The last of them? A new relic karaurid stem salamander from the Lower Cretaceous of Western Siberia, Russia

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Abstract

A new karaurid stem salamander, *Kuzbassia sola* gen. et sp. nov., from the Lower Cretaceous (Aptian) Ilek Formation of Shestakovo 1 locality in Western Siberia, Russia, is described on the basis of isolated vertebrae, including incomplete atlantal and trunk vertebral centra. The new taxon is diagnosed by the following unique combination of vertebral characters: the presence of a shallow dorsolateral depression and low ridges (longitudinal, vertical and oblique ridges) flanking this depression on the lateral surface of the atlantal centrum; the absence of deep lateral grooves or depressions on the lateral surfaces and ventral depression on the ventral surface of the atlantal centrum; the absence of ventro-lateral ridges, transverse processes and alar processes associated with the transverse processes on the atlantal centrum; anterior cotyles with elliptical anterior outline, located at an angle of approximately 150–160 degrees to each other; and the presence of a pair of rugose surfaces with low tubercles (= ?anterior basapophyses) on the ventral surface of the anterior portion of the trunk vertebral centrum. *Kuzbassia sola* gen. et sp. nov. is the last karaurid salamander in the fossil record to date.

Keywords: Caudata, stem salamanders, Karauridae, Early Cretaceous, Western Siberia, Russia, Shestakovo 1 locality

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Introduction

The Lower Cretaceous (Aptian) temperate-latitude Shestakovo vertebrate assemblage (paleolatitude estimate N 49°–52° in paleolatitude.org; http://paleolatitude.org/; van Hinsbergen et al., 2015) derives from several localities of the Ilek Formation in Western Siberia, Kemerovo-Kuzbass oblast, Russia. Among vertebrate localities of the Ilek Formation, the Shestakovo 3 locality in Kemerovo Province is famous due to the discovery of articulated skeletons of the basal ceratopsian *Psittacosaurus sibiricus* (Averianov, Voronkevich, Leshchinskiy, and Fayngertz, 2006; Lopatin et al., 2015), whereas the Shestakovo 1 locality is known for numerous microvertebrates including salamanders (Skutschas, 2013, 2014).

The Shestakovo assemblage is similar in composition to that of the Lower Cretaceous high-latitude Teete locality (paleolatitude estimate of N 62° in Averianov et al., 2019b; N 66.5° in Fossilworks, http://fossilworks.org; N 63°–65° in paleolatitude.org, http://paleolatitude.org/, van Hinsbergen et al., 2015) of the Batylykh Formation in southwestern Yakutia (Eastern Siberia, Russia) (Averianov et al., 2018, 2019a; Skutschas et al., 2018, 2021). Both the Teete and Shestakovo assemblages include taxa with Jurassic affinities (namely stem karaurid salamanders, primitive choristoderes, paramacellodid lizards, stegosaurs, tritylodont mammaliamorphs, and docodont mammaliaforms) that survived as relics into the Early Cretaceous of present-day Siberia (e. g., Averianov et al., 2018; Skutschas et al., 2018). The similarity of the high-latitude assemblage of Teete and the mid-latitude vertebrate assemblage of Shestakovo suggests that the territory of a geographically vast "Great Siberian refugium" (sensu Skutschas et al., 2021) for Jurassic vertebrate relicts covered the northeastern part of the Asiatic continent during the Early Cretaceous (Averianov et al., 2018; Skutschas et al., 2018).

The Shestakovo 1 locality has produced remains of two salamander taxa. In 2002, A. O. Averianov and A. V. Voronkevich described a possible crown-group salamander *Kiyatriton leshchinskiyi* based on a fragmentary atlas and femoral fragments (Averianov, Voronkevich, 2002). Later, P. P. Skutschas provided a detailed redescription of type and newly collected material on *Kiyatriton leshchinskiyi*, consisting of isolated and incomplete cranial and postcranial bones and suggested that *Kiyatriton leshchinskiyi* is a crown group salamander with possible cryptobranchoid affinities (Skutschas, 2014). The finding of the second species of *Kiyatriton* (*K. krasnolutskii*) in the Middle Jurassic (Bathonian) Itat Formation of the Berezovsk Quarry locality in Western Siberia, Russia extended the stratigraphic range of the genus *Kiyatriton* backward some 40 million years and indicated that *K. leshchinskiyi* from the Shestakovo 1 locality survived as a relic into the Early Cretaceous of present-day Western Siberia (Skutschas, 2016a). In 2016, an incomplete trunk vertebra of a relic stem salamander from the Shestakovo 1 locality was described (Skutschas, 2016b). Later, the two additional specimens (incomplete atlantal centra) of a stem salamander from the Shestakovo 1 locality were recognized among microvertebrate remains collected by several expeditions with participants from Tomsk and Saint Petersburg state universities and from Paleontological and Zoological institutes of the Russian Academy of Sciences at Shestakovo localities. Here we formally describe the stem karaurid salamander taxon from the Shestakovo 1 locality and discuss some aspects of the evolution of karaurid salamanders. This new taxon is the most recent karaurid salamander in the fossil record known to date.

Institutional abbreviations. The material used in this study is deposited in following institutional collections: ZIN PH, Paleoherpetological collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; LMCCE, Laboratory of Mesozoic and Cenozoic Continental Ecosystems, Tomsk State University, Western Siberia, Tomsk, Russia.

Material and methods

The fossil material derives from the Shestakovo 1 locality which is situated in Western Siberia, near Shestakovo village in Chebula district of Kemerovo–Kuzbass oblast, Russia (GPS coordinates: N 55°54.60′, E 87°56.90′; Fig. 1). The fossiliferous level is confined to the upper part of the Ilek Formation with a currently estimated Early Cretaceous age (Aptian) based on spore-pollen spectra, see Bugdaeva, Markevich, and Volynets (2017); the geologi-

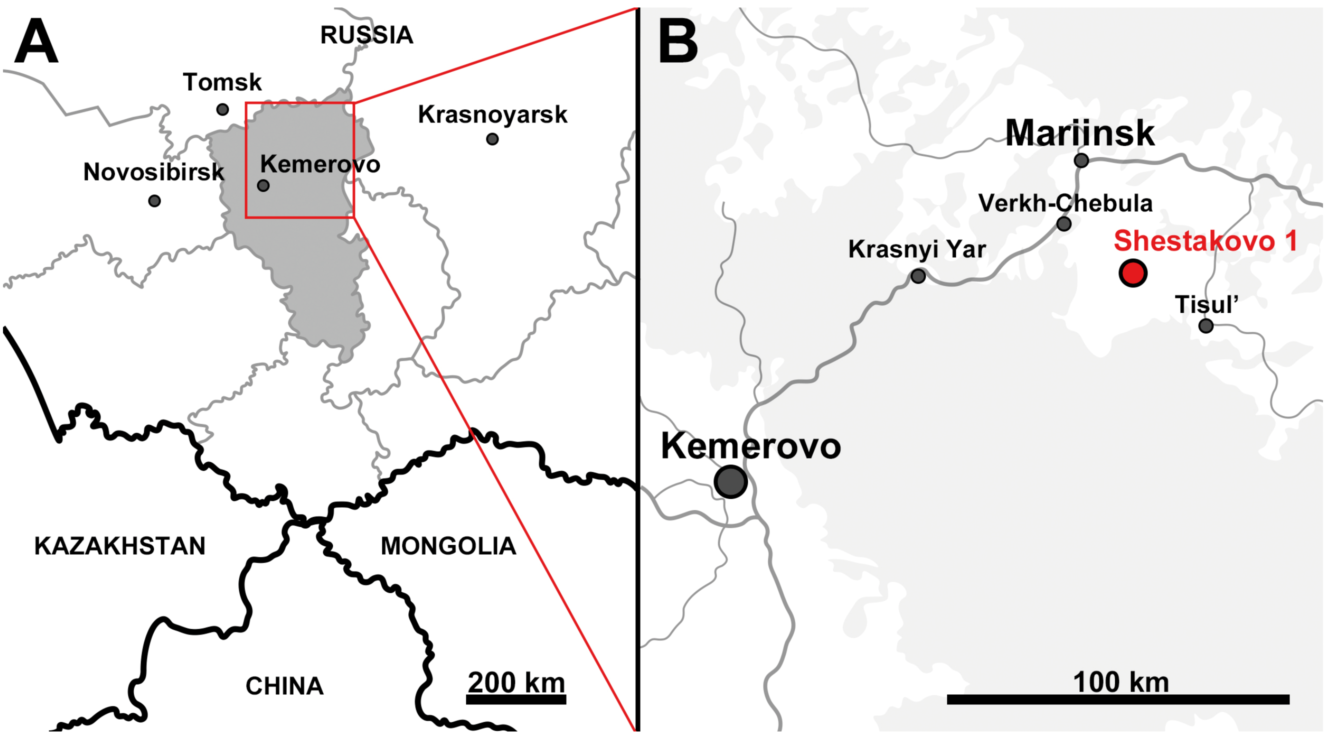

Fig. 1. Geographic setting of Shestakovo 1 locality.

cal settings of the Shestakovo localities and discussion of their age are given in Averianov et al. (this issue).

The study material comprises two incomplete atlantal centra (ZIN PH 18–19/173). To prepare accurate figures and to gain microanatomical information, all atlantal specimens of *Kuzbassia sola* gen. et sp. nov. were X-ray microCT scanned at the Saint Petersburg State University Research Centre for X-ray Diffraction Studies (Saint Petersburg, Russia) using a microtomography scanner Skyscan 1172. Settings comprised: voltage = 71 kV; current = 0.13mA; pixel size = 2.7 µm; and output = 1500 × 1500 pixels per slice.

The atlases of *Egoria, Kokartus* and *Kulgeriherpeton* (used for comparisons) were CT-scanned (at 70 kV and 139 µA, generating a nominal resolution of 2.97 µm, with cubic voxels and an output of 2472 × 2472 pixels per slice for *Egoria* and *Kokartus* and at 100 kV and 100µA, generating a nominal resolution of 4.48 µm, with cubic voxels and an output of 4000 × 4000 pixels per slice for *Kulgeriherpeton*) 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 (FEIVSG Company). The CT scans of incomplete atlantal centra of *Kuzbassia sola* gen. et sp. nov. were used to create surface models of these centra. The surface models were imported in Blender 3.6.4, where they were duplicated, mirrored and adjoined to each other based on the structure of preserved parts, to create the reconstruction of the centrum shown in this paper.

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 paleontology

Amphibia Linnaeus, 1758
Caudata Scopoli, 1777
Karauridae Ivakhnenko, 1978
Genus *Kuzbassia* nov.
Type species: *Kuzbassia sola* sp. nov., monotypic; see below.
Etymology: From Kemerovo–Kuzbass oblast, Russia.
Kuzbassia sola sp. nov.
Figs. 2, 3, 4A–E.
Etymology: From Latin *solum*, single, lonely; in reference that it is the last karaurid salamander in the fossil record to date.
Holotype: ZIN PH 18/173, fragmentary atlantal centrum.
Referred material: ZIN PH 19/173, fragmentary atlantal centrum; LMCCE 1/4, fragmentary trunk vertebral centrum.
Type locality: Shestakovo 1, Western Siberia, Kemerovo–Kuzbass oblast, Russia.
Type horizon: Ilek Formation, Aptian, Lower Cretaceous.

Diagnosis. — Referred to karaurid 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 presence of an anteroposteriorly short neural arch with an anterior border that is situated far from the level of anterior cotyles, the atlantal cotyle larger than the neural canal, and its relatively large size (the estimated maximum anterior width is about 4–5 mm and the ventral midline length, excluding the intercotylar tubercle is about 3–3.5 mm). Differs from all other karaurid salamanders for which the morphology of the atlantal centrum is known (namely *Kokartus* from the Middle Jurassic (Bathonian) of Kyrgyzstan, *Marmorerpeton* from the Middle Jurassic (Bathonian) of England and Scotland, *Urupia* and *Egoria* from the Middle Jurassic (Bathonian) and *Kulgeriherpeton* from the Lower Cretaceous (Berriasian-Barremian) of Siberian Russia) by following combination of characters: the presence of a shallow elliptical dorsolateral depression flanked by three low ridges (a longitudinal lateral ridge flanking its ventral border, a vertical ridge flanking its anterior border, and an oblique ridge, flanking its posterior border); the lack of lateral grooves or depressions on the lateral surfaces of the atlantal centrum (there is such a lack also in *Marmorerpeton wakei*); the lack of a ventral depression on the ventral surface of the atlantal centrum (lack also in *Egoria, Marmorerpeton wakei*); the lack of ventro-lateral ridges (lacks also in *Kulgeriherpeton*, *Egoria, Kokartus, Marmorerpeton wakei* and *M. kermacki*); anterior cotyles with elliptical anterior outline, located at an angle of approximately 150–160 degrees to each other (similar outline of anterior cotyles is present in *Kokartus*, see Fig. 4); the lack of transverse processes and alar processes associated with the transverse processes (lack also in *Marmorerpeton wakei*).

Differs from all other stem salamanders for which the morphology of the trunk vertebral centra is known (namely *Urupia*, *Egoria, Kokartus*, *Marmorerpeton*, and *Kulgeriherpeton*) in having a pair of rugose surfaces with low tubercles (= ?anterior basapophyses) on the ventral surface of the anterior portion of the trunk vertebral centrum.

Description. The atlas is known from two fragmentary centra of different sizes (the estimated maximum anterior width (i. e., between the lateral rims of the anterior cotyles) 4–5 mm). The atlantal centrum (Fig. 2, 4A–E) is wider than long. The anterior cotyles (Fig. 2A, I, 4A) are large, elliptical in anterior outline (ratio of maximum height: width is about 0.87) and they are located at an angle of approximately 150–160 degrees to each other. The articular surfaces of the anterior cotyles are

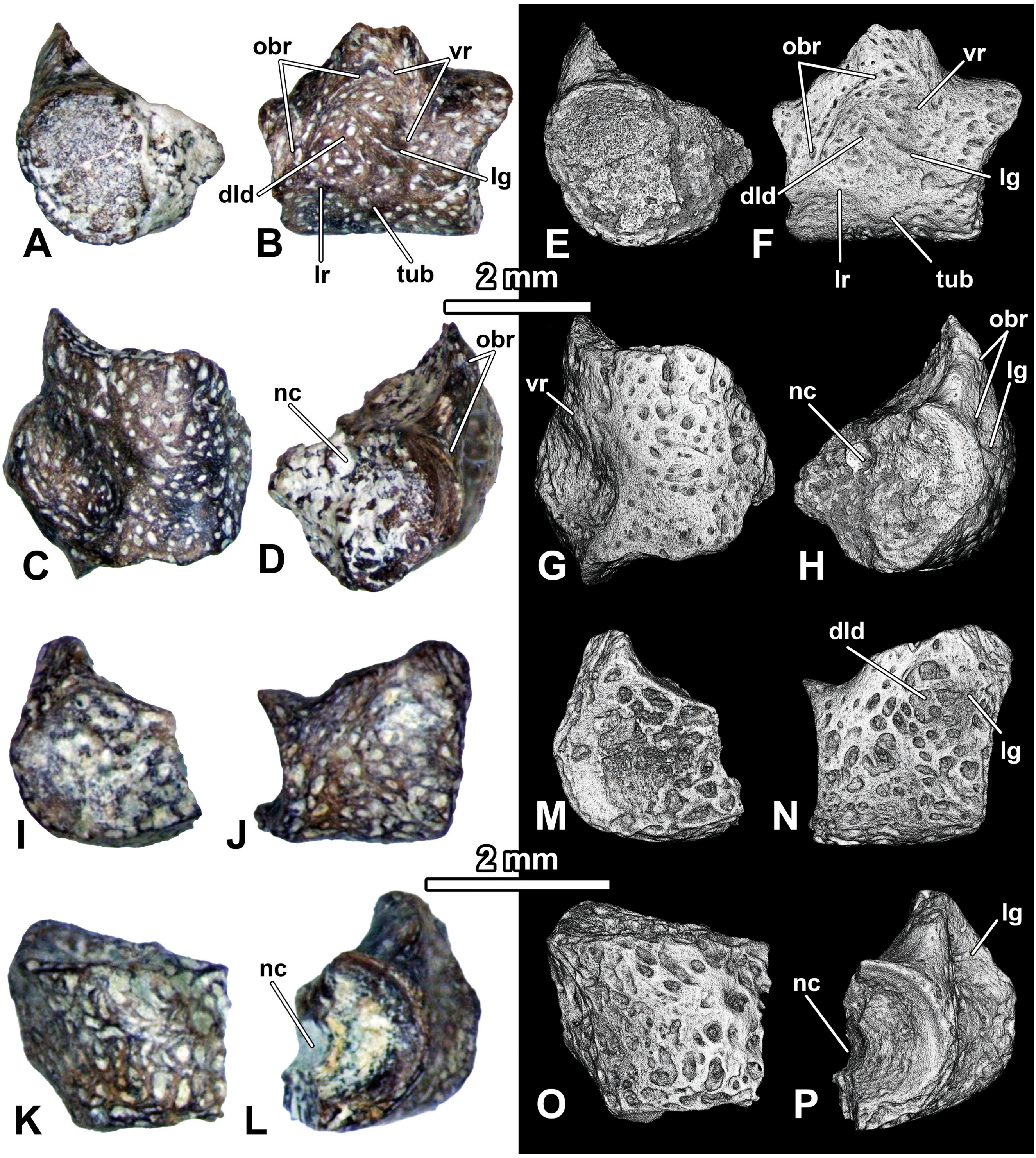

Fig. 2. *Kuzbassia sola* gen. et sp. nov., photo and tomographic reconstructions of specimens ZIN PH 18-19/173. A–D — photo of holotype ZIN PH 18/173 in anterior (A), lateral (B), ventral (C) and posterior (D) views; E–H — tomographic reconstruction of holotype ZIN PH 18/173 in anterior (E), lateral (F), ventral (G) and posterior (H) views; I–L — photo of centrum fragment ZIN PH 19/173 in anterior (I), lateral (J), ventral (K) and posterior (L) views; M–P — tomographic reconstruction of centrum fragment ZIN PH 19/173 in anterior (M), lateral (N), ventral (O) and posterior (P) views. Abbreviations: dld — dorsolateral depression, lg — longitudinal groove, lr — longitudinal ridge, nc — notochordal canal, obr — oblique ridge, tub — tubercle, vr — vertical ridge.

moderately dorsoventrally concave. The posterior cotyle is circular in posterior outline (Fig. 4B). The inner surface of the posterior cotyle is deeply concave and bears a notochordal canal in its central part (Fig. 2D, H, L, P).

The ventral surface of the centrum is flat with no ventral (= median) depression. Ventrolateral ridges are absent.

The lateral surface of the larger centrum (specimen ZIN PH 18/173, holotype, Fig. 2A–H) has a shal-

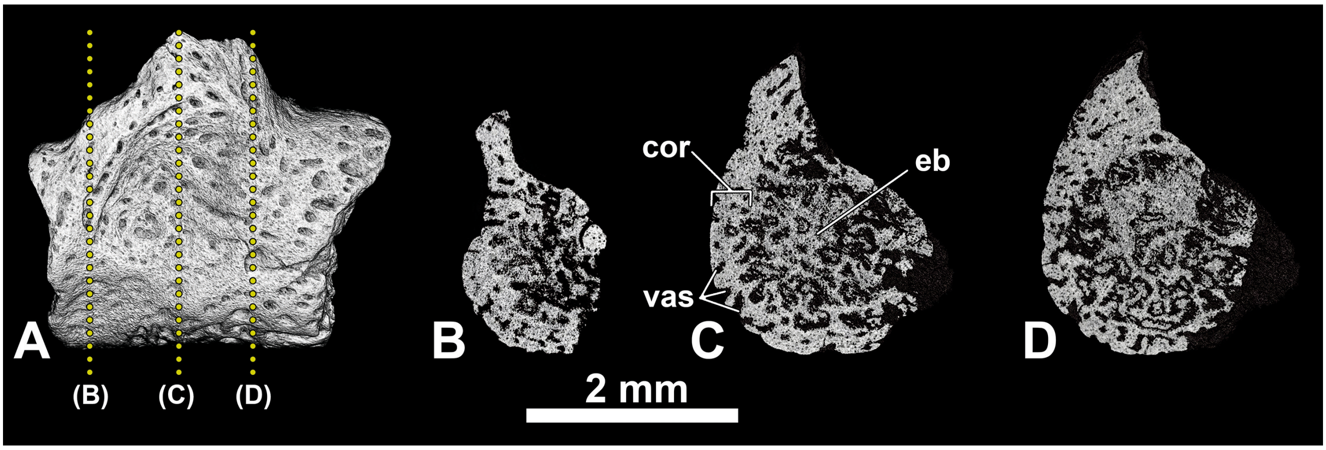

Fig. 3. *Kuzbassia sola* gen. et sp. nov., virtual sections showing microanatomy of the holotype ZIN PH 18/173. A — tomographic reconstruction in lateral view showing the level of virtual sections, B–D — virtual sections. Abbreviations: cor — cortex, eb — endochondral bone, vas — vascular canals.

low elliptical dorsolateral depression. This depression is flanked by low ridges: a longitudinal lateral ridge flanking its ventral border, a vertical ridge flanking its anterior border, and an oblique ridge, running from the base of neural arch to lateral surface of the rim of the posterior condyle, flanking its posterior border. A low tubercle is present at the fusion of longitudinal and vertical ridges. A small longitudinal groove is present in the anterior part of the dorsolateral depression, approximately at mid height of the centrum. The transverse processes, distinct alar processes associated with the transverse processes, and lateral grooves or depressions are absent.

The lateral surface of the smaller centrum (specimen ZIN PH 19/173, Fig. 2I–P) has less prominent ridges, flanking the dorsolateral depression, and the longitudinal groove is positioned slightly higher, close to the base of the neural arch (Fig. 2N, P).

The pedicels of the neural arch are anteroposteriorly short, massive and its anterior borders are situated behind the level of the anterior cotyle. The spinal nerve foramen is absent.

The internal microanatomical organization (Fig. 3) of the centrum is characterized by the presence of a thick compact periosteal cortex and an inner cancellous endochondral bone. The periosteal cortex is heavily vascularized by a network of short vascular canals. These canals exit on the ventral and lateral surfaces of the centrum through large rounded foramina, forming a characteristic pitted sculpture. The endochondral bone is formed by numerous trabeculae of varying thickness. Internally, the vascular canals of the cortex are connected with erosion bays of the inner cancellous endochondral bone.

The structure of the trunk vertebral centrum was described and figured by Skutschas (2016b: fig. 1). A unique feature of the trunk vertebral centrum is the presence of paired rugose surfaces that bear distinct tubercles located in the approximate position of (and perhaps homologous with) the anterior basapophyses (Skutschas, 2016b: fig. 1).

Comparisons and discussion

Kuzbassia sola gen. et sp. nov. can be assigned to stem karaurid salamanders on the basis of the following characteristic combination of features: the absence of spinal nerve foramina in the atlas; the presence of pitted ventral and lateral surfaces of the atlas; and an antero-posteriorly short neural arch with its anterior border situated behind the level of the anterior cotyles (Skutschas, 2016b; Skutschas et al., 2020; Jones et al., 2022).

Among karaurid salamanders, the atlas of *Kuzbassia sola* gen. et sp. nov. most closely resembles that of *Marmorerpeton wakei* from the Middle Jurassic (Bathonian) of Scotland in the presence of slight dorsoventral compressions at the anterior cotyles, in the absence of transverse processes and associated alar processes, in the absence of the lateral grooves or depressions on the lateral surfaces and the ventral depression on the ventral surface of the atlantal centrum (Jones et al., 2022: fig. 2A–D). The trunk vertebral centrum referred to *Kuzbassia sola* gen. et sp. nov. is similar to those of other karaurid salamanders in having ventral and lateral surfaces roughened and indented by scattered, small, rounded and oval pits, but differs in having paired rugose surfaces with distinct tubercles located in the approximate position of (and perhaps homologous with) the anterior basapophyses seen in some crown-group salamanders (Skutschas, 2014).

Karaurids are robustly built neotenous stem salamanders that are characterized by several synapomorphies (an interorbital distance greater than the width of the orbit, a posterolateral process of the prefrontal, heavy sculpture on the skull roofing bones, and vertebral cotyles that are greater in diameter than the neural

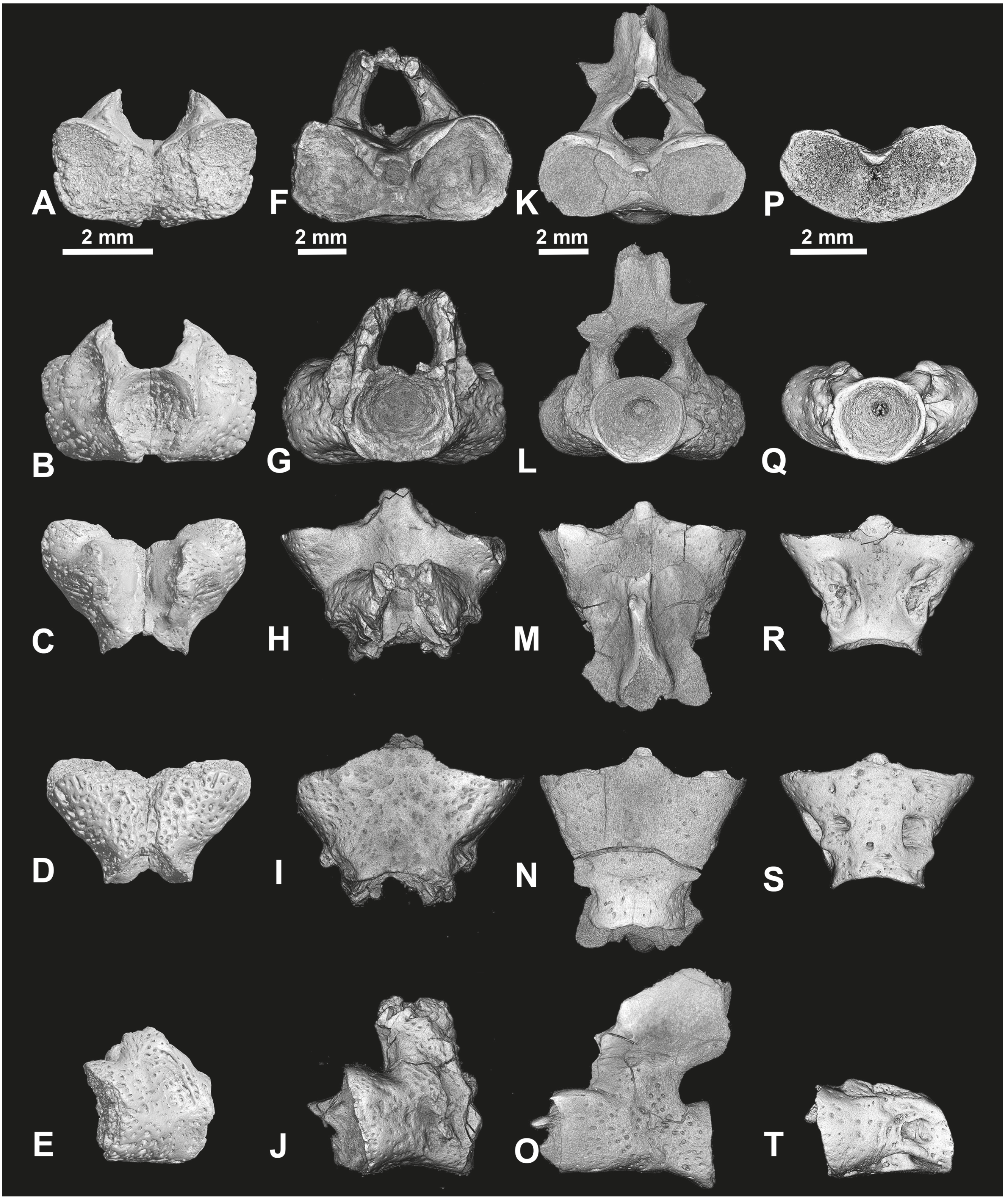

Fig. 4. Atlantal centrum of *Kuzbassia sola* gen. et sp. nov., and atlases of karaurid salamanders used for comparison: A–E — *Kuzbassia sola* gen. et sp. nov., reconstruction based on specimens ZIN PH 18-19/173; F–J — *Kokartus honorarius*, ZIN PH 3/47 (referred specimen) mirrored for comparison; K–O — *Kulgeriherpeton ultimum,* ZIN PH 3/246 (holotype); P–T — *Egoria malashichevi,* ZIN PH 40/144 (holotype).

canal; Jones et al., 2022), and a suite of features of uncertain polarity (e.g., atlas and other vertebrae sculptured and lacking spinal nerve foramina; the presence of an anteroposteriorly short neural arch with an anterior border that is situated far from the level of anterior cotyles; amphicoelous post-atlantal vertebrae lacking basapophyses; ribs bicapitate; Skutschas and Martin, 2011; Skutschas et al., 2018).

Karaurids first appear in the fossil record in the Middle Jurassic (Bathonian). The oldest karaurids are represented by *Kokartus honorarius* from Kyrgyzstan, *Marmorerpeton* spp. (three species) from the United Kingdom, and *Urupia monstrosa* and *Egoria malashichevi* from Siberian Russia (Evans, Milner, and Mussett, 1988, Nesov, 1988; Evans and Milner, 1994; Skutschas and Krasnolutskii, 2011; Skutschas and Martin, 2011; Skutschas, 2013; Skutschas et al., 2020; Jones et al., 2022). Karaurids were the dominant salamander component in the Bathonian vertebrate assemblages of present-day Great Britain, Kyrgyzstan and Western Siberia.

The next youngest karaurid salamanders date from the Late Jurassic. These include two Kimmeridgian occurrences, namely *Karaurus sharovi* from the Karabastau Formation in Kazakhstan and "cf. *Marmorerpeton*" (sensu Wiechmann, 2000) from Portugal (Ivakhnenko, 1978; Milner, 2000; Wiechmann, 2000). *Karaurus sharovi* is known by a well-preserved, nearly complete and articulated skeleton (Ivakhnenko, 1978). The salamander remains from Portugal identified as "cf. *Marmorerpeton*" have never been described and figured and their karaurid affinities should be tested in the future. We know very little about Late Jurassic karaurids, especially about their abundance and role in ecosystems.

The Early Cretaceous record of karaurids is restricted to *Kulgeriherpeton ultimum* from the Berriasian–Barremian of Yakutia, Eastern Siberia (Skutschas et al., 2018) and the new salamander *Kuzbassia sola* gen. et sp. nov. from the Aptian of Kemerovo–Kuzbass oblast, Western Siberia, Russia. *Kulgeriherpeton ultimum* is the dominant salamander component in the vertebrate assemblage of Yakutian Teete locality and the largest (the estimated body length of *Kulgeriherpeton,* based on the proportions of the stem salamander *Karaurus*, is about 35 cm) aquatic predator of the local ecosystem (PPS, VVK, pers. obs.). The remains of the new salamander *Kuzbassia sola* gen. et sp. nov. are extremely rare in the Siberian Shestakovo 1 locality and its dominant salamander component is a possible crown group salamander *Kiyatriton leshchinskiyi*. Karaurids are not known from the post-Aptian deposits, so *Kuzbassia sola* gen. et sp. nov. is the last karaurid salamander in the fossil record to date survived as a relic in the "Great Siberian refugium". The absence of karaurids in the younger deposits suggests karaurids became extinct after the Aptian.

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