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Middle Jurassic vertebrate assemblage of Berezovsk coal mine in western Siberia (Russia)

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Abstract: The Berezovsk coal mine in western Siberia has yielded the most diverse Middle Jurassic limnic and terrestrial vertebrate assemblage of Asia. The vertebrate remains were recovered by screen washing from flood-plain deposits on top of a thick coal seam of the Bathonian Itat Formation. A total of 29 vertebrate taxa has been recorded so far, including hybodontiform sharks, acipenseriforms, palaeonisciforms, amiiforms, dipnoans, anurans, caudates, turtles, squamates, choristoderans, crocodyliforms, pterosaurs, dinosaurs, tritylodontids, and a diverse mammaliaform and mammalian assemblage (eleutherodontids, docodontans, ? amphilestids, dryolestids, and zatherians). The caudates are among the oldest in the fossil record and the anurans represent the oldest Asian record of this group. Among the mammals, *Anthracolestes* is the oldest and most basal known member of Dryolestidae and so far the only record from Asia. The vertebrate assemblage from the Berezovsk coal mine is very similar to that from the British Forest Marble Formation (Bathonian) and suggests a limited provincialism in the Middle Jurassic Laurasian landmass.

Key words: vertebrate assemblage; Berezovsk coal mine; Middle Jurassic; western Siberia; Russia

1 Introduction

The first vertebrate fossils of the Berezovsk coal mine in western Siberia were discovered in 2000 by S. A. Krasnolutskii (Alifanov *et al.*, 2001; Averianov *et al.*, 2005). Vertebrate fossils occur in fluvial flood-plain deposits that continuously overlay massive coal seams (more than 50 m thickness) of the Middle Jurassic (Bathonian) Itat Formation. The Berezovsk mine is located at the southeastern flank of the West Siberian Basin (Fig. 1), and coal formation occurred in depressions of pre-Jurassic relief, a depth of the peat mire of 60-100 m is assumed (Le Heron *et al.*, 2008). By mid-Jurassic times, a low profile alluvial plain had developed that was characterized by anastomosing rivers and well defined floodplains (Le Heron

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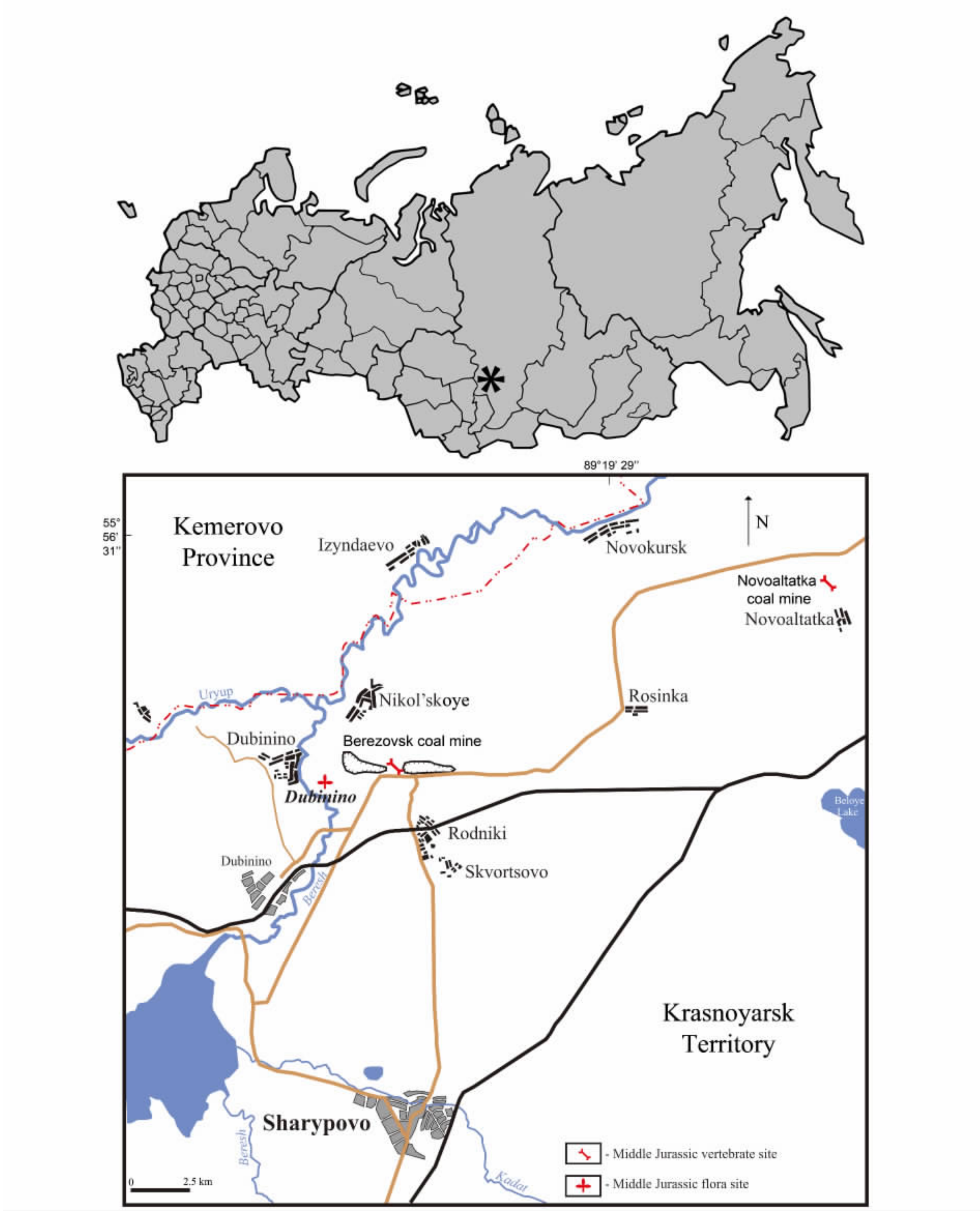


Fig. 1 Maps showing the position of the study area on the map of Russia (asterisk, top) and vertebrate bearing localities in Berezovsk and Novoaltatsk coal mines and plant fossil bearing locality near Dubinino settlement (bottom)

et al., 2008: fig. 10B). These floodplains were favorable for the deposition of vertebrate remains such as scales, bones, and teeth. Due to the fluvial origin of the sediments, vertebrate remains are mostly disarticulated and often somewhat water worn. Exceptions are partial skeletons of dinosaurs and partial turtle shells as well as a layer with more than a dozen of articulated palaeonisciform fish skeletons which was discovered in 2012. The mostly good preservation of the vertebrate remains demonstrates that they have not been transported over long distances. The vertebrate remains are concentrated in layers and the most productive layer proved to be a soft, slightly sandy siltstone layer of 20–30 cm thickness. The age of the Upper Member of the Itat Formation is Bathonian according to the pollen complex including *Cyathidites minor*, *Piceapollenites indet.*, *Eboracia torosa*, *Quadraeculina limbata*, and *Classopollis* sp. (Raevskaya *et al.*, 1993).

Extensive screen washing operations by the Russian-German expeditions (2010–2013) of about 15 tons of fossiliferous soft silt- and sandstones yielded a wealth of vertebrate remains that provide a detailed insight into terrestrial vertebrate evolution in northern Central Asia in Middle Jurassic times. The picking of the concentrate is going on, and this report gives a state-of-the art of the work on the Berezovsk vertebrate assemblage. But already by now, this locality has produced the largest diversity of Middle Jurassic terrestrial vertebrates in Asia. The preliminary results of the studies on Berezovsk vertebrates were presented in various symposia (Lopatin & Averianov, 2006, 2007b; Martin *et al.*, 2011; Danilov & Krasnolutskii, 2012; Danilov *et al.*, 2013; Schultz *et al.*, 2013; Averianov *et al.*, 2014b; Martin *et al.*, 2014; Martin *et al.*, 2015; Obraztsova & Danilov, 2014, 2015; Skutschas, 2015). In this report the hybodontiform sharks, acipenseriform and amiiform fishes, Dipnoi, Pterosauria, Dinosauria, and Tritylodontidae were described by Averianov. Palaeonisciform fishes were described by Sytschevskaya, Amphibia, Squamata, and Choristodera by Skutschas, Testudines (turtles) by Danilov and Obraztsova, Crocodyliformes by Kuzmin, and Mammalia by Averianov, Martin and Lopatin.

2 Berezovsk vertebrate assemblage

Hybodontiformes

A single shark specimen from the Berezovsk coal mine is a partial tooth of *Hybodus* sp. with heavily worn main cusp and two pairs of stout cusplets (ZIN PH 14/117; Fig. 2A-C). The missing root suggests that the tooth was shed during tooth replacement. The main cusp has no sigmoidal curve, with convex labial and slightly flattened lingual surfaces. The cutting edges on the main cusp are equidistant from the labial and lingual sides. There are numerous fine striations on the labial side and fewer coarser folds on the lingual side, avoiding the central flattened surface of the main cusp on the lingual side. The folds are not bifurcating and have no nodes. ZIN PH 14/117 is quite different from the hybodontid species known from the Bathonian of England and Moscow Province (Bragina, 2005; Rees & Underwood, 2008). The crown shape is similar to that of *Hybodus antingensis* Liu, 1962 from the Middle Jurassic of China (Zhang, 2007), but differs by finer striations on the labial side. The ornamentation of ZIN PH 14/117 is similar to that of the Early Jurassic *Hybodus reticulatus* Agassiz, 1837 from England (Maisey, 1987; Cappetta, 2012), but its main cusp is more stout and was apparently higher.

Acipenseriformes

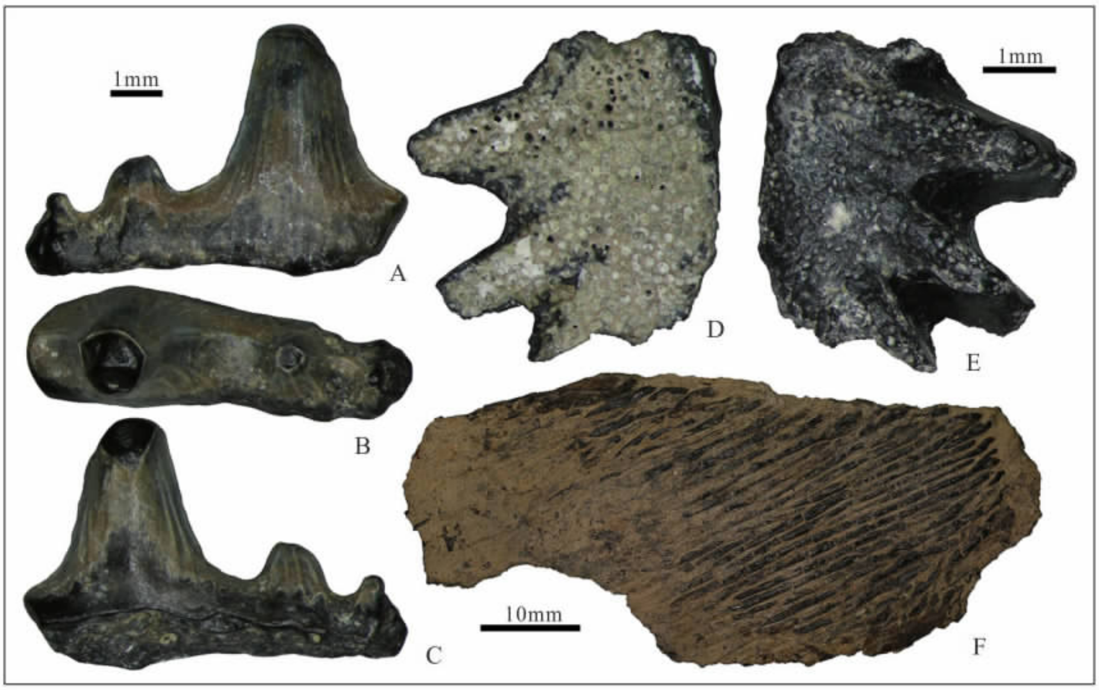
The acipenseriform fishes are represented by sheet fragments of tightly interlocking rhomboid scales of the upper caudal lobe, caudal fulcra, tiny three- and four-radiate scales, and pectoral fin spines. The apparent absence of trunk scutes in the Berezovsk taxon suggests that it is a non-acipenserid acipenseriform (Grande & Bemis, 1996). It is not referable to the Peipiaosteidae because the rhomboid scales of the upper caudal lobe are absent in that group (Zhou, 1992; Sytchevskaya, 2009). In the largest fragment of the caudal sheet (ZIN PH 15/117; Fig. 2F) there are at least 28 rows of rhomboid scales. The Early Jurassic *Chondrosteus acipenseroides* Egerton, 1858 from England shows only 10–13 rows of scales in the caudal sheet (Hilton & Forey, 2009). The number of these rows is ontogenetically controlled (Grande & Bemis, 1996). In comparison, the stellate scales of the Berezovsk acipenseriform are quite different from the scales of Peipiaosteidae and Polyodontidae (Grande & Bemis, 1991, 1996; Grande *et al.*, 2002), but may represent an ancestral morphotype for polyodontid scales. *Asiacipenser kotelnikovi* Nessov et Fedorov, 1990, a true acipenserid with trunk scutes, is present in the Bathonian Zindan Formation of the Fergana Valley, Kyrgyzstan (Nesov *et al.*, 1990).

Palaeonisciformes

The majority of fish skeletons, represented mainly by posterior fragments, belongs to a new palaeoniscid genus which will be named elsewhere. It is characterized by a long tail with the upper lobe completely covered by scales. The scales are compact, largely overlapping, with diagonal ridges. The posterior edge of the scales is smooth, without spines. There are well developed fulcra with ridges similar to that of the scales. The Berezovsk taxon is very similar to the Asiatic genera *Palaeoniscinotus* Rohon, 1890 and *Pteroniscus* Berg, 1949. These genera differ from the Berezovsk taxon by thinner and less overlapping scales, with spines along the posterior edge. These two genera also show less developed fulcra: in *Pteroniscus* there are no abdominal fulcra, one anal fulcrum, and few fulcra at the dorsal fin and the ventral lobe of the caudal fin. In *Palaeoniscinotus* the fulcra are rudimentary.

Amiiformes

The amiiform fishes are represented by abundant vertebrae, jaws and vomer fragments, as well as isolated teeth, and numerous isolated rhomboidal scales. The vertebrae are subcircular, with an open notochordal canal, and a well-developed constriction at mid-length. The teeth are hollow inside, ornamented with vertical folds, and have a pointed enameloid cusp.



A-C, *Hybodus* sp., tooth (ZIN PH 14/117), in labial (A), occlusal (B), and lingual (C) views; D, E, *Ferganoceratodus* sp., pterygopalatine tooth plate (ZIN PH 18/117) in dorsal (D) and ventral (E) views; F, Acipenseriformes indet., rhomboid scales of the upper caudal lobe (ZIN PH 15/117), in lateral view.

Fig. 2 Vertebrate remains from Berezobsk coal mine

Dipnoi

Dipnoan remains are extremely rare in the Berezovsk vertebrate assemblage. There are one complete upper (pterygopalatine) tooth plate (ZIN PH 18/117; Fig. 2D, E) and several tooth plate fragments consisting of tubular dentine. The upper tooth plate has five ridges and an inner angle of 87°. The first ridge is very short and its length decreases from the second to the last ridge. There are four denticles on the second ridge and two denticles on the third ridge. The two last ridges are narrowly spaced. This specimen closely resembles the upper tooth plates of *Ferganoceratodus* spp. from the Middle Jurassic of Kyrgyzstan, and from the Upper Jurassic to Lower Cretaceous of Thailand (Nesov & Kaznyshkin, 1985; Kaznyshkin, 1993; Cavin *et al.*, 2007). In contrast to the dipnoan remains from the Berezovsk coal mine, remains of *Ferganoceratodus* are numerous in the Balabansai Formation of Kyrgyzstan (Nesov & Kaznyshkin, 1985).

Amphibia

The vertebrate assemblage of the Berezovsk coal mine is remarkable by the presence of one of the oldest salamanders in the fossil record. Apart from the salamander, only one anuran specimen is known from Berezovsk. The salamander is represented by several isolated cranial (dentaries, bones of the skull roof) and postcranial remains (vertebrae, limb bones, bones of pelvic girdle), while the anuran is represented by one single fragmentary atlas.

The first salamander remains (a dentary fragment and a femur) from the Berezovsk coal mine were found in 2003 (Skutschas *et al.*, 2005). Primarily, the fragment of the large dentary was assigned to the stem salamander clade Karauridae and the large short femur was identified as an indeterminate salamander (Skutschas *et al.*, 2005; Skutschas, 2006). Later, Skutschas & Martin (2011) showed that the dentary fragment from the Berezovsk coal mine differs strongly from the dentaries of karaurids and cannot be referred to this group. In 2011, on the basis of the previously described specimens and additional material (an incomplete atlas, an anterior fragment of the left dentary, and fragments of trunk vertebrae), a new genus and species of stem salamanders (*Urupia monstrosa*) was described (Skutschas & Krasnolutskii, 2011). *Urupia monstrosa* differs from other stem salamanders in possessing the following combination of characters: the presence of atlantal transverse processes, a deep depression on the ventral surface of the atlas, and distinct ventrolateral ridges on the atlas (Skutschas & Krasnolutskii, 2011). The attribution of *U. monstrosa* to stem-group salamanders is supported by its large size, the absence of spinal nerve foramina in the atlas and its sculptured vertebral surface texture (Skutschas & Krasnolutskii, 2011; Skutschas, 2013).

Later, in addition to the material assigned to *U. monstrosa*, remains of two other salamander taxa ("Berezovsk salamander A" and "Berezovsk salamander B") were described and figured (Skutschas, 2013). Like *U. monstrosa*, "Berezovsk salamander A" was considered a stem salamander on the basis of the absence of spinal nerve foramina in the atlas and its sculptured vertebral surface texture (Skutschas, 2013). The atlantes assigned to "Berezovsk salamander A" (Skutschas, 2013: Fig. 3d-f) differ from that of *U. monstrosa* in lacking both atlantal transverse processes and a deep depression on the ventral surface and in having more rounded anterior cotyles (vs. oval and dorsoventrally compressed in *U. monstrosa*; Skutschas & Krasnolutskii, 2011: Fig. 2; Skutschas, 2013: Fig. 3a-c). Trunk vertebrae of "Berezovsk salamander A" (Skutschas, 2013: Fig. 3j-k) differ from those of *U. monstrosa* (Skutschas & Krasnolutskii, 2011: Fig. 4; Skutschas, 2013: Fig. 3g-i) in being relatively shorter and in having more widely separated dia- and parapophyses. Additionally, dentaries were tentatively assigned to "Berezovsk salamander A" that differ from *U. monstrosa* (Skutschas, 2013: Fig. 3l) in lacking both a sharp ridge along the ventral edge of the presymphyseal region and sculpture on the lateral surface, in being smaller in size and in the position and structure of Meckel's groove.

"Berezovsk salamander B" was known by a fragmentary small dentary only (Skutschas, 2013: Fig. 3n) and was considered as a possible crown salamander on the basis of its small size and in possessing a dentary that is lightly built, lacks sculpture on its external surface and bears pedicellate teeth (Skutschas, 2013). In 2014, new material of "Berezovsk salamander B" (atlantes, trunk vertebrae and fragmentary cranial and postcranial bones) was found (Skutschas, 2016). This material was described as the new species *Kiyatriton krasnolutskii* Skutschas, 2016 of the crown-group salamander genus *Kiyatriton*, previously only known by the type species from the Early Cretaceous (Aptian-Albian) of Western Siberia (Skutschas, 2016). *Kiyatriton krasnolutskii* possesses characters diagnostic for the genus *Kiyatriton* (e. g., sharp ridge along the ventral edge of the presymphyseal region of the dentary; intercotylar tubercle of the atlas with a low median ridge and distinct medial groove on its ventral surface; femur with a reduced trochanteric crest, spur-like trochanter and ossified epiphyses; see Skutschas, 2014, 2016), but differs from the type species by the following features: the ventrolateral ridges on the atlas are sharper anteriorly, more ventrally oriented and reach up to the anterior cotylar rims, and the dental parapet on the dentary is taller (Skutschas *et al.*, 2016).

The salamander component of the vertebrate assemblage of the Berezovsk coal mine is generally similar to that from the Kirtlington locality of the Forest Marble Formation (England, UK): both assemblages include two taxa of stem salamanders and one taxon of crown salamanders (Evans *et al.*, 1988; Evans & Milner, 1994; Evans & Waldman, 1996; Milner, 2000; Evans *et al.*, 2006; Skutschas, 2016).

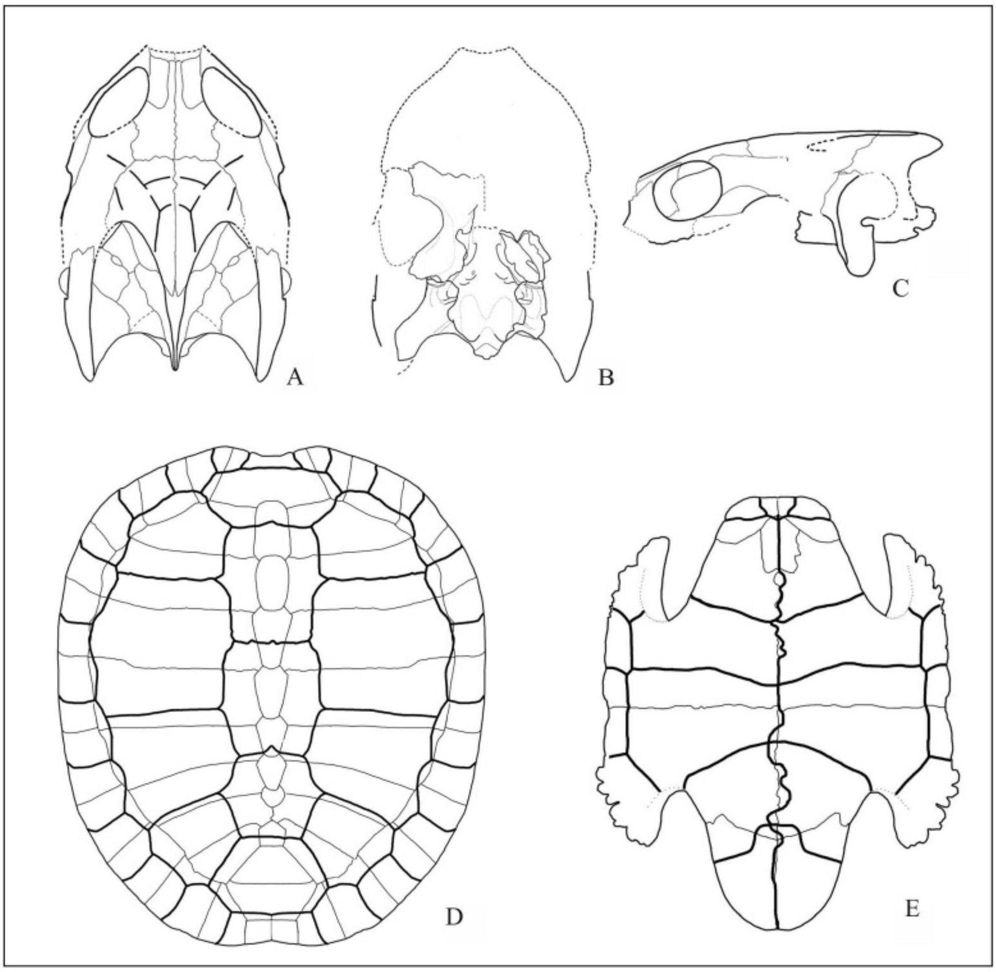
An anuran atlantal centrum from the Berezovsk coal mine was tentatively referred to the lalagobatrachian genus *Eodiscoglossus* based on its dorsoventrally flattened shape, the dorsoventrally compressed and slightly separated anterior cotyles, lack of a medial ventral crest, and the confluent articular cotyles (Skutschas *et al.*, 2016). If the assignment of the atlantal centrum from the Berezovsk coal mine to *Eodiscoglossus* is correct, this finding represents one of the oldest crown-group frogs in the fossil record. However, the atlantal centrum of ? *Eodiscoglossus* sp. represents the first unambiguous record of Anura in the Jurassic of Asia (Skutschas *et al.*, 2016).

Testudines

The first turtle material from the Berezovsk coal mine was represented by few isolated shell plates, and was attributed to two unnamed families of freshwater turtles (Chelonia indet.; Alifanov *et al.*, 2001). The study of more abundant material allowed to establish a single turtle taxon, primarily determined as *Xinjiangchelys* sp. of the basal cryptodiran family Xinjiangchelyidae (Danilov *et al.*, 2005; Skutschas *et al.*, 2009) and later as *Annemys* sp. of the same family (Danilov & Krasnolutskii, 2012; Danilov *et al.*, 2013; Obraztsova & Danilov, 2014, 2015; Danilov & Obraztsova, 2015). Further study revealed four specimens which are morphologically different from *Annemys* sp. and which were determined as Testudines indet. 1–3 (Obraztsova & Danilov, 2016).

The *Annemys* sp. material consists of thousands of isolated bones and several fragmented specimens, including three partial braincases and larger fragments of connected shell parts (Fig. 3). Attribution of this material to the family Xinjiangchelyidae is based on the following characters (Tong *et al.*, 2012b, with changes): shell height moderate to low domed, thoracic rib 1 reduced and reaching only half-way to the axillary buttress; peripherals 7 to 11 transversely expanded; middle marginals extend on to the costals; dorsal processes of epiplastra present; mesoplastra absent; pectorals and abdominals similar in length, pectorals can be slightly longer; musk ducts present. Attribution of this material to the genus *Annemys* is based on a combination of the following characters (Rabi *et al.*, 2014, with changes): presence of a ligamentous plastron-carapace connection; vertebral 1 noticeably wider than vertebrals 2 and 3; length of vertebral 2 equal or greater than its width; cervical scute trapezoid, and about four times wider than long; entoplastron longer than wide and placed between the hyoplastra; four pairs of inframarginals; pectorals and abdominals similar in length, pectorals can be slightly longer; anals usually form a Ω-shaped anterior projection extending on to the hypoplastra; cervical vertebrae short.

Annemys sp. from the Berezovsk coal mine is cha



A-C, skull in dorsal (A), ventral (B) and left lateral (C) views; D, carapace in dorsal view; E, plastron in ventral view. Not to scale.

Fig. 3 Composite reconstructions of skull and the shell of *Annemys* sp. from Berezovsk coal mine

racterized by the following characters: 1) reconstructed width to length ratio of the skull about 0.75; 2) equal height of the braincase anteriorly and posteriorly; 3) frontals fully separate the prefrontals; 4 and 5) extensive contribution of the frontal (4) and the jugal (5) to the orbital rim; 6) eight neurals; 7) neural 1 tetragonal or hexagonal and short-sided posteriorly; 8) midline contact of costals 7 and 8 can be present or absent; 9) two or three suprapygals; 10) vertebral 1 wider than the nuchal; 11) extension of vertebral 1 on to peripheral 2 can be present or absent; 12) vertebrals 2 and 3 narrower than vertebral 1; 13 and 14) sulcus between vertebrals 3 and 4 straight or V-shaped (13) and located on neural 5 or 6 (14); 15) extension of vertebral 5 on to peripheral 10 present or absent; 16) marginals extending on to costals 2 to 6; 17) marginal 12 extending on to the posterior suprapygal; 18) posterior margin of the epiplastra almost perpendicular to the midline or directed posterolaterally from the midline; 19) entoplastron rhomboid, oval or hexagonal; 20) extension of the gulars on to the entoplastron weak or absent; 21) posterior plastral lobe length to width ratio 0.72–0.73; 22) extension of the anals on to the hypoplastra can be present or absent; 23) anterior projection of the anals can be present or absent; 24) width of the anterior projection of the anals (when present) to width of the posterior plastral lobe ratio 0.29–0.32; 25) the midline sulcus of the plastron can be straight or sinuous.

Annemys sp. from the Berezovsk coal mine differs from *A. latiens* Sukhanov & Narmandakh, 2006 from the Late Jurassic of Mongolia (see Rabi *et al.*, 2014) by characters 1, 4, 5, and 24; from *A. levensis* Sukhanov & Narmandakh, 2006 from the Late Jurassic of Mongolia (see Rabi *et al.*, 2014) by characters 1–3, 10, 21, and 24; from *A. wusu* Rabi *et al.*, 2013 from the Middle Jurassic of China (as *Xinjiangchelys wusu*; Rabi *et al.*, 2013) by characters 1, 21, and 24; from *Annemys* sp. from the Middle Jurassic of Uurusay, Kyrgyzstan ("*Plesiochelys*" sp.; Nesov & Kaznyshkin, 1985) by character 16; from *Annemys* sp. from the Late Jurassic of the "Mesa Chelonia", China (Wings *et al.*, 2012) by characters 1, 10, and 21; and from *Annemys* sp. from the Middle Jurassic of Wucaiwan, China (Brinkman *et al.*, 2012) by characters 1, 2, and 5. The listed differences indicate that *Annemys* sp. from the Berezovsk coal mine represents a distinct species of the genus, of which a detailed description will be published elsewhere (Danilov & Obraztsova, in prep.).

In addition to the variable characters of the shell mentioned above (7–9, 11, 13–15, 18–20, 22, 23, 25), *Annemys* sp. from the Berezovsk coal mine also demonstrates a variation of skull characters, of which only preliminary data on the basisphenoid have been reported (Obraztsova & Danilov, 2014). These include the degree of ossification of the posterior projection of the parasphenoid; presence/absence of basipterygoid processes; presence/absence of basisphenoid pits and their position in relation to the posterior margin of the basisphenoid; degree of development of the basisphenoid rostrum; presence/absence of the intertrabecular fossa; presence/absence of bony bridges below the posterior part of the internal carotid canal; cerebral canals that are closed or opened from below; number of sulci for palatine arteries; presence/absence of the overhang of the dorsum sellae over the sella turcica; close or distant position of the pits for the retractor bulbae muscles to each other; close or distant position of the anterior foramina of the cerebral canals. Detailed study on the basisphenoid variation in *Annemys* sp. from the Berezovsk coal mine will be published elsewhere (Obraztsova & Danilov, in prep.).

Obraztsova & Danilov (2015) briefly reported on the morphology of the cervical vertebrae of *Annemys* sp. from the Berezovsk coal mine, including their formula: (2(3()4()5()6()7()8) or (2(3()4()5()6()7()8(, that is different from the condition in other xinjiangchelyids, which previously were thought to have a completely amphicoelous series of cervical vertebrae (Kaznyshkin *et al.*, 1990; Peng & Brinkman, 1993; Matzke *et al.*, 2004; Brinkman *et al.*, 2012; Rabi *et al.*, 2013). In addition to the cervical formula, cervical vertebrae of *Annemys* sp. from the Berezovsk coal mine differ from those of other xinjiangchelyids in having relatively short centra, different shapes of the central articulations, and different patterns of cervical rib attachments (Obraztsova & Danilov, 2015).

Danilov & Krasnolutskii (2012) and Danilov *et al.* (2013) included *Annemys* sp. from the Berezovsk coal mine in a cladistic analysis of Xinjiangchelyidae (Xinjiangchelyidae and Bashuchelyidae were considered to represent a monophyletic group, and *Kayentachelys aprix* was used as an outgroup). This analysis revealed a sistergroup relationship with *A. latiens* and *A. levensis* supported by two synapomorphies (vertebrals 2 and 3 narrower than vertebral 1; sulcus between vertebrals 3 and 4 V-shaped). However, the relationship of the new taxon within the *Annemys* clade remains unresolved.

A detailed description of Testudines 1–3 is given by Danilov *et al.* (in press) but in the following the main characteristics are summarized. Testudines indet. 1 is represented by a single costal 8, which is significantly thicker than costals 8 of *Annemys* sp. This specimen lacks scute sulci and sculpturing on the external surface and has a very strong rib thickening on the internal surface. The absence of scute sulci on this costal suggests that the vertebrals were wide, a character typical for some basal turtles. Among Jurassic turtles of Asia wide vertebrals are known in basal members of the family Sichuanchelyidae (Tong *et al.*, 2012a; Brinkman *et al.*, 2012). The strong rib thickening on costal 8 distinguishes Testudines indet. 1 from other turtles. The histology of Testudines indet. 1 supports its attribution to basal turtles with aquatic specialization.

Testudines indet. 2 is represented by two shell fragments (presumably plastron) with surface sculpturing consisting of elongated tubercles. This kind of sculpturing is not known in other Jurassic turtles of Asia and somewhat similar to the surface sculpturing of Pleurosternidae and Solemydidae, with a Jurassic record outside Asia (Gaffney, 1979; Joyce *et al.*, 2011). However, the histology of these shell fragments appeared to be similar to that of *Annemys* sp. For this reason, these shell fragments may represent abnormal variants of shell bones of *Annemys* sp.

Testudines indet. 3 is represented by a distal fragment of a humerus, which is two times larger than those known from *Annemys* sp. and distinguished from the latter by a wider and lower distal condyle. A similar morphology of the humerus is seen in some basal turtles (*Mongolochelys efremovi* Khosatzky, 1998 from the Late Cretaceous of Mongolia; Suzuki & Chinzorig, 2010, Fig. 8). Histologically, Testudines indet. 3 is similar to *Annemys* sp., with a low density of bone that indicates an aquatic mode of life (Nakajima *et al.*, 2014). It is possible that the humerus fragment of Testudines indet. 3 belongs to the same taxon as Testudines indet. 1. Thus, Testudines 1 and 3 belong to one or two taxa of aquatic basal turtles, whereas Testudines indet. 2 probably represents abnormal specimens of *Annemys* sp.

The presence of two to four turtle taxa in the Berezovsk coal mine, including representatives of basal turtles (Testudines indet. 1, 3, and probably 2) and basal cryptodires (*Annemys* sp.) corresponds to the diversity of other Middle Jurassic turtle assemblages of Asia. For instance, the turtle assemblage of the Shishugou Formation (Xinjiang, China, Callovian–Oxfordian) includes *Annemys* sp. and the basal turtle ? *Sichuanchelys* sp. (Brinkman *et al.*, 2012), whereas the turtle assemblage of the Xiashaximiao Formation (Sichuan, China, Middle Jurassic) includes *Sichuanchelys* spp. and representatives of basal cryptodires – Bashuchelyidae and Xinjiangchelyidae (Tong *et al.*, 2012a). The turtle assemblage from the Berezovsk coal mine is the oldest well dated, and the northernmost in Asia.

Lepidosauromorpha

Lepidosauromorphs of the Berezovsk coal mine are represented by several taxa, including a basal form and two lizards. The basal lepidosauromorph is known by several fragments of dentaries and maxillae. It is similar to the contemporaneous genus *Marmoretta* from the Forest Marble and Kilmaluag formations (UK; Evans, 1991; Waldman & Evans, 1994) in the following features: a weak pleurodont dentition, with sharp and conical teeth, and a maxilla with low dorsal process.

Remains of lizards are rare in the Berezovsk coal mine assemblage. Valeev (2008) reported and figured fused premaxillae and two dentary fragments and assigned them to Scincomorpha indet. The specimens were referred to Scincomorpha on the basis of the closely spaced and highly pleurodont teeth, the high subdental shelf, the ventrally open Meckel's canal and the fused premaxillae (Valeev, 2008). New material (several fragmentary maxillae and dentaries) shows the presence of at least two scincomorph lizards in the assemblage that differ from each other in size and shape of the tooth crowns. The larger form is characterized by closely spaced highly pleurodont teeth with chisel-like, slightly asymmetrical (and slightly medially concave) crowns. The previously published lizard material (Valeev, 2008) can be tentatively referred to this taxon on the basis of similar size (premaxillae) and morphology (dentary fragments). The second scincomorph lizard (known from two dentary fragments) is about two times smaller than the first one and differs by sharper tooth crowns that are slightly curved posteriorly. A detailed description of the material of lepidosauromorphs from the Berezovsk coal mine and discussion of their affinities will be given elsewhere.

Choristodera

Isolated cranial (skull roof bones, maxillary and dentary fragments) and postcranial bones (vertebrae, ribs) of choristoderes are common in the Berezovsk coal mine assemblage. All these specimens are comparable to one another in size and can be assigned to the taxon *Cteniogenys* sp. The choristodere from the Berezovsk coal mine demonstrates a suite of primitive characters (e. g., relatively small body size; conical teeth with a striated tip and smooth base lacking dentine folds; fused neural arches and centra (= closure of the neurocentral sutures) of the cervical and dorsal vertebrae; elongated cylindrical vertebrae retaining a notochordal pit) that suggests its basal position within Choristodera. Based on these characters the choristodere from the Berezovsk coal mine is morphologically very similar to the basal choristodere *Cteniogenys* from the Middle-Late Jurassic (Euramerica; Evans, 1990). A detailed description of the material of the choristodere from the Berezovsk coal mine and discussion of its affinities will be given elsewhere.

Crocodyliformes

Crocodyliform remains are relatively rare in the assemblage of the Berezovsk coal mine, and are represented by several dozens of isolated teeth, osteoderms, and a few cranial fragments. The cranial bones (fragments of maxilla, nasal and splenial), osteoderms, and teeth were assigned to one neosuchian taxon – Goniopholididae indet. (Kuzmin *et al.*, 2013). The goniopholidid affinities of the crocodyliform from the Berezovsk coal mine are supported by the following combination of characters: presumably narrow and long snout, splenial contributing to the mandibular symphysis, dermal sculpturing consisting of almost circular and slightly elongated oval pits, polygonal ventral osteoderms, and presence of conical teeth with strongly striated crowns and unserrated lateral carinae (Kuzmin *et al.*, 2013). The goniopholidid from the Berezovsk coal mine represents the northernmost occurrence of this group in the Jurassic of Asia and one of the oldest goniopholidid records in Asia (Kuzmin *et al.*, 2013). Other Middle to Late Jurassic occurrences of goniopholidids in Asia have been reported from Kyrgyzstan (Averianov, 2000), northwestern China (Wu *et al.*, 1996; Maisch *et al.*, 2003; Schellhorn *et al.*, 2009) and Mongolia (Efimov, 1988a,b).

Pterosauria

The pterosaurs are represented in the Berezovsk coal mine by numerous isolated teeth and very rare bone fragments. The teeth have an asymmetrical enamel distribution and smooth enamel. Previously the pterosaur remains from the Berezovsk coal mine have been referred to the Pterodactyloidea based on tooth morphology (Table 1). However, very similar teeth, labiolingually compressed and lingually curved, have been reported for the rhamphorhynchid *Sericipterus* from the Upper Jurassic of Xinjiang, China (Andres *et al.*, 2010). Thus, the assignment of the pterosaurs from the Berezovsk coal mine to Rhamphorhynchidae seems more likely.

Dinosauria

The sauropods of the Berezovsk coal mine are known from numerous isolated teeth and two platycoelous posterior caudal vertebrae. The sauropod material was previously assigned to the Titanosauriformes (Table 1) based on *Pleurocoelus*-like teeth. However, a now largely expanded sample of isolated teeth shows that the tooth morphology is more primitive and therefore more consistent with the placement of this taxon among non-neosauropod eusauropods. The teeth have narrow to broad spatulate crowns, sometimes with a median ridge on the concave (lingual) side. The enamel is smooth in most specimens. Very few teeth have the wrinkled enamel texture typical for Eusauropoda. Some teeth have lost their enamel layer post mortem most likely due to chemical etching during digestion. Most teeth lack denticles, but in few specimens there are well developed denticles on the mesial and distal crown edges. Some teeth show variably developed V-shaped wear facets. At least one posterior tooth with a small crown and large denticles has an apical wear facet. The teeth and caudal vertebrae closely resemble those of *Mamenchisaurus* (Young &

Table 1 The known vertebrate assemblage of Itat Formation at Berezovsk coal mine, Krasnoyarsk Territory, Russia

Hybodontiformes	
	Hybodus sp. (Skutschas *et al*., 2009).
Acipenseriformes	
	Acipenseriformes indet.
Palaeonisciformes	
	Palaeonisciformes indet. [=Palaeoniscidae indet. in Alifanov *et al*. (2001)] (Averianov *et al*., 2005; Skutschas *et al*., 2009).
Amiiformes	
	Sinamiidae indet. (Skutschas *et al*., 2009).
Dipnoi	
	Ferganoceratodus sp. [=Dipnoi indet. in Averianov *et al*. (2005); Skutschas *et al*. (2009)]
Anura	
	?*Eodiscoglossus* sp. (Skutschas *et al*., 2016).
Stem Caudata	
	Urupia monstrosa Skutschas et Krasnolutskii, 2011 [=cf. Karauridae indet. in Averianov *et al*. (2005); =Karauridae? indet. in Skutschas *et al*. (2005); =Caudata indet. in Skutschas *et al*. (2005); =Karauridae indet. in Skutschas *et al*. (2009)] (Skutschas and Krasnolutskii, 2011).
	Berezovsk salamander A (Skutschas, 2013).
Crown Caudata	
	Kiyatriton krasnolutskii Skutschas, 2015 [=Berezovsk salamander B in Skutschas (2013)] (Skutschas, 2016).
Testudines	
	Annemys sp. [=Chelonia indet. in Alifanov *et al*. (2001); =*Xinjiangchelys* sp. in Averianov *et al*. (2005) and Skutschas *et al*. (2009)] (Danilov and Krasnolutskii, 2012; Obraztsova and Danilov, 2015).
	Testudines indet. 1
	Testudines indet. 2
	Testudines indet. 3
Squamata	
	Scincomorpha indet. [=cf. Paramacellodidae indet. in Averianov *et al*. (2005); =Paramacellodidae indet. in Skutschas *et al*. (2009)] (Valeev, 2008).
Choristodera	
	Choristodera indet. [=*Cteniogenys* sp. in Skutschas *et al*.(2009)]. (Skutschas and Efimov, 2015)
Crocodyliformes	
	Goniopholididae indet. [=*Sunosuchus* sp. in Alifanov *et al*. (2001); =cf. *Sunosuchus* sp. in Averianov *et al*. (2005)] (Skutschas *et al*., 2009; Kuzmin *et al*., 2013; Skutschas *et al*., 2015).
Pterosauria	
	Rhamphorhynchidae indet. [=Pterodactyloidea indet. in Averianov *et al*. (2005); Skutschas *et al*. (2009); =Pterodactylida indet. in Averianov (2008)].
Sauropoda	
	Mamenchisauridae indet. [=Sauropoda indet. (Alifanov *et al*., 2001); =Titanosauriformes indet. in Averianov *et al*. (2005) and Skutschas *et al*. (2009)].
Theropoda	
	Kileskus aristotocus Averianov *et al*., 2010 [=Allosauroidea indet. in Alifanov *et al*. (2001); =Dromaeosauridae indet. in Alifanov *et al*. (2001); =cf. Dromaeosauridae indet. in Averianov *et al*. (2005); =Tetanurae indet. in Skutschas *et al*. (2009); =*Kileskus aristotokus* [sic] in Alifanov (2012)] (Averianov *et al*., 2010a).
Ornithopoda	
	Ornithopoda indet. (Alifanov *et al*., 2001).
	Heterodontosauridae indet. (Averianov *et al*., 2005; Skutschas *et al*., 2009).
Stegosauria	
	Stegosauria indet. (Alifanov *et al*., 2001; Averianov *et al*., 2005; Averianov and Krasnolutskii, 2009; Skutschas *et al*., 2009).
Tritylodontidae	
	Tritylodontidae indet. (Averianov *et al*., 2005; Skutschas *et al*., 2009).
Eleutherodontidae	
	Sineleutherus issedonicus Averianov *et al*., 2011 [=Haramiyida indet. in Skutschas *et al*. (2009); =*Allodacus butleri* [nomen nudum] in Skutschas *et al*. (2009)] (Averianov *et al*., 2011).
Simpsonodontidae	
	Simpsonodon sibiricus Averianov *et al*., 2010 [=*Simpsonodon* sp. in Lopatin and Averianov (2009)] (Averianov *et al*., 2010b).
Tegotheriidae	
	Hutegotherium yaomingi Averianov *et al*., 2010 (Averianov *et al*., 2010b).
Docodonta incertae sedis	
	Itatodon tatarinovi Lopatin et Averianov, 2005 (Lopatin and Averianov, 2005, 2006, 2009; Skutschas *et al*., 2009; Averianov *et al*., 2010b).
	Docodonta indet. (Averianov *et al*., 2005; Skutschas *et al*., 2009).
?Amphilestidae	
	Amphilestidae indet. (Skutschas *et al*., 2009).
	Eutriconodonta indet. (Averianov *et al*., 2008).
Dryolestidae	
	Anthracolestes sergeii Averianov *et al*., 2014 [=Dryolestidae indet. in Skutschas et al. (2009)] (Averianov *et al*., 2014).
Zatheria	
	Amphibetulimus krasnolutskii Lopatin & Averianov, 2007 (Lopatin and Averianov, 2007; Skutschas *et al*., 2009; Averianov *et al*., 2015).

Chao, 1972; Russell & Zheng, 1994; Ouyang & Ye, 2002) and therefore the sauropod remains from the Berezovsk coal mine may well belong to the Mamenchisauridae.

The proceratosaurid *Kileskus aristotocus* from the Berezovsk coal mine is one of the oldest members of

Tyrannosauroidea and Coelurosauria (Averianov *et al.*, 2010a; Brusatte *et al.*, 2010). Its original description was based on the premaxilla, maxilla, a mandible fragment, and several limb bone parts (Averianov *et al.*, 2010a). Newly collected material includes cervical and caudal vertebrae. The numerous isolated laterally compressed dentary and maxillary and variously asymmetrical ("D-shaped") premaxillary theropod teeth from the Berezovsk coal mine are all attributable to *Kileskus*.

Isolated leaf-like maxillary and dentary teeth with marginal and cingular denticles, as well as premaxillary teeth with swollen recurved crown having few or none marginal denticles are common. These teeth closely resemble those of Heterodontosauridae (Sereno, 2012) and indicate the presence of this ornithopod taxon in the vertebrate assemblage of the Berezovsk coal mine.

Numerous stegosaur postcranial elements have been excavated from the top of the Itat Formation section in the Berezovsk coal mine, and were described as Stegosauridae indet. (Averianov & Krasnolutskii, 2009). Isolated stegosaur teeth are quite common in the microvertebrate samples. The stegosaur material from the Berezovsk coal mine is one of the oldest occurrences of this group in the fossil record.

Tritylodontidae

The Tritylodontidae from the Berezovsk coal mine are represented by isolated incisors and cheek teeth. Complete cheek teeth are rather rare but tooth fragments are common. The Berezovsk taxon belongs to a derived tritylodontid clade with the upper teeth cusp formula 2: 2: 2. This clade includes *Bocatherium*, *Polistodon*, *Stereognathus*, *Xenocretosuchus*, and *Montirictus* (Setoguchi *et al.*, 1999; Tatarinov & Maschenko, 1999; Matsuoka *et al.*, 2016). The Berezovsk tritylodontid is more closely related to the last three genera in having subequal cusps on the upper teeth.

Enigmatic non-mammalian amniote

Among the most enigmatic findings from the Berezovsk coal mine are small amniote vertebrae with a very unusual morphology of the neural spines. The neural spines of those vertebrae are sharp, very high and lanceolate (Fig. 4). They so far could not be confidently assigned to any amniote taxon known from the Berezovsk coal mine or from elsewhere. Pending on further discoveries that could clarify affinities of these enigmatic vertebrae from the Berezovsk coal mine locality (e. g. articulated skeletons), we assign them only to Amniota indet.

Mammaliaformes

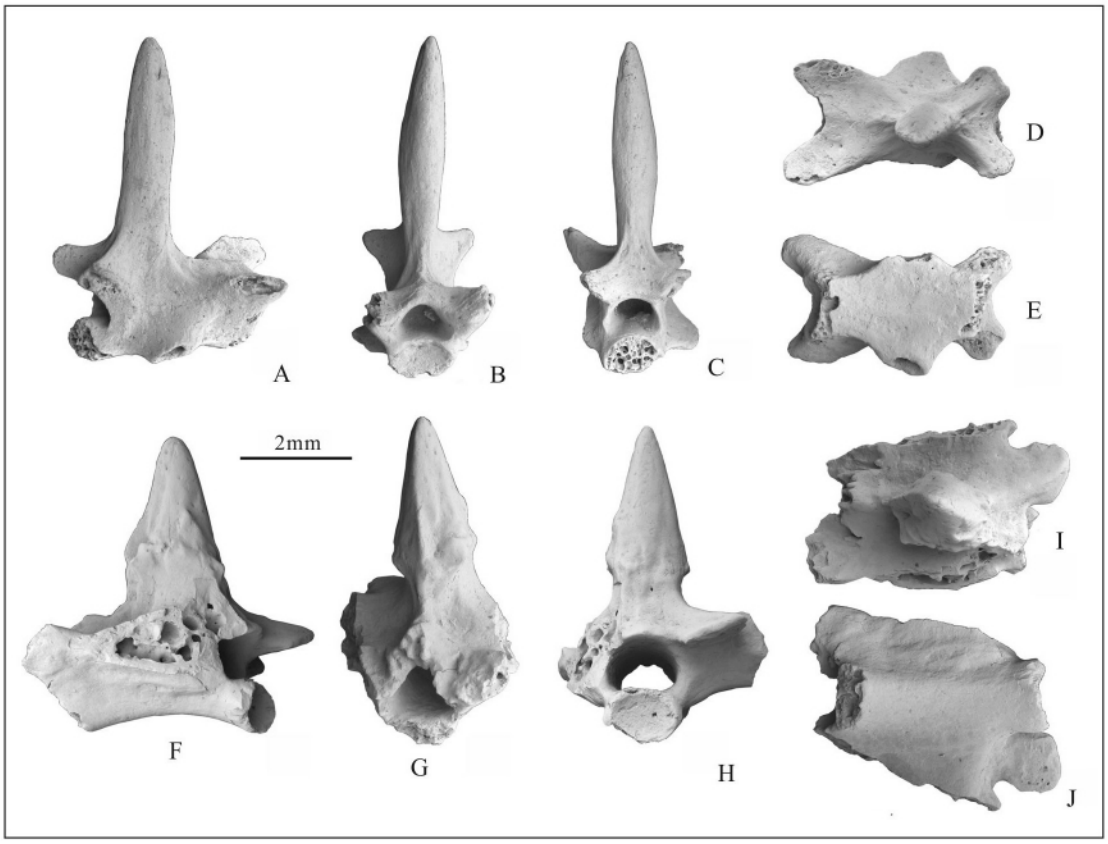
The mammaliaform and mammalian assemblage of the Berezovsk coal mine is diverse and the specimens are surprisingly common, even surpassing the number of tritylodontid remains. The most common remains are edentulous dentary fragments, isolated teeth, and postcranial bones, which is typical for fluvial deposits. Cranial elements are extremely rare and include some maxillary fragments and isolated petrosals. There are at least two types of petrosals, both referable to docodontans (Schultz *et al.*, 2013).

Haramiyidans include the described eleutherodontid *Sineleutherus issedonicus* Averianov *et al.*, 2011 (Averianov *et al.*, 2011) and at least one undescribed taxon of arboroharamiyidan.

Docodontans are the dominant group of mammaliaforms in the Berezovsk coal mine vertebrate assemblage. There are three named taxa: *Itatodon tatarinovi* Lopatin et Averianov, 2005, *Simpsonodon sibiricus* Averianov *et al.*, 2010, and *Hutegotherium yaomingi* Averianov *et al.*, 2010, as well as indeterminable edentulous dentary fragments (Averianov *et al.*, 2005; Lopatin & Averianov, 2005; Averianov & Lopatin, 2006; Averianov *et al.*, 2010b). *Simpsonodon sibiricus* differs from *Simpsonodon oxfordensis* Kermack *et al.*, 1987 from the Forest Marble Formation of England (Kermack *et al.*, 1987) by subtle dental characters. Isolated docodontan teeth, very similar to those of *Simpsonodon*, are also known from the Callovian Balabansai Formation of Kyrgyzstan (Martin & Averianov, 2010). *Simpsonodon* and *Dsungarodon* from the Upper Jurassic of Xinjiang, China (Pfretzschner *et al.*, 2005; Martin *et al.*, 2010), were referred to the Simpsonodontidae (Aver-

ianov et al., 2010b). *Hutegotherium* is referred to the Tegotheriidae which also includes *Krusatodon* from the Middle Jurassic of England (Sigogneau-Russell, 2003), *Tegotherium* from the Upper Jurassic of Mongolia and Xinjiang, China (Tatarinov, 1994; Martin *et al.*, 2010), and *Sibirotherium* from the Lower Cretaceous of Siberia, Russia (Maschenko *et al.*, 2003; Lopatin *et al.*, 2009). In the phylogenetic analysis by Averianov *et al.* (2010b) *Itatodon* was found to be a basal docodontan. In spite of the reduction of crest a–b on the lower molariform teeth, *Itatodon* is a typical docodontan (contra Wang & Li, 2016). It has the longitudinal groove along the inner (interradical) surface of the lower molariform roots, as observed in all docodontans. This groove houses a bone projection on the septum separating the tooth alveolus which is assumed to serve as a strengthening of the tooth implantation in the jaw. This peculiar structure is not known from any symmetrodontan, including *Shuotherium*.

Eutriconodontans are very rare and represented by one rather large *Gobiconodon*-like tooth (Averianov *et al.*, 2008) and several tooth fragments.



A–E, ZIN PH 16/117, in right lateral (A), anterior (B), posterior (C), dorsal (D), and ventral (E) views; F–J, ZIN PH 17/117, in right lateral (F), anterior (G), posterior (H), dorsal (I), and ventral (J) views.

Fig. 4 Enigmatic vertebrae of Amniota indet. from the Berezovsk coal mine

Multituberculates from the Berezovsk coal mine are represented by molariforms of a yet undescribed taxon. This is one of the oldest evidences of multituberculates in the fossil record. Other Middle Jurassic multituberculates are known from the Forest Marble Formation of England (Butler & Hooker, 2005).

The dryolestid *Anthracolestes sergeii* Averianov *et al.*, 2014 from the Berezovsk coal mine, represented by isolated teeth and edentulous dentary fragments, is the oldest, most basal, and only Asiatic member of Dryolestidae (Averianov *et al.*, 2014a). A molar fragment of a stem dryolestid ("paurodontid") has been reported from the Middle Jurassic Balabansai Formation of Kyrgyzstan (Martin *et al.*, 2010). While dryolestidans are common faunal elements in the Jurassic of western Laurasia (Europe and North America), they are extremely rare resp. absent in contemporaneous strata in Asia.

The stem therian (zatherian) mammals of the Berezovsk coal mine include the relatively large *Amphibetulimus krasnolutskii* Lopatin & Averianov, 2007 (Lopatin & Averianov, 2007a; Averianov *et al.*, 2015) and the smaller *Amphitherium* sp. The latter is represented by undescribed upper and lower molars and an edentulous dentary fragment.

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