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A NEW GENUS AND SPECIES OF BASAL SALAMANDERS FROM THE MIDDLE JURASSIC OF WESTERN SIBERIA, RUSSIA

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ABSTRACT

A new basal stem salamander, *Urupia monstrosa* gen. et sp. nov., is described based on an atlantal centrum (holotype), fragments of trunk vertebrae, and some associated elements (fragmentary dentaries and a femur) from the Middle Jurassic (Bathonian) Itat Formation of Krasnoyarsk Territory in Western Siberia, Russia. The new taxon is characterized by the following combination of characters: lack of the spinal nerve foramina in the atlas, presence atlantal transverse processes and a deep depression on the ventral surface of the atlas; lateral surface of anterior part of the dentary is sculptured by oval and rounded pits; very short diaphyseal part of femur. The absence of intercotylar tubercle on the atlas and presence of atlantal transverse processes support for neotenic nature of *Urupia monstrosa* gen. et sp. nov. Large size, presence of sculpture on vertebrae, and the absence of spinal nerve foramina in the atlas suggest that *Urupia monstrosa* gen. et sp. nov. is a stem group salamander. The phylogenetic relationships of *Urupia monstrosa* gen. et sp. nov. with other stem group salamanders cannot be established on the available material.

Key words: Caudata, Itat Formation, Jurassic, Russia

НОВЫЙ РОД И ВИД БАЗАЛЬНЫХ ХВОСТАТЫХ АМФИБИЙ ИЗ СРЕДНЕЙ ЮРЫ ЗАПАДНОЙ СИБИРИ, РОССИЯ

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РЕЗЮМЕ

Новая базальная стволовая хвостатая амфибия, *Urupia monstrosa* gen. et sp. nov., описана по телу атласа (голотип), фрагментам туловищных позвонков и некоторым другим костям (фрагменты зубных костей, бедренная кость), ассоциированных с данным таксоном из среднеюрской (батский ярус) итатской свиты в Красноярском Крае, Западная Сибирь, Россия. Новый таксон характеризуется следующей комбинацией признаков: отсутствие в атласе отверстий для выхода спинномозговых нервов; присутствие поперечных отростков на атласе и глубокой депрессии на вентральной поверхности атласа; латеральная поверхность зубной кости скульптурирована овальными и округлыми ямками; диафиз бедренной кости очень короткий. Отсутствие интеркотилярного бугорка и наличие поперечных отростков на атласе указывают на неотеническую природу *Urupia monstrosa* gen. et sp. nov. Крупный размер, присутствие скульптуры на позвонках и отсутствие в атласе отверстий для выхода спинномозговых нервов поддерживают положение *Urupia monstrosa* gen. et sp. nov. среди стволовой группы хвостатых амфибий. Филогенетические отношения *Urupia monstrosa* gen. et sp. nov. с другими стволовыми хвостатыми амфибиями пока неясны.

Ключевые слова: Caudata, итатская свита, юра, Россия

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INTRODUCTION

The most primitive basal stem salamanders are known from the Middle Jurassic of Great Britain (*Marmorerpeton kermacki* Evans, Milner et Mussett, 1988, *M. freemani* Evans, Milner et Mussett, 1988, Kirlington salamander A; Evans et al. 1988; Evans and Waldman 1996; Milner 2000) and Kyrgyzstan (*Kokartus honorarius* Nessov, 1988; Nessov 1988; Nessov et al. 1996; Milner 2000; Averianov et al. 2008b; Skutschas and Martin 2011), from the Late Jurassic of Kazakhstan (*Karaurus sharovi* Ivachnenko, 1978; Ivakhnenko 1978) and the USA (cf. Karauridae indet.; Nessov 1993). Additionally, stem salamanders (cf. Karauridae indet.) have been reported from the Middle Jurassic (Bathonian) Berezovsk Quarry locality in Western Siberia, Russia on the basis of a single heavily sculptured dentary fragment (Skutschas et al. 2005; Skutschas 2006). The second salamander specimen (robust femur) from the Berezovsk Quarry locality was determined as Caudata indet. (Skutschas et al. 2005; Skutschas 2006). Later, Skutschas and Martin (2011) showed that the dentary fragment from the Berezovsk Quarry differs strongly from the dentaries of karaurids (*Karaurus* Ivachnenko, 1978 and *Kokartus* Nessov, 1988) and cannot be referred to the Karauridae Ivachnenko, 1978. They also suggested that this specimen may belong to non-lissamphibian temnospondyls.

During last five years several new salamander specimens were found in the Berezovsk Quarry locality. This material shows that salamanders in the Berezovsk Quarry vertebrate assemblage were diverse and represented by several taxa. Most of this new material and the previously described salamander specimens from the Berezovsk Quarry (Skutschas et al. 2005; Skutschas 2006) can be referred to one large salamander taxon, which we describe here. Description of other salamander taxa from this locality is deferred, pending new informative material.

Institutional abbreviations. ZIN PH, Paleoherpetological collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; PM TGU, Paleontological Museum, Tomsk State University, Tomsk, Russia.

Locality. The salamander remains were recovered from grey clays in the upper part of the Itat Formation (=Svita), exposed in the Berezovsk Quarry, in the south of the Krasnoyarsk Territory, Western Siberia, Russia (for the detailed geological setting see Averianov et al. [2005]). The Itat Formation has been dated as Bathonian based on spores and palynomorphs (Alifanov et al. 2001). The Berezovsk Quarry locality has yielded a diverse vertebrate assemblage, which (besides salamanders) includes hybodont sharks, palaeonisciform and amiiform actynopterygians, dipnoans, xinjiangchelid turtles, primitive lepidosauromorphs, scincomorph lizards, choristoderes, crocodiles, various ornithischian and saurischian dinosaurs, pterosaurs, tritylodontids and diverse mammals (Alifanov et al. 2001; Averianov et al. 2005, 2008a, 2010a, b; Lopatin and Averianov 2005, 2006, 2007, 2009; Skutschas et al. 2005; Averianov and Lopatin 2006; Skutschas 2006; Averianov and Krasnolutskii 2009). The composition of this vertebrate assemblage is generally similar to that of the contemporary Forest Marble (Great Britain) and Balabansai (Kyrgyzstan) formations, especially in the mammalian component (Averianov et al. 2010b).

SYSTEMATICS

Amphibia Linnaeus, 1758

Caudata Scopoli, 1777

***Urupia* gen. nov.**

Etymology. After Urup River, which flows near Berezovsk Quarry.

Type species. *Urupia monstrosa* sp. nov.

Differential diagnosis. Differs from crown-group salamanders in lacking spinal nerve foramina in the atlas. Differs from *Marmorerpeton* Evans, Milner et Mussett, 1988 in the presence of atlantal transverse processes and a deep depression on the ventral surface of the atlas; from *Kokartus* by the presence of distinct ventrolateral ridges on the atlas.

Remarks. Comparison with *Karaurus* is not possible because the detailed structure of the atlas and trunk vertebrae is not described for this taxon (Ivakhnenko 1978). Isolated salamander atlantes from the Upper Jurassic Morrison Formation, USA, were referred to the Karauridae by Nessov (1993) without further explanation, and this material never has been described or figured. Atlantes are undescribed in Kirlington salamander A from the Middle Jurassic of the Great Britain, but the structure of trunk vertebrae of this form differs from that of *Urupia monstrosa* gen. et sp. nov. in the oblique orientation of the bases and articular surfaces of transverse processes (=rib-bearers).

Urupia monstrosa **sp. nov.**
(Figs 1–5)

cf. Karauridae indet. [part.], Skutschas et al. 2005: 122, fig. 1A–D; Skutschas 2006: 124, fig. 1F–G.
Caudata indet. [part.], Skutschas et al. 2005: 122, fig. 1E–K; Skutschas 2006: 124, fig. 1A–E.

Etymology. From the Latin *monstrum,* for abnormal or supernatural wonder (monster), in reference to the size of this species compared to the Late Jurassic and Early Cretaceous crown-group salamanders.

Holotype. ZIN PH 1/144, incomplete atlas.

Type locality and horizon. Berezovsk Quarry, 2 km south of Nikol'skoe village, Sharypovo District, Krasnoyarsk Territory, Western Siberia, Russia. Grey clays of the upper part of the Itat Formation, Middle Jurassic, Bathonian.

Material. PM TGU 200/10, anterior fragment of left dentary; PM TGU 200/11, left femur; ZIN PH 2/144, anterior fragment of left dentary; ZIN PH 3/144, 4/144, fragments of trunk vertebrae.

Distribution. Bathonian, south of the Krasnoyarsk Territory, Western Siberia, Russia.

Description. *Dentary.* The structure of the anterior portion of the dentary PM TGU 200/10 was described and figured by Skutschas et al. (2005) and Skutschas (2006). The newly collected anterior fragment of a left dentary ZIN PH 2/144 (Fig. 1E–H) shows the same morphology. The lateral surface of the anterior part of the dentary is sculptured by oval and rounded pits. It has a relatively sharp ridge along the ventral edge of the presymphyseal region and a robust convex subdental shelf on the medial surface. The Meckelian groove is very narrow and does not reach the symphysis. The Meckelian groove is exposed medially (more posterior part) and ventromedially (anterior end). The symphysis is expanded, but the structure of its medial face is unknown.

Atlas. The atlantal centrum (ZIN PH 1/144; Figs 2–3) is large and relatively elongated, with a maximum anterior width (i.e., between lateralmost edges of the rims of the anterior cotyles) of about 11 mm and a ventral midline length (i.e., between the anterior edge of intercotylar area and the posterior edge of the posterior cotylar rim) of about 8.5 mm (ratio of maximum anterior width:ventral midline length about 1.3). The anterior cotyles are dorsoventrally compressed (ratio of maximum height:width about 0.5) and elliptical in anterior view, with the medial end narrower.

The articular surfaces of the anterior cotyles are moderately concave. The dorsal, ventral and medial edges of the rims of the anterior cotyles project anteriorly, while lateral edges project anterolaterally. The anterior surface of the atlantal centrum lacks the intercotylar tubercle and only the notochondral central pit is present. The anterior cotyles do not extend onto the lateral sides of a thin layer of periosteal bone which surrounds the notochordal pit (the left anterior cotyle is fully separated from the notochordal pit; the right anterior cotyle and the notochordal pit are connected only by a narrow transverse groove). The areas between the medial edges of the rim of the anterior cotyles, the notochordal pit and the anteromedial edge of the centrum are perforated by two pairs of foramina.

The posterior cotyle is subcircular in posterior outline. In lateral view, the ventral rim of the posterior cotyle lies well below the level of the ventral rim of the anterior cotyles. The inner surface of the posterior cotyle is deeply concave.

The ventral surface of the centrum has a deep medial depression. The ventrolateral ridges extend anterolaterally from the ventrolateral edge of the rim of the posterior cotyle to the level of the deepest part of the medial depression. Both ventrolateral ridges are clearly distinct (the left ridge is relatively low and swollen; the right one is sharp and bears a protuberance in its middle part). The ventral surface of the centrum is sculptured by rounded and oval pits (several large pits in the medial depression and numerous relatively small pits along the ventrolateral ridges and on the posteroventral surface of the anterior cotyles). A similar sculpture (numerous relatively small pits) is present on the posterolateral and posterodorsal surfaces of the anterior cotyles.

The lateral surface of the centrum has a well-developed bipartite transverse process. The upper (diapophysis) and lower (parapophysis) parts of the transverse process are ridge-like and do not bear articular surfaces for the contact with the atlantal rib. There is a short vertical ridge which connects the upper and lower parts of the transverse process. There is a large foramen anteriorly to this vertical ridge. Three short ridges are associated with the upper part of the transverse process. The dorsal ridge is low, swollen, extends anterodorsally from the upper part of the transverse process and is clearly distinct only on the left side of the atlas. The dorsoposterior ridge and posterior ridges are sharp flanges which extend,

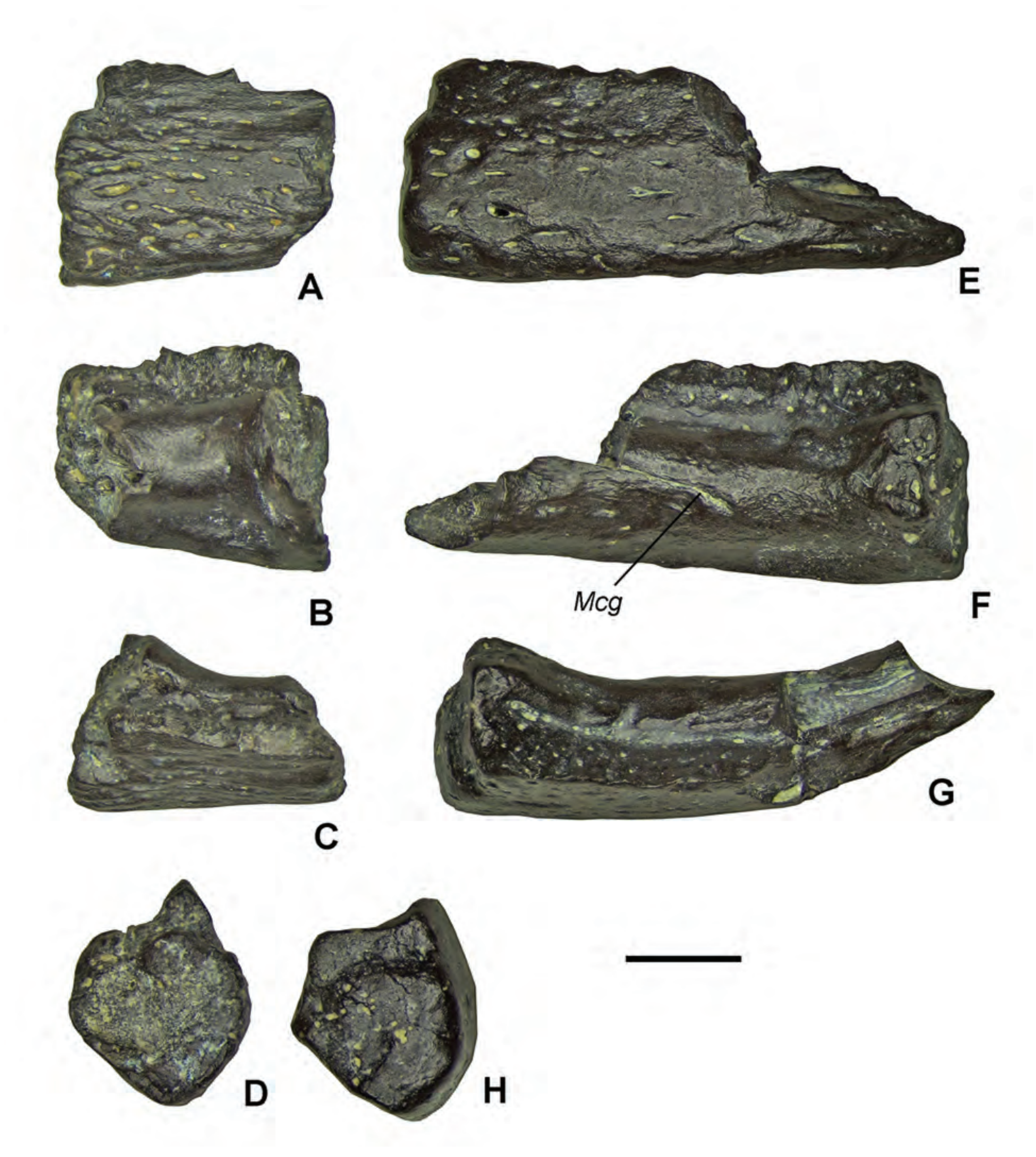

Fig. 1. Anterior fragments of left dentaries of *Urupia monstrosa* gen. et sp. nov. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic): A–D – PM TGU 200/10, in lateral (A), medial (B), dorsal (C) and anterior (D) views; E–H – ZIN PH 2/144, in lateral (E), medial (F), dorsal (G) and anterior (H) views.

Abbreviations: *Mcg* – Meckelian groove. Scale bar = 2 mm.

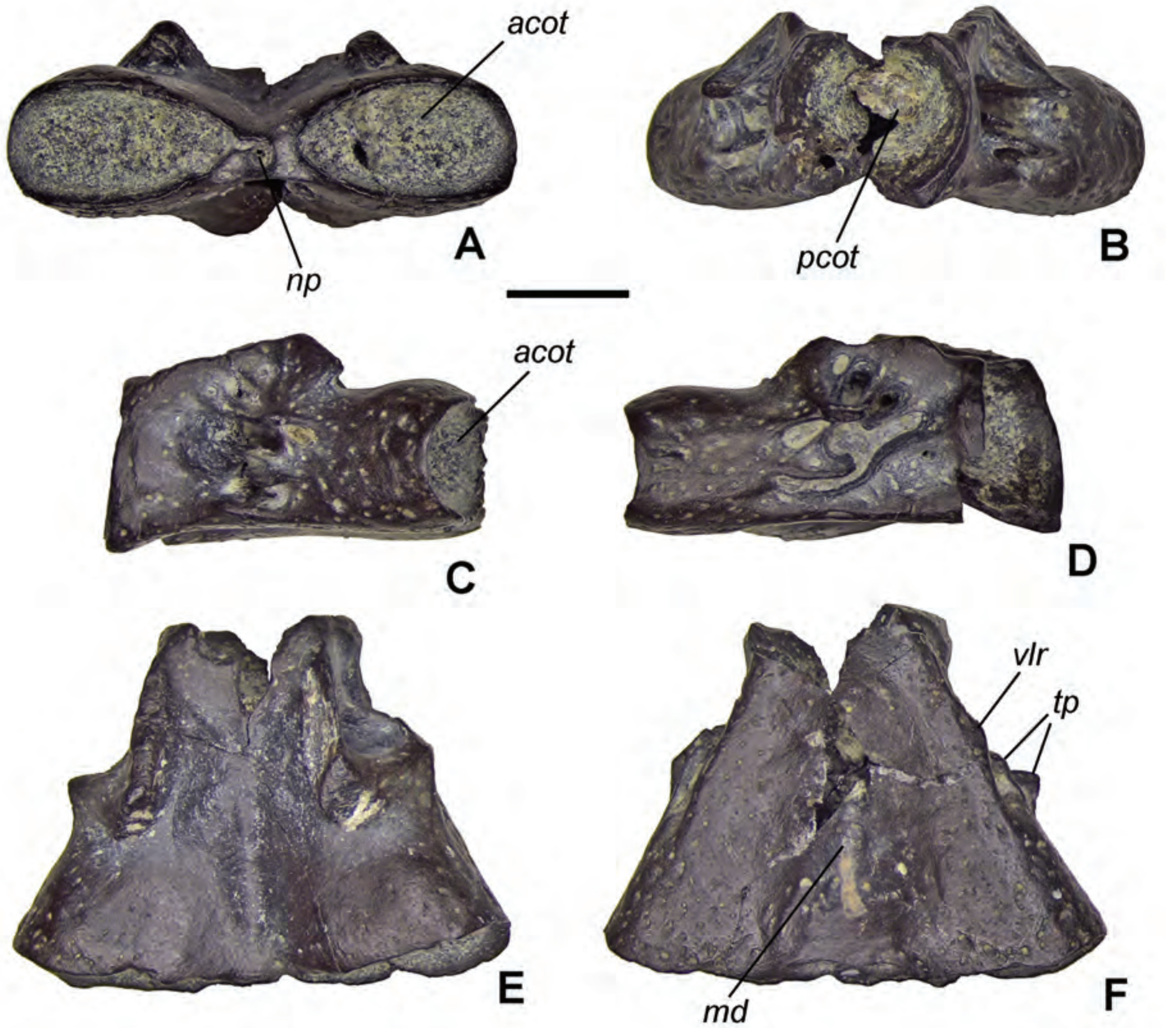

Fig. 2. ZIN PH 1/144, holotype, incomplete atlas of *Urupia monstrosa* gen. et sp. nov. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic), in anterior (A), posterior (B), right (C), left (D), dorsal (E) and ventral (F) views.

Abbreviations: *acot* – anterior cotyle; *md* – medial depression; np – notochordal pit; *pcot* – posterior cotyle; *tp* –transverse proccess; *vlr* – ventrolateral ridge. Scale bar = 2 mm.

respectively, dorsoposteriorly and posteriorly from the upper part of the transverse process. These ridges are distinct on both sides of the atlas and flank a large foramen. Another large foramen is situated just above the upper part of the transverse process and it is flanked posteriorly by the dorsoposterior ridge. Anterodorsal to this large foramen, there is a considerably smaller foramen which is present only on the left side of the atlas. There is a deep lateral depression of a complex shape on the lateral surface of the atlas. The anterodorsal edge of this depression is formed by a vertical ridge between the upper and lower parts of the transverse process, the posterior part of the upper part of the transverse process, the posterior ridge and the lower part of the transverse process. On the left side of the atlas, the posteroventral edge of this depression is flanked by an elongated, "S"-shaped ridge; on the right side this ridge is not developed and the posteroventral edge is smooth. In the posteroventral corner of the lateral surface there is a shallow depression (more pronounced on the left side) into which open several small foramina.

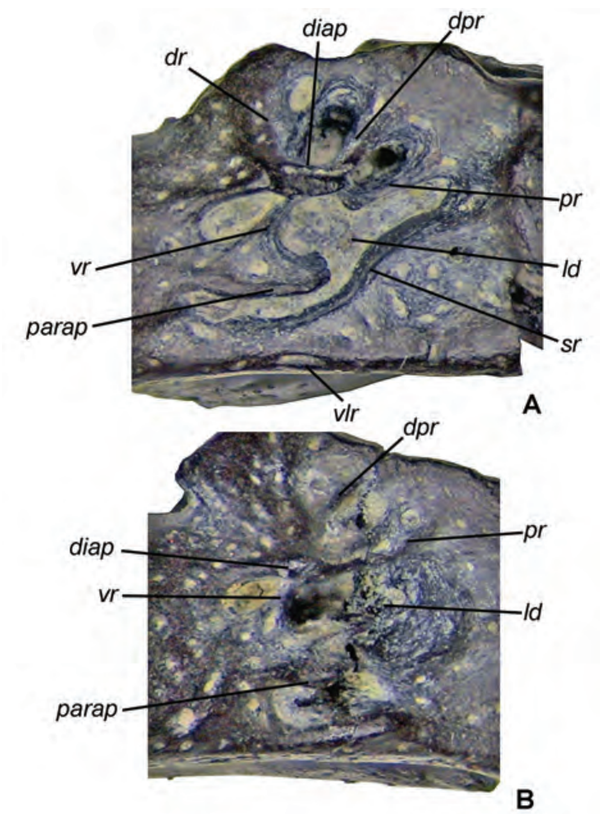

Fig. 3. ZIN PH 1/144, holotype, lateral surfaces of an incomplete atlas of *Urupia monstrosa* gen. et sp. nov. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic), in left (A) and reversed right (B) views.

Abbreviations: *diap* – diapophysis; *dpr* – dorsoposterior ridge; *dr* – dorsal ridge; *ld* – lateral depression; *parap* – parapophysis; *pr* – posterior ridge; *sr* – "S"-shaped ridge; *vlr* – ventrolateral ridge; *vr* – vertical ridge.

Trunk vertebrae. The two referred specimens (ZIN PH 3/144, 4/144) are incomplete centra with the bases of neural arches. The centrum ZIN PH 3/144 (Fig. 4A–C) is large (the ventral midline length is about 7.6 mm) and is sculptured by rounded and oval pits. In lateral view, the centrum is relatively short and deep (ratio of ventral midline length: maximum height is about 1.4). Judging by its deep subcentral keel, the vertebra is probably from the anterior part of the trunk series. The centrum is amphicoelous and both cotyles are deeply concave. The preserved posterior cotyle is nearly circular with a slightly projecting ventral edge (due to the presence of the deep subcentral keel). The notochordal pit opens in the dorsal half of the posterior cotyle. Basapophyses and spinal nerve foramina are absent. The subcentral keel is a deep ridge extending between the ventral rims of the anterior and posterior cotyles. Subcentral foramina are large and nearly equal in size (the right foramen is slightly larger). A small foramen is present anterior to each subcentral foramen. The transverse process (= rib-bearer) is bicipital, short, and extends posterolaterally. The base of the transverse process is perforated by a vertebrarterial canal. The distal end of the transverse process bears a pair of deep indentations that, in life, were presumably finished in cartilage. The anterior alar process is a relatively short low flange that extends anteriorly from the base of the lower part of the transverse process (parapophysis). The posterior alar process is not developed. Three ridges are associated with the upper part of the transverse process (diapophysis): the dorsal alar process and the accessory posterior and anterior ridges. The dorsal alar process is low, swollen, and extends dorsally from the upper part of the transverse process. The accessory anterior ridge is a sharp flange which extends anteriorly from the upper part of the transverse process. The accessory posterior ridge is a short and sharp flange which extends posteriorly from the upper part of the transverse process. The dorsal alar process and accessory anterior ridge flank a deep depression. There are three foramina in a floor of this depression.

The centrum ZIN PH 4/144 (Fig. 4D–F) is smaller than ZIN PH 3/144 (the ventral midline length is about 6.9 mm). It differs from ZIN PH 3/144 in having a shallower subcentral keel and, judging by this feature, the vertebra was probably from a more posterior part of the trunk series. The right subcentral foramen is large and single but on the left side there are three foramina which are different in size. The two largest of these foramina are separated by a short transverse ridge.

Femur. The structure of a nearly complete left femur PM TGU 200/11 was described and figured by Skutschas et al. (2005) and Skutschas (2006). The femur (Fig. 5) is short (the fragment is about 14.2 mm long; the estimated length of the bone is about 15–16 mm) and robust (ratio of length of the estimated length: minimal width of the shaft is about 4.5–5). There is a high, massive trochanteric crest extending distolaterally from a well developed, blunt trochanter. The diaphyseal part is extremely short. The proximal and distal heads are flattened and have deep indentations that, in life, were presumably filled

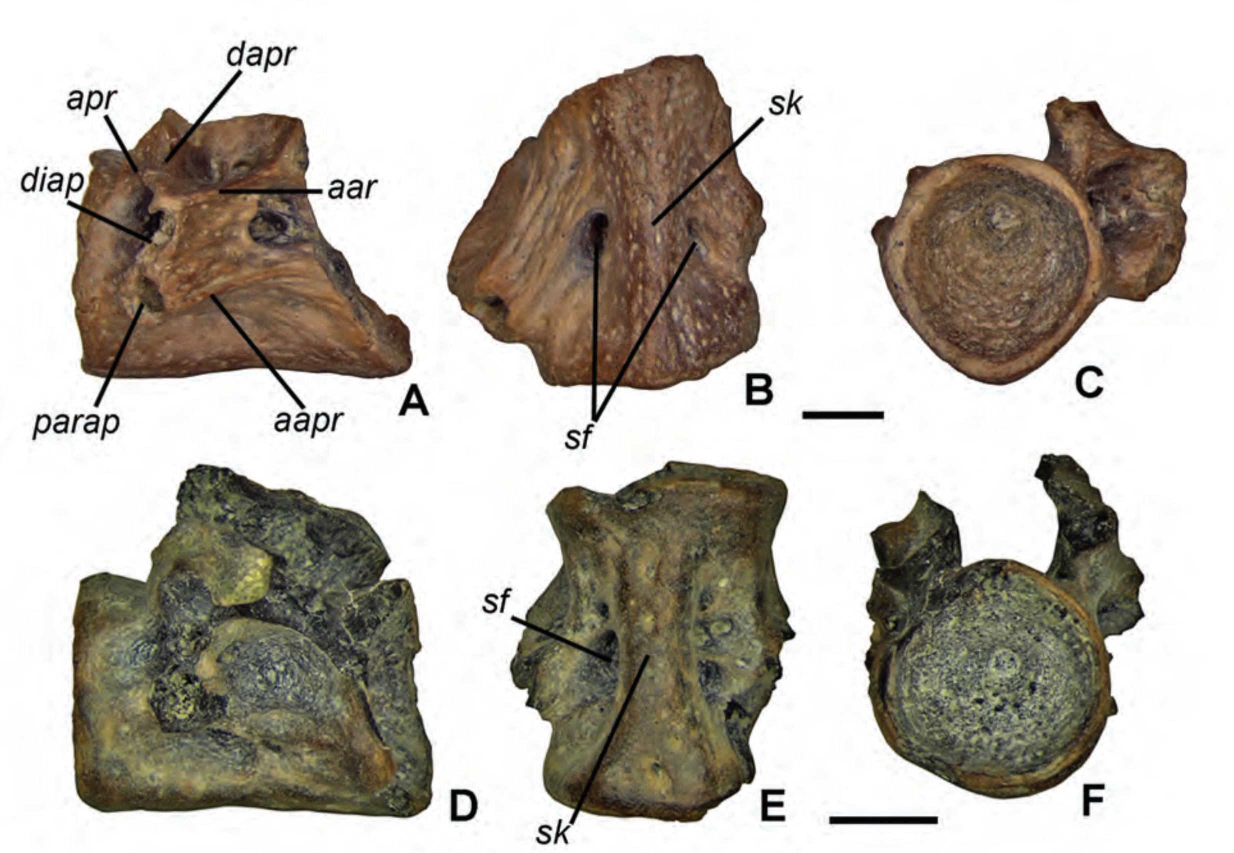

Fig. 4. Fragments of trunk vertebrae of *Urupia monstrosa* gen. et sp. nov. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic): A–C – ZIN PH 3/144, in lateral (A), ventral (B) and posterior (C) views; D–F – ZIN PH 4/144, in lateral (D), ventral (E) and anterior (F) views.

Abbreviations: *aapr* – anterior alar proccess; *aar* – accessorial anterior ridge; *apr* – accessorial posterior ridge; *dapr* – dorsal alar proccess; *diap* – diapophysis; *parap* – parapophysis; *sf* – subcentral foramen; *sk* – subcentral keel. Scale bar = 2 mm.

by cartilage. The plane of the proximal head is twisted about 50 degrees in relation to that of the distal head. In proximal view, 9–10 rings of growth are visible in the indentation of the proximal head.

DISCUSSION

The atlas ZIN PH 1/144 and fragments of trunk vertebrae ZIN PH 3/144, 4/144 are comparable in size and morphology, so all of these newly collected specimens are assigned to *Urupia monstrosa* gen. et sp. nov. We also refer the anterior dentary fragments PM TGU 200/10, ZIN PH 2/144 and femur PM TGU 200/11 to this new taxon because these specimens are in the same size category as vertebrae referred to *Urupia monstrosa* gen. et sp. nov. and differ from those of other undescribed salamander taxa from the Berezovsk Quarry.

Urupia monstrosa gen. et sp. nov. can be placed outside the crown-group (Urodela) on the base of a combination of vertebral characters which is characteristic for stem group salamanders: large size, presence of sculpture composed of numerous pits, and the absence of the spinal nerve foramina in the atlas. The relationships of *Urupia monstrosa* gen. et sp. nov. to other stem group salamanders are uncertain because there is limited information about the anatomy of the new taxon and and of some other basal salamanders (*Marmorerpeton*, Kirlington salamander A and salamander from the Morrison Formation).

If our assignment of the femur PM TGU 200/11 to *Urupia monstrosa* gen. et sp. nov. is correct, then

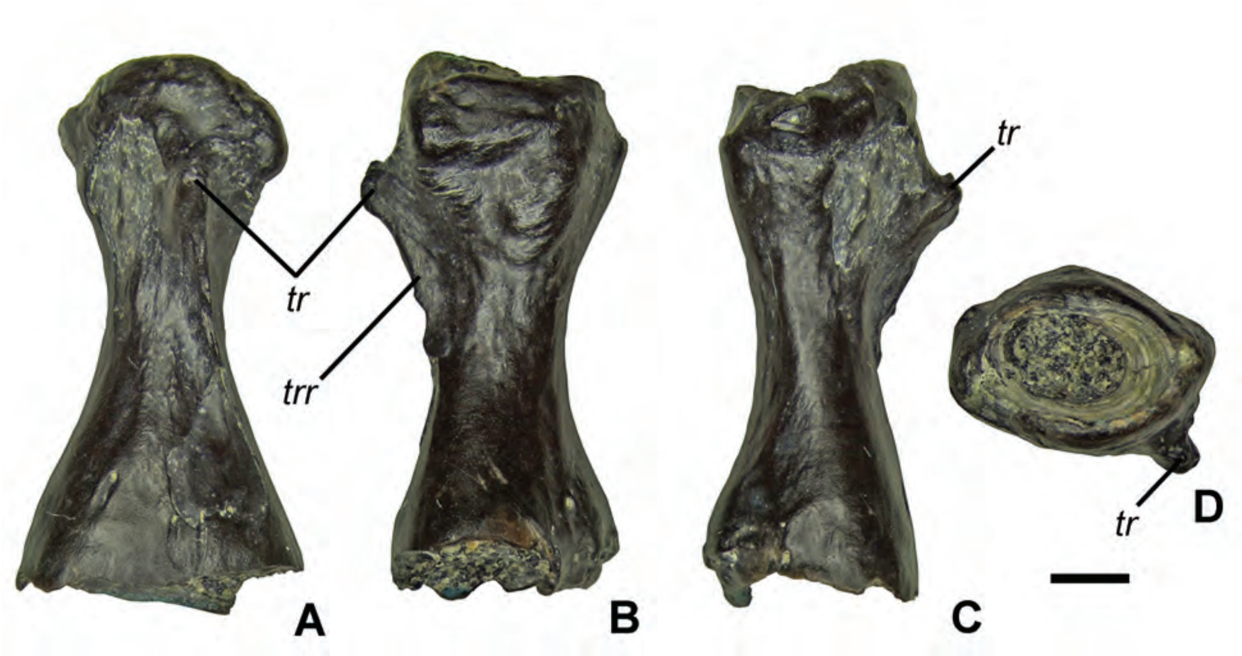

Fig. 5. PM TGU 200/11, left femur of *Urupia monstrosa* gen. et sp. nov. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic), in ventral (A), lateral (B), medial (C) and proximal (D) views.
Abbreviations: *tr* – trochanter; *trr* –trochanteric ridge. Scale bar = 2 mm.

this taxon is apparently unique among salamanders in having a femur with an extremely short diaphyseal part. In all salamanders (except modern sirenids which lack hindlimbs) the femur has an elongated diaphyseal part, even in aquatic obligatory neotenic forms (i.e. cryptobranchids, amphiumids, proteids). The short femur in *Urupia monstrosa* gen. et sp. nov. is probably the result of a general reduction in the hindlimbs of this taxon, but more distal elements need to be discovered to test this suggestion.

The absence of intercotylar tubercle and presence of atlantal transverse processes argue for the neotenic nature of *Urupia monstrosa* gen. et sp. nov. According to their morphology, all other described stem salamanders (*Marmorerpeton*; *Karaurus*, *Kokartus*), were also neotenic forms and neoteny was a common life strategy for basal salamanders (Skutschas and Martin 2011). The large size of these stem salamanders (compared with Jurassic and Early Cretaceous salamanders) is also probably correlated with obligatory neoteny, as in extant salamanders (Wiens and Hoverman 2008).

Bathonian salamander records in the Great Britain (Forest Marble and Kilmaluag formations), Kyrgyzstan (Balabansai Formation) and Siberia (Berezovsk Quarry locality, Itat Formation) are the oldest indisputable occurrences for Caudata. The presence of diverse salamander taxa in the geographically distant Berezovsk Quarry and the Forest Marble vertebrate assemblages indicates that early episodes of primary diversification of Caudata took place well before the Bathonian.

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