Correction

EVOLUTION, GEOLOGY


The authors note that on page 5772, left column, first full paragraph, lines 17–20 to lines 1–2 of the adjacent right column, “This evidence, in keeping with our previous report of an early cryptobranchid from Inner Mongolia (9), rejects the purported timing of 140 Ma for this cladogenetic event (16), but supports a more recent study based on complete mitochondrial genomes for a Middle Jurassic divergence of the Salamandroidea from Cryptobranchioidea (8)” should instead appear as “This evidence, in keeping with our previous report of an early cryptobranchid from Inner Mongolia (9), supports molecular calibrations that imply Middle Jurassic divergence of the Salamandroidea from Cryptobranchioidea (8, 16).”

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Late Jurassic salamandroid from western Liaoning, China

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A Jurassic salamander, Beiyangerpeton jianpingensis (gen. et sp. nov.), from a recently found site in western Liaoning Province, China is the earliest known record of Salamandroidea. As a Late Jurassic record of the group, it extends the range of the clade by ~40 Ma. The Late Jurassic taxon is neotenic and represented by exceptionally preserved specimens, including fully articulated cranial and postcranial skeletons and bony gill structures close to the cheek region. The fossil beds, consisting of dark-brown volcanic ash shales of the Upper Jurassic Tiaojishan (Lanqi) Formation (Oxfordian), underlie trachyanidesite rocks that have yielded a SHRIMP zircon U-Pb date of 157 ± 3 Ma. The fossiliferous beds are substantially older than the Jehol Group, including the Xiyian Formation (40Ar/39Ar dates of 122–129 Ma), but slightly younger than the Middle Jurassic Daohugou horizon (40Ar/39Ar date of 164 ± 4 Ma). The early fossil taxa shares with extant salamandroids derived character states, including: separated nasals lacking a midline contact, angular fused to the prearticular in the lower jaw, and double-headed ribs on the presacral vertebrae. In contrast to extant salamandroids, however, the salamander shows a discrete and tooth-bearing palatine, and unequivocally nonpedicellate and monocupid marginal teeth in large and presumably mature individuals. The finding provides insights into the evolution of key characters of salamanders, and also provides direct evidence supporting the hypothesis that the split between Cryptobranchioidea and Salamandroidea had taken place before the Late Jurassic Oxfordian time. In this aspect, both paleontological and molecular data now come to agree.

Salamanders are a diverse group of modern amphibians, with high ecological diversity and extreme morphological conservatism (1–4). Among the 10 extant families, the Hynobidae and Cryptobranchidae are classified in the suborder Cryptobranchioidea, and the remaining families (except for the Sirenidae) in another suborder, Salamandroidea. Phylogenetic relationships of the Sirenidae remain contentious, and recent phylogenetic analyses place the family in either basal or crownward positions (5–8). The Cryptobranchioidea have their earliest record from the Middle Jurassic in Asia (9–13), and the Salamandroidea have an Early Cretaceous record from Europe (14). Indotriton was described as a putative salamandroid from the Upper Jurassic Morrison Formation (15), but our evaluation of the available data suggest that it is probably a cryptobranchoid (see SI Appendix for details). Within the phylogenetic framework of the Urodela, the split of the Salamandroidea from the Cryptobranchioidea is a major cladogenetic event in the evolution of salamanders, but the timing for this major event is still in dispute (8, 16–18), largely because of lack of early fossil evidence. New molecular data (8) point to a substantially earlier age for this split than does the existing fossil record (14) before the finding of the fossils reported in this article.

The salamandroid described herein is based on the specimens collected from the Guancaishan site near the county town of Jianping in western Liaoning Province, China (Fig. 1). With a radiometric date of 157 ± 3 Ma from the overlying rocks (12), the fossil beds of the Upper Jurassic Tiaojishan (Lanqi) Formation consist of volcanic ash deposited in a lake during Oxfordian time (19). Thus, this Late Jurassic fossil taxon documents the earliest known record of the Salamandroidea, predating a previously Early Cretaceous record (Valdositrion, 116–114 Ma) by some 40 Ma (14). In contrast to the salamander fossils from the nearby Daohugou site, specimens from Jianping are all preserved with genuinely fossilized skeletons rather than preserved as natural molds or impressions resulting from postmortem dissolution of the skeletons. The superb preservation of skeletal details shads new light on the key characters, including palatal structures and marginal teeth. In addition, a phylogenetic study incorporating this important fossil taxon supports the hypothesis that the divergence of the Salamandroidea from their sister clade Cryptobranchioidea likely took place before the Late Jurassic on the Eurasian continent (8).

Systematic Paleontology

Amphibia Linnaeus, 1758; Lissamphibia Haeckel, 1866; Caudata Scopoli, 1777; Urodela Duméril, 1806; Suborder Salamandroidea Noble, 1931; Beiyangerpeton jianpingensis gen. et sp. nov.

Etymology. Beiyan (ancient place name, meaning Northern Yan State) + herpeton (Greek: creeping animal); Jianping, county town nearby the type locality.

Holotype. Peking University Paleontological Collection (PKUP) V0601, a nearly complete skeleton exposed in ventral view.

Referred Specimens. PKUP V0602-0606, and several unnumbered specimens; all preserved as articulated cranial and postcranial skeletons.

Type Locality and Horizon. Guancaishan, near Jianping, Liaoning Province, China; Upper Jurassic Tiaojishan (Lanqi) Formation.

Diagnosis. A Late Jurassic neotenic salamandroid diagnosed by the following unique combination of character states: Skull relatively wider than long, both anterodorsal and anteromedial fenestrae developed; sensory canal present on external surface of premaxilla and maxilla; prefrontal present; lacrimal retained; palatine present as a discrete and dentate element; marginal teeth nonpedicellate, simple peg-like and significantly shorter than vomerine teeth; posterolateral wings of parasphenoid grooved for internal carotid artery; operculum separate from stapes; hypobranchial I and II well ossified; basibranchial I and II co-ossified; angular lost by fusion with prearticular; presacral vertebrae 15 in number; vertebral centrum short, strongly constricted, with prominent subcentral keel; phalangeal 2-2-3-2/3 in manus, and 2-2-3-4-3 in pes.

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Description and Comparison. As best shown by the holotype (PKUP V0601), the salamandroid is a medium-sized salamander with a standard snout-vent length of ~100 mm (Fig. 2). Bony structures of gill rakers (branchial denticles) are preserved in all large specimens known for the taxon, giving clear indication of the gill structure for suction feeding as a neotenic feature of the Late Jurassic salamander. The tail is roughly the same length as the trunk, as shown in PKUP V0602. Caudal vertebrae are dorsoventrally expanded, reflecting a laterally compressed tail, which, in keeping with the presence of gill structures and lack of ossification of the mesopodium, implies an aquatic habitat of the salamander.

In the skull roof, the premaxillae are paired tooth-bearing elements, each of which carries ~30 monocuspid and non-pedicillate teeth. These teeth are short, thick, and loosely spaced. The premaxilla has a well-developed triangular dorsal process overlapping the nasal (Fig. 3). The partes dentales of the premaxillae are medially in contact, but the pars dorsalis (dorsal process) along with the nasals are widely separated from one another by a large anterodorsal fenestra. The external surface of the pars dentalis carries a deep groove for the sensory canal leading to the narial opening. The paired frontals have an extensive midline sutural contact, but are anteriorly notched for the anterodorsal fenestra. Prefrontals and lacimals are present, and the former element has a posterior process that contacts the anterior extension of the parietal. The lacrimal is a small element articulated medially with the prefrontal and laterally with the dorsal process of the maxilla (PKUP V0604, V0605). Among extant salamander families, the lacrimal is present in Hynobiidae, Rhyacotritonidae, and Dicamptodontidae, but is lost in all other families (20, 21).

Like other skull roof elements, the paired parietals have a smooth dorsal surface, but dorsolaterally develop a curved crest for attachment of adductor muscles. The posterior border of the parietals does not form the dorsal rim of the foramen magnum, because two sides of the otic-occipital complex contact each other below the parietals (best shown in PKUP V0604). The squamosal in dorsal view is essentially a transverse bar, but has an expanded medial end overlapping the boot-shaped posterolateral process of the parietal, and a relatively narrow lateral end above the quadratojugal as part of the crano-mandibular joint.

The maxilla is short, with a pointed posterior extremity free from articulation with any bony elements. Similar to the premaxilla, the lateral surface of the maxilla also has a deep groove running horizontally towards the external narial opening. This groove may indicate the anterior extension of the infraorbital sensory canal as a branch of the Cranial Nerve V (22). The maxilla develops a low dorsal process, the anterior border of which is slightly notched for the narial opening. Close to this notch, the inner surface of the maxilla is grooved for articulation with a small septomaxilla (PKUP V0604, V0605). In those salamanders with this element present, the septomaxilla is the last cranial element to ossify ontogenetically (21), and the presence of this element indicates maturity of these individuals. The maxillary teeth are extremely short, simple and monocuspid, and the tooth row extends close to the posterior extremity of the maxilla.

In the palate, the vomers are narrow strip-like elements that are widely separated from one another by an anteromedial fenestra. The vomer lacks a posterior process that is commonly seen in more derived salamandroids, but has a small notch at its posterolateral border for the choana. Vomerine teeth are closely spaced and aligned to form a single tooth row (monostichous teeth), which is curved along the anterior border of the vomer, paralleling the marginal tooth row. The palate as a discrete tooth-bearing element is clearly identifiable in several specimens, including the holotype. This small element is anteriorly articulated to the vomer and posteriorly to the pterygoid. The palate carries a single tooth row, different from sirensids, which have multiple tooth rows. The parapophyseal is anteriorly notched for the anteromedial fenestra and the posterolateral wing is grooved for the internal carotid artery. The pterygoid (palatopterygoid of some other authors) is triradiate, with a sickle-shaped anterior process curved anteromedially to meet the palate. The anterior process bears small denticles forming a single tooth row. The medial process is extremely short, contacting the lateral wing of the parapophyseal just anterior to the otic capsule. The quadrate process of the pterygoid is much wider than the anterior or the medial processes and extends posterolaterally to contact the quadrate.
from a stratigraphically slightly lower (older) Beiyanerpeton jianpingensis Holotype of
indeed has nonpedicellate and lacking marginal teeth in greatly reduced premaxilla, maxilla, including sirenids. Extant sirenids are highly specialized in monocuspid marginal teeth are different from all extant salamanders (20, 21). In addition, a free operculum is present in most salamanders and loss of this element presumably covers part of the otic capsule, but cannot be ascertained, although the foramina can be clearly identified and mushroom-like (24).

Also in palatal view, hypobranchial I and II are ossified as short bar-like structures, arranged obliquely and roughly parallel to one another. Basibranchial I and II are co-ossified as a trident-shaped structure with slender arms extending anteriorly and anterolaterally (counterpart of PKUP V0601, V0602). The sphenethmoid (orbitosphenoid) forms a narrow strip covering the lateral side of the neurocranium.

The otic-occipital complex of the recently identified salamander consists of the prootic, exoccipital, and opisthotic as separate elements. The dorsal exposure of the complex is limited to the posterior end of the skull, lacking an anterolateral extension between the parietal and squamosal. A stapes (columella) is clearly present with its footplate covering the fenestra ovalis and a short, thick, rod-like stylus extending laterally (Fig. 3). A stapes is present in most salamanders and loss of this element is known for all salamandrids, and some but not all plethodontids and sirenids (20, 21). In addition, a free operculum is clearly identifiable as a thin, oval, and domed plate (Fig. 3). In life, this element presumably covers part of the otic capsule, but has been taphonomically dislocated to a posterior position close to the base of the squamosal. Loss of the operculum is a phylogenetically significant feature, independently occurring in at least seven families of salamanders (SI Appendix).

The mandible consists of only two dermal elements, a derived feature of Salamandroidea: the tooth-bearing dentary and the large prearticular formed by fusion with the articular and angular. Marginal teeth, as shown in several specimens including the holotype, are extremely short, thick, loosely spaced, and clearly nonpedicellate, as none of the well-preserved teeth show a bipartite structure. The tooth crown is a simple cone without any indication of bicuspidation. The nonpedicellate and monocuspid marginal teeth are different from all extant salamanders including sirenids. Extant sirenids are highly specialized in lacking marginal teeth in greatly reduced premaxilla, maxilla, and the dentary; those monocuspid teeth covering the vomer and palatine can be weakly pedicellate or nonpedicellate (21, 23). Early fossil sirenid Habrosaurus indeed has nonpedicellate and monocuspid marginal teeth, although the teeth may be either chisel-shaped or inflated and mushroom-like (24).

The vertebral column of the Late Jurassic salamander consists of 15 presacrals, including the atlas, a single sacral, and about 30 caudals (PKUP V0601, V0602). All trunk vertebrae are amphicoelous, and ventrally have a well-developed subcentral keel. Presacral ribs are clearly bicipitate, having an expanded head and a slender shaft. The anteriormost three pairs are more robust than the others, and have both proximal and distal ends expanded. The last three-to-four pairs of ribs are significantly shorter than the others, but the sacral ribs are robust and elongate, as curved rods in articulation with the pelvic girdle. The presence or absence of spinal nerve foramina on trunk vertebrae cannot be ascertained, although the foramina can be clearly identified on the caudal vertebrae. The first two caudal vertebrae are exposed in dorsal or ventral view and show free ribs in articulation with the transverse processes. The remaining part of the caudal series is twisted at a 90° angle, and thus is exposed in lateral view. The third and more posterior caudal vertebrae bear no free ribs, but dorsally carry a high neural spine and, ventrally, an elongate chevron, forming a deep and laterally compressed tail.

The scapulocoracoid as a single ossification has a narrow and elongate scapular blade, and a thickened coracoid process, which is only slightly expanded, differing from the squared configuration in Chunerpeton from a stratigraphically slightly lower (older) horizon (9). The humerus has a low and thick delto-pectoral crest, and well-ossified epiphysis as an indication of the maturity of the individual at death. The ulna and radius are short, subequal in length; and more distally, no carpal but distal carpal and phalanges are ossified. The manus shows a phalangeal formula of 2-2-3-2 in the holotype, but 2-2-3-3 in PKUP V0602.
Both the ilium and ischium are well preserved in the pelvis, but an ossified pubis, as commonly seen in other salamanders, is lacking. The iliac shaft is elongate, more than two-thirds the length of the femur. The acetabular fossa is shallow, but has a well-developed crest to form the dorsal border of the acetabulum. The ischium is a small and thick plate, which hardly contributes to any part of the acetabulum. The femoral trochanter is weakly developed as a small tubercle, different from the twig-like process in more advanced salamanders. The epipodial segment is extremely short, being roughly one-third the length of the prospodial. The pes has a phalangeal formula of 2-2-3-4-3, as shown on both sides of PKUP V0602.

Results and Discussion

The assessment of these specimens as neotenic is based on a suite of diverse characters. The holotype and the referred specimens are relatively large individuals, with a snout-vent length of greater than 100 mm. These specimens show fully ossified nasals and septomaxillae, both frontals and parietals closely articulating along the midline, and well-ossified hyobranchium, including co-ossification of basibranchials I and II to form a trident-shaped structure. In the postcranial skeleton, all specimens show a well-ossified epiphysis of the long bones as well. Although all these features indicate maturity of the individual specimens (21, 25), retention of gill structures as a larval feature in these relatively large and presumably mature salamanders confirms the neotenic status of the Late Jurassic taxon.

This Late Jurassic salamander is placed in the suborder Salamandroidea because this fossil taxon shares with extant salamandroids several derived character states, including: nasals separated by anterodorsal fenestra without a midline contact; angular fused to prearticular; articular absent by fusion to prearticular; double-headed ribs associated with dorsal vertebrae; anterior process of parietal extending to midlevel of orbit; and parietal-prefrontal contact medially above orbit. Other diagnostic features of the Salamandroidea, mostly soft anatomical or genetic characters, cannot be determined for this fossil taxon, and these include: lateral wall of nasal capsule incomplete; microchromosome absent; spermathecase in cloaca present; and internal fertilization (see SI Appendix for citations). Within the phylogenetic framework of the Salamandroidea, results of the phylogenetic analysis place the Late Jurassic salamander as the most basal taxon within the clade (Fig. 4 and SI Appendix, Figs. S1 and S2). This basal position is secured for the salamander by its possession of diagnostic features of the Salamandroidea, as mentioned above, and in its lack of other features of extant salamandroids, including: dorsal process of premaxilla extending to contact frontal and separating nasals; dorsal exposure of the otic-occipital complex between the parietal and the squamosal; and absence of a squamosal-parietal contact. Forceful grouping the unique taxon with the Cryptobranchioidea or moving it to a more crownward position in the Salamandroidea requires a minimum cost of five (235 vs. 240) and four (235 vs. 239) additional steps, respectively, none of which would be a parsimonious hypothesis. The relationships within the Salamandroidea
and that of the Sirenidae with other salamanders, as resulted from our morphology-based analysis (Fig. 4 and SI Appendix, Figs. S1 and S2), show topological differences from those of molecular-based studies (8, 17, 26), as have been foreshadowed by previous research (5, 6). Although resolving the molecular/morphological conflict is beyond the scope of this study, topological changes within the Salamandroidea have little impact on the phylogenetic position of the fossil taxon reported in this article.

The fossil finding in western Liaoning provides paleontological evidence for understanding the fundamental patterns of character evolution in salamanders. One of these patterns of character evolution concerns the loss of the palatine. The presence or absence of a dentate palatine in salamanders has been in dispute: some authors (27, 28) regarded all mature salamanders as lacking a palatine as in frogs and caecilians, and other authors (21, 29) have shown that a palatine in most salamanders is present in early ontogeny, but subsequently fuses to the pterygoid. Sirenids present an exception, as they retain the palatine as a discrete element in the mature stage (21, 24). The Late Jurassic salamandroid from western Liaoning is so far the only nonsirenid fossil taxon known with a "larval type of palatine" in seemingly mature individuals.

This finding, in keeping with ontogenetic evidence, indicates that the presence of a separate palatine as a tooth-bearing element in the palate indeed occurred in early evolution of true salamanders as a primitive morphology. Temnospondyls, such as branchiosaurids and amphibamids, contenders as probable salamander ancestors, also retain a discrete but greatly reduced palatine (25, 30), supporting this interpretation. The actual condition in stem caudate Karaurus remains uncertain. Although the palate of this Middle–Late Jurassic stem-group caudate is reconstructed as lacking a palatine, the type and only known complete specimen is not exposed in palatal view.

Another key character seen in the recently identified salamander is its nonpedicellate and monocuspid marginal dentition. Pedicellate teeth with bicuspid crowns have been widely accepted as unchallenged synapomorphies, supporting a single origin of the Lissamphibia (salamanders, frogs, caecilians). With the exception of sirenids that possess monocuspid but weakly pedicellate or nonpedicellate teeth in mature individuals (21, 23), most extant salamanders have pedicellate and monocuspid teeth replaced by bicuspid teeth at metamorphosis, and neotenic salamanders at sexual maturity may show positional or regional

Fig. 4. Calibrated cladogram showing the relationships of Beiyanerpeton to other fossil and extant salamander clades, and the timing of the Salamandroidea splitting from Cryptobranchoidea (solid dot) as indicated by the fossil record. For details on phylogenetic analysis and stratigraphic range of major salamander clades see text and SI Appendix.
variations with a mixture of monocusp and bicuspid marginal teeth in the same individual (31). Surprisingly, the Late Jurassic salamander from western Liaoning, China, clearly shows non-pedicellate teeth that have a monocuspid crown at maturity. The tooth morphology is uncommon for the stem caudate Karaurus and Marmorpeton (14, 32), but a recent study has shown that the Middle Jurassic Kokoartus as another stem caudate has indeed monocuspid and nonpedicellate teeth (33). The salamander from western Liaoning, as a basal salamandrid, provides unequivocal evidence showing that primitive crown-group salamanders may have had nonpedicellate and monocuspid teeth as the stem caudate Kokoartus. Furthermore, this finding indicates that the pedicelly and bicuspid crown patterns are most likely derived, as the fossil material remains undescribed. In that context, the Late Jurassic salamander from western Liaoning also provides, so far, the most reliable palaeontological evidence to estimate the timing for the split of Salamandridae from its sister clade Cryptobranchidae. Because the fossil beds described herein, in western Liaoning, are stratigraphically below the trachyandesite rocks that have been dated at 157 ± 3 Ma (12), the fossil occurrence indicates that the Salamandridae/Cryptobranchidae split, a major cladogenetic event in salamander evolution, had taken place before the Late Jurassic. This evidence, in keeping with our previous report of an early cryptobranchid from Inner Mongolia (9), rejects the purported turning of 140 Ma for this cladogenetic event (16), but supports a more recent study based on complete mitochondrial genomes for a Middle Jurassic divergence of the Salamandridae from Cryptobranchidae (8).

With a plausible estimation of the origin of living salamanders at ~183 Ma in the Early Jurassic (8), there is still a considerable gap to be filled between this early fossil record of the Salamandridae and the Middle Jurassic origin of the group.

Materials and Methods

The dataset constricted for the phylogenetic study comprised 105 characters coded across 26 basic taxa, with the stem caudate Karaurus designated as the outgroup (SI Appendix, Table S1). Source of character information and explanation on sampling of taxa are given in the SI Appendix. Phylogenetic analysis is performed using the Macintosh version of PAUP* 4.0 (34) under a branch-and-bound search option, and trace of character evolution is carried out by using MacClade 4.06 (35).

The initial analysis of the dataset found 40 most parsimonious trees (TL = 235 steps, CI = 0.506, RI = 0.727), and all of the most parsimonious trees have the taxon Beijinerpeton placed as a basal salamandrid, as shown in the strict consensus tree (SI Appendix, Fig. S1). Because the relationships within the Cryptobranchidae and among several salamandrid clades are poorly resolved, further analysis of the dataset is carried out after character resampling by maximum value of rescaled consistency indices (36). The latter analysis generated 10 most parsimonious trees (TL = 9,131 steps, CI = 0.695, RI = 0.852). Both the strict and Adams consensus trees are given in the SI Appendix, and the Adams consensus tree is converted into a calibrated cladogram as presented in Fig. 4.

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