

A new relict stem salamander from the Early Cretaceous of Yakutia, Siberian Russia

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A new stem salamander, *Kulgeriherpeton ultimum* gen. et sp. nov., is described based on a nearly complete atlas from the Lower Cretaceous (Berriasian–Barremian) Teete vertebrate locality in southwestern Yakutia (Eastern Siberia, Russia). The new taxon is diagnosed by the following unique combination of atlantal characters: the presence of a transversal ridge and a depression on the ventral surface of the posterior portion of the centrum; ossified portions of the intercotylar tubercle represented by dorsal and ventral lips; the absence of a deep depression on the ventral surface of the anterior portion of the centrum; the absence of pronounced ventrolateral ridges; the absence of spinal nerve foramina; the presence of a pitted texture on the ventral and lateral surfaces of the centrum and lateral surfaces neural arch pedicels; the presence of a short neural arch with its anterior border situated far behind the level of the anterior cotyles; moderately dorsoventrally compressed anterior cotyles; and the absence of a deep incisure on the distal-most end of the neural spine. The internal microanatomical organization of the atlas is characterized by the presence of a thick, moderately vascularized cortex and inner cancellous endochondral bone. The recognition of stem salamanders and other vertebrates with Jurassic affinities in the Early Cretaceous high-latitude (paleolatitude estimate N 63–70°) vertebrate assemblage of Teete suggests that: (i) the large territory of present day Siberia was a refugium for Jurassic relicts; (ii) there were no striking differences in the composition of high-latitude Yakutian and mid-latitude Western Siberian Early Cretaceous vertebrate assemblages; and (iii) there was a smooth transition from the Jurassic to Cretaceous biotas in North Asia.

Key words: Amphibia, Caudata, stem salamanders, Cretaceous, Russia, Siberia.

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Introduction

Stem salamanders are critical for documenting primitive character states and patterns of character state transformations within Caudata. The geologically oldest stem salamanders include the following taxa: *Kokartus* Nesov, 1988 from the Middle Jurassic (Bathonian) of Kyrgyzstan; *Marmorherpeton* Evans, Milner, and Mussett, 1988 (two spe-

cies *M. kermacki* and *M. freemani*) and “Kirtlington salamander A” (sensu Evans and Milner 1994), all from the Middle Jurassic (Bathonian) of Great Britain; and *Urupia* Skutschas and Krasnolutskaa, 2011 and “Berezovsk salamander A” (sensu Skutschas 2013), both from the Middle Jurassic (Bathonian) of Russia (Evans et al. 1988; Nesov 1988; Evans and Milner 1994; Evans and Waldman 1996; Milner 2000; Skutschas and Krasnolutskaa 2011; Skutschas and Martin



Fig. 1. A, B. Maps showing the geographic location of the Lower Cretaceous Teete locality (asterisk) in Eastern Siberia, Russia.

2011; Skutschas 2013, 2016a). The next younger stem salamanders date from the Late Jurassic. These include two Kimmeridgian occurrences, namely *Karaurus* Ivachnenko, 1978 from the Karabastau Formation in Kazakhstan and “cf. *Marmorherpeton*” (sensu Wiechmann 2000) from Portugal (Ivachnenko 1978; Milner 2000; Wiechmann 2000), plus a possible stem salamander from the Kimmeridgian–early Tithonian (Morrison Formation) of the USA (Nesov 1992; Evans and Milner 1993; Gardner and DeMar 2013). Outside China, all Bathonian vertebrate assemblages containing salamanders are dominated by stem salamanders but later, at the end of the Middle Jurassic and into the Late Jurassic, crown group salamanders became the dominant salamander component in vertebrate assemblages everywhere. Except for a possible stem salamander in the Early Cretaceous of North America (Gardner and DeMar 2013), there had been no unequivocal evidence of stem salamanders in post Jurassic deposits, and it was suggested that they became extinct before the Jurassic–Cretaceous boundary (Skutschas 2013). In 2016, a fragmentary trunk vertebra of a stem salamander from Lower Cretaceous (Aptian–Albian) deposits at Shestakovo in Western Siberia was described (Skutschas 2016b). That discovery was the first conclusive evidence that the stem salamanders survived beyond the Jurassic–Cretaceous boundary and co-existed with crown group salamanders during approximately the first 40 million years of the known history of salamanders.

In 2017 PS, RS, and DV conducted field work at the Lower Cretaceous Teete locality in southwestern Yakutia (Eastern Siberia, Russia; Fig. 1). That locality was formed close to Mesozoic polar latitudes (paleolatitude estimate 63–70° N) and has become known for its polar dinosaurs (Rich et al. 1997, 2002). On-site excavation and screen-washing of 500 kg of fossiliferous matrix produced numerous vertebrate microfossils, including remains of fishes, salamanders, turtles, choristoderes, lizards, dinosaurs, tritylodontids, and mammals. Among the vertebrate remains collected in 2017 at Teete, one atlas (ZIN PH 3/246) erected as the holotype of the new stem salamander taxon described herein. This is additional evidence for a survival of stem salamanders

beyond the Jurassic–Cretaceous boundary and the presence of a vast Early Cretaceous Siberian refugium for Jurassic relicts among vertebrates.

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

Material and methods

The atlas ZIN PH 3/246 (holotype of *Kulgeriherpeton ultimum* gen. et sp. nov.) is fragile and is partly embedded in matrix (Fig. 2), therefore some details of its structure are not visible. To overcome this problem and to gain additional morphological information, ZIN PH 3/246 was CT scanned (at 100kV and 0.1 mA, generating a resolution of 4.4 μ m of pixel size and an output of 4000 \times 4000 pixels per slice) at the Saint Petersburg State University Research Centre for X-ray Diffraction Studies (Saint Petersburg, Russia) using a Skyscan 1172. Segmentation of the CT scan data and 3D model reconstructions were made with Amira 6.3.0 (FEI-VSG Company).

ZIN PH 3/246 is stored at the Paleoherpological collection (ZIN PH) of the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

The CT data are deposited in the Department of Vertebrate Zoology of the Saint Petersburg State University, Saint Petersburg, Russia and can be made available by the corresponding author for the purpose of scientific study.

Systematic palaeontology

Amphibia Linnaeus, 1758

Caudata Scopoli, 1777

Genus *Kulgeriherpeton* nov.

Type species: *Kulgeriherpeton ultimum* sp. nov., monotypic; see below.

Etymology: From Yakutian *kulgeri*, lizard, salamander; and Greek *ἑρπετόν* [*herpeton*], a creeping animal.

Kulgeriherpeton ultimum sp. nov.

Figs. 2–4, 5A.

Etymology: From Latin *ultimus*, last; in reference to the relict nature of this stem salamander.

Holotype: ZIN PH 3/246, nearly complete atlas partially embedded in matrix.

Type locality: Teete, Suntar Ulus, Yakutia, Eastern Siberia, Russia.

Type horizon: Batylykh Formation, Sangar Series, Berriasian–Barremian, Lower Cretaceous, for geological settings see Kolosov et al. (2009); Averianov et al. (2018).

Diagnosis.—Placed outside the crown group (Urodela) and referred to stem group salamanders based on the absence of spinal nerve foramina in the atlas, the presence of a pitted texture on the ventral and lateral surfaces of the atlas, the

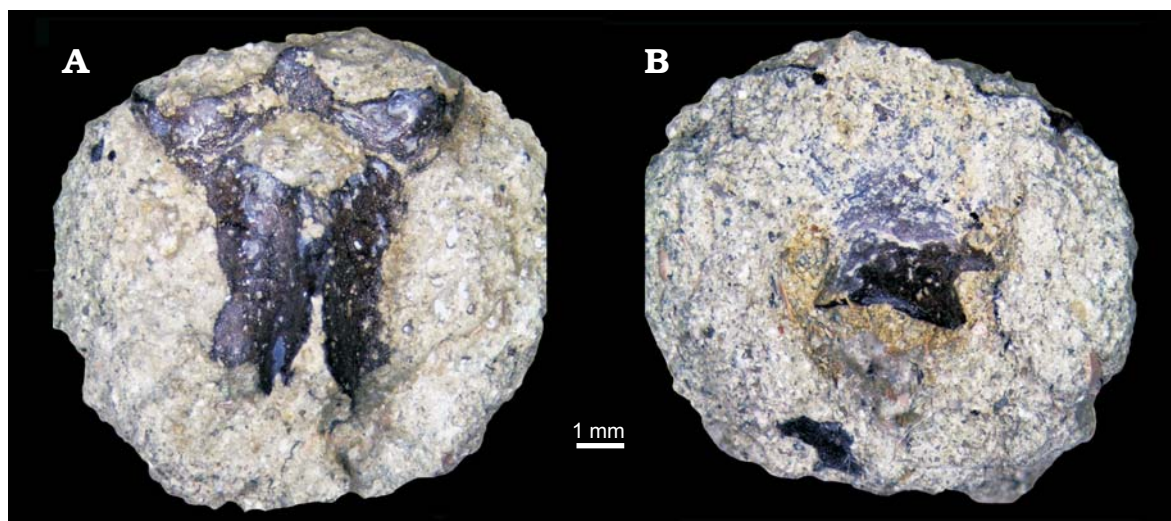


Fig. 2. Stem salamander *Kulgeriherpeton ultimum* gen. et sp. nov. from Teete locality, Yakutia, Eastern Siberia, Russia; Sangar Series, Batylykh Formation, Berriasian–Barremian, Lower Cretaceous. Atlas ZIN PH 3/246 (holotype) in dorsal (A) and ventral (B) views, with anterior end to top of figure.

presence of an anteroposteriorly short neural arch with an anterior border that is situated far from level of anterior cotyles, and its relatively large size (the maximum anterior width is about 8.8 mm and the ventral midline length, excluding the intercotylar tubercle is about 6.4 mm). Differs from all other stem salamanders for which the morphology of the atlantal centrum is known (namely *Kokartus* from the Middle Jurassic (Bathonian) of Kyrgyzstan, *Marmorherpeton* from the Middle Jurassic (Bathonian) of Great Britain, and *Urupia* and “Berezovsk salamander A” from the Middle Jurassic (Bathonian) of Russia) in the presence of a transversal ridge and a depression on the ventral surface of the posterior portion of the centrum. Differs further from *Marmorherpeton*, *Urupia*, and “Berezovsk salamander A” by presence of an intercotylar tubercle on the atlas with ossified dorsal and ventral lips (vs. absence of the intercotylar tubercle and presence of only the notochondral central pit in *Urupia*, “Berezovsk salamander A” and *M. freemani*; and no division of the intercotylar tubercle into dorsal and ventral lips in *M. kermacki*). Additionally, *Kulgeriherpeton* differs from *Urupia* by the lack of a deep depression on the ventral surface of the anterior portion of the atlantal centrum, by the lack of pronounced ventro-lateral ridges on the atlas, and by less dorso-ventrally compressed atlantal anterior cotyles (ratio of maximum height/width about 0.79 vs. about 0.5 in *Urupia*); additionally differs from “Berezovsk salamander A” in the atlantal centrum being relatively longer (ratio of maximum anterior width, i.e., between lateral rims of the anterior cotyles), midline length (excluding intercotylar tubercle) is about 1.37 vs. about 1.75 in “Berezovsk salamander A”; and additionally differs from *Karaurus* in the absence of a deep incisure on the distal-most end of the atlantal neural spine.

Description.—The atlantal centrum (Figs. 2A, 3) is slightly wider than long: the maximum anterior width (i.e., between the lateral rims of the anterior cotyles) is about 8.8 mm and the ventral midline length, excluding the intercotylar tubercle

(= odontoid process), is about 6.4 mm (ratio of maximum anterior width/ventral midline length without intercotylar tubercle about 1.38). The anterior cotyles (Fig. 3K) are large and slightly dorso-ventrally compressed (ratio of maximum height/width about 0.8). The articular surfaces of the anterior cotyles are moderately concave. The intercotylar tubercle is not fully ossified and is represented by dorsal and ventral lips that are separated by a narrow strip of the articular surface extending between the anterior cotyles. The posterior cotyle is nearly circular in posterior outline (Fig. 3G). The inner surface of the posterior cotyle is deeply concave (Fig. 3G, J, L).

The ventral surface of the centrum has a shallow median depression (Fig. 3H). The surface of the median depression is perforated by three relatively large subcentral foramina. Antero-lateral to the medial depression, there is a pair of narrow oblique grooves. Ventro-lateral ridges are absent. A distinct transverse ridge and a relatively deep transverse depression, the latter being situated just behind the transverse ridge, extend across the ventral surface of the posterior portion of the centrum.

The lateral surfaces of the centrum (Fig. 3A–D, F, I, J, L) have distinct unipartite transverse processes (the left transverse process is more prominent). The transverse processes are short and do not project far from the lateral wall of the centrum. There are relatively deep lateral depressions on the lateral surfaces of the centrum. There are three ridges on the lateral surface of the centrum; two are short (anterior and posterior alar processes) and are associated with the transverse process and one longitudinal lateral ridge flanks the dorsal border of the lateral depression. Like the transverse processes, the three ridges are more distinct and prominent on the left side. Hypapophyses and basapophyses are absent.

The neural arch is high and antero-posteriorly short, with its anterior border situated far (about one third of the length of the centrum) behind the level of the anterior cot-

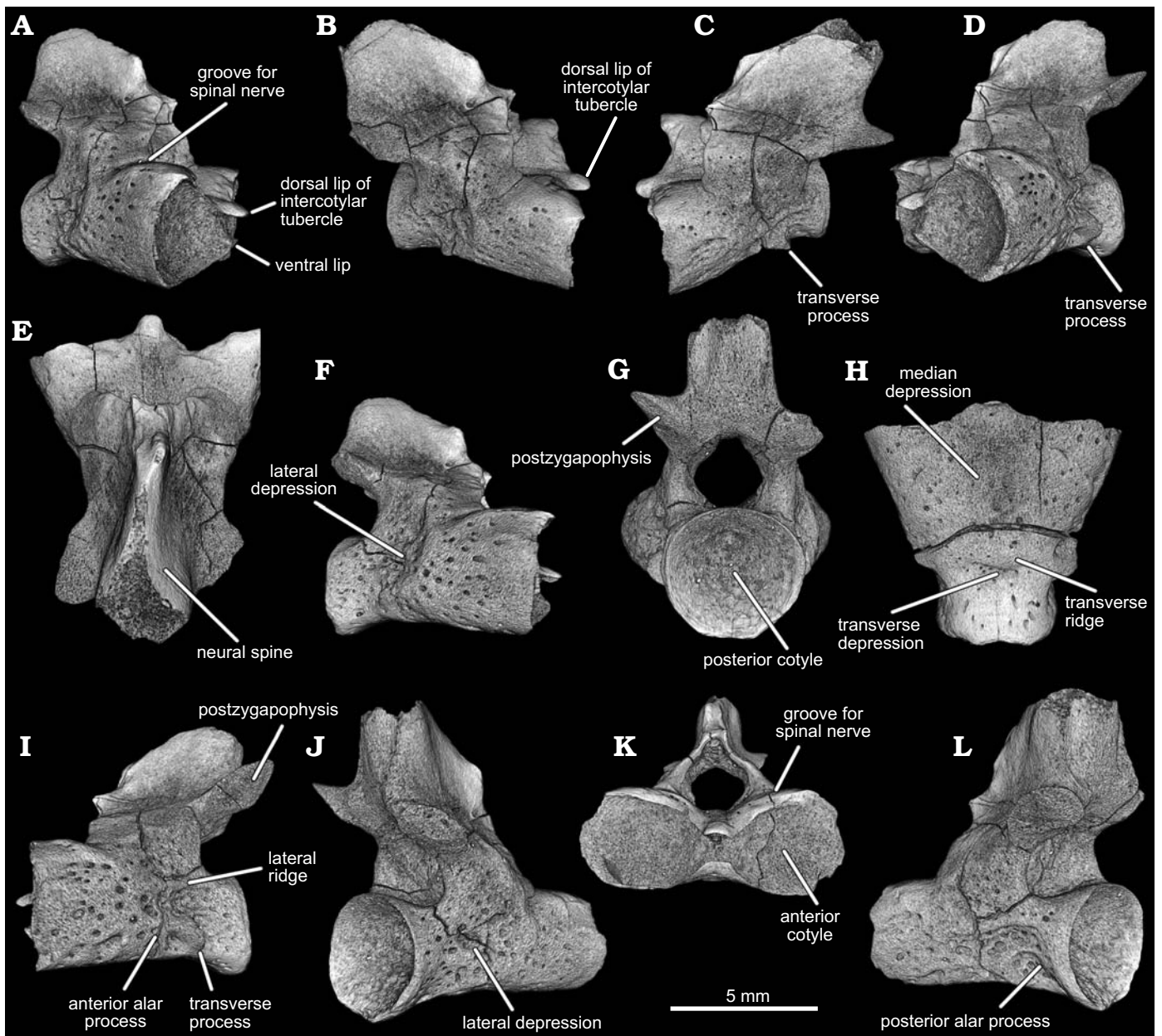


Fig. 3. Stem salamander *Kulgeriherpeton ultimum* gen. et sp. nov. from Teete locality, Yakutia, Eastern Siberia, Russia; Sangar Series, Batylykh Formation, Berriasian–Barremian, Lower Cretaceous. Digital restoration of atlas ZIN PH 3/246 (holotype) in right antero-lateral (A), right dorso-lateral (B), left dorso-lateral (C), left antero-lateral (D), dorsal (E), right lateral (F) posterior (G), ventral (H), left lateral (I), right postero-lateral (J), anterior (K), and left postero-lateral (L) views.

yles (Fig. 3E, F, L). The pedicels of the neural arch are massive. The spinal nerve foramen is absent, but there is a groove for passage of the first spinal nerve on the anterior edge and the antero-lateral part of the pedicel of the neural arch (Fig. 3A, K). The neural canal is broad and low in anterior and posterior view (Fig. 3G, K). The neural arch roof is posteriorly short and extends back only to about the level of the rim of the posterior cotyle (Fig. 3F, L).

The dorso-median surface of the neural arch roof bears a high, posteriorly massive neural spine. The postero-dorsal end of the neural spine terminates in a deeply concave scar indicating that in life the distal-most end of the spine was

cartilaginous. The posterior surface of the neural spine has a pair of dorso-ventrally elongated lateral depressions. The postzygapophyseal processes project postero-laterally (approximately 45° from the midline). The postzygapophyseal facets are relatively wide, oval in outline and face ventrally and slightly laterally (Fig. 3G, L).

The ventral and lateral surfaces of the centrum and the lateral surfaces of the neural arch pedicels are rugose and indented by scattered, small, rounded and oval pits.

The internal microanatomical organization of the centrum is characterized by the presence of a thick compact periosteal cortex and an inner cancellous endochondral bone

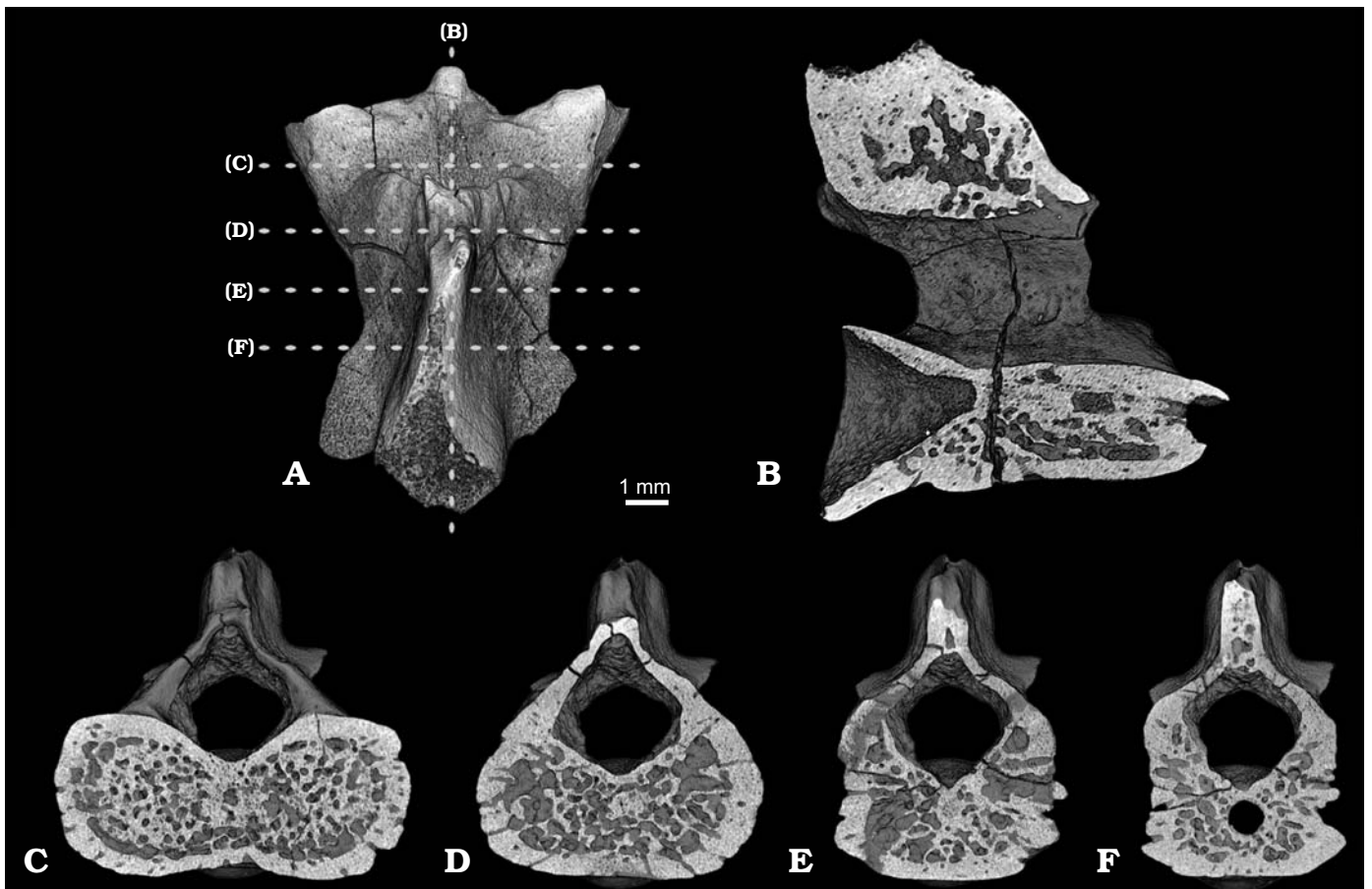


Fig. 4. Stem salamander *Kulgeriherpeton ultimum* gen. et sp. nov. from Teete locality, Yakutia, Eastern Siberia, Russia; Sangar Series, Batylykh Formation, Berriasian–Barremian, Lower Cretaceous. Digital restoration of atlas ZIN PH 3/246 (holotype), detailed anatomy with the locations of the microCT digital sections, dorsal view (A); longitudinal section, vertical plane (B); transverse sections (C–F).

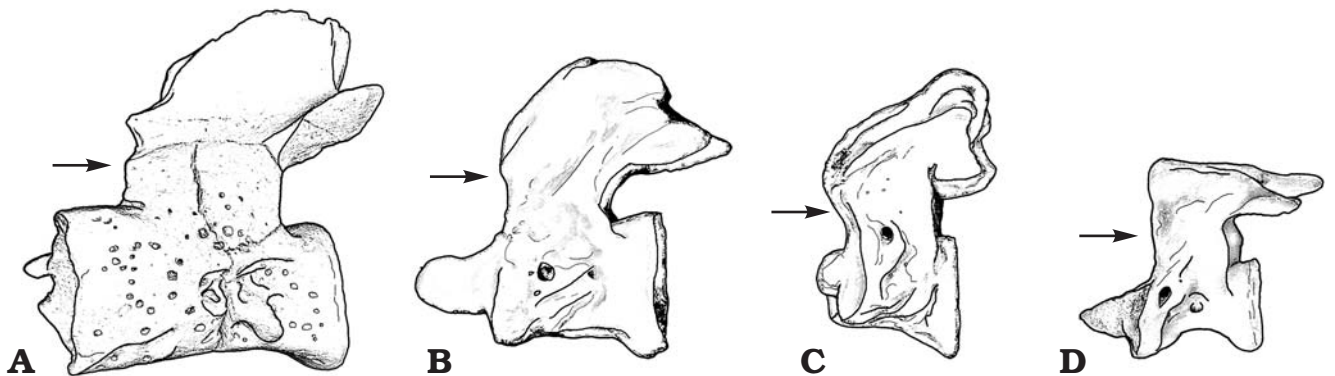


Fig. 5. Drawings of atlas of stem (A) and extant crown (B–D) salamanders in lateral views. A. *Kulgeriherpeton ultimum* gen. et sp. nov. B. *Cryptobranchus*. C. *Amphiuma*. D. *Hynobius*. Note the antero-posteriorly short neural arch with its anterior border situated far behind the level of the anterior cotyles in stem salamanders (A) and long neural arch with its anterior border is situated at the level of the anterior cotyles in crown salamanders (B–D). Arrows show the anterior border of the neural arch. Not to scale.

with numerous erosion bays that are separated by irregularly arranged trabeculae of varying thickness (Fig. 4). The periosteal cortex is moderately vascularized by a network of short vertical and subvertical vascular canals. These vascular canals access the external surface of the bone where they are visible as rounded and oval pits forming a characteristic pitted texture. Internally, the vascular canals of the cortex are connected with erosion bays of the inner cancellous en-

dochondral bone. A narrow notochordal canal is present and centrally located. The notochordal canal is partly infilled by a bone. The neural arch has a microanatomical organization similar to that of the centrum, but differs in a lower degree of vascularization of the cortex.

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion and conclusions

Kulgeriherpeton ultimum gen. et sp. nov. is placed outside the crown group (Urodela) based on a combination of at-lantal features that is primitive for crown salamanders and characteristic for stem group salamanders: the absence of spinal nerve foramina in the atlas (vs. spinal nerve foramen fully enclosed by bone in crown salamanders); the presence of pitted ventral and lateral surfaces of the atlas (vs. smooth external vertebral surface in most crown salamanders); and its relatively large size (vs. relatively smaller size in the most of early diverging crown group members (see e.g., Skutschas 2016b). Additionally, *Kulgeriherpeton ultimum* gen. et sp. nov., like all other stem salamanders, is characterized by an antero-posteriorly short neural arch with its anterior border situated far behind the level of the anterior cotyles (vs. long neural arch with its anterior border situated at the level of the anterior cotyles in crown salamanders) (Jim Gardner, personal communication 2016; Fig. 5). *Kulgeriherpeton ultimum* gen. et sp. nov. shares several at-lantal features with the karaurid stem salamander *Kokartus* from the Middle Jurassic (Bathonian) of Kyrgyzstan (the atlas is partly visible in the articulated holotype skeleton of the karaurid *Karaurus*) namely: similar proportions of the anterior cotyles; an intercotylar tubercle that is represented by dorsal and ventral lips; the absence of distinct ventro-lateral ridges; and the presence of transverse processes). Those similarities indicate a possible karaurid affinity for the new stem salamander from Teete.

According to previously known and recently collected material, the high latitude vertebrate assemblage of Teete includes paleonisciform and amiid fishes, two salamander taxa (*Kulgeriherpeton ultimum* gen. et sp. nov. and a small undescribed crown salamander), paramacellodid lizards, primitive (= non-neochoristoderan) choristoderes, turtles, various dinosaurs (stegosaurs, ornithopods, theropods, and sauropods), the tritylodontid synapsid *Stereognathus kolossovi* and three mammaliaform taxa (haramiyid cf. *Sineleutherus* sp., a new genus of tegotheriid docodont and a new genus of eutriconodont) (Kurzanov et al. 2000, 2003; Lopatin and Agadjanian 2008; Kolosov et al. 2009; Averianov et al. 2018). In spite of the Early Cretaceous age of the fossiliferous sediments at Teete (Kolosov et al. 2009), the mammaliaform, tritylodontid, salamander and dinosaur components of the Teete vertebrate assemblage have a distinctive Jurassic appearance, being similar to Middle–Late Jurassic vertebrate assemblages known from Western Siberia (Russia), Xinjiang (China), and Great Britain (Evans and Milner 1994; Evans and Waldman 1996; Maisch et al. 2001, 2003; Martin et al. 2010; Skutschas 2013; Averianov et al. 2016, 2018; Skutschas et al. 2016a).

On the other hand, the Teete vertebrate assemblage shares many components (namely stem salamanders, primitive choristoderes, paramacellodid lizards, stegosaurs, tritylodonts and eutriconodont and docodont mammaliaforms) with the Early Cretaceous vertebrate assemblage of the

Shestakovo locality (Ilek Formation) in Western Siberia (Russia) (Averianov et al. 2006; Skutschas 2016b). As suggested earlier, Western Siberia possibly was a refugium where vertebrates with Jurassic affinities (including relict salamanders) survived (Leshchinskiy et al. 2001; Skutschas 2016b). The similarity of the high-latitude vertebrate assemblage of Teete and the mid-latitude vertebrate assemblage of Shestakovo suggests that the territory of a refugium for Jurassic vertebrate relicts was not restricted to modern day Western Siberia in the Early Cretaceous, but spread farther into the northeastern part of the Asiatic continent. It also indicates the lack of striking faunistic differences between high-latitude (Teete) and some mid-latitude (Shestakovo) Early Cretaceous vertebrate assemblages of Siberia. Finally, the presence of vertebrates with Jurassic affinities (including stem salamanders) in the Early Cretaceous of Siberia supports the hypothesis (Averianov et al. 2018) that the transition from the Jurassic to Cretaceous biotas in North Asia, in contrast to the environmental perturbations that occurred in other regions at the Jurassic/Cretaceous boundary (Tennant et al. 2017), was smooth.

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