to an almost vertical position compared with the more inclined position of the floor of Meckel's groove, which gives impression that the groove widens dorsoventrally posteriorly. The mandibular foramen is placed in the deep ante-

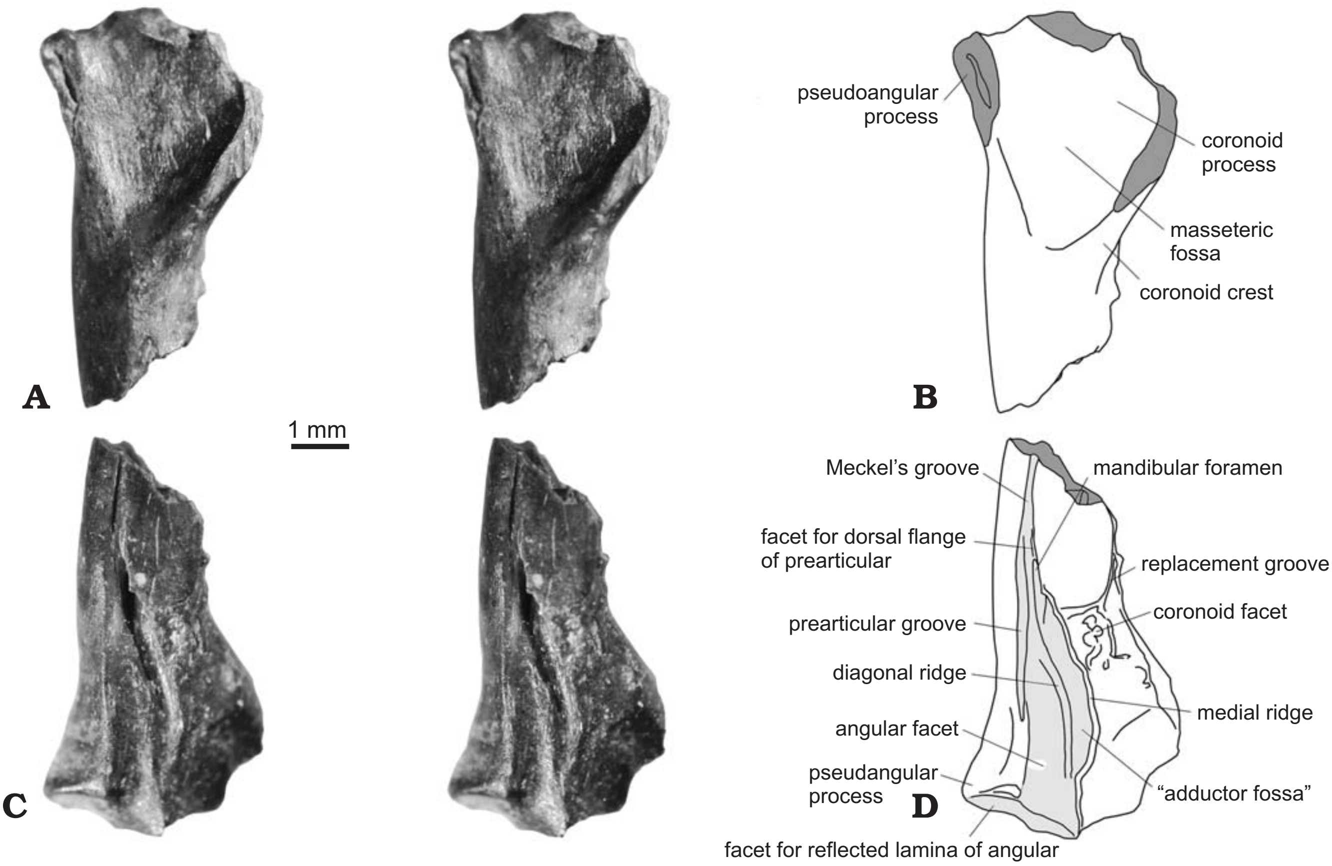

Fig. 3. Docodonta indet., Berezovsk Quarry, Krasnoyarsk Territory, Russia; Itat Formation, Middle Jurassic. Damaged bone is shown in dark grey, area occupied by Meckel's cartilage and postdentary is shown in light grey. PIN 5087/1, right dentary fragment, labial view (**A**, stereopair), lingual view (**C**, stereopair), and outline drawings (**B**, **D**). Anterior is to the bottom (A, B) and top (C, D).

rior portion of the postdentary trough and facing posteriorly. Ventral to the mandibular foramen there is a faint ridge which possibly delimits the dorsal border of the prearticular dorsal flange facet. The postdentary trough is deep throughout the fragment preserved, without a diagonal ridge on the floor. Possibly all this part of the postdentary trough is represented by "adductor fossa". There is no groove for the replacing dental lamina, or coronoid attachment area visible. There is breakage ventral to the anterior alveolus of the ultimate molar which exposes the molar root. There is no pseudangular process preserved and the ventral border of the dentary is convex throughout the entire fragment, without a concavity which should be anterior to the pseudangular process. This might mean that the pseudangular process was located relatively far posterior from the preserved posterior end. The masseteric fossa is shallower and the coronoid crest is weaker than in PIN 5087/1, but this might be related to a prominent water abrasion of PM TGU 200/3-BR-1.

Mammalia indet.

Fig. 5.

Locality and horizon: Berezovsk Quarry, Krasnoyarsk Territory, Russia; Upper Member of Itat Formation, Bathonian, Middle Jurassic.

Material.—PM TGU 200/3-BR-2, tooth.

Description.—PM TGU 200/3-BR-2. The crown is 0.6 mm long, 0.3 mm width, and 0.6 mm high. The complete tooth is 1.5 mm high. The crown is single-cusped, with a small posterior denticle and without an anterior denticle. The bulbous anterior side of the crown projects anteriorly beyond the root. One crown side (labial?) is little more convex than the opposite side. There is no cingulum. There is a single long and robust root, without any trace of subdivision. Its distal end is narrowed before a distalmost widening.

Discussion

The most diagnostic feature of the dentaries from Berezovsk Quarry is presence of a trough for the postdentary bones. This is a plesiomorphic feature occurring in various stem mammals which retained compound (dentary-squamosal and articular-quadrate) craniomandibular articulation. In more derived mammals the single (dentary-squamosal) temporomandibular joint was established and postdentary bones were successively detached from the dentary and incorporated in the middle ear (Kielan-Jaworowska et al. 2004 and references therein). There are nine taxa of stem mammals retaining the postdentary trough with the medial ridge overhanging the trough (charac-

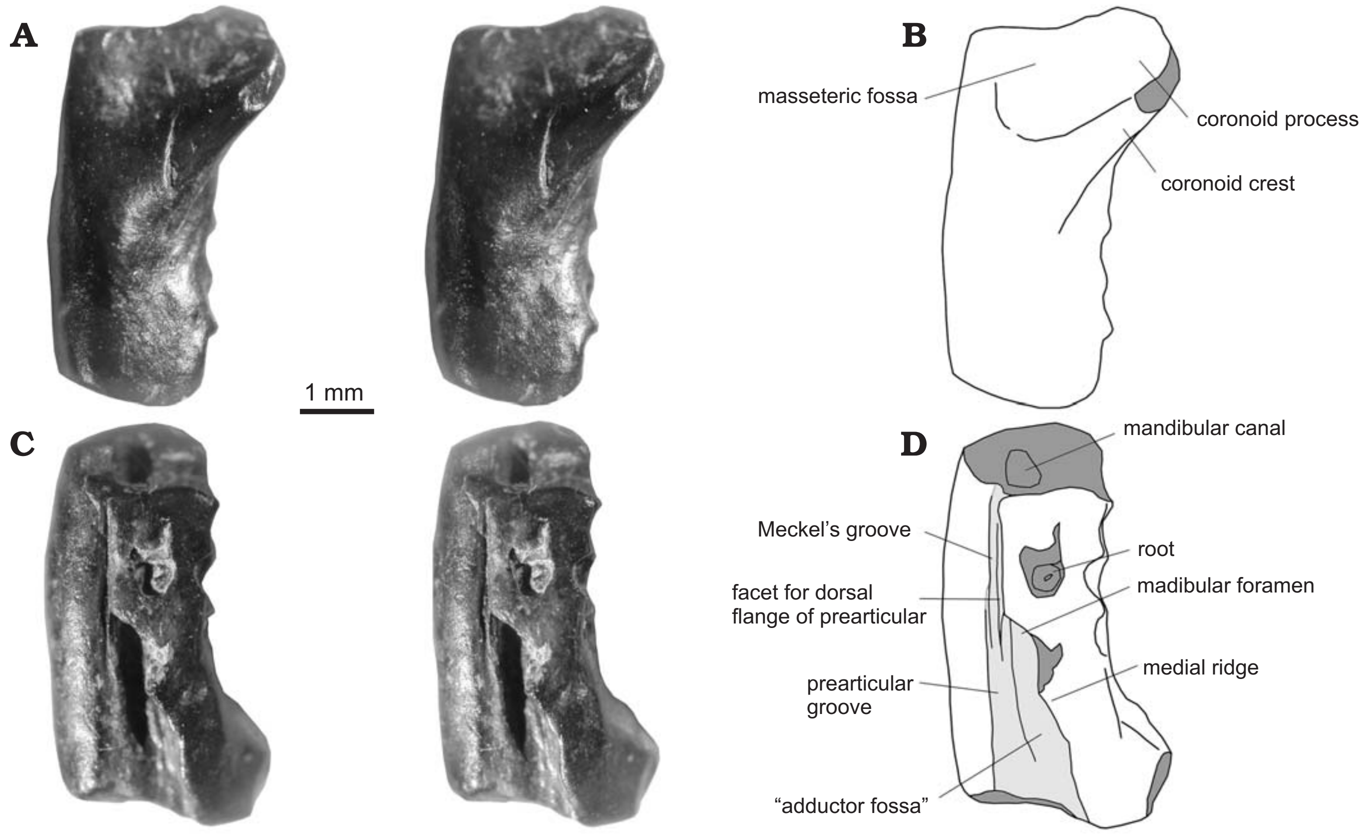

Fig. 4. Docodonta indet., Berezovsk Quarry, Krasnoyarsk Territory, Russia; Itat Formation, Middle Jurassic. Damaged bone is shown in dark grey, area occupied by Meckel’s cartilage and the postdentary bones is shown in light grey. PM TGU 200/3-BR-1, right dentary fragment, labial view (**A**, stereopair), lingual view (**C**, stereopair), and outline drawings (**B**, **D**). Anterior is to the bottom (A, B) and top (C, D).

ter 1 in Luo et al. 2002): *Haramiyavia*, *Sinoconodon*, Morganucodonta, Docodonta, Kuehneotheriidae, and *Shuotherium*. Among endemic Gondwanan mammals Australosphenida the postdentary trough is well developed in *Asfaltomylos* and unnamed new taxon from the Middle–Late Jurassic of South America (Rauhut et al. 2002; Forasiepi et al. 2004), and reduced in *Ausktribosphenos* from the Early Cretaceous of Australia (Rich et al. 1997, 1998, 1999). In *Bishops*, another Early Cretaceous australosphenidan taxon from Australia, the postdentary trough was not described originally (Rich et al. 2001), but Luo et al. (2002: character 1) interpret *Bishops* as having postdentary trough (“incomplete, but its anterior part is visible”). However, we see no basis for such interpretation. What is visible in two specimens of *Bishops whitmorei* is best interpreted as the Meckel’s groove (Rich et al. 2001: figs. 1, 2). The presence of a postdentary trough in the Early Cretaceous Australian monotreme *Steropodon* is also problematic (Luo et al. 2002). This structure is absent in the Early Cretaceous monotreme *Teinolophos* (as exemplified by the type specimen) and in more derived monotremes. Recently Rich et al. (2005) described “additional specimen” of *Teinolophos* having a well developed trough for postdentary bones. However, attribution of this specimen to *Teinolophos* is problematic, it might rather belong to an ausktribosphenid. When present, the postdentary trough in australosphenidans is different from that in the Siberian jaws in lacking the medial ridge overhanging the trough and the diagonal ridge. So, there is no basis to assume close relationships between australosphenidans and the Siberian taxon.

Another diagnostic feature of the Siberian mammals, seen in PIN 5087/1, is the pseudangular process with internal fossa for the angular bone. In *Kuehneotherium* (the only member of Kuehneotheriidae with dentary known) and *Shuotherium* the pseudangular process is lacking and these taxa are omitted from future comparisons. This process, serving for support of the reflected lamina of the angular in cynodonts and stem mammals with attached postdentary bones and placed relatively anteriorly on the dentary, is termed here the pseudangular process following some authors (Patterson 1956; Jenkins et al. 1983; Jenkins 1984; Crompton and Sun 1985; Gow 1986; Crompton and Luo 1993; Hopson 1994). We consider the “pseudangle” of stem mammals as not homologous with the neomorph (“true”) angular process of Cladotheria, having a more posterior position on the dentary and serving for insertion of the masseter superficialis muscle. Other researches consider these structures to be homologues (e.g., Parrington 1959; Kermack et al. 1973; Gambaryan and Kielan-Jaworowska 1995; Kielan-Jaworowska 1997; Luo et al. 2001; Luo, Kielan-Jaworowska and Cifelli 2002; Kielan-Jaworowska et al. 2004).

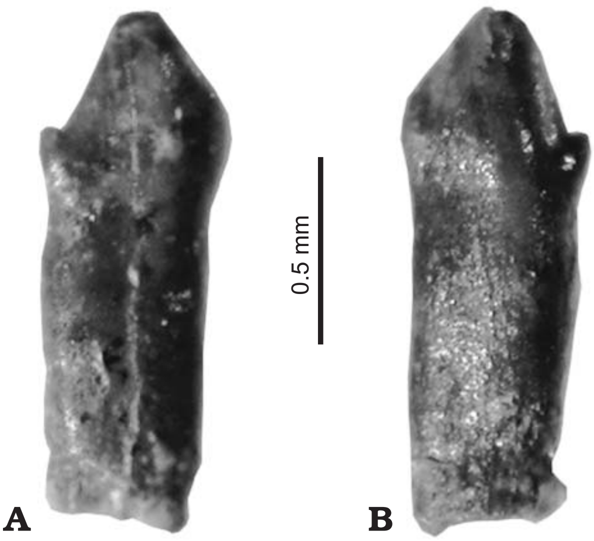

Fig. 5. Mammalia indet., Berezovsk Quarry, Krasnoyarsk Territory, Russia; Itat Formation, Middle Jurassic. PM TGU 200/3-BR-2, a tooth in lingual? (**A**) and labial? (**B**) views.

The combination of the postdentary trough with a well-developed pseudangular process, having a fossa for the angular, is found in *Sinoconodon*, *Morganucodon* (one of two members of Morganucodontidae with dentary known), and Docodonta. Moreover, among stem mammals only in these three taxa there is a facet for the reflected lamina of angular on the pseudangular process. In *Haramiyavia* and Megazostrodontidae (*Megazostrodon* and *Dinnetherium*) the pseudangular process with the angular fossa is present, but much weaker. It should be noted here that in *Erythrotherium*, which is now considered as a member of Morganucodontidae closely related to *Morganucodon* (Kielan-Jaworowska et al. 2004), the dentary angle is as small as in megazostrodontids (Crompton 1964: fig. 1).

Among *Sinoconodon*, *Morganucodon*, and Docodonta the Siberian jaws are more similar with Docodonta. In *Sinoconodon* the pseudangular process is large, but posteriorly rather than posteroventrally projecting, with its ventral margin confluent with the ventral margin of the rest of dentary (Crompton and Luo 1993). Among docodontans the posterior region of dentary is known for *Haldanodon* and *Docodon*. In both genera it is generally very similar to the condition of *Morganucodon*. The only difference between these taxa, first noted by Kermack and Mussett (1958: 208) is that in *Morganucodon* "the internal medial groove [=Meckel's groove] does not extend posterior to the mandibular foramen". This posterior part of Meckel's groove, which extends in Docodonta posterior to the mandibular foramen is interpreted here as the prearticular groove. In *Haldanodon* this groove was described earlier under name "sulcus primordialis" (Krusat 1980: pl.1), but later this term was abandoned by Lillegraven and Krusat (1991). In *Morganucodon* there is no prearticular facet ventral to the angular facet and the prearticular is reconstructed as lying medial to the angular posteriorly to the mandibular foramen (Kermack et al. 1973: fig. 7B). In both PIN 5087/1 and PM TGU 200/3-BR-1 the prearticular groove extends posteriorly ventral to the angular facet and it reaches the anterior end of pseudangular process in PIN 5087/1. This character is considered here as sufficient difference between mandibular structure in Docodonta and *Morganucodon*, which allows referring Siberian jaws to Docodonta. This difference has one substantial functional consequence. *Haldanodon*, as reconstructed by Lillegraven and Krusat (1991: fig. 14) differs from other mammals with a double jaw joint in having the articular complex that contacts the ventral side of the dentary condyle, while in *Morganucodon* and *Sinoconodon* it is situated medial to the dentary condyle (Kielan-Jaworowska et al. 2004). The position of the prearticular facet ventral to the angular facet is consistent with such reconstruction. But, if articular complex in *Haldanodon* really had a ventral position, this animal could not have a double jaw joint. The mandible is inserted to the skull like a door to the jamb: it may be held by a number of hinges, but all of them should be lying in the same line. In a double jaw joint all hinges should lie on the same transverse axis, i.e., the articular-quadrate hinge should be medial to the dentary-squamosal hinge (like in *Morganucodon*), not ventral. Ventral position of articular complex in *Haldanodon* indicates that it was used only for sound transmission, not for jaw articulation. This is supported also by large size of glenoid fossa and dentary condyle in *Haldanodon*, which apparently formed the only functional jaw articulation in this animal, as was suggested previously by Lillegraven and Krusat (1991).

According to Lillegraven and Krusat (1991: fig. 17) Docodonta occupy very basal position on the mammal cladogram, inferior to *Sinoconodon* and Morganucodonta. This view contradicts with the classic concept that docodontans are derivates of morganucodontans (Patterson 1956; Crompton and Jenkins 1968; Crompton 1974; Kron 1979), and numerous more recent cladistic studies (Wible and Hopson 1993; Luo 1994; Wible et al. 1995; Rougier, Wible and Hopson 1996; Luo et al. 2001, 2002, 2003; Wang et al. 2001; Ji et al. 2002), which place Docodonta superior to Morganucodonta on the tree. If docodontans have functionally single jaw articulation and postdentary bones were used solely for sound transmission, they are clearly more derived than morganucodontans and other stem mammals with compound jaw articulation.

In PIN 5087/1 there is a distinct groove for the replacement dental lamina. This character is a symplesiomorphy inherited from cynodonts and found among few stem mammals: *Sinoconodon*, *Morganucodon*, and *Megazostrodon* (Crompton and Luo 1993; Luo et al. 2002: character 7). This groove was not reported previously for a docodont.

Both dentary specimens (PIN 5087/1 and PM TGU 200/3-BR-1) agree in size and general morphology and differ in minor details outlined above. The most important differences are more prominent prearticular groove, especially posteriorly, absence of a diagonal ridge, and lacking of the replacement dental lamina in PM TGU 200/3-BR-1. In this specimen the diagonal ridge may appear further posterior on the trough, which is consistent with a reconstructed similarly posterior position of the pseudangular process. Lacking of the groove for the replacement dental lamina in PM TGU 200/3-BR-1 could be due to its worse preservation or older individual age when tooth eruption and replacement is finished. Nevertheless, difference in the shape and extend of the prearticular groove between PIN 5087/1 and PM TGU 200/3-BR-1 might be taxonomically important. At the moment we cannot decide if both specimens belong to the same taxon or different taxa, and both are referred here as Docodonta indet.

The tooth PM TGU 200/3-BR-2 from Berezovsk Quarry is not diagnostic itself and currently cannot be determined beyond Mammalia indet. Although PM TGU 200/3-BR-2 is not a splendid specimen, it is historically important (at least for the national paleontology) as the first tooth of a Jurassic mammal found in Russia.

The occurrence of Docodonta in the Middle Jurassic of Siberia agrees with the presence of docodontans in similar Middle Jurassic (Bathonian–Callovian) vertebrate faunas of Kyrgyzstan and Xinjiang, China (Martin and Pfretzschner 2003; Martin and Averianov 2004a, b). A docodont is the only mammal found in a slightly younger, Late Jurassic Sharteg fauna in Mongolia (Tatarinov 1994). All these faunas are also united by presence of a primitive cryptodiran turtle (*Xinjiangchelys*) and this faunistic complex is called here the *Xinjiangchelys*-Docodonta association. Records of docodontans in this association are among the oldest fossil records for the group, which is present also in the Bathonian of Great Britain (Waldman and Savage 1972; Freeman 1979; Kermack et al. 1987; Sigogneau-Russell 2001, 2003).

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