



A relict stem salamander: Evidence from the Early Cretaceous of Siberia

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The early evolution of salamanders, which are one of the three living groups of lissamphibians, is not well known. Both stem- and crown-group salamanders first appeared in the Middle Jurassic (Bathonian), but subsequently had different evolutionary histories: stem salamanders were thought to have gone extinct in the Late Jurassic, while crown salamanders persist to the present day. Here, I report the discovery of an indeterminate stem salamander in the Lower Cretaceous (Aptian–Albian) Ilek Formation of Western Siberia. This is new evidence that the most basal 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. The recognition of stem salamanders in the Early Cretaceous of Western Siberia adds to the inventory of taxa that suggest this area was a refugium for various groups of vertebrates with Jurassic affinities.

Introduction

Salamanders (Caudata) are one of the three living clades of lissamphibians. The first salamanders appeared in the fossil record in the Middle Jurassic (Bathonian) and are represented by taxa of varying grades of evolution, some of which may co-occur at the same localities. These salamanders include the following: the stem-group taxa *Kokartus* Nesov, 1988, from Kyrgyzstan, *Marmorperpeton* Evans, Milner, and Mussett, 1988, and “Kirtlington salamander A” (sensu Evans and Milner 1994), both from Great Britain, and *Urupia* Skutschas and Krasnolutskii, 2011, and “Berezovsk salamander A” (sensu Skutschas 2013), both from Russia (Evans et al. 1988, Nesov 1988; Evans and Milner 1994; Evans and Waldman 1996; Milner 2000; Skutschas and Krasnolutskii 2011; Skutschas 2013); the possible crown-group taxa “Kirtlington salamander B” (sensu Evans and Milner 1994) from Great Britain and “Berezovsk salamander B” (sensu Skutschas 2013) from Russia (Evans and Milner 1994; Milner 2000; Skutschas 2013); and the unambiguous crown-group taxa *Chunerpeton* Gao and Shubin, 2003, *Jeholotriton* Wang, 2000, and *Liaoxitriton* Dong and Wang, 1998, all from China (see review by Gao et al. 2013). The next youngest, previously reported stem salamanders date from the Late Jurassic. These include two Kimmeridgian occurrences, namely *Karaurus* Ivachnenko, 1978, from Kazakhstan and “cf. *Marmorperpeton*” (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 1996; Gardner and DeMar 2013). Outside China, all Bathonian vertebrate assemblages containing salamanders are dominated by stem-group 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.

There has been only one report of possible stem salamanders in post Jurassic deposits: three atlantal centra from the Aptian–Albian Cloverly Formation of Wyoming, USA (Gardner and DeMar 2013: 486, fig. 1d). These atlantal centra could not be referred to any crown-group salamander family currently known from the North American Early Cretaceous, and generally resemble some Jurassic stem salamander atlantal centra (Gardner and DeMar 2013: 486). The assignment of atlantal centra from the Cloverly Formation to stem salamanders (as well the presence of stem-group salamanders in the Early Cretaceous of North America) needs to be verified in the future with detailed study of this material.

Except for the possible stem salamanders in the Early Cretaceous of North America (Gardner and DeMar 2013), there has been no evidence of stem salamanders in post Jurassic deposits, and it was suggested they became extinct before the Jurassic–Cretaceous boundary (Skutschas 2013).

Here I present evidence for an Early Cretaceous stem salamander from Aptian–Albian deposits in Western Siberia.

Institutional abbreviations.—LMCCE, Laboratory of Mesozoic and Cenozoic Continental Ecosystems, Tomsk State University, Western Siberia, Tomsk, Russia.

Systematic paleontology

Amphibia Linnaeus, 1758

Lissamphibia Haeckel, 1866

Caudata Scopoli, 1777 (sensu Milner, 1988)

Genus et species indet.

Material.—LMCCE 1/4, fragmentary trunk vertebra (Fig. 1). Shestakovo locality (Shestakovo 1 local site), bluff on right (i.e., east) side of Kiya River, 1.5 km downstream from Shestakovo village, Kemerovo Region, Western Siberia, Russia. Coarse-grained sand and sandstone of the Ilek Formation. Early Cretaceous or Aptian–Albian in age. For more details on

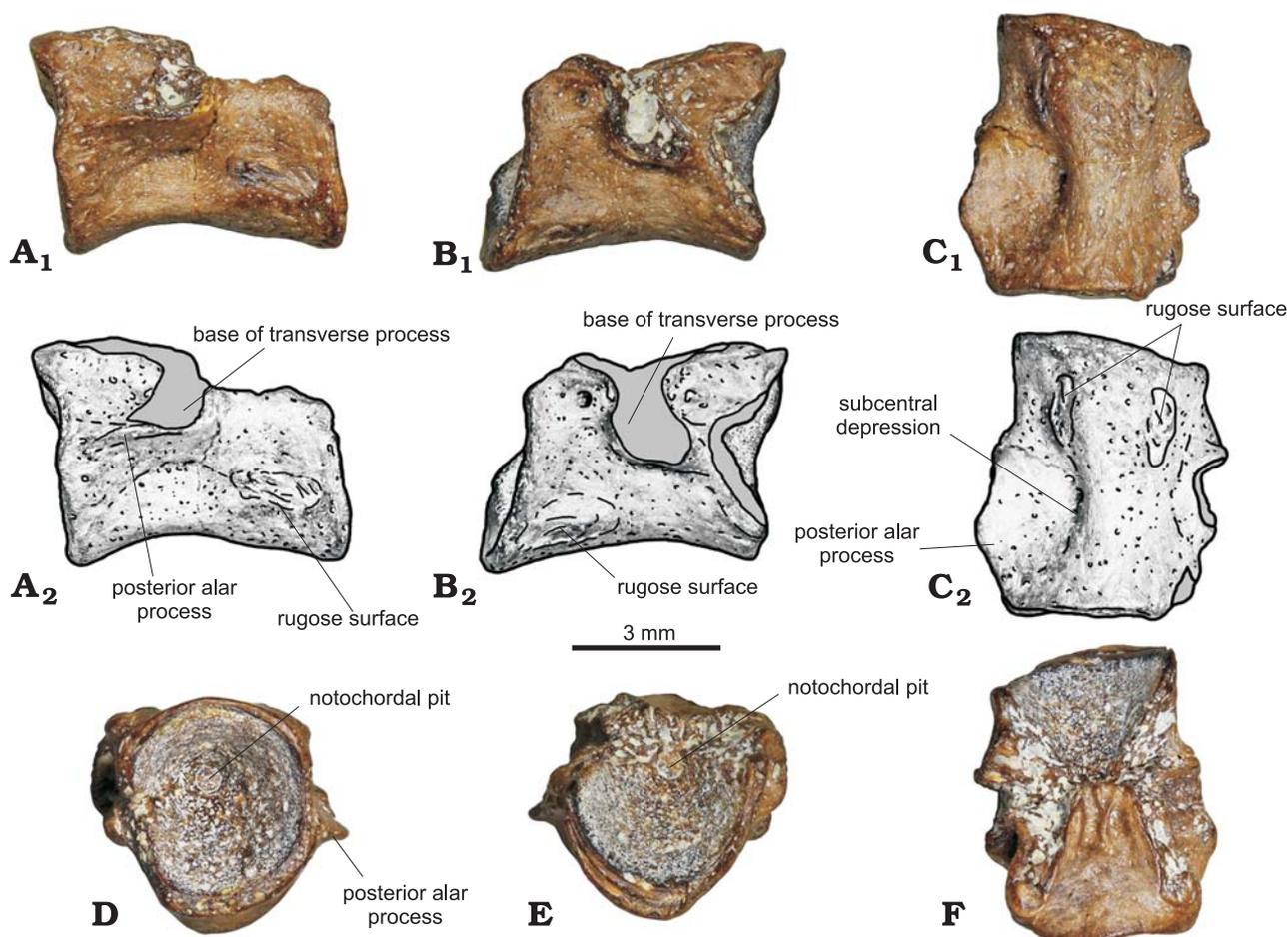


Fig. 1. Fragmentary trunk vertebral centrum (LMCCE 1/4) of stem salamander *Caudata*, gen. et sp. indet. from the Shestakovo locality, Lower Cretaceous (Aptian–Albian), Ilek Formation, Western Siberia, Russia; in right lateral (A), left lateral (B), ventral (C, anterior towards top), posterior (D), anterior (E), and dorsal (F, anterior towards top) views. Photographs (A₁–C₁, D–F) and interpretive drawings (A₂–C₂).

the Shestakovo locality and its vertebrate assemblage, see Averianov et al. (2006: 361, fig. 1); Skutschas (2014: 89, fig. 1).

Description.—LMCCE 1/4 is an incomplete trunk vertebral centrum that lacks the anterodorsal portion of the anterior cotyle (Fig. 1). It is large (relative to trunk vertebrae of the possible cryptobranchoid *Kiyatriton leshchinskiyi* from the same locality, see Skutschas 2014: fig. 4), with a ventral midline length of about 5.5 mm. LMCCE 1/4 is heavily ossified vertebra (= heavily built) that appears to have an endochondral component. The lateral and ventral surfaces of the centrum (Fig. 1A–C) are roughened and indented by scattered, small, rounded and oval pits (= pitted texture). These numerous pits are not densely situated and do not form a net-like texture. In lateral view, the centrum is relatively short anteroposteriorly and deep (ratio of ventral midline length vs. maximum height is about 1.3) and its ventral surface is broadly concave dorsally. The centrum is amphicoelous and both cotyles are deeply concave. The posterior cotyle is intact and nearly circular in posterior outline, with the ventral portion slightly narrower than the dorsal (Fig. 1D); the anterior cotyle is missing its dorsal portion, but it probably had a similar outline (Fig. 1E, F). Both cotyles retain a modest-sized notochordal pit. That pit is

located slightly above the dorsoventral midpoint of posterior cotyle and it likely was in about the same location in the anterior cotyle. The inner walls of both cotyles are lined with a thin layer of calcified cartilage. The ventral surface lacks a subcentral keel. Instead, the ventral surface is moderately broad, shallowly convex from side-to-side and bracketed on either side by a shallow subcentral depression. Those depressions are perforated by small and nearly equal-sized subcentral foramina (not visible in figure); there are three foramina in the right subcentral depression and two in the left. Anteroventral to each subcentral depression, there is an anteroposteriorly elongate patch having a weakly rugose surface and bearing along its posterior portion a low, but distinct tubercle (= ?anterior basapophysis). Bases of transverse processes (= rib-bearers) are present higher up and midway along the lateral sides of the centrum, but those bases are too damaged to determine whether the transverse processes were bicipital or unicipital. As best shown on the left side, the anterior and posterior bases of the transverse process are perforated by a small canal. Best preserved on the right side, the posterior alar process is an anteroposteriorly short flange that extends posteriorly from the base of the lower part of the transverse process.

Discussion

The fragmentary trunk vertebral centrum LMCCE 1/4 from the Shestakovo locality can be assigned to the Caudata based on the following features: deeply amphicoelous, notochordal centrum (common feature for lissamphibians), longer than wide (difference from frogs), the absence of prominent anterior basapophyses and/or anteroventral extensions of the basapophyses into bilateral flanges which are associated with specialized hypaxial musculature (difference from caecilian), and lacking the thickened rims around the anterior and posterior cotyles (difference from albanerpetontids) (e.g., Milner 2000; Evans and Sigogneau-Russell 2001; Gardner et al. 2013). The fragmentary centrum LMCCE 1/4 from the Shestakovo locality differs from those of crown-group salamanders (including the possible cryptobranchoid *Kiyatriton leshchinskiyi* from the same locality; see Skutschas 2014: fig. 4) and resembles other stem-group salamanders in showing the following combination of features: relatively large size, especially when compared with the most of known Jurassic or Early Cretaceous crown-group salamanders; heavy build; and ventral and lateral surfaces roughened and indented by scattered, small, rounded and oval pits (for examples of stem salamander trunk vertebrae see Evans et al. 1988: fig. 8; Evans and Waldman 1996: fig. 1; Skutschas and Krasnolutskii 2011: fig. 4; Skutschas 2013: fig. 3).

Large size is characteristic for stem salamanders. Most stem-group salamanders had a skull length of approximately 40–50 mm and an estimated body length of approximately 200–400 mm (Skutschas and Martin 2011; Buffrénil et al. 2015), whereas the most of early crown-group members had a skull length of approximately 20 mm and an estimated body length of approximately 120–180 mm (Wang and Evans 2006: 68). There are two Jurassic crown-group salamanders with body sizes comparable to stem-group taxa: the cryptobranchid *Chunerpeton* (the total body length of holotype is approximately 180 mm; Wang and Evans 2006: 68) and the salamandroid *Beiyanerpeton* Gao and Shubin, 2012 (the estimated body length of holotype is slightly more than 160 mm; Gao and Shubin 2012: fig. 2). The lengths of trunk vertebrae centra are approximately 4 mm in *Chunerpeton* (Gao and Shubin 2003: fig. 1) and approximately 5 mm in *Beiyanerpeton* (Gao and Shubin 2012: fig. 2), which is comparable in size with LMCCE 1/4 from the Shestakovo locality (about 5.5 mm). As a result, large size could be a primitive feature of the Caudata and by itself should not be used for systematic identification of the fragmentary trunk vertebral centrum LMCCE 1/4 from the Shestakovo locality.

On the other hand, LMCCE 1/4 is a heavily ossified vertebra (= heavily built) that appears to have an endochondral component. This morphology differs from that of crown-group salamanders which have notochordal ectochordal vertebrae (= lightly built) which are formed from membrane bone (Evans et al. 2005: 611). Another unique feature which supports the assignment of LMCCE 1/4 to stem-group salamanders is the presence of specific texture on the vertebral surface. The ventral and lateral surfaces of LMCCE 1/4 are roughened and

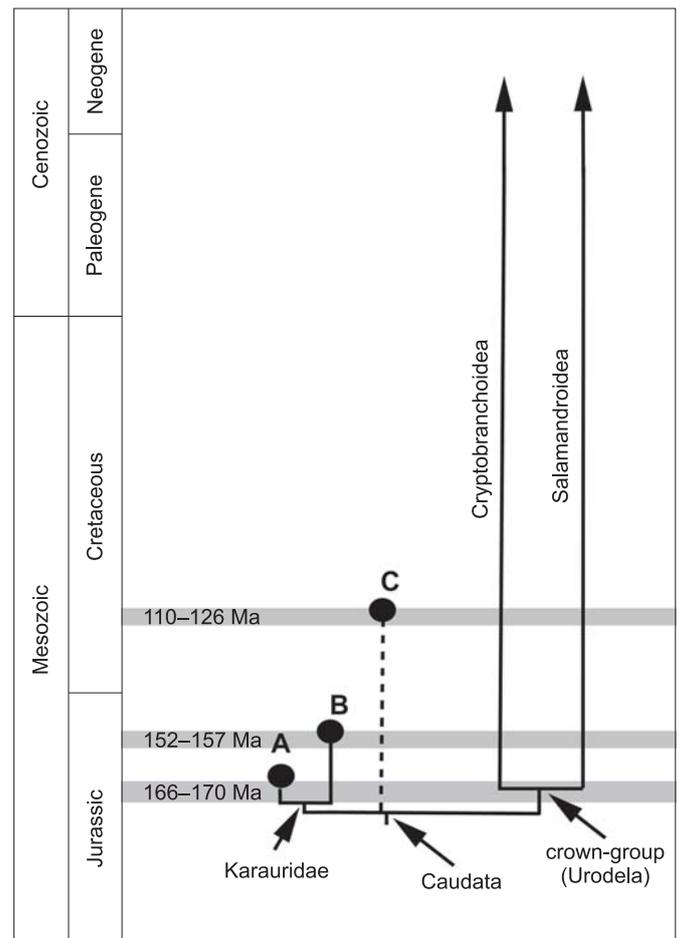


Fig. 2. Simplified relationships and temporal ranges of stem- and crown-group salamanders. Stem salamanders are represented only by Karauridae (i.e., *Kokartus* + *Karaurus*). A, stratigraphic placement (Bathonian) of the stem salamander *Kokartus* (note that the stem salamanders *Marmorerperton*, “Kirtlington salamander A”, *Urupia*, and “Berezovsk salamander A” have the same stratigraphic placements). B, stratigraphic placement (Kimmeridgian) of *Karaurus* (note that salamanders “cf. *Marmorerperton*” from Portugal and the possible “stem salamander” from the USA have approximately the same stratigraphic placements). C, stratigraphic placement (Aptian–Albian) of the stem salamander Caudata, Gen. et sp. indet. reported here from the Shestakovo locality and possible stem salamanders from the Cloverly Formation of USA.

indented by scattered, small, rounded and oval pits (= pitted texture). The same pitted texture is present on atlasses and trunk vertebrae of stem salamanders with described or/and figured detailed vertebral morphology (*Kokartus*, *Marmorerperton*, “Kirtlington salamander A” [sensu Evans and Milner 1994], *Urupia*, “Berezovsk salamander A” [sensu Skutschas 2013]). Most of crown-group salamanders have smooth vertebral surface, with only a few exceptions (e.g., the large-bodied extant cryptobranchid *Andrias* and the Paleocene scapherpetontid *Piceoerperton*, Gardner 2012: 615, fig. 2; in the moderate-bodied extant cryptobranchid *Eoscaferpeton* rare pits found only in few largest specimens, PPS personal observation). However, the pits do not form a net-like texture and are not so dense on the vertebral surface in stem salamanders compared with *Andrias* and *Piceoerperton* (for comparison see Gardner

2012: fig. 2 and Skutschas 2013: fig. 3), and pitted texture is much more pronounced in stem salamanders (even on relatively small vertebrae) than in the largest vertebral specimens of *Eoscapherpeton* (for comparison see Skutschas 2013: figs. 3, 5). As a result, the pitted texture of stem salamanders could be a primitive character for the Caudata and the smooth vertebral surface is a possible synapomorphy of crown-group salamanders. Densely pitted or net-like texture, as well as appearance of rare pits on the vertebral surface, may have been developed secondarily in some crown-group salamanders.

LMCCE 1/4 is generally similar in its morphology to the vertebral centra of Jurassic stem salamanders, but differs in having paired rugose surfaces that bear distinct tubercles located in the approximate position of (and perhaps homologous with) the anterior basapophyses seen in some crown-group salamanders, such as sirenids and amphiumids. Relationships of the stem salamander from Shestakovo to other stem-group salamanders are uncertain, because there is limited information about both its anatomy and the anatomy of some other basal salamanders. Despite the presence of an apparently unique feature (i.e., paired rugose surfaces with distinct tubercles), the fragmentary nature of LMCCE 1/4 plus the absence of any other referable bones (e.g., cranial bones and atlantes) does not allow for the description of new taxon. Pending the discovery of additional material, I conservatively identify LMCCE 1/4 as stem Caudata, gen. et sp. indet.

LMCCE 1/4 (possibly together with three atlantal centra from the Cloverly Formation of Wyoming, USA) extends the stratigraphic range of stem salamanders forward some 25 million years into the Aptian–Albian, from the previously youngest records in the Kimmeridgian of Kazakhstan and Portugal and, perhaps, the Kimmeridgian–early Tithonian of the USA (Ivachnenko 1978; Nesov 1992; Evans and Milner 1996; Wiechmann 2000; Gardner and DeMar 2013; Fig. 2). It therefore provides a new example of the “Lazarus effect”: the reappearance of a group in the fossil record long after it was thought to have become extinct (Jablonski 1986). The absence of stem salamanders in any Asian Cretaceous localities (except Shestakovo) suggests that Western Siberia was a refugium where basal salamanders survived.

To date, stem salamanders in Western Siberia are known from two localities: the Bathonian age Berezovsk Quarry (Skutschas and Krasnolutskii 2011; Skutschas 2013) and the Aptian–Albian age Shestakovo locality. Despite the considerable age difference between them, the faunal compositions of Berezovsk Quarry and the Shestakovo locality are similar in sharing stem salamanders, primitive choristoderes, paramacellodid lizards, tritylodonts and docodont cynodonts (Averianov et al. 2005, 2006). Moreover, the vertebrate assemblage of the Shestakovo locality also includes additional vertebrates with Jurassic affinities that are not known from the Berezovsk Quarry (e.g., “protosuchian” and shartegosuchid crocodyliforms; Leshchinskiy et al. 2001). Similarities between vertebrate assemblages of the Middle Jurassic Berezovsk Quarry and the Early Cretaceous Shestakovo locality and the presence of additional vertebrates with Jurassic affinities in Shestakovo

suggest that paleoenvironmental conditions in Western Siberia were more-or-less stable for an extended interval from the Bathonian to Aptian–Albian. That stability presumably was an important factor in allowing the survival of so many Jurassic taxa as relics into the Early Cretaceous of present day Western Siberia.

The first unambiguous crown-group salamanders are known from the Jurassic (Bathonian) Daohugou beds in China (e.g., Gao et al. 2013) and they are the same age as the oldest stem salamanders from Kyrgyzstan, Great Britain, and Russia (Evans et al. 1988; Nesov 1988; Evans and Milner 1994; Evans and Waldman 1996; Milner 2000; Skutschas and Krasnolutskii 2011; Skutschas 2013). After the Bathonian, stem salamanders co-existed for approximately 40 million years with crown-group salamanders until the Aptian–Albian. Such lengthy temporal co-existence of stem- and crown-group members is not known for either of the other living lissamphibian clades.

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