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## RE-EVALUATION OF *MYNBULAKIA* NESOV, 1981 (LISSAMPHIBIA: CAUDATA) AND DESCRIPTION OF A NEW SALAMANDER GENUS FROM THE LATE CRETACEOUS OF UZBEKISTAN

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**ABSTRACT**—Isolated skull and postcranial bones previously assigned to the monotypic batrachosauroidid salamander genus *Mynbulakia* Nesov, 1981 (Uzbekistan, Byssekty Formation, Turonian) are re-interpreted as a mixture of two salamander taxa. The holotype maxilla of *Mynbulakia surgayi* Nesov, 1981, and dentaries, parietals, and femora previously referred to that species belong to smaller and, presumably, younger individuals of the cryptobranchid *Eoscapherpeton asiaticum* Nesov, 1981. Atlantes and trunk vertebrae previously referred to *M. surgayi*, along with additional vertebrae collected more recently from the Byssekty Formation, belong to *Nesovtriton mynbulakensis* gen. et sp. nov.. The structure of the atlas, the absence of spinal nerve foramina in the trunk and anterior caudal vertebrae, and the presence of unicipital transverse processes on the trunk vertebrae suggest that *N. mynbulakensis* may be a member of the Cryptobranchioidea. Two salamander taxa (*E. asiaticum* and *N. mynbulakensis*) are currently known from the Byssekty Formation and no salamander families are shared between the Late Cretaceous tetrapod assemblages of Asia and Euramerica.

### INTRODUCTION

The sparse Late Cretaceous record of salamanders in Asia is limited largely to the Kyzylkum Desert in Uzbekistan, where three genera have been identified based on isolated skull and postcranial bones: *Horezmia* Nesov, 1981, is from the Cenomanian Khodzhakul Formation and *Eoscapherpeton* Nesov, 1981, and *Mynbulakia* Nesov, 1981, are from the Turonian Byssekty Formation (Nesov, 1981, 1988, 1997; Duellman and Trueb, 1986; Milner, 2000; Shishkin, 2000). Because the Kyzylkum Desert contains the only record of Late Cretaceous salamanders in Asia, fossils from that region are potentially significant for clarifying the evolutionary history of salamanders during that interval on the Asian continent.

Expeditions to the Kyzylkum Desert in 1977–1994 by L.A. Nesov and in 1997–2006 by the international Uzbek/Russian/British/American/Canadian Joint Paleontological Expeditions (URBAC) yielded several thousand Upper Cretaceous salamander bones, which are deposited in the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia. Much of this material is being used to study ontogenetic and individual variation within *Eoscapherpeton asiaticum* and to clarify the phylogenetic relationships of *Eoscapherpeton* and *Horezmia* (a monographic treatment of these two taxa is in preparation by the author). Other specimens have proven informative for re-evaluating the status of *Mynbulakia*. In this paper I argue that specimens previously assigned to *Mynbulakia* are a mixture of two salamander taxa: the holotype maxilla and referred dentaries, parietals, and femora of *M. surgayi* (the type and only previously accepted species) belong to small and, presumably, young individuals of *E. asiaticum*, whereas referred atlantes and trunk vertebrae and other vertebrae discovered during the URBAC expeditions belong to a previously unrecognized salamander taxon, which is formally named and described here as *Nesovtriton mynbulakensis* gen. et sp. nov.

**Institutional Abbreviations**—CCMGE (=“UFG” in Nesov, 1981), Chernyshev’s Central Museum of Geological Exploration,

Saint Petersburg, Russia; ZIN PH, Paleoherpetological collection, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

### DISCUSSION OF “MYNBULAKIA”

Nesov (1981) named and described the genus *Mynbulakia* and two species: the type species *M. surgayi* from the Turonian Byssekty Formation and *M. nongratis* from the Cenomanian Khodzhakul Formation, Kyzylkum Desert, Uzbekistan. *Mynbulakia surgayi* Nesov, 1981, was based on the holotype maxilla and a substantial collection of referred specimens, including five dentaries, four parietals, three atlantes, about one hundred trunk vertebrae, and several femora (Nesov, 1981: 68). Only the holotype maxilla and seven referred specimens (i.e., one dentary, one atlas, four trunk vertebrae, and one femur) were figured (Nesov, 1981: pl. XI, fig. 10–11, 14–19; 1988: pl. XIV, fig. 22–23; 1997: pl. X, fig. 5–11). The second species of *Mynbulakia*, *M. nongratis* was described by Nesov (1981) for one fragmentary dentary with transversely expanded tooth bases. Later, this taxon was implicitly rejected by Nesov (1988: 481) and the genus *Mynbulakia* became monotypic.

According to Nesov (1981:67, 68) and Shishkin (2000:306), *Mynbulakia* is characterized by the following unique combination of features: (1) maxilla anteroposteriorly short, with relatively deep ascending process (= dorsal process), anteroposteriorly short pterygoid process bent medially near its end, and subhorizontal ridge on external side above and parallel to tooth row (as in *Horezmia* and *Eoscapherpeton*); (2) dentary deepest immediately behind tooth row, with Meckelian groove strongly narrowed anteriorly and reaching symphysis (Shishkin (2000:306) incorrectly stated that the Meckelian groove did not reach the symphysis); (3) teeth relatively large, transversely expanded, bearing nearly blunt apex, and not set very close to each other (about 12 teeth per 5 mm); (4) atlas with rounded anterior facets, intercotylar tubercle large, and lacking hypapophysis on ventral surface of centrum; (5) trunk vertebrae elongate, with ventral

median ridge (= subcentral keel) reduced or absent, transverse processes (= rib-bearers) thin and elongate, neural spines low, and zygapophyses extend anteroposteriorly; (6) femur short and stout, with crista trochanterica strong and plate like. Nesov (1981) originally assigned *Mynbulakia* to the Batrachosauroididae based on general similarities with the maxillae and dentaries (small size of these bones, maxilla and dentary anteroposteriorly short, dentary deepest immediately behind tooth row) of Euramerican batrachosauroidids such as *Palaeoproteus* and *Opisthotriton* and this familial assignment was accepted by all subsequent workers (Duellman and Trueb, 1986; Milner, 2000; Shishkin, 2000).

The holotype of "*Mynbulakia surgayi*" (ZIN PH K77-3; Nesov, 1981:pl. XI, fig. 10a, b; Fig. 1A) is a short left maxilla with a subhorizontal ridge on its external side, an anteroposteriorly short pterygoid process, and eleven relatively large, transversely expanded teeth. The referred dentaries (e.g., CCMGE 50/11657; Nesov, 1981:pl. XI, fig. 11) are deepest immediately behind the tooth row, have a narrow Meckelian groove reaching the symphysis, and 13–15 relatively large, transversely expanded teeth that lack intact crowns. I interpret these specimens as belonging to smaller and, presumably, younger individuals of *Eoscapherpeton* because differences noted by Nesov (1981) between jaws of "*Mynbulakia*" and *Eoscapherpeton* are ontogenetically controlled characters. In the reconstructed ontogenetic series of maxillae and dentaries presented here (Figs. 1 and 2A–C, respectively) for "*Mynbulakia*"–*Eoscapherpeton*, the following size related changes are seen: (1) teeth increase in number and their shape changes from transversely expanded to rounded in cross-section; (2) bones become absolutely longer and processes and ridges on maxilla become relatively longer;

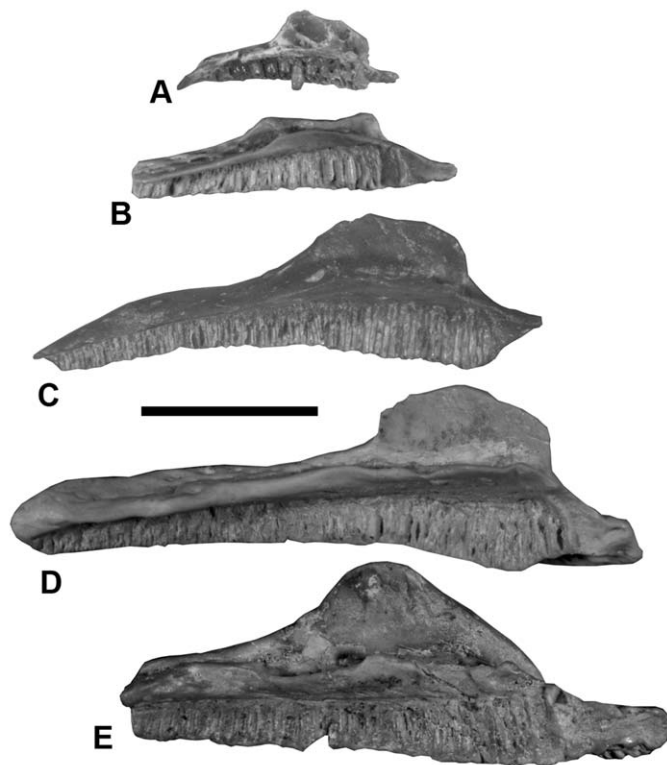


FIGURE 1. Size series of *Eoscapherpeton asiaticum* maxillae, all in medial view. **A**, holotype of "*Mynbulakia surgayi*," left maxilla, ZIN PH K77-3; **B**, left maxilla, ZIN PH 9/85; **C**, right maxilla (reversed), ZIN PH 10/85; **D**, left maxilla, ZIN PH 11/85; **E**, holotype of *Eoscapherpeton asiaticum*, left maxilla, ZIN PH K77-1. Scale bar equals 5 mm.

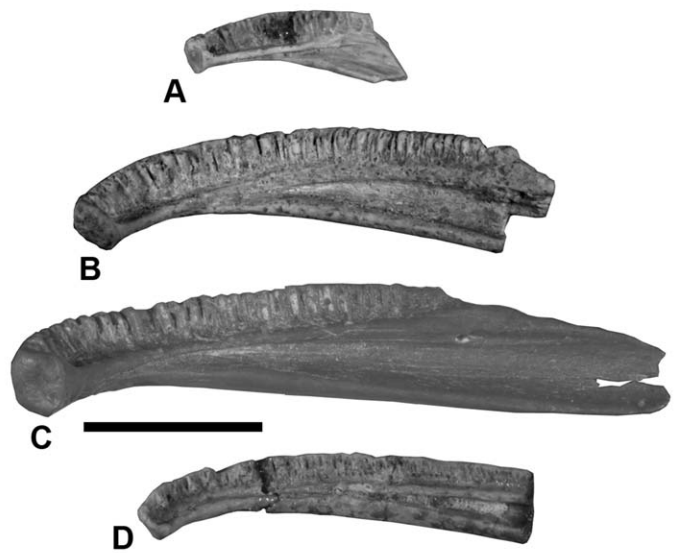


FIGURE 2. Dentaries of *Eoscapherpeton asiaticum* and *Nesovtriton mynbulakensis*, gen. et sp. nov., all in medial view. **A–C**, size series of *E. asiaticum* dentaries: **A**, right dentary, ZIN PH 12/85; **B**, right dentary, ZIN PH 13/85; **C**, left dentary (reversed), ZIN PH 14/85. **D**, *N. mynbulakensis*, right dentary, ZIN PH 2/85. Scale bar equals 5 mm.

(3) Meckelian groove becomes relatively shorter; and (4) maximum depth of dentary displaced forward to level of posterior end of tooth row. Similar ontogenetic modifications of the maxilla and dentary were noted in the Siberian newt (*Salmandrella keyserlingii*) and some other modern salamanders (*Ranodon sibiricus*, *Pleurodelus waltlii*, *Triturus cristatus*) by Lebedkina (1979, for an English translation of this book see Lebedkina, 2004). In salamanders, the number of teeth on the maxillae and dentaries increases and teeth are replaced throughout the post-metamorphic life (Lebedkina, 1979). During ontogeny, morphology of salamander teeth changes from non-pedicellate monocuspid (early larval stages) to monocuspid subpedicellate (late larval–early postmetamorphic stages) and, finally, to definitive bicuspid pedicellate. Each tooth generation contains teeth of a single morphological pattern (Vassilieva and Smirnov, 2001, and references therein) and conspecific salamanders of different ages may have teeth that look very different. Thus, differences in tooth shape in smaller and larger *Eoscapherpeton* maxillae and dentaries—which presumably are from younger and older individuals—could be explained by the presence of teeth at different ontogenetic stages of development in different-sized jaws. Attribution of the holotype of "*Mynbulakia surgayi*" to a small individual of *Eoscapherpeton* also is supported by the presence of a subhorizontal ridge on the external side, which is a synapomorphic character of *Eoscapherpeton* and *Horezmia* (the latter taxon is known only from the Khodzhaikul Formation, Nesov, 1981, 1988, 1997; pers. obs., 2007).

The parietals (CCMGE 173 and 174/11657) described, but never figured, by Nesov (1981:68) for "*Mynbulakia surgayi*" are long, with a ventrally oriented ridge along the medial edge of the bone. These specimens are similar to those of *Eoscapherpeton* in shape (Nesov, 1988: pl. XV, fig. 23–24; 1997: pl. IX, fig. 14) and in the presence of the ventral ridge and differ from *Eoscapherpeton* only by their smaller size. I thus interpret these parietals as belonging to smaller and, presumably, younger individuals of *Eoscapherpeton*.

The structure of the atlas CCMGE 53/11657 (Nesov, 1981:pl. XI, fig. 14a, b) and other atlantes referred by Nesov (1981) to



"*Mynbulakia surgayi*" differs significantly from referred atlantes of *Eoscapherpeton* (Nesov, 1981: pl. IX, fig. 16a and pl. XI, fig. 25a, b; 1988, pl. XV, fig. 1–4) in two features: hypapophysis absent and anterior cotyles nearly circular in outline in "*M. surgayi*" versus hypapophysis present and ventrally elongate and anterior cotyles slightly compressed laterally in *Eoscapherpeton* (Fig. 3A–D versus E, F). These differences are so substantial that the two kinds of atlantes cannot reasonably be interpreted as belonging to the same genus. The atlantes of *Horezmia* (Nesov, 1981: pl. VIII, fig. 8) are similar to those of *Eoscapherpeton* (hypapophysis present and ventrally elongate) and strongly differ from atlantes referred by Nesov (1981) to "*Mynbulakia surgayi*". Trunk vertebrae of "*Mynbulakia*" (Nesov, 1981: pl. XI, figs. 15–18) also differ from those of *Eoscapherpeton* (Nesov, 1981: pl. XII, fig. 1a, b) and *Horezmia* (pers. obs., 2008) in lacking sculpture and a hypapophysis on the centrum, in being more elongate, and in having a relatively lower neural arch with a lower neural spine.

The only figured femur CCMGE 56/11657 (Nesov, 1981: pl. XI, fig. 19) and other femora referred to "*Mynbulakia surgayi*" (Nesov, 1981: 68) are short and bear a deep, plate-like crista trochanterica. The referred femora of *Eoscapherpeton* (Nesov, 1981: pl. X, fig. 6b) have similar proportions and also bear a plate-like crista trochanterica and I interpret femur CCMGE 56/11657 (and other femora referred to "*Mynbulakia surgayi*" by Nesov (1981)) as belonging to small and, presumably, younger individuals of *Eoscapherpeton*.

Because I interpret the holotype of "*Mynbulakia surgayi*" as belonging to a small and, presumably, younger individual of *Eoscapherpeton asiaticum* and because the former name has page priority (Nesov, 1981: 61 versus 67), I consider the names *Mynbulakia* Nesov, 1981, and *Mynbulakia surgayi* Nesov, 1981, to be junior subjective synonyms of, respectively, *Eoscapherpeton* Nesov, 1981, and *Eoscapherpeton asiaticum* Nesov, 1981, according to the action of the first reviser (Articles 24.2.1 and 24.2.2 of the International Code of Zoological Nomenclature). Atlantes and trunk vertebrae referred to "*Mynbulakia*" by

Nesov (1981) and additional vertebrae collected by the URBAC expeditions are comparable in size and morphology, so all of those specimens are assigned to the new salamander genus and species described below.

## SYSTEMATIC PALEONTOLOGY

LISSAMPHIBIA Haeckel, 1866

CAUDATA Scopoli, 1777

URODELA Duméril, 1806

*NEOVTRITON*, gen. nov.

**Type Species**—*Nesovtriton mynbulakensis*, sp. nov.

**Diagnosis**—As for type and only species.

**Etymology**—"Nesov", in honor of Lev Nesov in recognition of his pioneering work on Late Cretaceous salamanders from the Kyzylkum Desert, and Greek "triton", in Greek mythology, a marine God with man's body and fish's tail.

*NEOVTRITON MYNBULAKENSIS*, sp. nov.

(Figs. 2D, 3A–D, 4)

**Holotype**—ZIN PH 1/85, atlas (Fig. 3A–D)

**Etymology**—After Mynbulak Village in the Kyzylkum Desert, Uzbekistan.

**Type Locality and Horizon**—Site CBI-14, Dzharakuduk locality, Itemir-Dzharakuduk Depression, central Kyzylkum Desert, Navoi Viloyat, Uzbekistan. Bissekty Formation (Upper Cretaceous, Turonian).

**Referred Specimens**—Dentary: ZIN PH 2/85, Site CBI-17, Dzharakuduk locality; atlantes: ZIN PH 5/49, ZIN PH 3/85, ZIN PH 4/85, ZIN PH 5/85, Site CBI-14, and CCMGE 53/11657, site unknown, Dzharakuduk locality; trunk vertebrae: ZIN PH 6/85, ZIN PH 7/85, Site CBI-4V, and CCMGE 54/11657, 55/11657, 56/11756, and 57/16, site unknown, Dzharakuduk locality; and anterior caudal vertebra ZIN PH 8/85, Site CBI-14, Dzharakuduk locality; additionally, uncatalogued fragmentary dentaries figured by Nesov (1988: pl. XIV, figs. 24, 25; 1997: pl. IX, figs. 25) and atlantes, trunk vertebrae mentioned by Nesov (1981: 68) from Dzharakuduk locality.

**Diagnosis**—(primitive (-), derived (+), and uncertain polarity (?) character states). Differs from stem caudates *Marmorerpiton*, *Kokartus*, and *Karaurus* in having fully enclosed spinal nerve foramina in atlas (+) and lightly built vertebrae (+) and in lacking any sculpture on vertebrae (+). Differs from other Mesozoic crown caudates, except *Iridotriton*, *Chunerpeton*, *Sinerpeton*, *Jeholotriton*, *Laccotriton*, *Liaoxitriton*, *Pangerpeton*, *Kiyatriton*, *Eoscapherpeton*, and *Horezmia* in having uncapitate transverse processes on trunk vertebrae (?). Among Mesozoic crown caudates differs further from batrachosauroidids in retaining prominent intercotylar tubercle (-) and in having flat anterior cotylar surfaces on atlas (?); from scapherpetids in lacking any constriction at base of intercotylar tubercle (-); from *Iridotriton* in lacking spinal nerve foramina in caudal vertebrae (-), in having Meckelian groove in dentary not reaching symphysis (-), and in having subcentral keel on trunk vertebrae (?); from *Chunerpeton* in more posterior orientation of transverse processes on trunk vertebrae (ca. 75–85° from midline in *Chunerpeton* versus 55–65° in *Nesovtriton*) (?) and in having more elongate trunk vertebrae (ratio of maximum width of centrum:ventral midline length ca. 0.4 in *Nesovtriton* versus 0.6–0.7 in *Chunerpeton*) (+); from *Sinerpeton* and *Jeholotriton* in having relatively more elongate trunk vertebrae (ratio of maximum width of centrum:ventral midline length ca. 0.8–0.9 in *Sinerpeton* and *Jeholotriton*) (+); from *Liaoxitriton* and *Pangerpeton* in having subcentral keel on trunk vertebrae (?); from *Kiyatriton* in lacking median ridge on dorsal surface of intercotylar tubercle (?) and tripartite posterior cotyle with dorsoventral compression on atlas (?); and from *Eoscapher-*

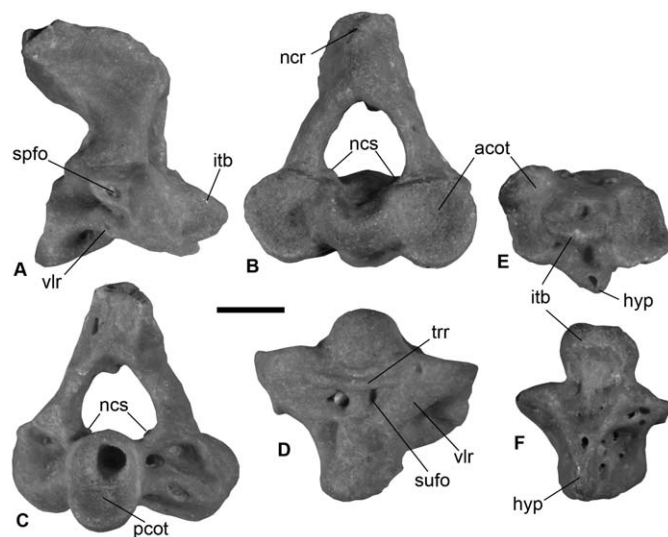


FIGURE 3. Atlantes of *Nesovtriton mynbulakensis*, gen. et sp. nov. and *Eoscapherpeton asiaticum*. A–D, holotype of *N. mynbulakensis*, ZIN PH 1/85, in (A) right lateral, (B) anterior, (C) posterior, and (D) ventral views. E–F, atlantal centrum of *E. asiaticum*, ZIN PH 1/85, in (E) anterior and (F) ventral views. **Abbreviations:** acot, anterior cotyle; hyp, hypapophysis; itb, intercotylar tubercle; ncr, neural crest; ncs, neural canal support; pcot, posterior cotyle; spfo, spinal foramen; sufo, subcentral foramen; trr, transversal ridge; vlr, ventrolateral ridge. Scale bar equals 1 mm.

*peton* and *Horezmia* in lacking hypapophyses on atlas and trunk vertebrae(-).

**Comments**—Comparisons with *Laccotriton* are not possible and the characters used above to distinguish *Nesovtriton* from *Chunerpeton*, *Sinerpeton*, *Jeholotriton*, *Pangerpeton*, and *Liaoxitriton* are tentative because detailed information about the structure of the dentaries and vertebrae in those Chinese taxa is limited or, in some cases, unknown.

## Description

The best preserved dentary ZIN PH 2/85 (Fig. 2D) is broken posteriorly near the end of the tooth row. ZIN PH 2/85 is slender and relatively low, with closely spaced teeth that lack intact crowns. The Meckelian groove is exposed medially and its anterior end lies more dorsally just below the tooth row (not ventromedially as in *Eoscapherpeton*) and does not reach the symphysis. The symphysis is moderately expanded and has a flat medial face. The post-symphyseal expansion of the subdental ridge is absent. Other incomplete dentaries similar to ZIN PH 2/85 were figured by Nesov (1988:pl. XIV, figs. 24, 25) as “dentaries with specific Meckelian groove” and “dentary of *Caudata* gen et sp. nov” (1997:pl. IX, figs. 25), but were not described.

The atlas is known from five complete or nearly complete specimens. The atlantal centrum (Nesov, 1981:pl. XI, fig. 14; 1988:pl. XIV, fig. 26; Fig. 3A–D) is relatively short and broad. The maximum anterior width (i.e., between lateral rims of the anterior cotyles) is about 3–4 mm and the ventral midline length, excluding the intercotylar tubercle (= odontoid process), is about 1.8–2.5 mm ( $n = 5$ ; ratio of maximum anterior width:ventral midline length without intercotylar tubercle about 1.5–1.7). The anterior cotyles are large and slightly dorsoventrally compressed or nearly circular in outline (ratio of maximum height:width about 1–1.2). The anterior cotyles are strongly inclined dorsally (at about 20° from the vertical plane) and their articular surfaces are nearly flat. The anterior cotylar surfaces are continuous medially across the lateral and ventral surfaces of the intercotylar tubercle. The intercotylar tubercle is large and moderately elongate, about 25–30 percent of the total ventral midline length of the bone. The intercotylar tubercle is gutter-like in anterior view, and is not constricted at its base. In lateral view, the ventral rim of the posterior cotyle lies well below the level of the ventral rim of the anterior cotyles. The anterior cotyles are relatively shorter than the posterior cotyle (ratio of maximum height of anterior cotyle:maximum height of posterior cotyle about 0.7–0.9). The posterior cotyle is laterally compressed and oval in outline, with the ventral end narrower. The inner surface of the posterior cotyle is deeply concave, has no a layer of calcified cartilage and bears a notochordal pit in its dorsal half. The ventrolateral ridges are low and swollen. Between the ventrolateral ridges, the ventral surface of the centrum may be perforated by one to three relatively large subcentral foramina and several small subcentral pits. A short, posteriorly curved transversal ridge extends across the ventral surface, just behind the intercotylar tubercle. Hypapophyses and basapophyses are absent. The spinal nerve foramen is fully enclosed by bone and opens in the upper part of the posterolateral surface of the anterior cotyle, close to the lateral rim of its articular surface. A short, but massive ridge extends posterodorsally from the upper part of the posterolateral surface of the anterior cotyle to the neural arch pedicel. Two foramina open behind the spinal nerve foramen, in the depression between this ridge and the ventrolateral ridge.

The atlantal neural arch is high. In the lateral view, the anterior edge of the neural arch is straight and vertical and the dorsal edge of the neural arch roof is almost horizontal. The anterior end of the neural arch is not modified, which differs from the typical condition in batrachosauroids where this part of the arch is often elaborated with prongs or a bony swelling

(J. Gardner, pers. comm., 2008). In anterior view the neural canal is nearly triangular in outline, with the ventral part wider than the intercotylar tubercle. The inner surface of the base of the neural arch bears a pair of small bony thickenings (= neural cord supports) that extend dorsomedially into the neural canal. The neural arch roof is posteriorly short and extends back only to about the level of the rim of the posterior cotyle. The dorsomedian surface of the neural arch roof bears a low neural crest. A posterodorsal end of the neural crest terminates in a scar for attachment of an unossified neural spine.

The six referred specimens collectively document the structure of the middle trunk vertebrae. The middle trunk vertebrae (Nesov, 1981:pl. XI, fig. 15–18; Fig. 4A–C) are relatively elongate, narrow, and low and consistently lack sculpture. The centrum is amphicoelous. In lateral view, the centrum is longer than wide (ratio of maximum centrum width:ventral midline length about 0.4) and its ventral surface is dorsally concave. The cotyles are circular in outline and bear a notochordal pit in the central part. Anterior basapophyses are variably present as anteriorly elongate knobs along the ventrolateral side of the anterior cotylar rim. Posterior basapophyses and spinal nerve foramina are consistently absent. The subcentral keel typically is a broad and shallow ridge extending between the ventral rims of the anterior and posterior cotyles. Subcentral foramina are small or absent.

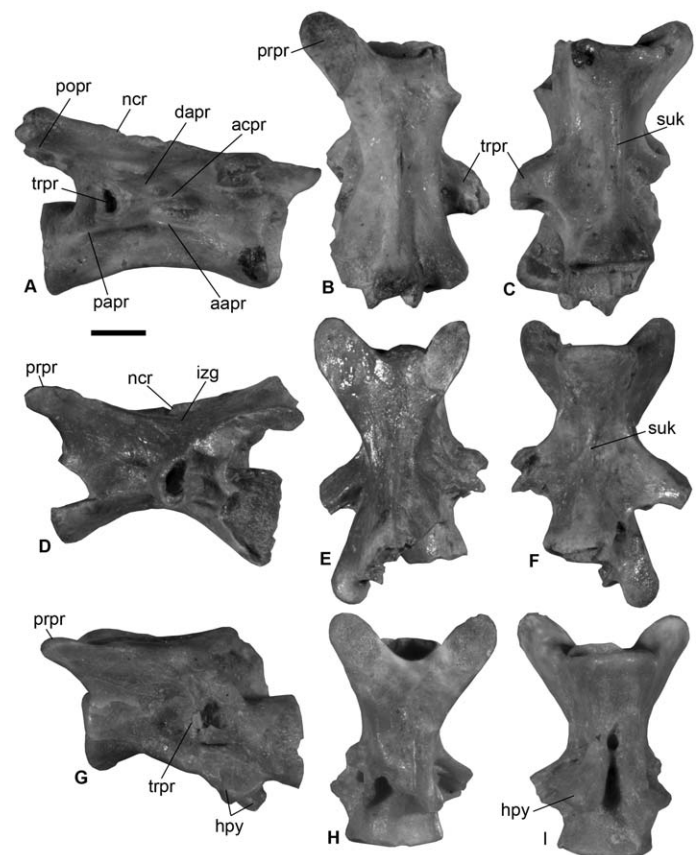


FIGURE 4. Postatlantal vertebrae of *Nesovtriton mynbulakensis*, gen. et sp. nov. A–C, middle trunk vertebra, ZIN PH 6/85, in (A) right lateral, (B) dorsal, and (C) ventral views; D–F, posterior trunk vertebra, ZIN PH 7/85, in (D) left lateral, (E) dorsal, and (F) ventral views; G–I, anterior caudal vertebra, ZIN PH 8/85, in (G) left lateral, (H) dorsal, and (I) ventral views. **Abbreviations:** aapr, anterior alar process; acpr, accessory alar process; dapr, dorsal alar process; hpy, haemapophysis; izg, interzygapophyseal ridge; ncr, neural crest; papr, posterior alar process; popr, postzygapophyseal process; prpr, prezygapophyseal process; trpr, transverse process; suk, subcentral keel. Scale bar equals 2 mm.



The transverse processes (= rib-bearers) are unicipital, elongate, and extend posterolaterally. Four alar processes (= laminae) are associated with the transverse process. The anterior alar process is a relatively short low flange that extends anteriorly from the base of the transverse process. The posterior alar process is a sharper and slightly shorter flange (in comparison with the anterior alar process) that extends posteriorly from the base of the transverse process. The dorsal alar process is low, swollen, and extends anterodorsally from the upper part of the transverse process; this is the shortest of the three main alar processes. A small, indistinct, ridge-like accessory process is present on most specimens between the dorsal and anterior alar processes. This accessory alar process is similar in length to or slightly shorter than the anterior alar process. The base of the transverse process is perforated anteriorly and posteriorly by a vertebral canal.

The neural canal is broad and low in anterior or posterior view. In dorsal outline, the roof of the neural arch is elongate and hourglass-shaped, with its lateral edge moderately constricted midway along the length of the arch at about the level of the base of the transverse process. The prezygapophyseal processes are oriented anterolaterally (at approximately 45° from the midline) and are elongate and narrow in dorsal outline, with a rounded anterolateral edge and straight lateral and medial margins. The prezygapophyseal processes project posterolaterally at complementary angles and the posterior border is straight and nearly transverse in dorsal or ventral views to the sagittal axis of the centrum. The prezygapophyseal articular surfaces are elliptical in outline and face dorsally, whereas the postzygapophyseal articular surfaces are oval in outline and face ventrally. The interzygapophyseal ridge is absent or weakly developed. The neural spine is reduced to a low median ridge which extends just past the posterior end of the neural arch roof. The posterior part of the spine is bifurcate and ends in a scar indicating that in life the distal-most end of the spine was finished in cartilage.

The posterior trunk vertebra is known from one nearly complete specimen ZIN PH 7/85 (Fig. 4D–F). The posterior trunk vertebra differs from the middle trunk vertebrae in having a more reduced subcentral keel and higher neural spine and, in most specimens, the accessory alar process is absent.

The anterior caudal vertebra is known from one specimen ZIN PH 8/85 (Fig. 4G–I), which lacks a posterior portion of the neural arch. The anterior caudal vertebra generally resembles the posterior trunk vertebrae, but differs in lacking the anterior alar process and in having a pair of short haemapophyses; the latter processes extend posteroventrally and have free distal ends. The presence of unicipital transverse processes indicates that this vertebra is from the anterior part of the caudal series.

## DISCUSSION

Atlantes, and trunk vertebrae referred to “*Mynbulakia*” by Nesov (1981) and the newly collected additional vertebrae are comparable in size and morphology, so all of these specimens are assigned to *Nesovtriton mynbulakensis* gen. et sp. nov. The dentary ZIN PH 2/85 and dentaries figured by Nesov (1988:pl. XIV, figs. 24–25; 1997: pl. IX, fig. 25) are in the same size category as vertebrae referred to *Nesovtriton mynbulakensis* gen. et sp. nov. and strongly differ in size from that of *Eoscapherpeton asiaticum* (the other salamander taxon from the vertebrate assemblage of the Byssesky Formation), so the assignment of this material to *Nesovtriton mynbulakensis* gen. et sp. nov. is the simplest assumption.

*Nesovtriton mynbulakensis* gen. et sp. nov. can be assigned to the Caudata based on the following features: dentary thin and elongate, having closely spaced teeth; atlas with prominent intercotylar tubercle bearing an articular surface for contact with ventral and lateral walls of foramen magnum; postatlantal vertebrae without a suture between the neural arch and cen-

trum, longer than wide, and may bear anterior basapophyses (Duellman and Trueb, 1986; Milner, 2000).

Another common character of *Nesovtriton* and caudates is the presence of spinal cord supports in the neural canal of the vertebrae. Spinal cord supports were first described by Wake and Larson (1973) in the recent plethodontid salamander *Eurycea bislineata* (Wake and Lawson, 1973). These bony thickenings extend into the neural canal and, in life, contact with strands of fibrous tissue extending along the ventrolateral surface of the nerve cord (Wake and Lawson, 1973:fig. 36; pers. obs., 2008). This structure is unique to caudates and absent in other vertebrates, including anurans and caecilians (Wake and Lawson, 1973). My observations on available specimens of recent and extinct salamanders also reveals the presence of this structure in hynobiids (*Salamandrella*), cryptobranchids (*Cryptobranchus* and *Andrias*), ambystomatids (*Ambystoma*), salamandrids (*Salamandra*), and Cretaceous crown group salamanders such as *Kiyatriton*, *Eoscapherpeton*, and *Scapherpeton*. Spinal cord supports are also present in the stem salamander *Kokartus* (pers. obs., 2008). The distribution of this structure among the above-mentioned salamanders suggests that the presence of the spinal cord supports is a synapomorphy of the Caudata.

*Nesovtriton mynbulakensis* gen. et sp. nov. can be placed in the clade of crown group salamanders (Urodela) because it has spinal nerve foramina fully enclosed by bone in the atlas, and lightly built vertebrae (Milner, 2000).

Among urodeles, the atlas of *Nesovtriton mynbulakensis* gen. et sp. nov. most closely resembles those of recent cryptobranchoids (hynobiids and cryptobranchids) in the following features: centrum relatively short; intercotylar tubercle gutter-like and without a constricted base; anterior cotyles flat and tilted dorsally; anterior cotylar surfaces continuous across lateral and ventral surfaces of intercotylar tubercle; ventrolateral ridges low and swollen; anterior edge of neural arch straight and vertical in lateral view; and neural crest low. None of those atlantal features are synapomorphic for cryptobranchoids. Postatlantal vertebrae of *Nesovtriton* retain the primitive caudate morphology (e.g., amphicoelous centra and absence of spinal nerve foramina) and most closely resemble those of cryptobranchoids (except hynobiids *Parahynobius* and *Onychodactylus*) in the presence of unicipital transverse processes. However, unicipital transverse processes are not a uniquely cryptobranchoid character (see discussion of this character in Evans et al., 2005) and, thus, this feature on its own cannot strongly support placing *Nesovtriton* in the Cryptobranchioidea. *Nesovtriton* has no derived characters of salamandroids (i.e., urodeles that are not cryptobranchoids) and, thus, can not be referred to this clade. Based on current evidence, *Nesovtriton* is best interpreted as a primitive crown group salamander with possible cryptobranchoid affinities. A more precise placement for this new taxon must await the recovery of more informative specimens and better resolution of the phylogenetic relationships among other basal crown caudates, particularly *Iridotriton* and taxa from the Jehol biota.

As currently understood, the vertebrate assemblage of the Byssesky Formation contains two salamander taxa: *Eoscapherpeton asiaticum* and *Nesovtriton mynbulakensis* gen. et sp. nov. *Eoscapherpeton* and *Horezmia*, the second of which is known only from the Cenomanian Khodzshakul Formation, share with cryptobranchids such characters as: midline contact along the dorsal processes of the premaxillae; frontal-maxillary contact; parietals strongly overlapped by frontals, no distinct medial process on the pterygoid; and pterygoid-parasphenoid contact (Gao and Shubin, 2003). Based on this suite of features, *Eoscapherpeton* and *Horezmia* can be referred to the Cryptobranchidae.

Attribution of *Eoscapherpeton* to the Scapherpetidae and “*Mynbulakia*” to the Batrachosauroididae, as originally proposed by Nesov (1981) and accepted by most subsequent workers (Duellman and Trueb, 1986; Milner, 2000; Shishkin, 2000), is

not supported by the current study. Thus, there are no salamander families common to the Late Cretaceous tetrapod assemblages of Asia and Euramerica. In North America, Late Cretaceous salamanders are represented by sirenids (*Habrosaurus*), amphiumids (*Proamphiuma*), batrachosauroidids (*Opisthotriton*, *Parrisia*, and *Prodesmodon*), and scapherpetids (*Scapherpeton* and *Lisserpeton*) (Holman, 2006). In Asia, Late Cretaceous salamanders are represented by cryptobranchids (*Eoscapherpeton* and *Horezmia*) and a crown group salamander with possible cryptobranchoid affinities (*Nesovtriton*). During the Mesozoic, the only salamanders common to both Asia and Euramerica were karaurids (stem caudates) during the Middle and Late Jurassic (Milner, 2000; Evans et al., 2005; Averianov et al., 2008). This distribution pattern could be a result of long, independent evolution of salamanders in Asia and Euramerica during the Cretaceous and it agrees with the vicariance model proposed by Milner (1983).

### CONCLUSIONS

- (1) Specimens previously assigned to *Mynbulakia surgayi* Nesov, 1981, represent a mixture of two salamander taxa: the holotype maxilla of *M. surgayi* and referred dentaries, frontals, and femora belong to small and, presumably, young individuals of *Eoscapherpeton asiaticum*, whereas referred atlantes and trunk vertebrae belong to the new salamander taxon *Nesovtriton mynbulakensis*, gen. et sp. nov. The names *Mynbulakia* Nesov, 1981, and *Mynbulakia surgayi* Nesov, 1981, are designated as junior subjective synonyms of, respectively, *Eoscapherpeton* Nesov, 1981, and *Eoscapherpeton asiaticum* Nesov, 1981.
- (2) The cryptobranchoid-like morphology of the atlas, the absence of spinal nerve foramina in the trunk and anterior caudal vertebrae, and the presence of unicipital transverse processes suggest that *Nesovtriton mynbulakensis* is a basal crown group salamander with possible cryptobranchoid affinities.
- (3) The vertebrate assemblage of the Byssekty Formation (Turonian) in Uzbekistan contains two salamander taxa: the possible cryptobranchoid *Nesovtriton mynbulakensis* and the cryptobranchid *Eoscapherpeton asiaticum*.
- (4) In contrast to previous interpretations, at present there is no evidence of any salamander families that were common to the Late Cretaceous tetrapod assemblages of Asia and Euramerica.

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