Proceedings of the Zoological Institute RAS
Vol. 317, No. 4, 2013, pp. 452–458

УДК 57.072:551.762.2

GONIOPHOLIDID CROCODYLOMORPH FROM THE MIDDLE JURASSIC BEREZOVSK QUARRY LOCALITY (WESTERN SIBERIA, RUSSIA)

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ABSTRACT

Excavations and sediment screenwashing at the Middle Jurassic Berezovsk Quarry locality in Krasnoyarsk Territory, Russia, yielded rare isolated teeth, osteoderms and fragments of cranial bones of crocodyliforms. All these remains were referred to Goniopholididae indet. on the basis of the following combination of features: a relatively narrow and long snout, contribution of splenials to the mandibular symphysis, dermal sculpturing consists of almost circular and slightly elongated oval pits, polygonal ventral osteoderms, and conical teeth with strongly striated crowns with weakly developed unserrated lateral carinae. The Berezovsk goniopholidid represents one of the oldest goniopholidid records in Asia and, geographically, the northernmost occurrence of this group in the Jurassic of Asia.

Key words: Crocodyliformes, Goniopholididae, Itat Formation, Jurassic, Russia

ГОНИОФОЛИДИДНЫЙ КРОКОДИЛОМОРФ ИЗ СРЕДНЕЮРСКОГО МЕСТОНАХОЖДЕНИЯ «БЕРЕЗОВСКИЙ РАЗРЕЗ» (ЗАПАДНАЯ СИБИРЬ, РОССИЯ)

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РЕЗЮМЕ

Раскопки и промывка породы в среднеюрском местонахождении Березовский разрез в Красноярском Крае (Россия) позволила обнаружить редкие изолированные зубы, остеодермы и фрагменты черепных костей крокодилиформ. Все эти остатки были отнесены к Goniopholididae indet. на основании следующей комбинации признаков: передняя часть морды сравнительно узкая и длинная, пластинчатые кости участвуют в формировании нижнечелюстного симфиза, скульптура покровных костей состоит из практически округлых или слабо удлиненных овальных ямок, вентральные остеодермы полигональной формы, зубы конические, с сильной струйчатостью и слабо развитыми незубчатыми латеральными гребнями. Гониофолидид из Березовского разреза один из древнейших представителей Goniopholididae в Азии и, географически, представляет собой наиболее северную находку этой группы в юре Азии.

Ключевые слова: Crocodyliformes, Goniopholididae, итатская свита, юра, Россия

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INTRODUCTION

The Middle Jurassic (Bathonian) microvertebrate Berezovsk Quarry locality (Western Siberia, Russia) has yielded remains of diverse fresh-water and terrestrial vertebrates (Alifanov et al. 2001; Averianov et al. 2005, 2008, 2010a, b; Lopatin and Averianov 2005, 2006, 2007, 2009; Skutschas et al. 2005; Averianov and Lopatin 2006; Skutschas 2006; Averianov and Krasnolutskii 2009). Crocodyliforms are among the rarest components of the Berezovsk Quarry vertebrate assemblage and during more than ten years of regular excavations and intensive screenwashing several dozen of isolated teeth, osteoderms and very few fragments of cranial bones were found. The most diagnostic specimens are described in this paper.

Institutional abbreviations. ZIN PH, Paleoherpetological collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

Locality. The Berezovsk Quarry locality is situated 500 m south of Nikol'skoe village, Sharypovo District, Krasnoyarsk Territory, Russia. Vertebrate remains from the Berezovsk Quarry locality were found in grey clays and sands in the upper part of the Bathonian Itat Formation (for the detailed geological setting see Averianov et al. [2005]). The Berezovsk Quarry vertebrate assemblage (besides crocodyliforms) includes hybodont sharks (cf. *Hybodus* sp.), palaeonisciform (Palaeonisciformes indet.) and amiiform (Amiiformes indet.) actynopterygians, dipnoans (Dipnoi indet.), salamanders (*Urupia monstrosa* and two undescribed taxa) , xinjiangchelid turtles (*Xinjiangchelys* sp.), primitive lepidosauromorphs (Lepidosauromorpha indet.), scincomorph lizards (Scincomorpha indet.), choristoderes (Choristodera indet.), various ornithischian (Stegosauria indet., Ornithischia indet.) and saurischian (Titanosauriformes indet., theropod *Kileskus aristotocus*) dinosaurs, pterosaurs (Pterosauria indet.), tritylodontids (Tritylodontidae indet.) and diverse mammals (the eleutherodontid haramiyid *Sineleutherus issedonicus*, the docodonts *Itatodon tatarinovi*, *Simpsonodon sibiricus*, and *Hutegotherium yaomingi*, an amphilestid-grade eutriconodontan, the stem therian *Amphibetulimus krasnolutskii* and an undescribed dryolestid) (Alifanov et al. 2001; Averianov et al. 2005, 2008, 2010a, b, 2011; Lopatin and Averianov 2005, 2006, 2007, 2009; Skutschas et al. 2005; Averianov and Lopatin 2006; Skutschas 2006, 2013; Averianov and Krasnolutskii 2009). All vertebrates in the Berezovsk Quarry assemblage are fresh-water or terrestrial, indicating an in-land vertebrate community (Averianov et al. 2005).

SYSTEMATICS

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone and Whybrow, 1983

Neosuchia Benton and Clark, 1988

Goniopholididae Cope, 1875

Goniopholididae indet.
(Figs. 1–3)

Material. ZIN PH 1/176, maxillary fragment; ZIN PH 2/176, fragment of left nasal; ZIN PH 3/176, anterior fragment of right splenial; ZIN PH 4-8/176, teeth and 17 unnumbered teeth; ZIN PH 9/176, fragment of the dorsal osteoderm; ZIN PH 10/176, fragmentary ventral osteoderm.

Description. *Maxilla*. ZIN PH 1/176 is dorsoventrally flattened, small maxillary fragment with broken palatal process (Fig. 1A–B). The fragment is mediolaterally narrow, like in long-snouted crocodyliform taxa. In ventral view, there are two distinct alveoli and a bifurcating groove along medial edge of the bone. This groove likely corresponds to a part of a passage for the maxillary branch of the trigeminal nerve. The medial surface of the fragment is nearly flat, straight in dorsal view and bears a facet for the nasal. The dorsal surface is sculptured by almost circular and slightly anteroposteriorly elongated oval pits. A neurovascular foramen is present dorsally to the lateral margin of the fragment.

Nasal. ZIN PH 2/176 is a plate-like small fragment of the left nasal (Fig. 1C–D). The fragment is mediolaterally narrow and slightly tapers anteriorly. The ventral surface has two longitudinal grooves separated from each other in the posterior part of the fragment by a relatively high ridge. The medial groove is shallower and narrower than the lateral one. These grooves correspond to the bony walls of the nasal passages. The preserved part of facet for the left nasal on the medial surface is flat and straight in the dorsal view. The facet for maxilla on the lateral surface is slightly inclined. Sculpture of the dorsal surface is generally similar to that of maxilla, but differs in the presence of more anteroposteriorly elongated pits.

Splenial. ZIN PH 3/176 is the anteriormost fragment of the right splenial with a partly preserved

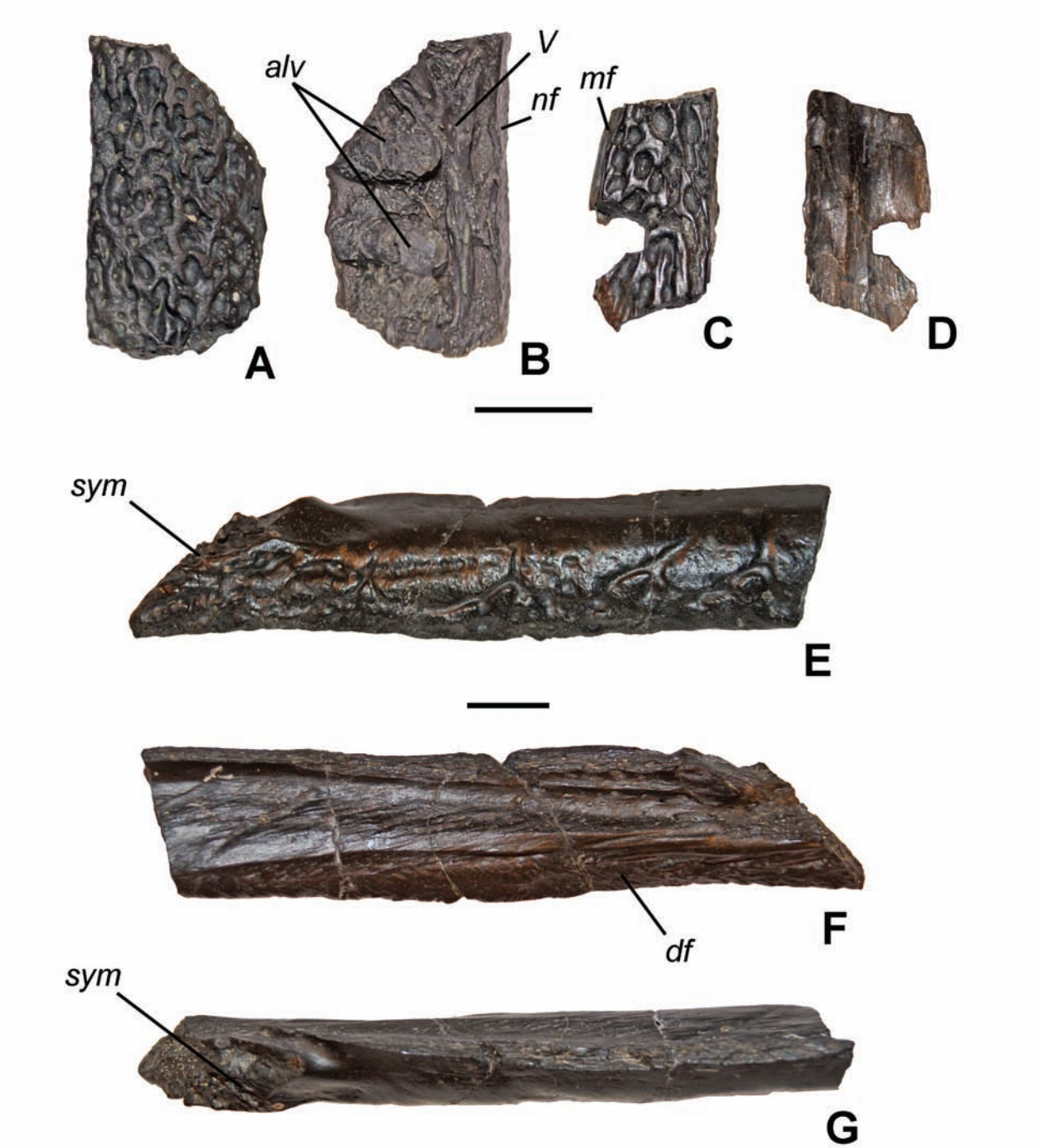

Fig. 1. Fragments of cranial bones of Goniopholididae indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic): A–B – ZIN PH 1/176, maxillary fragment, in dorsal (A) and ventral (B) views; C–D – ZIN PH 2/176, fragment of left nasal, in dorsal (C) and ventral (D) views; E–G – ZIN PH 3/176, anterior fragment of right splenial, in medial (E), lateral (F) and dorsal (G) views. *Abbreviations*: *alv* – alveoli; *df* – dentary facet; *mf* – maxillary facet; *nf* – nasal facet; *sym* – symphysis; *V* – groove for the trigeminal nerve;. Scale bar = 1 cm.

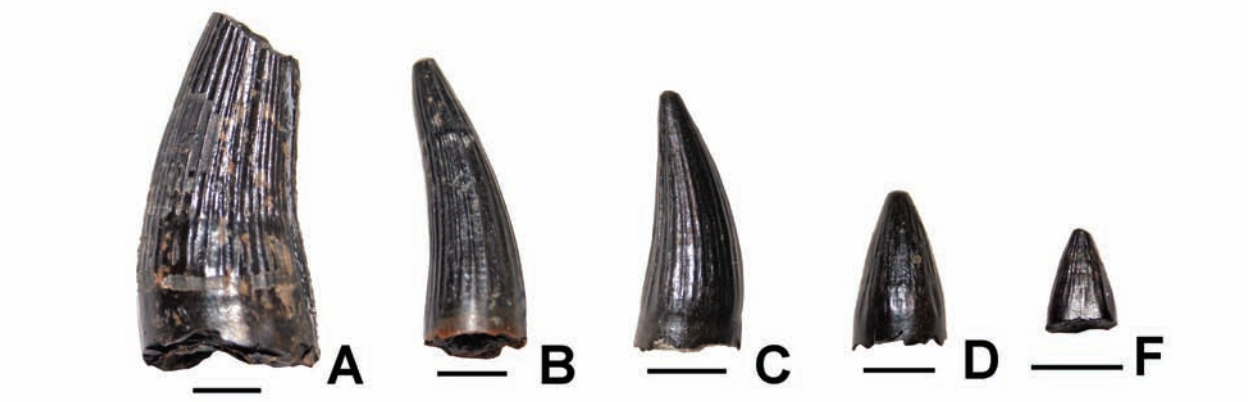

Fig. 2. Isolated teeth of crocodyliform Goniopholididae indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic): A – ZIN PH 4/176, teeth of morphotype 1 in lateral view; B – ZIN PH 5/176, teeth of morphotype 1 in lateral view; C – ZIN PH 6/176, teeth of morphotype 1 in lateral view; D – ZIN PH 7/176, teeth of morphotype 2 in labial view; F – ZIN PH 8/176, teeth of morphotype 2 in lingual view. Scale bar = 3 mm.

symphyseal region and a broken dorsal edge (Fig. 1E–G). The fragment is robust and convex medially. The ventromedial surface is sculptured by shallow pits and relatively deep grooves. The ventral edge is almost straight in lateral and medial views. Along ventral edge, the lateral surface has a longitudinal facet for the dentary which is deep near the symphysis and gradually tapering posteriorly. According to the presence of the symphysis on the medial surface of the anterior part of the fragment, the splenials are in contact medially and contribute to the mandibular symphysis. Dorsally to the posterior end of the symphysis, at the broken area, there is a groove which corresponds to the floor of the canal for the passage of the branches of V cranial nerve and the medial end of this groove is a part of the foramen intermandibularis oralis.

Dentition. Isolated teeth (specimens ZIN PH 4-8/176 and 17 unnumbered teeth; Fig. 2) are represented only by their crowns. Teeth vary in shape and size (total crown height ranges from 2 to about 20 mm), but all demonstrate similar configuration of the striae and carinae. The enamel is ornamented by regular coarse striae, which extend vertically from the tooth base over the entire height of the crown and merge at the apex. The striae, covering each single tooth, are nearly same in size, but the distribution of them is slightly irregular: lingual surface bears a higher number of striae comparing with labial surface. Weakly developed, unserrated mesial and distal carinae are present. Both carinae are equally pronounced and are more distinct closer to the tooth apex than towards its base.

Among isolated teeth two distinctive morphotypes can be recognized. The first morphotype includes the most of specimens (n = 17) and represented by highly conical teeth with rounded base and acute tip (Fig. 2A–C). Teeth of this morphotype are slightly lingually curved and circular or almost circular in cross section (only the smallest teeth are slightly labiolingually compressed). Total crown height ranges from 2 to about 20 mm (height of the fragment of the largest tooth ZIN PH 4/176 is about 15 mm and estimated total height of this tooth is about 20 mm). Notably, the smallest teeth of the first morphotype have actually a slightly labiolingually compressed base rather than round. One peculiar tooth (ZIN PH 5/176; Fig. 2B) belonging to this morphotype, is very highly conical and has a sigmoid flexure (the tip of the crown is slightly curved labially). This tooth also has a circular ridge at the level of three-quarter of its height. Three teeth of the first morphotype (ZIN PH 6/176 and two unnumbered teeth; Fig. 2C) have a slight constriction of the base, near the transition to the root.

The second morphotype (Fig. 2D-F) consists of low conical, weakly lingually curved stout teeth, with an acute tip and without any constriction of the base (n = 5, ZIN PH 7/176, ZIN PH 8/176 and three unnumbered teeth). The larger teeth of this morphotype (total crown height ranges from 4 to 7 mm) have rounded broad bases, which are nearly circular in cross section. The two smaller teeth (ZIN

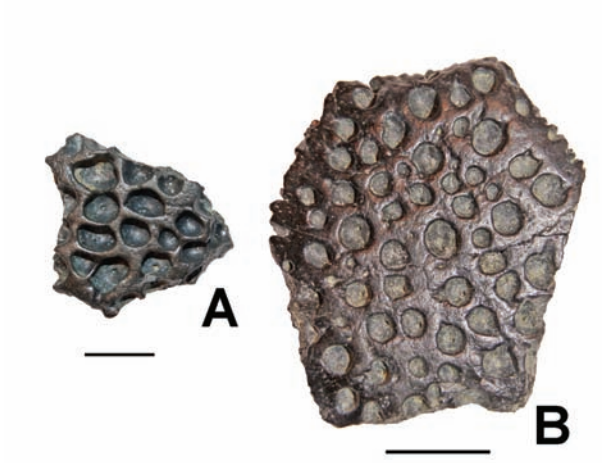

Fig. 3. Fragmentary osteoderms of crocodyliform Goniopholididae indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic): A – ZIN PH 9/176, fragment of the dorsal osteoderm in dorsal view;): B – ZIN PH 10/176, fragment of the ventral osteoderm in ventral view. Scale bar = 1 cm.

PH 8/176 and one unnumbered tooth; total crown height about 3 mm) are low, conical and considerably labiolingually compressed, with a broad base and also ending in an acute tip.

Osteoderms. The two referred specimens (ZIN PH 9/176 and ZIN PH 10/176) are fragmentary ventral and dorsal osteoderms respectively. The external surface of ZIN PH 9/176 (Fig. 3A) is sculptured by large and deep oval and nearly circular pits, resembling dorsal osteoderm ornamentation of goniopholidids, so it is considered to be a fragment of a dorsal osteoderm. The internal surface is smooth, with rare small nutritive foramina. The preserved portion of its lateral margin reveals no sign of sutural contact with adjacent osteoderm. The fragmentary ventral osteoderm (ZIN PH 10/176, Fig. 3B) is an irregular plate, presumably hexagonal in shape. The external surface covered with shallow, small and nearly circular pits, which are separated by relatively wide ridges. The preserved edges of the ventral osteoderm have interdigitating sutures for the contacts with adjacent osteoderms.

COMPARISON AND DISCUSSION

All cranial bones (fragments of maxilla ZIN PH 1/176, nasal ZIN PH 2/176, splenial ZIN PH 3/176) and osteoderms (ZIN PH 9-10/176) are comparable in size and dermal sculpturing, so all of these specimens are assigned to one taxon. The largest teeth of the morphotype 1 (ZIN PH 4/176) are comparable in size with cranial bones and osteoderms and assignment of all teeth of this morphotype to the same taxon is the simplest assumption. Teeth of other morphotype vary in size, but all demonstrate the pattern of striae and carinae similar to that of the morphotype 1. The differences between teeth morphotypes may be the result of ontogenetic or individual variations (even within one tooth row) and we tentatively refer all teeth specimens to the same taxon. Notably, the smallest teeth of both morphotypes are labiolingually compressed and this, presumably, may represent a juvenile morphological feature.

The Berezovsk crocodyliform is generally characterized as a mid-sized form, having an elongated, narrow and flattened snout (according to mediolaterally narrow and flattened maxilla and nasal) and a ventral bony armor containing polygonal osteoderms. These features are not unambiguous synapomorphies of any crocodyliform clade, but suggest mesoeucrocodylian rather than basal crocodyliform (= "protosuchian") affinities of the Berezovsk crocodyliform (for the list of synapomorphies of crocodyliforms see e.g. Andrade et al. 2011). Among mesoeucrocodylians, the Berezovsk crocodyliform closely resembles those of Asiatic Jurassic goniopholidid "*Sunosuchus*" Young 1948 in the following combination of morphological features: a relatively narrow and long snout, contribution of splenials to the mandibular symphysis, dermal sculpturing consists of almost circular and slightly elongated oval pits, polygonal ventral osteoderms, and conical teeth with strongly striated crowns with unserrated lateral carinae (see characters of "*Sunosuchus*" in Buffetaut and Ingavat 1980, 1984; Wu et al. 1996; Averianov 2000; Schellhorn et al. 2009; Wings et al. 2010). Additionally, the Berezovsk crocodyliform differs from the only known longirostrine non-goniopholidid Middle-Late Jurassic Asiatic mesoeucrocodylian *Hsisosuchus* Young et Chow 1953 by the flattened snout (Gao 2001; Peng and Shu 2005) and non-ziphodont teeth (ziphodont teeth in *Hsisosuchus* according to Andrade et al. 2011).

Based on current evidence, the Berezovsk crocodyliform is best interpreted as a goniopholidid with unknown affinities. Assignment of the Berezovsk goniopholidid to *Sunosuchus* is unlikely in following reasons: (1) the most recent cladistic analyses of goniopholidids (Andrade et al. 2011; Halliday et al. in press) suggest that this genus is polyphyletic and

Sunosuchus miaoi Young 1948 is the only taxon to retain the generic name, as the type species of the genus and (2) the Berezovsk goniopholidid does not share any synapomorphies with the type species *Sunosuchus miaoi*. A more precise placement for the Berezovsk goniopholidid must await the recovery of more informative specimens and better resolution of the phylogenetic relationships among Goniopholididae.

If our assignment of different teeth morphotypes to the one taxon is correct, then the Berezovsk goniopholidid had a slight "heterodonty" dentition. Variations in teeth morphology were not reported for Asiatic Jurassic goniopholidids, except "*Sunosuchus*" sp. from the Upper Toutunhe Formation (Middle Jurassic, ?Bathonian-Callovian) in China (Maisch et al. 2003). The Chinese "*Sunosuchus*" sp. has at least two types of teeth: pointed, strongly curved, and almost non-carinate anterior, and strongly carinate, bulbous and heavily striated, small posterior teeth (Maisch et al. 2003). The Berezovsk goniopholidid also has two very similar dental morphotypes, except that of low conical and stout teeth (morphotype 2) are less carinate than similar teeth morphotype of the Chinese "*Sunosuchus*" sp.

Crocodyliforms are rare component of the vertebrate assemblage of the Berezovsk Quarry locality. The reason for the rarity of crocodyliform remains in the Berezovsk Quarry locality is unclear and it could be a result of taphonomic as well as ecological factors.

Despite that the material on the goniopholidid from the Berezovsk Quarry locality is scarce, it extends the known geographical range of Goniopholididae and represents the northernmost occurrence of this group in Jurassic of Asia. Moreover, it is also one of the oldest goniopholidid records in Asia. The other oldest Asiatic goniopholidids (all Middle Jurassic in age) are known from Kyrgyzstan ("*Sunosuchus*" sp.) and China ("*Sunosuchus*" *shunanensis* Fu et al. 2005, "*Sunosuchus*" sp.) (Averianov 2000; Maisch et al. 2003; Fu et al. 2005). The findings of the oldest Asiatic goniopholidids in several geographically distant Middle Jurassic localities suggest that this group was widely distributed at that time and became one of the dominating crocodyliform component in vertebrate faunas (till the Early Cretaceous).

ACKNOWLEDGMENTS

We are grateful to all the members of the expeditions to the Berezovsk Quarry locality for their help. Support for our work was provided by the general director of OAO SUEK Krasnoyarsk A.V. Fedorov and by the chief manager of the Berezovsk Quarry M.V. Palshin. We thank I.G. Danilov (ZIN), M. Delfino (University of Torino, Italy), and an anonymous reviewer for useful comments. We thank N.B. Ananjeva (ZIN) for providing access in the Department of Herpetology to a stereomicroscope with a camera that was used to photograph some specimens. The research has been supported by the Deutsche Forschungsgemeinschaft (DFG) grant MA 1643/14-1 and the Russian Foundation for Basic Research (project 11-04-91331-NNIO).

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Submitted 30 October, 2013; accepted 10 December, 2013.