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A new salamander from the late Paleocene–early Eocene of Ukraine

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A new neotenic salamander, *Seminobatrachus boltyschkensis* gen. et sp. nov., is described based on 14 skeletons of late Paleocene–early Eocene age preserved on drill core slabs from the Cherkassy Region, central Ukraine. The new taxon is diagnosed by the following unique combination of characters: dorsal process of premaxilla posteriorly elongate and overlaps frontal; maxilla greatly reduced in size; parietal–squamosal contact absent; vomerine tooth row long and parallel to maxillary arcade; pterygoid has long anterior process; quadrate ossified; marginal and palatal teeth pedicellate; trunk vertebrae amphicoelous, each having a subcentral keel, anterior basapophysis, and spinal nerve foramina; ribs bicipital; carpals and tarsals unossified; and phalangeal formulae of 2-2-3-2 and 2-2-3-4-2 for manus and pes, respectively. Phylogenetic analysis nests *S. boltyschkensis* within Urodela (i.e., crown-clade salamanders), but its exact phylogenetic position is equivocal, resolving in one of three ways: (1) in an unresolved trichotomy with *Salamandra* and (Ambystomatidae + (*Dicamptodon* + *Rhyacotriton*)) (results obtained in NONA v. 2.0, with the WINCLADA v. 1.00.08 interface; the parsimony ratchet (island hopper) algorithm), (2) as a sister taxon of (*Salamandra* + (Ambystomatidae + (*Dicamptodon* + *Rhyacotriton*))) clade (results obtained in TNT v. 1.1; the implicit enumeration search algorithm) or (3) as a sister taxon of Ambystomatidae (results obtained in PAUP v. 4.0b10; the branch-and-bound search algorithm).

Key words: Caudata, Urodela, phylogeny, Paleocene, Eocene, Ukraine.

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Introduction

Salamanders (Caudata) are one of the three modern clades of amphibians. After their first appearance in the fossil record in the Middle Jurassic (Evans et al. 1988, Nesov 1988; Evans and Waldman 1996; Milner 2000), salamanders underwent several episodes of considerable diversification and dispersal (Milner 1983, 2000; Duellman and Trueb 1986), the last taking place during the Late Cretaceous and the Paleocene–Eocene thermal maximum (Vieites et al. 2007). During these intervals of global warming several extant salamander families appeared in the fossil record (Sirenidae, Amphiumidae, Salamandridae, Proteidae, Plethodontidae, and Ambystomatidae sensu Frost et al. 2006) and some major clades of the most diverse modern salamander families, the Plethodontidae and Salamandridae, were established (Vieites et al. 2007; Zhang et al. 2008).

The European Paleocene–Eocene salamander fossil record is relatively sparse and largely limited to Western Europe (Belgium, France, and Germany). Most of the Paleocene– Eocene salamander taxa are based on disarticulated material (usually isolated vertebrae) and very rarely on complete or partial skeletons (Estes 1981). Three salamander families have been reported for this interval in Europe: batrachosauroidids, "dicamptodontids", and salamandrids (Estes 1981; Milner 2000). Batrachosauroidids are represented by *Palaeoproteus* (late Paleocene–middle Eocene), "dicamptodontids" by two genera (*Geyeriella* and *Wolterstorffiella*, late Paleocene), and salamandrids by several genera (*Koalliella*, late Paleocene– early Eocene; *Chelotriton*, middle Eocene–Recent; *Chioglossa*, late Eocene–Recent; *Megalotriton*, late Eocene or early Oligocene–early Miocene; *Salamandra*, late Eocene– Recent; *Tylototriton*, middle Eocene–Recent; and *Triturus*, ?Eocene– Recent) (Estes 1981; Roček 1994; Venczel 2008).

Here we describe and discuss the phylogenetic affinities of a new genus and species of salamander based on 14 skeletons of late Paleocene–early Eocene age from Ukraine. These are the first record of Paleocene or Eocene salamanders in Eastern Europe. These specimens are part of a much larger collection of fish and invertebrate fossils that were identified in the late 1960s by the Soviet geologist A. Semin, in sapropelite layers in numerous cores that were drilled in 1967 near Boltyshka village, in the Cherkassy Region of central Ukraine.

Institutional abbreviations.—PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russian Federation.

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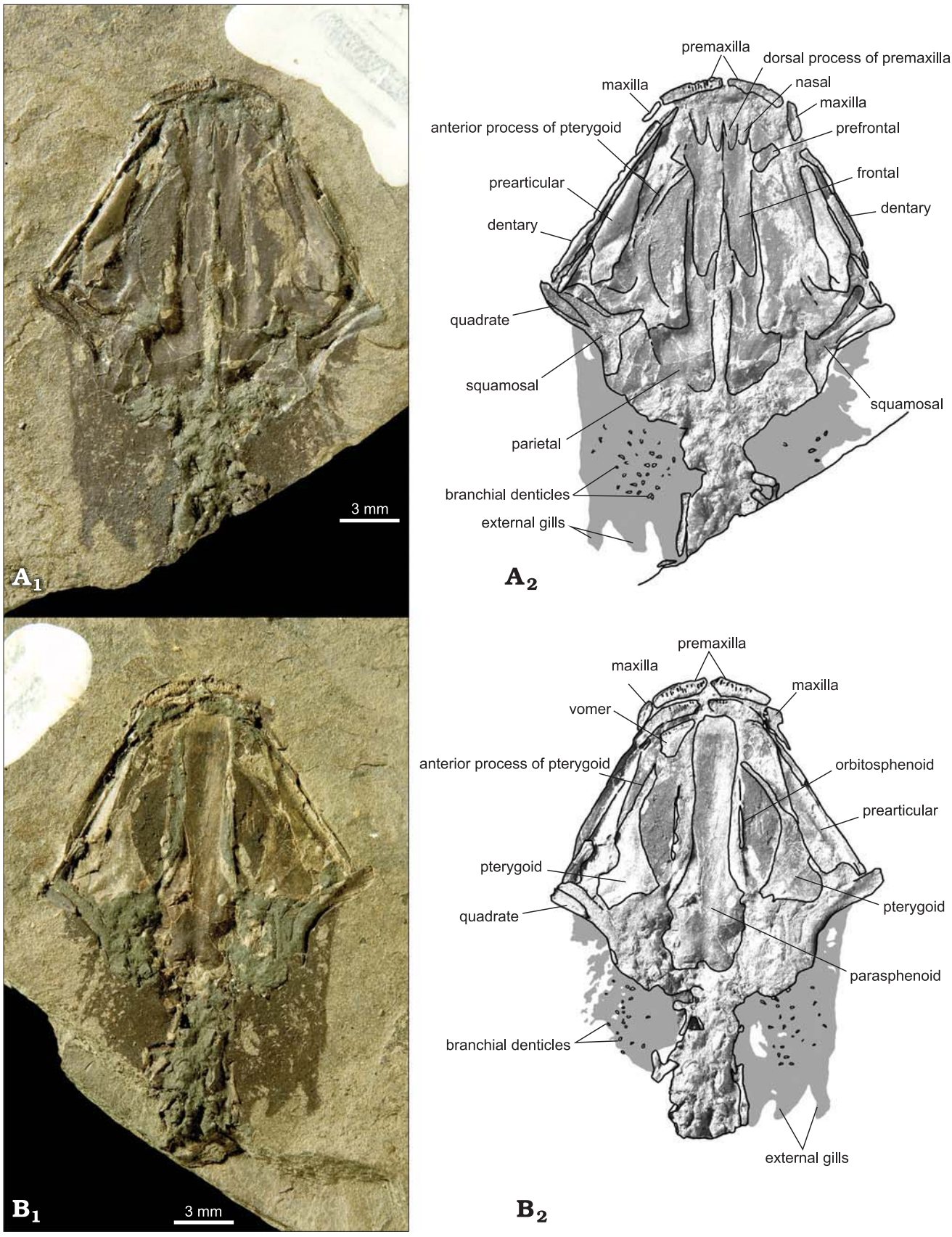

Fig. 1. A salamander *Seminobatrachus boltischki* gen. et sp. nov. from the lower unit of the Boltyshka sapropelite strata (late Paleocene–early Eocene, Ukraine), skull and anteriormost vertebrae with traces of soft tissue, holotype, PIN 3991/9. **A**. PIN 3991/9a, part in dorsal aspect. **B**. PIN 3991/9b, counterpart in ventral aspect. Photographs as exposed (A_1, B_1) and interpretative drawings (A_2, B_2). Grey areas in interpretive drawings represent soft tissues.

Material and methods

All of the salamander specimens from the Boltyshka sapropelites are housed in the collection of PIN. The specimens came from six drill cores, and they consist of articulated skeletons, none of which is complete. Most specimens are exposed on slabs preserved as part and counterpart; these are designated by, respectively, the suffixes "a" and "b" in the corresponding PIN number. The 14 skeletons reported here consist of one nearly complete skeleton (PIN 3991/14) and thirteen incomplete skeletons. Imprints of soft tissues are present on PIN 3991/4a, b, PIN 3991/6, PIN 3991/9a, b, PIN 3991/12a, b, PIN 3991/13a, b, and PIN 3991/14.

All specimens are morphologically similar and, therefore, are assigned to one species.

To gain additional information on vertebral morphology, micro-computer tomography was used to scan one specimen (PIN 3991/1a, articulated part of vertebral column and limbs) at the Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn, Bonn, Germany. Digital reconstructions were generated using AVIZO 5 (the 3D visualization Software for Scientific and Industrial data).

Geological setting and associated vertebrate assemblage

The sapropelite strata in the vicinity of Boltyshka village are overlain by deposits of the Kiev Svita (= "Formation"), which is dated as middle Eocene on the basis of its foraminifera (Ryabokon' 2002). The underlying, sapropelite part of the core samples has been dated as late Paleocene–early Eocene based on its molluscs, ostracods, insects, and fishes (Stanislavskiy 1968; Sytchevskaya 1986). The sapropelite strata are composed of three units: the upper unit (thickness up to 55 metres) lacks vertebrate fossils; the middle unit (thickness up to 130 metres) contains rare teleost fossils in its lower part; and the lower unit (known thickness at least 270 metres) contains most of the teleost and all of the salamander fossils. Apart from salamanders, the Boltyshka sapropelites have produced articulated remains of teleostean fishes, such as skeletons of *Thaumaturus avitus*, *Notogeneus gracilis*, *Boltyshia brevicauda*, *B. truncata*, and *Tretoperca vestita*, all found at depths of 230 to 430 metres (Sytchevskaya and Daniltschenko 1975; Sytchevskaya 1986).

The salamanders come from stratigraphically higher layers than the fishes (depths of 140 to 200 metres) with one exception—fragmentary skeleton PIN 3991/4 was found almost in 85 metres deeper than the others (depth 283.2 metres). The main salamander-bearing layers probably were deposited in more marshy conditions that were less hospitable or impossible for teleost fish colonization.

Systematic palaeontology

Amphibia Linnaeus, 1758

Caudata Scopoli, 1777

Urodela Duméril, 1806

Genus *Seminobatrachus* nov.

Type species.—*Seminobatrachus boltyschkensis* sp. nov.; see below.

Etymology: The genus is named after the geologist A. Semin who discovered this salamander material, and from Greek *batrachus* (βατραχος), frog.

Diagnosis.—As for type and only species (see below).

Seminobatrachus boltyschkensis sp. nov.

Etymology: From the Boltyshka locality.

Holotype: PIN 3991/9, part (PIN 3991/9a) and counterpart (PIN 3991/9b) skull and anteriormost vertebrae preserved on sapropelite slabs from a drill core, in dorsal and ventral aspects, respectively (Fig. 1).

Type locality: Drill hole near Boltyshka village, Cherkassy Region, central Ukraine.

Type horizon: Lower unit of unnamed sapropelite strata; late Paleocene–early Eocene.

Referred material.—Thirteen incomplete skeletons, all preserved on sapropelite slabs from drill cores: PIN 3991/1a, b, part and counterpart of articulated, incomplete vertebral column (trunk, sacral, and anterior caudal regions) in lateral aspect and limbs (Fig. 2); PIN 3991/3a, b, part and counterpart of skull, anterior part of vertebral column, and right forelimb in, respectively, dorsal and ventral aspects (Fig. 3); PIN 3991/4a, b, part and counterpart of skull, pre-sacral part of vertebral column, and forelimbs in, respectively, dorsal and ventral aspects (Fig. 4); PIN 3991/6a, b, part and counterpart of skull, anterior part of vertebral column, and left forelimb in, respectively, dorsal and ventral aspects (Fig. 5); PIN 3991/14, nearly complete skeleton in dorsal aspect (Fig. 6); PIN 3991/2a, b, part and counterpart of posterior part of vertebral column and hindlimbs, both in lateral aspect; PIN 3991/8a,b, part and counterpart of skull and anterior part of vertebral column in, respectively, ventral and dorsal aspects; PIN 3991/10a,b, part and counterpart of skull, anterior part of vertebral column, and forelimbs; PIN 3991/11a, b, part and counterpart of skull, anterior part of vertebral column, and forelimbs in, respectively, ventral and dorsal aspects; PIN 3991/12a, b, part and counterpart of skull, anterior part of vertebral column, and forelimbs in, respectively, ventral and dorsal aspects; PIN 3991/13a, b, part and counterpart of skull, anterior part of vertebral column, and forelimbs in, respectively, dorsal and ventral aspects; PIN 3991/19, of skull and anterior part of vertebral column in dorsal aspect; PIN 3991/20, middle part of vertebral column, limbs, and pelvic girdle.

Diagnosis.—Polarities of character states indicated using the following symbols: primitive (-); derived (+); and uncertain (?). Neotenic crown-group salamander characterized by the following, unique combination of characters: premaxilla with relatively wide, posteriorly elongated dorsal process (+) that overlaps frontal (+); maxilla small, abbreviated (+); nasal nar-

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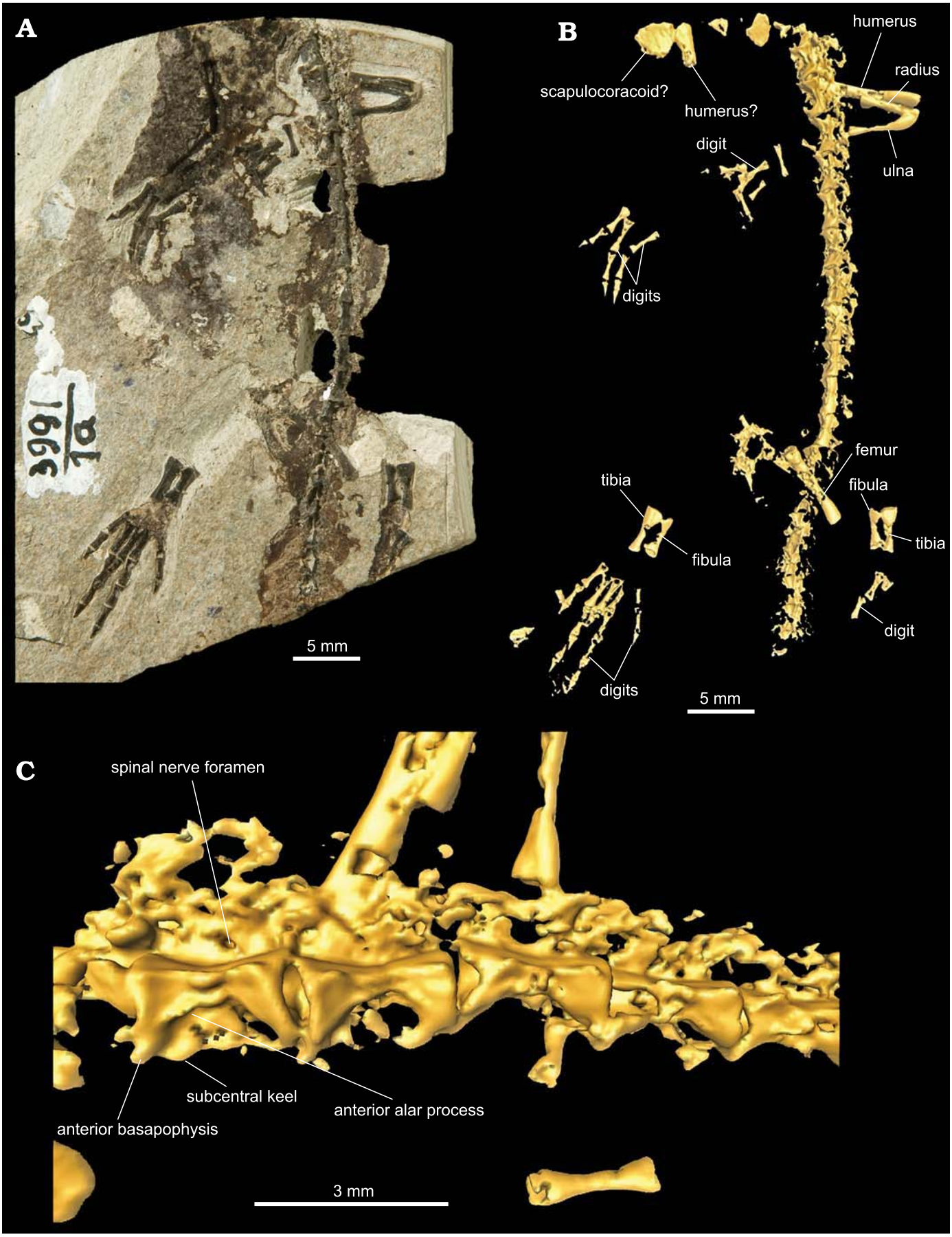

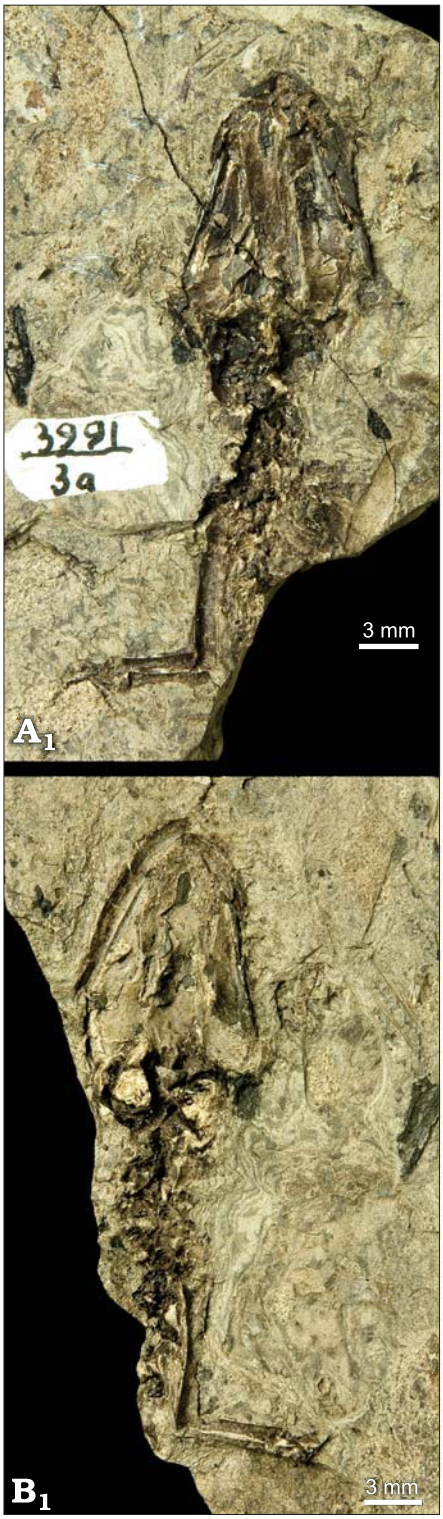

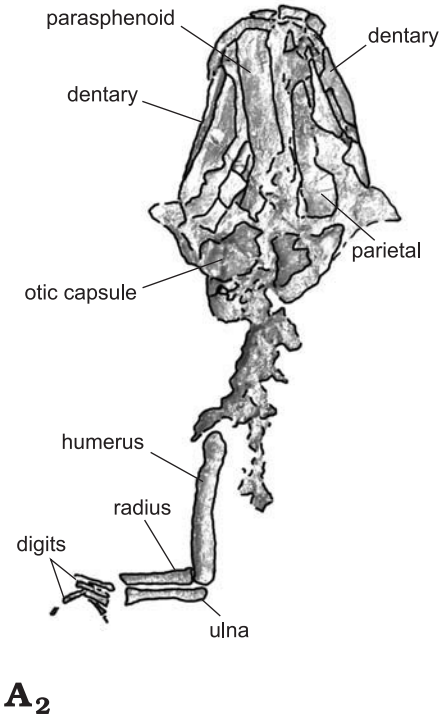

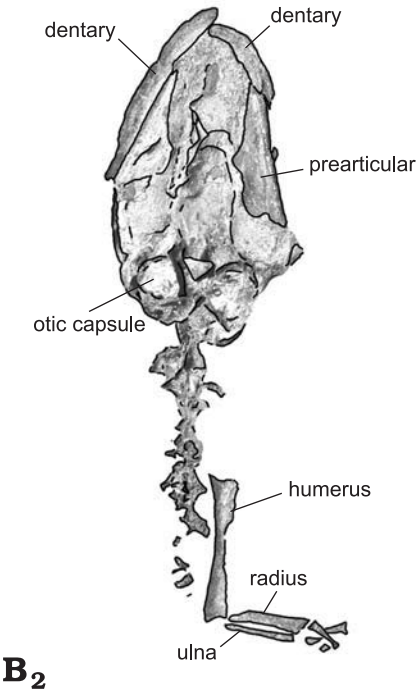

Fig. 3. A salamander *Seminobatrachus boltischki* gen. et sp. nov. from the lower unit of Boltyshka sapropelite strata (late Paleocene–early Eocene, Ukraine), part and counterpart of skull, anterior part of vertebral column, and right forelimb, PIN 3991/3. **A**. PIN 3991/3a, part in dorsal aspect. C, D. PIN 3991/3b, counterpart in ventral aspect. Photographs as exposed (A_1, B_1) and interpretative drawings (A_2, B_2).

← Fig. 2. A salamander *Seminobatrachus boltischki* gen. et sp. nov. from the lower unit of Boltyshka sapropelite strata (late Paleocene–early Eocene, Ukraine), articulated, incomplete vertebral column (trunk, sacral, and anterior caudal regions) and limbs, PIN 3991/1a, part in lateral aspect. **A**. Photograph as exposed. **B**, **C**. Digital reconstructions based on high-resolution computed tomography of entire specimen (**B**) and close up of pectoral region rotated 90° counterclockwise (**C**).

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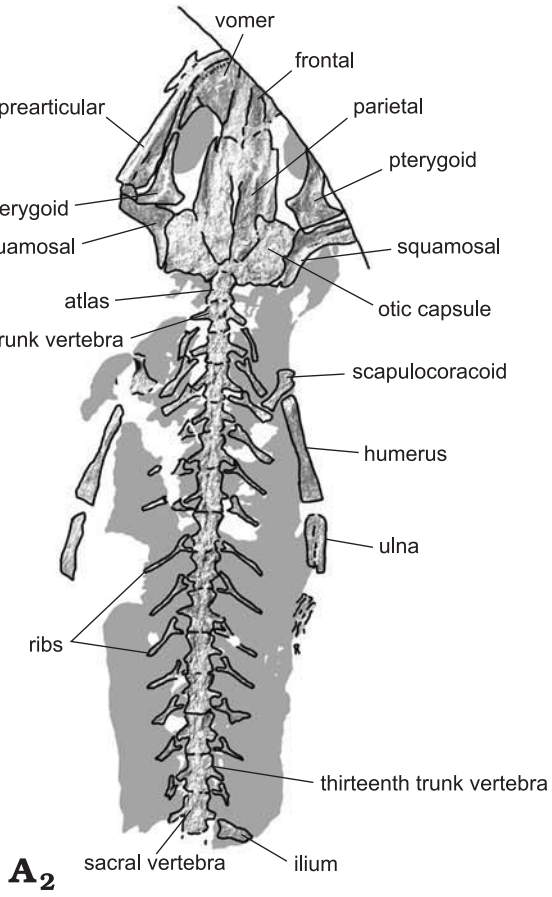

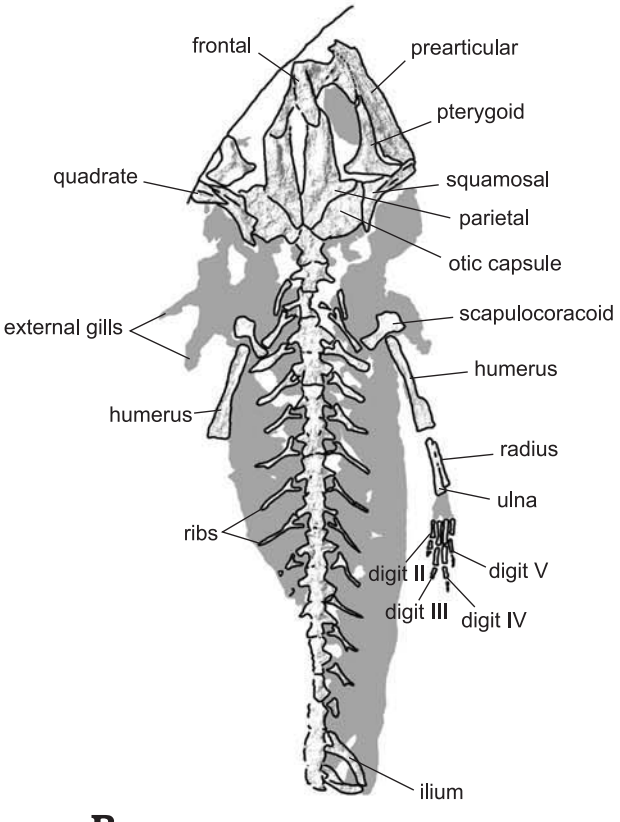

row and shorter than dorsal process of premaxilla (+); medial contact of nasals absent (+); parietal–squamosal contact absent (+); vomerine tooth row long and parallels maxillary arcade (-); pterygoid with long anterior process (-); ossified quadrate present (-); marginal and palatal teeth pedicellate (?); trunk vertebrae amphicoelous (-), with subcentral keel (+), spinal nerve foramina (+), and anterior basapophysis (+); bicipital ribs (-); carpals and tarsals not ossified (-); phalangeal formulae of 2-2-3-2 (?) and 2-2-3-4-2 (?) for manus and pes, respectively.

Stratigraphic and geographic range.—Late Paleocene–early Eocene, central Ukraine.

Remarks.—*Seminobatrachus* differs from stem caudates (Karauridae and *Marmorerpeton*) in lacking sculpture on the skull roof bones, in having lightly built vertebrae, and in having spinal nerve foramina in its trunk vertebrae. Differs from Hynobiidae and Cryptobranchidae in having spinal nerve foramina and bicipital transverse processes in trunk vertebrae. Differs from other crown-group salamanders, except Sirenidae, Salamandridae, Ambystomatidae, and Plethodontidae, in having spinal nerve foramina in trunk vertebrae. *Seminobatrachus* further differs from Salamandridae and Plethodontidae in having amphicoelous trunk vertebrae; from Sirenidae in having pedicellate marginal teeth and nasals lateral to the dorsal process of premaxilla, and from Ambystomatidae in having subcentral keel on trunk vertebrae and abbreviated maxilla.

Description

Skull overview.—Skulls and skull fragments are present in several specimens (Figs. 1, 3–6). The skull is relatively short (width to length ratio is about 1.1), with the widest part at the level of the jaw–skull articulation, and an anteriorly narrowing rostrum. The orbit is large and the cheek is widely emarginated from posterior abbreviation of the maxilla. The skull roof bones have no dorsal sculpture. The presence of lacrimals or septomaxillae cannot be confirmed in the available specimens.

Maxillary arcade and suspensorium.—The premaxilla (Figs. 1, 5) has an elongate maxillary process (= posterior process) and a narrow, relatively long and pointed dorsal process (= alary process); the latter arises from the medial part of the bone and posteriorly overlaps the anterior part of the frontals. The length of the dorsal process is nearly equal to the width of the dental margin. The dorsal processes on the paired premaxillae contact medially along their anterior halves.

The maxilla (Figs. 1, 5) is posteriorly abbreviated, but retains a short dorsal process and a slender posterior process. There is a large foramen in the anterior part of the dorsal process.

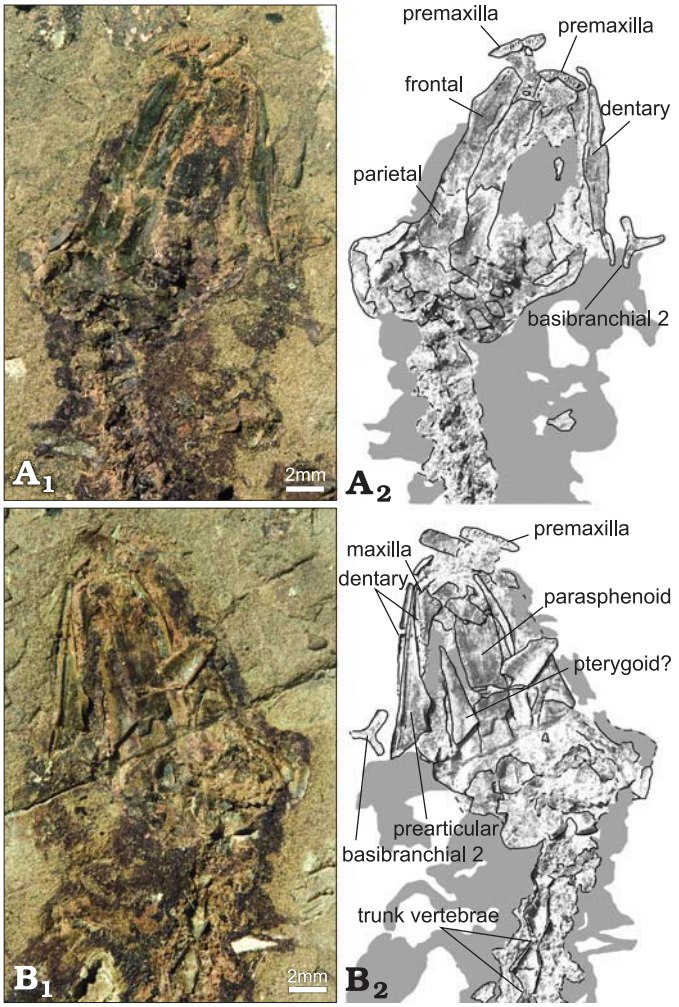

Fig. 5. A salamander *Seminobatrachus boltischki* gen. et sp. nov. from the lower unit of Boltyshka sapropelite strata (late Paleocene–early Eocene, Ukraine), close up of part and counterpart of skull, anterior part of vertebral column with traces of soft tissue, PIN 3991/6. **A**. PIN 3991/6a, part in dorsal aspect. **B**. PIN 3991/6b, counterpart in ventral aspect. Photographs as exposed (A_1, B_1) and interpretative drawings (A_2, B_2). Grey areas in interpretive drawings represent soft tissues.

The quadrate (Figs. 1, 4) is well ossified and has a typical salamander morphology, with expanded distal and narrow proximal portions.

Skull roof.—The nasal (Fig. 1) is small, with a narrow, triangular posterior portion that posteriorly overlaps the anterior part of the frontal and lies parallel and lateral to the dorsal process of the premaxilla. The nasal does not extend as far posteriorly as the dorsal process of the premaxilla. The structure of the anterior portion of the nasal is unknown.

The prefrontal (Figs. 1, 6) is larger than the nasal. The posterior portion of the prefrontal tapers posteriorly. The structure of the anterior portion of the prefrontal is unknown.

← Fig. 4. A salamander *Seminobatrachus boltischki* gen. et sp. nov. from the lower unit of Boltyshka sapropelite strata (late Paleocene–early Eocene, Ukraine), part and counterpart of skull, pre-sacral part of vertebral column, and forelimbs with traces of soft tissue, PIN 3991/4. **A**. PIN 3991/4a, part in dorsal aspect. **B**. PIN 3991/4b, counterpart in ventral aspect. Photographs as exposed (A_1, B_1) and interpretative drawings (A_2, B_2). Grey areas in interpretive drawings represent soft tissues.

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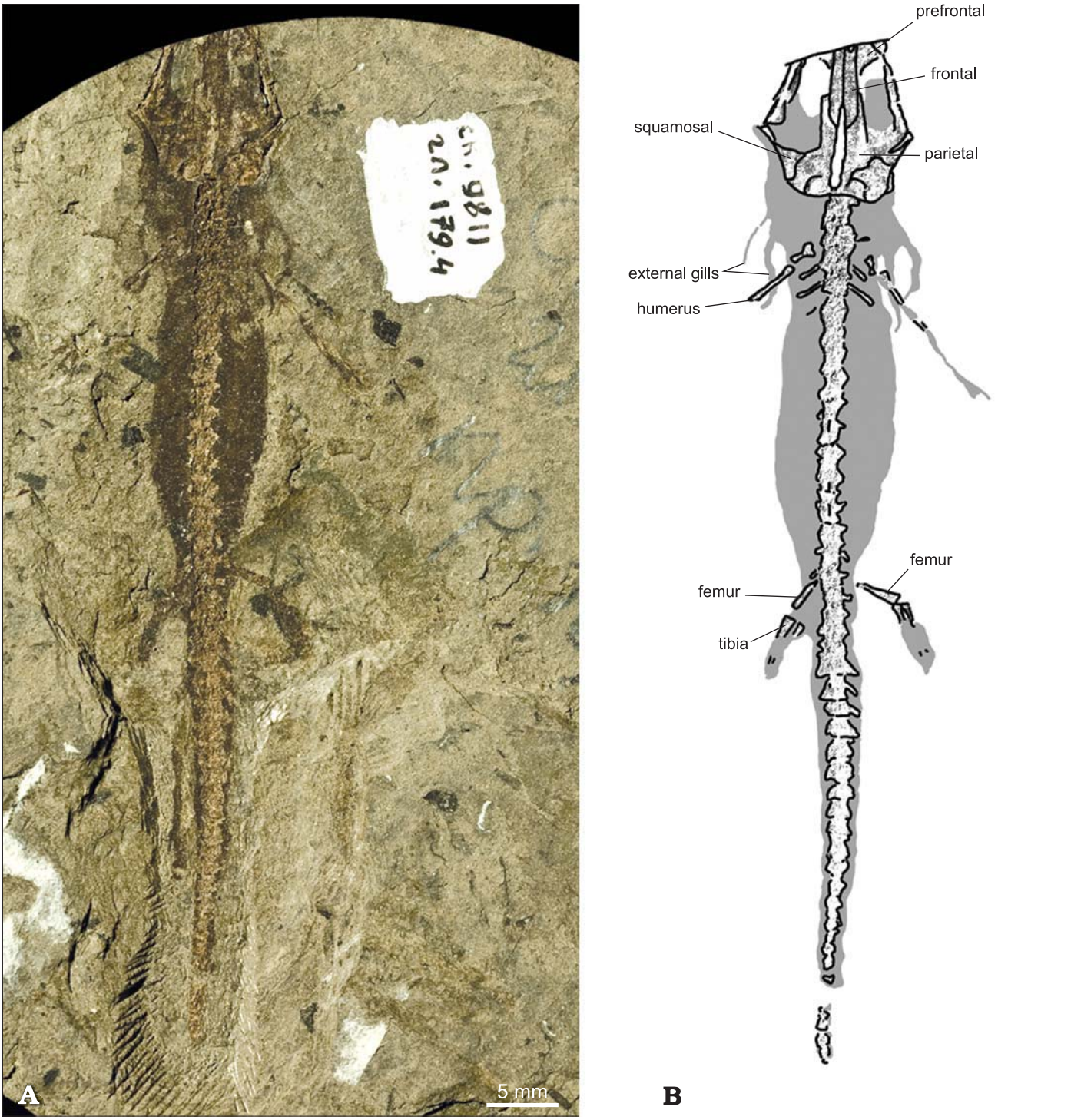

Fig. 6. A salamander *Seminobatrachus boltischki* gen. et sp. nov. from the lower unit of Boltyshka sapropelite strata (late Paleocene–early Eocene, Ukraine), nearly complete skeleton with traces of soft tissue, PIN 3991/14, in dorsal aspect. Photograph as exposed (**A**) and interpretative drawing (**B**). Grey areas in interpretive drawings represent soft tissues.

The frontal (Figs. 1, 3A, 4–6) is long, slender, and slightly tapered anteriorly, with nearly parallel lateral edges and a small anterolateral extension. The anterior portion is overlapped by the dorsal process of the premaxilla and the posterior portion of the nasal. The posterior portion is nearly triangular and overlaps the anterior portion of the parietal. The frontals contact one another only anteriorly, whereas more posteriorly they are separated by the median fontanelle. This fontanelle is elongate and rhomboidal in shape (with its widest part level with the anterior edge of the posterolateral extension of the parietal), and also separates the parietals posteriorly. The frontals contribute less than 50% of the orbital margin.

The parietal (Figs. 1, 3–6) is the longest bone of the skull roof (ratio of maximum lengths of frontal versus parietal is about 0.8), with a narrow and long posterolateral extension. The parietals appear to be slightly wider than the frontals. The posterior part of the parietal is curved and tapers posteriorly.

The squamosal (Figs. 1, 4, 6) is "T"-shaped bone, with a broad dorsal portion and a tapered ventral portion. It contacts the braincase dorsally, but has no contact with the posterolateral extension of the parietal. The ventral portion of the squamosal contacts the quadrate posteroventrally along most of its length.

Palate.—The vomer (Figs. 1, 4) is large, with a broad choanal notch and well-developed postchoanal flange. It clearly contacts the premaxilla anteriorly, but the detailed structure of the medial part of the vomer is unknown. The vomer has one tooth row that is long and extends close to and parallel with the maxillary arcade.

The triradiate pterygoid (Figs. 1, 4) has a wide and short medial process (= medial ramus or basipterygoid ramus). The structure of the pterygoid–parasphenoid contact (and basicranial articulation) is unknown but it seems to be loose. The anterior process (= palatine ramus) is long, strongly arcuate, and tapers anteriorly. The anterior portion of the anterior process is anteromedially oriented.

The parasphenoid (Figs. 1, 3, 5) is the largest bone of the palate. It has a long cultriform process that is relatively narrow, nearly parallel-sided in its medial part, and slightly expanded anteriorly. The cultriform process is overlapped anteriorly by the vomers (this feature is visible in PIN 3991/11, which is not figured in this paper). The lateral processes (= lateral ala) are not preserved.

Braincase.—The orbitosphenoid (Fig. 1) is long (about one-half the length of the cultriform process of the parasphenoid). The optic foramen is situated nearly at the anteroposterior midpoint of the orbitosphenoid. The otic capsule is well ossified, and there is no indication of a suture between the left and right otic capsules. The posterior end of the braincase bears a pair of large occipital condyles (Fig. 5B).

Mandible.—The mandibles are present in several specimens (Figs. 1, 3–6). Two bones are easily recognizable in all available specimens: dentary and prearticular. The dentary is elongate and deep. The medial surface has a wide Meckelian groove that narrows anteriorly and is bordered dorsally by a wide subdental shelf.

The prearticular (Figs. 1, 3–5) is long, has a narrow and tapering anterior part and an expanded posterior part. The posterior part has a sharp and high dorsomedial edge, which gradually decreases in size anteriorly, and a dorsomedially-oriented coronoid process. The posterior (the highest) part of the dorsomedial edge is nearly the same height as the coronoid process. The lateral edge of the prearticular is thickened, and there is a shallow groove between its lateral and dorsomedial edges.

Hyobranchial apparatus.—The only preserved element of the hyobranchial skeleton is basibranchial 2 (present in PIN 3991/6). Additionally, branchial denticles are present in the holotype PIN 3991/9 and three specimens (PIN 3991/4, 9, 6) have imprints of the external gills.

Basibranchial 2 (Fig. 5) is triradiate (inverted "Y"-shaped), with all three processes equal in size (as in the Early Cretaceous *Valdotriton*, ambystomatids, and some modern salamandrids; see Evans and Milner 1996; Rose 2003).

There are six rows of branchial denticles (Fig. 1) on the four branchial arches, having a configuration of 1.2.2.1. This linear arrangement of the branchial denticles allows us to reconstruct the presence of the four ceratobranchials: ceratobranchials 1 and 4 each support one row, whereas ceratobranchials 2 and 3 each support two rows of branchial denticles. Each denticle is conical, with an expanded base and a relatively thin, curved crown.

Only two pairs of external gills are present in any of the available specimens (Figs. 1, 4, 6). The first pair of external gills was supported by ceratobranchial 2 and the second by ceratobranchial 3. All external gills are nearly equal in size. If not a preservation artefact, the presence of only two pairs of external gills in *Seminobatrachus* is a unique feature among salamanders. Normally three pairs of external gills are present in larvae and in adults of those neotenic taxa, such as *Necturus*, that have external gills.

Dentition.—Marginal dentition is present on the premaxillae, maxillae, and dentaries. The number of teeth on the maxilla and dentary is unclear; the estimated premaxillary tooth count is 18–20. All marginal teeth are pedicellate. The tooth crowns of the marginal teeth are sharp but their detailed structure (e.g., number of cuspids) is unknown. Palatal dentition is present on the vomers; the estimated vomerine tooth count is more than 35–40. The vomerine teeth are smaller than the marginal teeth. The vomerine teeth are pedicellate as well, but the structure of their crowns is unknown.

Axial skeleton.—The vertebral column consists of 14–16 presacral vertebrae (15 or 16 in PIN 3991/14; 14 in PIN 3991/4) and more than 25 caudal vertebrae (the end of the tail is lacking in PIN 3991/14 and the estimated number of caudal vertebrae based on that specimen is 30–33). All trunk vertebrae were articulated with bicipital (= two-headed) ribs.

The detailed structure of the atlas (Fig. 4) is unknown. It is wider than the anterior trunk vertebrae in dorsal view and has no transverse processes. The length of the atlas is nearly equal to that of the following anterior trunk vertebrae.

The anterior trunk vertebrae (Figs. 2, 4) are relatively elongate, narrow, low, and consistently lack sculpture. The centrum is amphicoelous. In lateral view, the centrum is longer than wide, hourglass-shaped, and its ventral surface bears a prominent subcentral keel. Anterior basapophyses are present as anteriorly elongate knobs along the ventrolateral sides of the anterior cotylar rim. Posterior basapophyses are consistently absent. The transverse processes (= rib-bearers) are elongate, bipartite (inferred from the presence of bicipital ribs), and extend posterolaterally. The base of the transverse

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process is perforated by a vertebrarterial canal. Two alar processes (= laminae) are associated with the transverse process. The anterior alar process is a relatively long and wide flange that extends anteroventrally from the base of the transverse process and it almost reaches the anterior basapophysis. The base of the posterior alar process is nearly equal in length with that of the anterior alar process and extends posteroventrally from the base of the transverse process. The neural arches are poorly preserved and their structure is unknown. The spinal nerve foramen is visible on the inner surface of the base of the neural arch (Fig. 2C) just behind the anteroposterior midpoint of the vertebra.

The middle and posterior trunk vertebrae differ from the anterior trunk vertebrae in being more elongate and in having a shallower subcentral keel. Spinal nerve foramina are consistently present.

The sacral vertebrae are poorly preserved. According to specimen PIN 3991/4 (Fig. 4) the sacral vertebra does not differ in shape or size from the adjacent posterior trunk and anterior caudal vertebrae.

The anteriormost caudal vertebra (Figs. 2, 4) is as elongate as the posterior trunk vertebrae and it lacks haemapophyses. In successively more posterior caudal vertebrae, the centrum length gradually decreases and haemapophyses are consistently present. The latter processes are relatively narrow (in comparison with neural arches on the same vertebrae), rod-like, and extend posteroventrally. The depths of the haemapophyses decrease posteriorly along the caudal series.

All ribs are bicipital. The largest ribs are associated with the second and third trunk vertebrae. These robust ribs have expanded distal ends. The ribs become weaker and shorter towards the sacrum.

Pectoral girdle and forelimb.—The scapula and coracoid form a single ossification. The scapulocoracoid (Figs. 4, 6) has an expanded coracoid portion and an elongate scapular portion that is slightly constricted at its base. The humerus (Figs. 2–4, 6) is straight, with expanded and flattened proximal and distal ends. The ulna (Figs. 2–4) is slightly longer than the radius and roughly half the length of the humerus. The carpals are not ossified. Four digits (Fig. $4B_2$) are present in the manus, with digit IV the longest. The phalangeal formula of the manus is 2-2-3-2.

Pelvic girdle and hindlimb.—The ilium (Fig. 4) has a relatively long and narrow proximal part. The ischia are preserved in only one specimen (PIN 3991/20); they are kidney-shaped and contact one another medially along most of their lengths. The femur (Figs. 2, 6) is of similar length to the humerus, and the proximal and distal ends are expanded and compressed. The trochanter and crista trochanterica are well developed. The tibia and the fibula (Figs. 2, 6) are nearly similar in length. The tibia is more robust than the fibula and has a more expanded distal end. The fourth digit is the longest of the five (Fig. 2), and the phalangeal formula of the pes is 2-2-3-4-2.

Discussion

The specimens attributed to *Seminobatrachus boltyschkensis* gen. et sp. nov. have several salamander larval features: short maxillary arcade with reduced maxilla; vomerine tooth row long and parallel to the maxillary arcade; pterygoid with long, medially orientated anterior process; presence of external gills; and unossified carpals and tarsals. We interpret the specimens as neotenic, not juvenile, because they show adult features of well-developed skull bones (including ossified quadrate), pedicellate teeth (non-pedicellate or subpedicellate in salamander larvae; Vassilieva and Smirnov 2001), and relatively large body sizes (the estimated lengths of the largest individuals are about 10–12 centimetres).

Seminobatrachus boltyschkensis appears to be distinct from all the late Paleocene–early Eocene salamanders and can not be referred unambiguously to any extant or extinct salamander taxon. In order to elucidate the relationships of *S. boltyschkensis* within Caudata, a phylogenetic analysis was conducted using NONA v. 2.0 (Goloboff 1999), run with the WINCLADA v. 1.00.08 interface (Nixon 1999). We used the most recent matrix of Zhang et al. (2009), with the addition of three taxa (*Seminobatrachus* gen. nov., Batrachosauroididae, and *Kokartus*) and corrected, modified, or added states for seven characters to accommodate the conditions in *Karaurus*, Cryptobranchidae, Ambystomatidae, Hynobiidae, Ambystomatidae, Proteidae, and Amphiumidae (see Appendix 1). Multi-state characters were treated as unordered. One thousand repetitions of the parsimony ratchet (island hopper) algorithm recovered three most parsimonious trees (tree length 213; consistency index 0.43; retention index 0.56) where *Seminobatrachus boltyschkensis* gen. et sp. nov. is placed consistently in a clade with *Salamandra*, Ambystomatidae, *Dicamptodon*, and *Rhyacotriton* (Fig. 7A: clade L), but relationships of the new taxon with these taxa is only partly resolved in the strict consensus tree. Five synapomorphies support this clade (features which are not known for *Seminobatrachus boltyschkensis* gen. et sp. nov. written in italics): presence of articular as separate element [character 15(0)]; presence of postatlantal spinal nerve foramina in trunk, sacral and caudal vertebrae [character 24(3)]; presence of lateral narial fenestra [character 27(1)]; frontal contributes less than 50% of the orbital margin [character 32(1)]; and presence of separate, ossified operculum and stapes [character 65(0)]. The following possible positions of *Seminobatrachus boltyschkensis* gen. et sp. nov. within this clade were revealed: (1) as a basal member: *Seminobatrachus* + (*Salamandra* + (Ambystomatidae + (*Dicamptodon* + *Rhyacotriton*))); (2) as a sister taxon of *Salamandra*: (*Seminobatrachus* + *Salamandra*) + (Ambystomatidae + (*Dicamptodon* + *Rhyacotriton*)); and (3) as a sister taxon of the Ambystomatidae–*Dicamptodon*– *Rhyacotriton* clade: *Salamandra* + (*Seminobatrachus* + (Ambystomatidae + (*Dicamptodon* + *Rhyacotriton*))).

Our analysis also supports a basal position (but not basalmost) for Karauridae (*Kokartus* and *Karaurus*) within Cau-

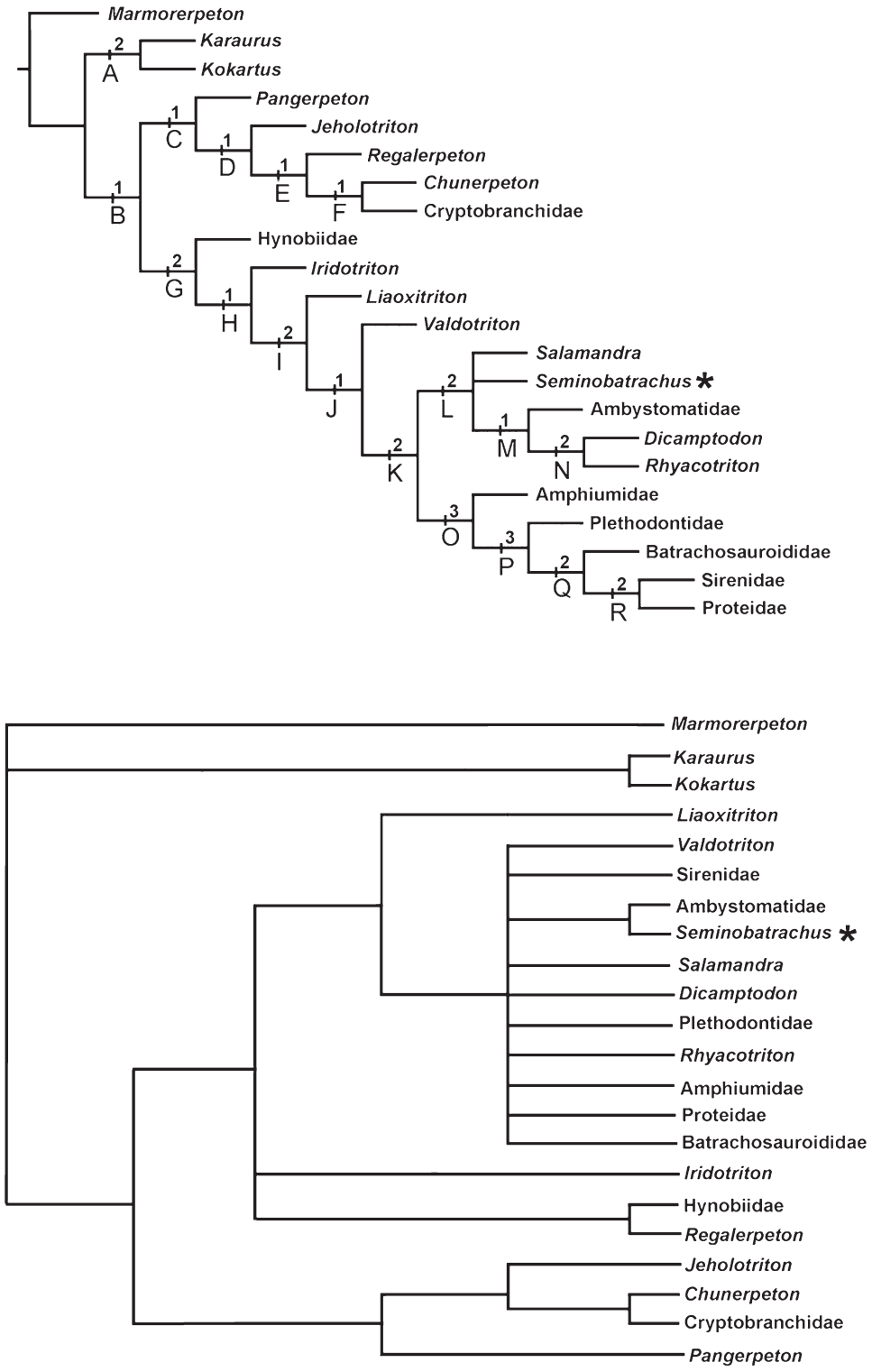

Fig. 7. Strict consensus of three most parsimonious trees obtained in NONA v. 2.0 with using the parsimony ratchet (island hopper) algorithm (**A**) and strict consensus of six most parsimonious trees obtained in PAUP v. 4.0b10 with using the branch-and-bound search algorithm (**B**) showing the position of *Seminobatrachus boltischki* gen. et sp. nov. within Caudata. *Seminobatrachus boltischki* gen. et sp. nov. is asterisked. The numbers are given above branches in A are Bremer support values.

data, monophyly of Karauridae exclusive of *Marmorerpeton*, and a sister-pair relationship between Karauridae + Urodela (crown-group salamanders); these results are similar to those in previous studies (Skutschas and Martin 2011 and references therein). The relationships of crown-group salamanders within the Urodela clade are largely resolved in our study (see Appendix 2 for synapomorphies supporting each clade) and two sister clades were recovered: the cryptobranchid clade

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(Fig. 7: clade C), which contains *Pangerpeton*, *Jeholotriton*, *Regalerpeton*, *Chunerpeton*, and the extant Cryptobranchidae, and the hynobiid–salamandroid clade (Fig. 7: clade G), which contains living hynobiids, some Mesozoic taxa (*Iridotriton*, *Liaoxitriton*, *Valdotriton*), extinct Batrachosauroididae and *Seminobatrachus boltyschkensis* gen. et sp. nov., and modern salamandroid taxa (*Salamandra*, Ambystomatidae, *Dicamptodon*, *Rhyacotriton*, Amphiumidae, Plethodontidae, Sirenidae, and Proteidae). In the hynobiid–salamandroid clade, living hynobiids are basal, three taxa (*Iridotriton*, *Liaoxitriton*, and *Valdotriton*) are placed in intermediate positions at successively higher nodes, and the other taxa form two sister-clades: the first (Fig. 7A: clade L) consists of an unresolved trichotomy among *Salamandra* + *Seminobatrachus boltyschkensis* + (Ambystomatidae + (*Dicamptodon* + *Rhyacotriton*)), and the second (Fig. 7: clade O) consists of Amphiumidae + (Plethodontidae + (Batrachosauroididae + (Sirenidae + Proteidae))). In our analysis, monophyly and relationships within the cryptobranchid-clade (*Pangerpeton* + (*Jeholotriton* + (*Regalerpeton* + (*Chunerpeton* + living Cryptobranchidae)))), the sister-pair of Sirenidae + Proteidae, and the clade of Ambystomatidae + (*Dicamptodon* + *Rhyacotriton*)) are all consistent with the results of Zhang et al. (2009). However, in contrast to Zhang et al.'s (2009) analysis, living hynobiids, the Late Jurassic *Iridotriton*, and the Late Jurassic–Early Cretaceous *Liaoxitriton* do not form a clade, but instead are basal taxa in the hynobiid–salamandroid clade. Further, whereas the position of the Early Cretaceous *Valdotriton* was unresolved by Zhang et al. (2009), in our analysis it is identified as the sister taxon of the salamandroid clade. Our placement of living hynobiids in a more inclusive clade with salamandroids conflicts with many previous analyses (e.g., Duellman and Trueb 1986; Gao and Shubin 2001; Frost et al. 2006) in which where hynobiids and cryptobranchids formed the monophyletic Cryptobranchoidea clade that was the sister of the Salamandroidea (± Sirenidae).

To evaluate the phylogenetic analysis obtained in NONA we ran the implicit enumeration search algorithm in TNT v. 1.1 (Goloboff et al. 2008) and branch-and-bound algorithm in PAUP v. 4.0b10 (Swofford 2002) to determine the most parsimonious trees for this data matrix. Additionally, we calculated bootstrap and Bremer (1994) support values in TNT and the bootstrap value in PAUP to evaluate the robustness of the nodes of the most parsimonious trees. The implicit enumeration search algorithm in TNT v. 1.1 (all parameters were left at their default settings) produced one tree with similar characteristics and topography to the trees obtained in NONA with the placement of *Seminobatrachus boltyschkensis* gen. et sp. nov. as a basal member of the clade *Seminobatrachus* + (*Salamandra* + (Ambystomatidae + (*Dicamptodon* + *Rhyacotriton*))). The branch-and-bound algorithm in PAUP v. 4.0b10 (all parameters were left at their default settings) retained six most parsimonious trees (tree length 178; consistency index 0.5; retention index 0.5). The strict consensus tree in PAUP differs from that in NONA (and from the single tree produced in TNT) in the following aspects (see Fig. 7B): (i) relationships between Karauridae (*Kokartus* and *Karaurus*) and *Marmorerpeton* are unresolved; (ii) *Regalerpeton* placed in the salamandroid clade as a sister taxon of hynobiids; (iii) presence of the unresolved trichotomy between hynobiids+*Regalerpeton* clade, *Iridotriton* and a clade united other salamandroids; (iv) relationships of the most of salamandroid taxa placed crownward of *Liaoxitriton* are unresolved; and (v) *Seminobatrachus boltyschkensis* gen. et sp. nov. placed as a sister taxon of the Ambystomatidae. Despite the differences mentioned above, the placement of hynobiids as basal salamandroids and *Seminobatrachus boltyschkensis* gen. et sp. nov. in a clade with the crownward salamandroids obtained in PAUP is in accordance with results from the NONA and TNT analyses. Additionally, we found no (in TNT; search trees with traditional search, number of replicates = 1000) or weak bootstrap support for Karauridae (52%), Cryptobranchidae+Chunerpeton (59%), Sirenidae+Proteidae (53%) (in PAUP; number of replicates = 100, heuristic search; 50% majority rule). The Bremer support values for the nodes of the tree obtained in TNT are relatively low and vary from 1 to 3 (Fig. 7A).

Our placement of hynobiids as basal salamandroids (obtained by phylogenetic analysis in all three programs), the Late Jurassic North American *Iridotriton*, Late Jurassic– Early Cretaceous Asian *Liaoxitriton*, and Early Cretaceous European *Valdotriton* as successively more derived salamandroids, and the remaining salamandroids in a crown clade (obtained in NONA and TNT) requires a more complex palaeobiogeograpical scenario than in the vicariance model proposed by Milner (1983). According to the vicariance model, salamandroids had a Euroamerican origin, cryptobranchoids had an Asian origin, and the dichotomy between the two corresponded to the isolation in the mid-Jurassic of East Asia from Euramerica by the Turgai Straits (Milner 1983, 2000). Considering that all basal members of the cryptobranchid clade (*Pangerpeton*, *Jeholotriton*, *Regalerpeton*, *Chunerpeton*) and one basal member of the hynobiid–salamandroid clade (*Liaoxitriton*) are known from the Late Mesozoic of Asia and that hynobiids are almost exclusively Asian in distribution, we suggest that the cryptobranchid and hynobiid–salamandroid clades could both have originated in Asia and that the origin and primary dichotomy of crown-group salamanders took place on that landmass. After those events, basal members of the hynobiid–salamandroid clade dispersed (probably several times) into Euramerica.

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Appendix 1

Additions and changes to the Zhang et al. (2009) data matrix used in the phylogenetic analysis.

1. A third character state (present, coarse and formed by tubercules and short ridges) was added to character 30 (dermal sculpture on skull roof: present, coarse (0); present, weak (1); absent (2)) to distinguish the specific sculpture of the skull roof bones in karaurids. Description of the character state (0) (present, coarse) was altered to "present, coarse and pitted". Character state (?) for amphiumids was changed to (1).
2. A fourth character state (on lateral surface of parietal and frontal) was added to character 38 (origin of m. adductor mandibulae internus superficialis) to distinguish the specific attachment of this muscle in karaurids.
3. The following data on *Kokartus* were added:
   010?0???10 0??0?0?030 ?000?????3 00000004?? ?????????? ???????100 ?102?0???? ??
4. The following data on *Seminobatrachus boltischki* gen. et sp. nov. were added:
   021?1???11 0?11?0?030 ?0?3?????2 0(1,2)01011??? ?????????? ??????111? 0010?1???? ??
5. The following data on Batrachosauroididae were added:
   030?1?1?3? 0?111000(2,3)(0,1) ?020?????2 1(1,2)0(1,2)111??? ?????????? ?????21110 2?02?1???? ??
6. Character 10, internal carotid foramina: present (0) or absent (1). Character state (1) for cryptobranchids was changed to (0).
7. Character 16, first hypobranchial and first ceratobranchial: the two elements separate (0); two elements fused (1). Character state (?) for *Karaurus* was changed to (0).
8. Character 23, atlantal spinal nerve foramen: absent (0); notch (1); fully enclosed (2). Character state (2) for *Karaurus* was changed to (?).
9. Character 61, number of presacrals: 15 or 16 (0); 14 or fewer (1); more than 16 (2). Character state (0) for *Karaurus* was changed to (1). Character state (?) for living hynobiids was changed to (2). Character state (?) for ambystomatids was changed to (1).
10. Character 62, shape of atlas centrum in ventral view: roughly equal in length to postatlantals (0), much shorter (1); longer (2). Character state (?) for ambystomatids was changed to (0). Character state (?) for proteids was changed to (1).

Appendix 2

Synapomorphies supporting each clade:

1. Clade A, Karauridae: 30(3), sculpture on skull roof: present, coarse and formed by tubercules and short ridges; 62(1), shape of atlas centrum in ventral view: much shorter.
2. Clade B, Urodela: 23(2), atlantal spinal nerve foramen: fully enclosed.
3. Clade C, Cryptobranchoidea: 66(1,2), vomerine dentition: marginal, tooth row parallel to premaxilla and maxilla (1); longitudinal row or patch (2).
4. Clade D: 9(1), pterygoid process: with an additional distinct anteromedial process; 19(3), palatine dentition: vomer, palatine and pterygoid (3).
5. Clade E: 32(1), medial border of orbit: frontal contributes less than 50% of the orbital margin; 34(1), anterolateral process of parietal: present but forms less than 50% of the total length of the parietal (1).
6. Clade F: 31(1), frontal anterior extension: does extend to lateral border of nasal; 32(2), medial border of orbit: frontal fully excluded from entering orbital margin.
7. Clade G, hynobiid–salamandroids: 10(1), internal carotid foramina: absent; 34(1), anterolateral process of parietal: present but forms less than 50% of the total length of the parietal; 37(1), squamosal contact with the parietal or other roofing elements: contact absent; 63(1), maximum skull length/width: 1.19-0.81.
8. Clade H: 8(1), prootic-exoccipital fused, separate opisthotic; 24(1), postatlantal spinal nerve foramina: spinal nerve foramina present in some caudal vertebrae.
9. Clade I: 13(1), angular: no distinct angular (absent or fused to prearticular in adult); 61(0), number of presacrals: 15 or 16.
10. Clade J: 22(0), postatlantal ribs: bicipital.
11. Clade K, Salamandroidea: 2(2), dorsal process of premaxilla: strong posterior extension separating nasals and contacting frontals; 5(1), nasal ossification: nasals separate without midline contact; 56(2), number of free ribs on anterior caudal vertebrae: free ribs absent; 66(1), vomerine dentition: marginal, tooth row parallel to premaxilla and maxilla.
12. Clade L: 15(0), articular: fused with prearticular; 24(3), postatlantal spinal nerve foramina: foramina in trunk, sacral and caudal; 27(1), lateral narial fenestra: present; 32(1), frontal contributes less than 50% of the orbital margin; 65(0), operculum: separate, ossified operculum and stapes.
13. Clade M: 29(0), nasolacrimal duct: present; 47(1), microchromosome: absent; 50(1), male cloacal folds: present; 66(0), vomerine dentition: transverse row, medial in the palate; 71(1), lateral pelvic glands: present.
14. Clade N, *Dicamptodon* + *Rhyacotriton*: 6(0), lacrimal: present; 8(0), prootic-exoccipital-opisthotic fusion: three separate elements; 24(2), postatlantal spinal nerve foramina: foramina present in caudal and sacral vertebrae.
15. Clade O: 9(3), pterygoid process: bar-like/vestigial; 39(1), ypsiloid cartilage: absent; 51(0), anteroventral glands in female: absent; 61(2), number of presacrals: more than 16; 62(1), shape of atlas centrum in ventral view: much shorter; 63(2), maximum skull length/width: 0.8 or less.
16. Clade P: 12(2), basilaris complex of inner ear: loss of entire basilaris complex; 47(1), microchromosome: absent; 48(1), ciliated epithelium of female cloaca: absent; 49(1).
17. Clade Q: 19(2), palatine dentition: vomer and palatine; 32(1), medial border of orbit: frontal contributes less than 50% of the orbital margin.
18. Clade R, Sirenidae+Proteidae: 33(1,2), frontal/maxillary contact: frontal contacts dorsal process of maxilla (1), contact absent because of loss of maxilla (2); 11(1), prefrontal: absent; 14(0), coronoid: present as a separate element; 33(2), frontal/maxillary contact: contact absent because of loss of maxilla.