



# A neotenic salamander, *Jeholotriton paradoxus*, from the Daohugou Beds in Inner Mongolia

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*Received 11 April 2011; revised 22 July 2011; accepted for publication 1 August 2011*

Over the past 10 years, there has been a wealth of discoveries of fossil salamanders from the Jehol Biota in northern China. These specimens have revealed many new species in addition to establishing probable divergence times and relationships among modern salamander families. Among these are numerous specimens of a neotenic species *Jeholotriton paradoxus*. In this study, we focused on this particular salamander species because its classification still remains enigmatic. The aim of this research was to determine the relationship of *Jeholotriton* with respect to other Jehol salamanders as well as modern salamander families. Although *Jeholotriton* has been described in previous studies, the discovery of new specimens and increasing knowledge of other Mesozoic salamanders has allowed for a more thorough description of the genus. *Jeholotriton* is known only from the Daohugou locality in Ningchen, south-eastern Inner Mongolia. It may be close to the base of the modern Urodele radiation, and might provide evidence of their transition from putative ancestors in the Permo-Triassic. We discovered that the fossil *Kokartus* (family Karauridae) and the living hynobiids (the most primitive group of modern salamanders) *Ranodon sibiricus* and *Hynobius maculosus*, as well as *Dicamptodontidae tenebrosus* all share some similarities with *Jeholotriton*. However, conclusive relationships could not be confidently established because of the unique combination of mature and larval characteristics in *Jeholotriton*.

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doi: 10.1111/j.1096-3642.2011.00777.x

ADDITIONAL KEYWORDS: Jehol biota – neoteny – Urodele.

## INTRODUCTION

Although the majority of our current knowledge of early salamanders has been gained from Cenozoic genera (Carroll, 2009), fossils from the Jehol Group in northern China, variably dated as ranging from the Middle Jurassic to Early Cretaceous, and *Karaurus* (Ivakhnenko, 1978), from the Upper Jurassic of Russia, document a much earlier radiation (Chen *et al.*, 2008; Liu *et al.*, 2006).

The Chinese specimens include unquestioned ancestors of the living Cryptobranchidae (Gao & Shubin, 2001), the hynobiids *Jeholotriton* and *Liaox-*

*itriton*, and several other genera, in which affinities with one another and with the various extant families remain elusive.

The greatest diversity of these fossils has been collected from the Daohugou locality, at the base of the Jehol Group (Chen *et al.*, 2008). The Daohugou locality is unique in many respects. It was not discovered until the fall of 1998, but has since yielded a very rich and diverse fauna. In addition to salamanders, these include the haired pterosaur *Jeholopterus ningchengensis*, the feathered theropod *Epidendrosaurus*, thousands of beautifully preserved insects, and a great diversity of plants.

These fossils have been preserved in great detail by the repeated falls of volcanic ash and concomitant diminution of oxygen that led to the death of the salamanders, but also to the preservation of

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thousands of fully articulated skeletons, complete with soft tissues, including skin, muscles, traces of blood vessel and nerves, tissues of the eye, and patterns of coloration. The areas of preservation were marked by many lakes, large and small, where they remained until they sank through the surface film and collected on the bottom where they accumulated in large numbers, in some cases by the thousands.

A general description of the Jehol Biota was published by Chen *et al.* 2008, discussing the fauna in general terms, as well as attempting to establish their related age and stratigraphic position. These studies have been further elaborated by Liu *et al.* (2006). According to Chen *et al.* (2008), the estimated age of the Daohugou salamanders ranged from the Middle Jurassic into the Early Cretaceous, comparable with the lower part of the Yixian Formation. In contrast, by making use of uranium–lead dating of zircon from the lava flows surrounding the salamander-bearing strata, Liu *et al.* supported a range of dates from 168 million years, from the Middle Jurassic, to a range of 164–152 million years in the early late Jurassic.

In terms of geology, the Jehol Biota developed in a relatively short period of time and quickly radiated within a large area in East Asia. Other major groups of vertebrates preserved in these deposits included fish, amphibians, turtles, aquatic reptiles, lizards, dinosaurs, birds, and mammals. The climate was warm, with ample rainfall. There were four significant cycles of volcanic eruptions related to the significant deposits of fossils within the lake basins. These remains are thought to represent a nearly complete history of the Jehol Biota.

## TAXON DESCRIPTION

### GENERAL DESCRIPTION

Numerous *Jeholotriton* specimens were examined. Latex casts of four adult specimens and one larva specimen were made from the dorsal and ventral surfaces of the original natural casts, so that the appearance of the bone surface could be replicated. This provided a very reliable means of studying the bones. In addition, one adult specimen and two larvae were studied on the basis of high-resolution photographs. The photographs and casts show a high degree of ossification of the skull (Fig. 1A and B). The length of the adult specimens (measured from the tip of the snout to the end of the tail), as represented by the bony elements and skin impression, varies from approximately 80 to 90 mm. Preserved soft tissue includes skin and gills (Fig. 2). In addition, most specimens preserve impressions of large eyes represented by circular structures distinguished by a dark

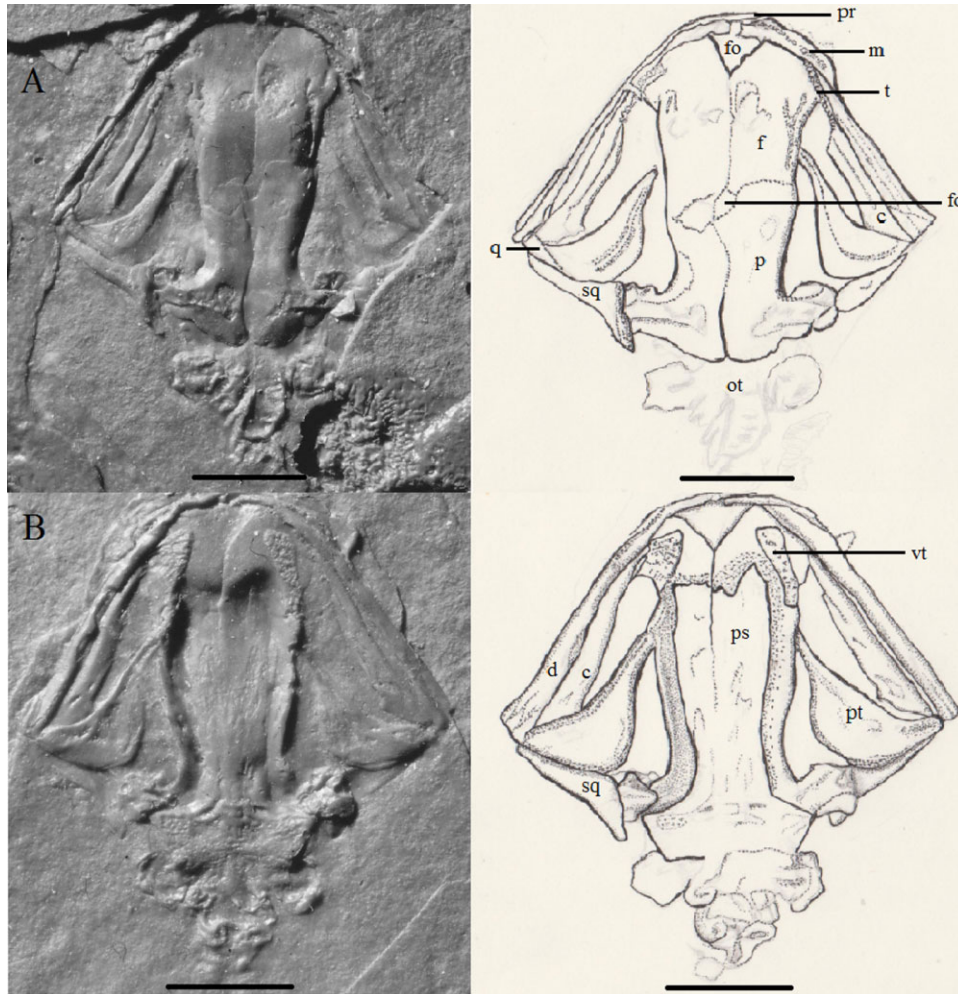
pigment. The adult skulls have an average length of 15.5 mm and an average width of 16 mm.

### SKULL

The skull is more or less triangular in dorsal view, with the occipital condyles well behind the jaw articulation. The bones of the skull roof are characterized by small circular pits on their external surface. All specimens possess two large dermal bones: the frontal and the parietal. In an earlier description of *Jeholotriton paradoxus* (Wang & Rose, 2005), nasal bones were identified. However, after careful investigation of all available specimens, the nasal bones, although common to most salamanders, cannot be recognized. Nasals are present in most modern salamanders, including hynobiids, cryptobranchids, salamandrids, and ambystomatids (Carroll & Holmes, 1980). Nevertheless, some extant salamanders, for example, some proteids (*Necturus*), certain plethodontids, and a dicamptodontid (*Dicamptodontidae tenebrosus*) do lack nasals (Carroll & Holmes, 1980; Rose, 2003). A faint ridge on the frontals of some specimens suggests that the nasals of *Jeholotriton* might be fused to the frontals, as suggested by Wang & Rose (2005). The paired frontals occupy on average 45% of the total length of the skull. They are roughly rectangular, with little or no lateral extension, and consistently overlap the parietal at its anterior end. In a few specimens, the anterior end of the frontals diverges laterally. The parietals are also very large bones, exceeding the length of the frontals. At the posterior end of each parietal bone is a lateral extension. Prefrontal bones appear to be missing. The lacrimal, extending from the frontal to the maxilla, is very small and bears a small nasolacrimal duct. All specimens have a diamond-shaped fontanelle where the frontals and parietals meet near the centre of the skull.

The premaxillae are short and narrow, with a small dorsal process that extends from the middle of the posterior margin, as well as a median fontanelle. The maxillae are short compared with those of most modern salamanders. Their shape is difficult to determine but they appear to be broken posteriorly in all specimens. The length of the maxillae is estimated to be around 6 mm: an accurate measurement is difficult to obtain because of the incomplete ossification. This is in accordance with Wang & Rose's (2005) measurement of the maxilla, which was noted to be 7 mm long. *Jeholotriton* has a maxilla length/skull length ratio of 39%. No septomaxillae could be recognized.

The squamosal is an anteroventrally oriented rod with an expanded proximal end that is in contact dorsally with the lateral extensions of the parietal and the otic capsule. The anteroventral end is in



**Figure 1.** A, dorsal view of *Jeholotriton* skull, specimen 0009B. B, ventral view of *Jeholotriton* skull; c, coronoid/prearticular; d, dentary; f, frontal; fo, fontanelle; m, maxillae; ot, otic capsule; p, parietal; pr, premaxilla; ps, parasphenoid; pt, pterygoid; q, quadrate; sq, squamosal; t, teeth; vt, vomerine teeth. Scale bars: 5 mm.

contact with the quadrate, although it is difficult to tell whether these bones are sutured or simply overlap. The presence of a quadratojugal cannot be confirmed from the available material.

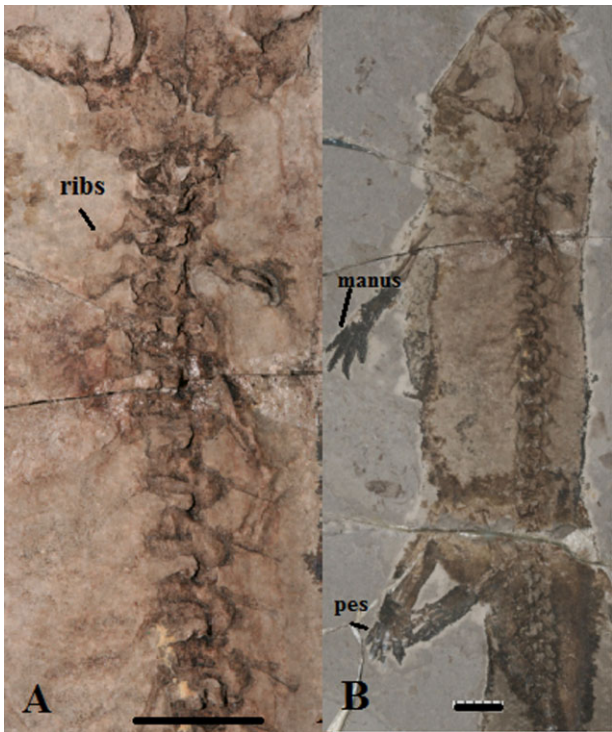
The palatal surface of the skull has two widely separated vomers. Each bears a large tooth plate with rows of teeth running obliquely posterolaterally. There are four rows of teeth with approximately ten teeth in each row. Each of the vomers has a narrow posterior extension. The parasphenoid occupies much of the palatal surface and is marked by irregular longitudinal ridges. It extends from near the anterior margin of the skull to the base of the otic capsules.

The pterygoid is a very conspicuous bone, approximately the same length as the parietal. It is essentially triradiate in appearance: wide at the base, with the anterior apex extending medially towards the

anterior end of the parasphenoid. At the most anterior end, the pterygoid has markings on the bone that were previously described as teeth (Wang & Rose, 2005). This, however, cannot be confirmed from the available casts and photographs. What seem to be teeth may only be the result of broken bone or an irregular surface. Were it to be confirmed that *Jeholotriton* does have denticles on its pterygoid, it would be an unusual characteristic, although it does occur in *Kokartus*, a member of the family Karauridae (Ivakhnenko, 1978) and *Regalerpeton* (Zhang *et al.*, 2009). The palatine and ectopterygoid could not be distinguished in any of the specimens.

The prootic, exoccipital, and opisthotic are fused to form the otic capsule. Short stapes, bearing a stapedial foramen, extend from the otic capsules. The otic capsules and the occipital condyles are both well ossified; none of the hyoid apparatus is evident.





**Figure 2.** Axial and appendicular skeleton of adult *Jeholotriton* specimen 0012B. Scale bars: 5 mm.

Neither hyobranchials nor ceratobranchials are visible in either the casts or the photographs.

#### MANDIBLE

There are two distinct bones making up the mandible: the dentary and the coronoid/prearticular. The dentary is both longer and slightly wider than the coronoid/prearticular. The dentary bears approximately 40 teeth. The teeth are long, narrow, and pointed, and there is no size variation. The teeth did not appear to be pedicellate. The angular could not be clearly observed, and nor could the articular.

#### AXIAL SKELETON

*Jeholotriton* has 16 presacral vertebrae, one sacral, and at least 18 caudals. The transverse processes that bear the ribs become noticeably shorter as the vertebrae column approaches the sacrum. The sacral vertebra has a pair of expanded ribs that support the ilium. As the caudal vertebrae extend posteriorly, the haemal arches replace the intercentra, although the first few caudal vertebrae have cylindrical centra. Whether the ribs are unicapitate or bicapitate is hard to determine from the available material. The centra in the trunk appear roughly rectangular in lateral

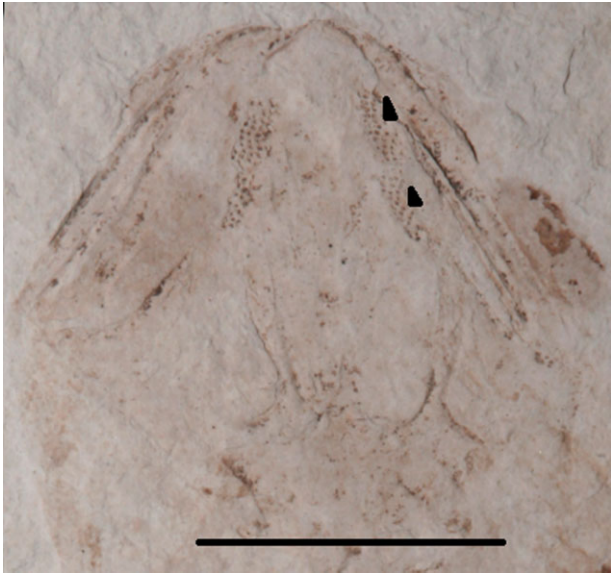
**Table 1.** Comparison of phalangeal formulas between *Jeholotriton* and other salamanders. L = left, R = right. The information for modern salamanders is from (Shubin & Wake, 2003)

	Manus	Pes
<i>Jeholotriton</i>	2-3-3-2	2-2-3-3-2
<i>Liaoxitriton</i>	2-2-3-2	2-2-3-4-2
<i>Sinerpeton</i>	1-2-3-2	1-2-3-4-2
<i>Pangerpeton</i>	2-3-3-2	2-2-3-3-2
	(L)/2-2-3-2 (R)	
<i>D. tenebrosus</i>	2-2-3-2	2-2-3-4-2
<i>Valdotriton</i>	2-2-3-2	2-2-3-4-2
Plethodontids/ Salamandrids	1-2-3-2	1-2-3-3-2
Hynobiids/ Cryptobranchids	2-2-3-2	2-2-3-3-2
Ambystomatids	2-2-3-2	2-2-3-3-2
Karaurus	2-2-3-2	2-2-3-3-3

view. The haemal arches were ossified before the centra in the tail, as in some hynobiids (Boisvert, 2008).

#### APPENDICULAR SKELETON

Although the scapulocoracoid is not clearly visible in the available specimens, it has been described as having a round coracoid section and a long scapular bar (Zhang *et al.*, 2009). Compared with the other Jehol salamanders, the coracoid is quite reduced in *Jeholotriton*. *Liaoxitriton*, *Pangerpeton*, *Regalerpeton*, and *Laccotriton* all have expanded coracoids that take on a rectangular shape (Zhang *et al.*, 2009). There are no dermal bones in the shoulder girdle, as is the case for all extant salamanders (Duellman & Trueb, 1994). The humerus of adults has a length of approximately 7.5 mm. The radius and the ulna are both well ossified. These two bones are similar to one another in length and are shorter than the humerus, with both having a length of approximately 4 mm. The ulna lacks an ossified olecranon. In the hindlimbs, the femur is poorly ossified, but with an estimated length of 7.0 mm. The fibia and tibia are of approximately the same size: about half the length of the femur. The manus of the *Jeholotriton* has four digits and a phalangeal formula of 2-3-3-2, whereas the pes has five digits and a phalangeal formula of 2-2-3-3-2. The carpals and tarsals cannot be seen in either the photographs or in the casts, indicating their immature, non-ossified condition. Most modern salamanders have a phalangeal formula of 2-2-3-2 in the manus and 2-2-3-4-3 in the pes (Carroll, 2009). See Table 1 for further comparisons of phalangeal formulae.



**Figure 3.** Larval skull of *Jeholotriton* specimen 0039B (ventral view). Note what seem to be distinct vomers and palatines. Scale bar: 5 mm.

#### SOFT ANATOMY

The presence of large eyes and skin are evident in most of the specimens. The skin appears to be smooth. Extensive external gills are retained in the fully ossified mature specimens, as well as in the larvae.

#### LARVAL SPECIMENS

The lengths of the larval specimens (tail included) range from 25 to 65 mm. Most are well preserved. Similar to the adults, the larvae have large eyes and external gills. The skull length to width ratio ranges from 4/6 mm to 13/15 mm. The frontals and parietals are present, although not clearly defined. In the cheek region, the squamosal is only present in specimens that had reached an advanced larval stage. The pterygoid retains its larval configuration throughout growth, with no evidence of the anterior process shifting to the more lateral orientation common in metamorphosing adults of non-neotenic salamanders. It remains poorly ossified and its length relative to the skull roof is reduced. Both the vomers and the palatine bones bear tooth patches (Fig. 3). It is unclear whether the larvae had pedicellate teeth. At metamorphosis, the palatine and the vomer become fused to one another. The parasphenoid is relatively smaller and not as well defined as in the adults. The otic capsule is ossified in all larval specimens. In the lower jaw, the dentary, angular, and coronoid/prearticular bones are present. None of the hyoid apparatus is visible. Little of the caudal vertebrae are

ossified. The smallest number of ossified caudals is eight. Ossification of the phalanges is also delayed.

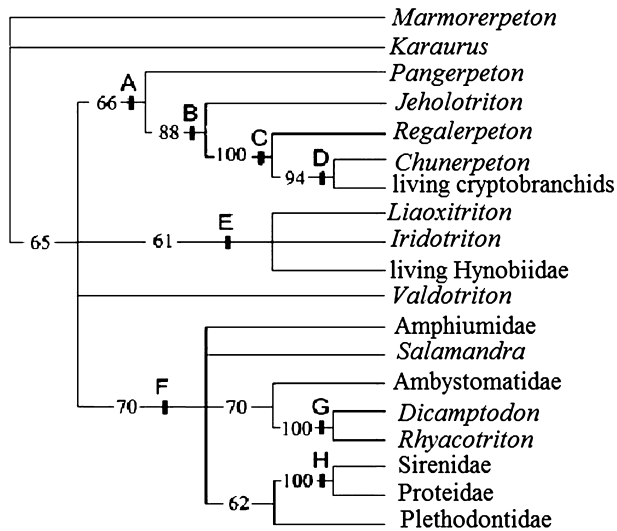
Rose (2003) investigated the ossification sequence of modern salamanders. He stated that the first bones to ossify were the lateral wall of the otic capsule and then the palatal and jaw bones (except for the maxilla, which is formed subsequently), along with the nasal, prefrontal, lacrimal, and septomaxilla. Later larval additions include the ossification of the stapes as well as the pterygoid. At metamorphosis, the maxilla attains its full length, the coronoid bone becomes reabsorbed, and the vomerine teeth appear. The ossification sequence of *Jeholotriton* differs from that described for modern metamorphosing salamanders in that the vomerine teeth appear early in development, the maxilla never attains its full length, and the coronoid bone is not reabsorbed. In most modern salamanders that undergo metamorphosis (such as the cryptobranchids and hynobiids), the orientation of the pterygoid changes gradually from pointing towards the anterior end of the parasphenoid to having its apex extending towards the margin of the skull. The differences between the sequence of ossification in *Jeholotriton* and modern transforming salamanders emphasize the neoteny of *Jeholotriton*.

#### COMPARISON AND DISCUSSION

The larval features of *Jeholotriton* include a pterygoid that is oriented towards the centre of the skull throughout growth, and the presence of external gills even in the most mature specimens. In addition, it retains a distinct coronoid bone that most salamanders reabsorb at metamorphosis (Rose, 2003). The maxilla also remains short throughout growth rather than increasing in relative length later in development – a factor that characterized metamorphosis among modern salamanders. Ossification of the vertebrae occurs in an anterior to posterior direction, and some of the largest specimens are fully ossified to almost the very end of the tail (preserved as an impression), indicating their adult condition.

#### TAXONOMIC POSITION

The position of *Jeholotriton* in the phylogenetic tree is difficult to specify because of its unique combination of mature and neotenic characteristics. The great extent of paedomorphosis exhibited by many lineages of both modern and extinct salamanders can make it difficult to establish patterns of relationships, as discussed by Wiens, Bonett & Chippindale 2005. In our study we chose to find the maximum number of synapomorphies in order to determine relatedness. The differences between *Jeholotriton* and other Inner Mongolia salamanders strongly suggest that *Jeholot-*



**Figure 4.** Phylogenetic tree based on a data matrix constructed for *Regalerpeton* (Zhang *et al.*, 2009).

*riton* is not closely related to any of the other salamander species from the Jehol Biota, although various previously published cladograms (Wang & Evans, 2006; Zhang *et al.*, 2009; see Fig. 4) have claimed this to be so. Both these studies made use of extensive data matrices (based on characters from Gao & Shubin, 2003). However, in this study, probable synapomorphies were used to establish plausible relationships instead of doing a parsimony analysis based on a large data matrix. The term synapomorphy is very specific: it refers to derived characters that are thought to have had a common ancestry, and thereby a common relationship. On the contrary, the term data matrix is very general. It may include a wide range of characters that are shared within a diversity of taxa, not all of which may be indicative of the degree of the relationship. Therefore, data matrices are not necessarily reliable for establishing sister-group relationships among salamanders, as there are great volumes of data that might be included. By investigating the anatomy of our specimens, we have noticed many characteristics that are not reflected in the cladograms that have been based on data matrices. This is most evident in the analysis of *Pangerpeton sinensis*, a salamander from the Liaoning deposit in Inner Mongolia. This species was described and analyzed by Wang & Evans (2006). However, it was only known in ventral view, precluding an adequate comparison with other species (Fig. 5).

The cladogram used suggested that *Pangerpeton* was a sister taxon to *Jeholotriton*. This relationship was based on a data matrix comparing *Pangerpeton* with many other salamanders, including those from the Jehol Biota (e.g. *Chunerpeton* and *Liaoxitriton*) as

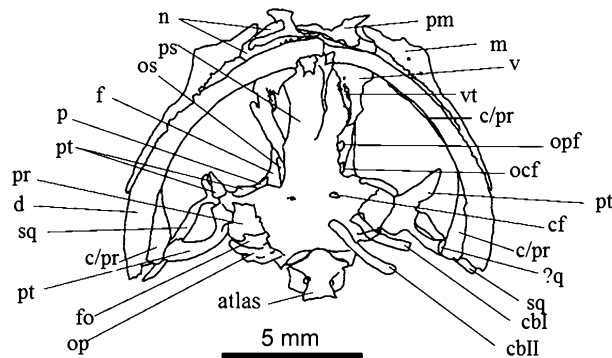
well as salamander families with living descendants (e.g. hynobiids and cryptobranchids). However, after comparing the character states of the two species, it is clear that there is not enough evidence to establish specific relationships between them. One of the most prominent characteristics of *Jeholotriton* is the medial orientation of its pterygoid. In contrast, *Pangerpeton* has a small pterygoid oriented away from the midline of the skull, long maxillae, and nasals (Wang & Evans, 2006), unlike *Jeholotriton*. The manus of *Pangerpeton* has an identical phalangeal formula to *Jeholotriton*, but the phalangeal formula of the pes is incompletely known (?-2-3-3-2); *Jeholotriton* pes, (2-2-3-3-2). The phalangeal count of the pes of *Pangerpeton* and *Jeholotriton* might have been the same, unless the first digit of the pes in *Pangerpeton* had less than two elements. The skull of *Pangerpeton* is also approximately half the length of *Jeholotriton* relative to the trunk length (Wang & Evans, 2006).

*Liaoxitriton daohugouensis* is another species from the Daohugou locality (the same locality as *Jeholotriton*), and shares many similarities with hynobiids. It was first described by Wang in 2004. It differs from *Jeholotriton* in having a very small pterygoid, oriented laterally, vomers that join at the midline, and pedicellate teeth. In addition it possesses long transverse processes and a very well ossified hyoid apparatus. The phalangeal formula also differs from *Jeholotriton*. *Liaoxitriton* has the formula of 2-2-3-2 in the manus and 2-2-3-4-2 in the pes (Wang, 2004), whereas *Jeholotriton* has a phalangeal formula of 2-3-3-2 in the manus and 2-2-3-3-2 in the pes. Juvenile *Jeholotriton* specimens were distinguished from *Liaoxitriton* by a shortened maxillae, as well as by the presence of vomerine tooth patches (*Jeholotriton*) instead of transverse vomerine tooth rows (*Liaoxitriton*). Another member of the genus *Liaoxitriton* is *Liaoxitriton zhongjiani*, from the Shuikouzi site in Liaoning province (Wang & Zhiming, 1998). The body of this salamander is 120 mm long, and differs from *Jeholotriton* in having well-developed maxillae and a pterygoid in which the apex reaches the posterior end of the maxilla (Wang & Zhiming, 1998).

Fossils of the salamander *Chunerpeton tianyiensis* (Fig. 6) are also known from the Daohugou locality (Gao & Shubin, 2003). This genus is the only Jehol salamander that has been classified as a member in one of the modern families: the Cryptobranchidae. *Chunerpeton* has a total length of 180 mm, and can be distinguished from *Jeholotriton* by the absence of a lacrimal, and by a pterygoid extending towards the lateral margin of the palate. Juvenile *Chunerpeton* specimens possess transverse vomerine teeth, unlike those of larval *Jeholotriton*.



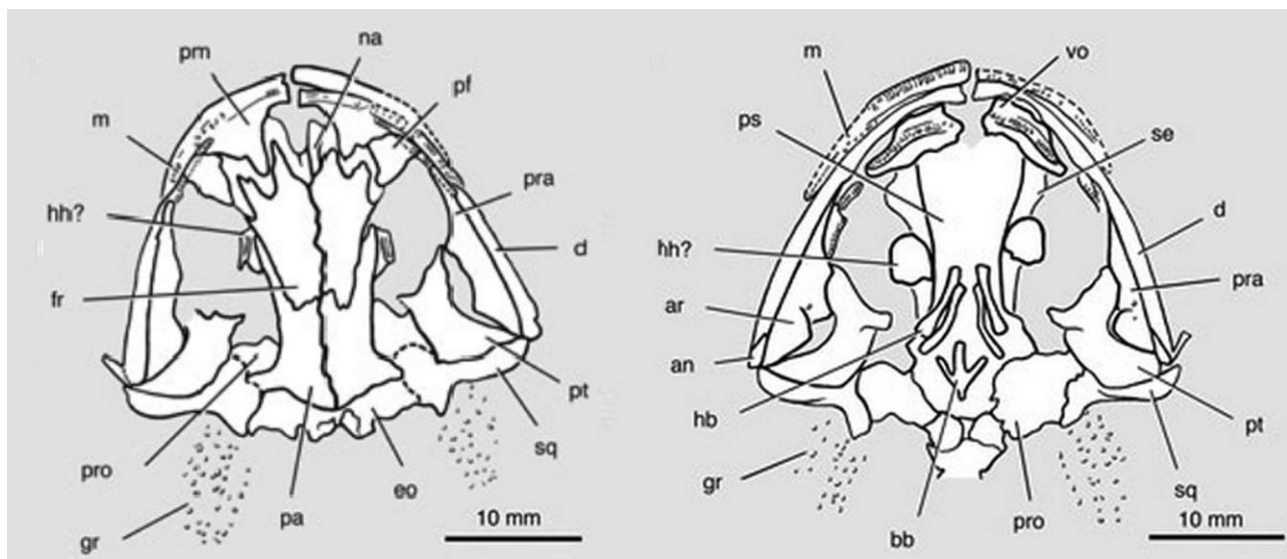
Modern cryptobranchids differ from *Chunerpeton* in only minor features. Cryptobranchids have a very well-developed maxilla, vomerine teeth that are parallel to the dentition in the upper jaw, well-ossified stapes, prefrontals, and nasals (Carroll, 2009). They do have a pterygoid similar in size and shape to that of the *Jeholotriton*. However, the orientation of the pterygoid in cryptobranchids is very different in that its apex points away from the midline of the skull.



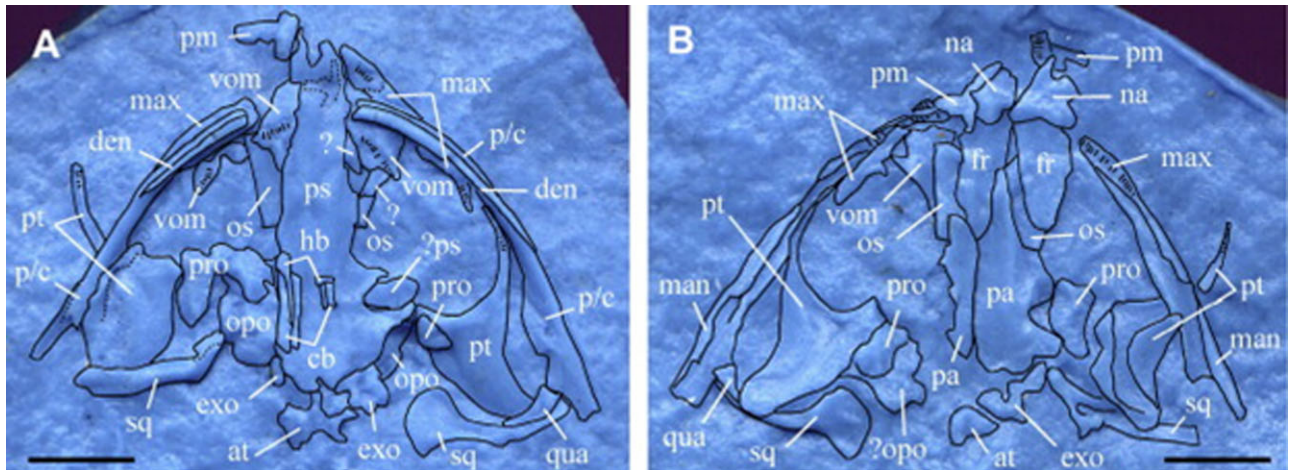
**Figure 5.** Ventral view of *Pangerpeton*; a, atlas; cbI/II, ceratobranchial I/II; cf, carotid foramen; c/pr, coronoid/prearticular; d, dentary; f, frontal; fo, fenestra ovalis; m, maxilla; n, nasal; ocf, oculomotor foramen; op, opisthotic; opf, optic foramen; p, parietal; pm, premaxilla; ps, parasphenoid; pt, pterygoid; q, quadrate; sq, squamosal; v, vomer; vt, vomerine teeth row. (Wang & Evans, 2006).

*Regalerpeton* (Fig. 7), from the Huajiyang Formation in the north-eastern part of China, is approximately the same age as *Jeholotriton* (Zhang *et al.*, 2009). Based on anatomical differences, it is unlikely that *Regalerpeton* and *Jeholotriton* are closely related. *Regalerpeton* has vomerine teeth rows that run parallel with the maxilla, unlike the teeth rows in *Jeholotriton* that run obliquely, and a pterygoid oriented away from the midline of the skull. Also, *Regalerpeton* has a well-ossified hyobranchium, along with ossified carpals and tarsals, which *Jeholotriton* lacks. Finally, there is no sign of external gills in *Regalerpeton*. The total length of *Regalerpeton* could not be determined because of the absence of the posterior trunk.

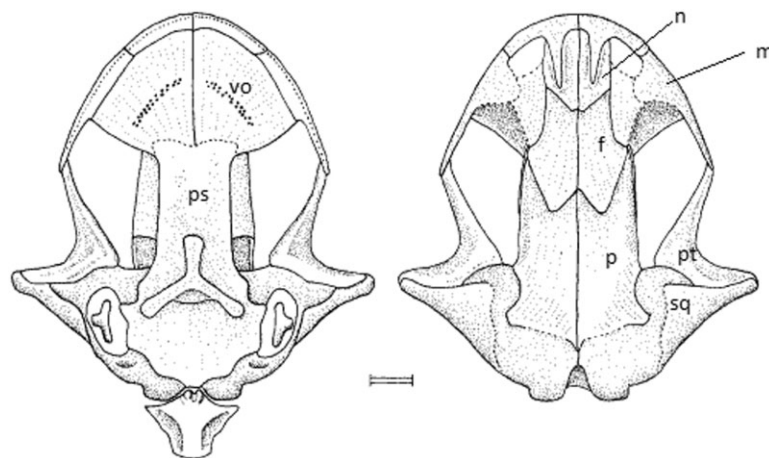
*Sinerpeton fengshaensis* and *Laccotriton subsolanus* are two additional salamander species from the late Jurassic Fengshan locality (China). They were described by Gao & Shubin in 2001. *Sinerpeton fengshaensis* differs from *Jeholotriton* in the small size of the frontals, ossified ceratobranchials, parietals with no lateral extensions, a pterygoid oriented away from the midline of the skull, five distinct bones in the mandible (angular, prearticular, articular, coronoid, and dentary), and a phalangeal formula of 1-2-3-2 in the manus and 1-2-3-4-2 in the pes (Gao & Shubin, 2001). Both the manus and the pes are different from *Jeholotriton*, which has a formula of 2-3-3-2 in the manus and 2-2-3-3-2 in the pes. *Sinerpeton* has a snout–vent length of 47 mm (Gao & Shubin, 2001), but is shorter than *Jeholotriton*, which has a



**Figure 6.** Skull of *Chunerpeton* (left, dorsal view; right, ventral view); an, angular; ar, articular; bb, basibranchial; d, dentary; fr, frontal; gr, gill rakers; hb, hypobranchial; hh?, hypohyal?; m, maxilla; na, nasal; pa, parietal; pf, prefrontal; pm, premaxilla; pra, prearticular; pro, pro-otic; ps, parasphenoid; pt, pterygoid; se, sphenethmoid; sq, squamosal; vo, vomer; vt, vertebra (Gao & Shubin, 2003).



**Figure 7.** Skull of *Regalrpeton* (A, ventral view; B, dorsal view); at, atlas; cb, ceratobranchial; den, dentary; exo, exoccipital; fr, frontal; hb, hypobranchial; man, mandible; max, maxilla; na, nasal; opo, opisthotic; os, orbitosphenoid; p/c, prearticular/coronoid; pa, parietal; pm, premaxilla; pro, prootic; ps, parasphenoid; pt, pterygoid; qua, quadrate; sq, squamosal; vom, vomer (Zhang *et al.*, 2009). Scale bars: 5 mm.



**Figure 8.** *Valdetrion*: reconstruction of skulls in palatal view (left) and dorsal view (right); F, frontal; m, maxilla; n, nasal; p, parietal; ps, parasphenoid; pt, pterygoid; sq, squamosal; vo, vomers. Scale bar: 1 mm. (Evans & Milner, 1996).

snout–vent length of approximately 62 mm. *Laccotriton subsolanus* also has short frontals, a prefrontal, and, like *Sinerpeton*, its mandible is made up of five separate elements.

Going beyond the Chinese Mesozoic salamanders, the genus *Valdetrion* (a sister group of the more advanced Urodeles: ambystomatids, amphiumids, sirenids, plethodontids, and proteids – see Fig. 8) is from the Las Hoyas locality in Spain (Evans & Milner, 1996). The age of the Las Hoyas locality is between 116 and 114 million years old, approximately 45 million years later than the specimens from the Daohugou locality. *Valdetrion* has an average snout–pelvis length of 34 mm, a well-developed pterygoid that points away from the midline of the skull, and a

fully ossified hyoid apparatus (Evans & Milner, 1996). In addition, it is characterized by long and slender prefrontals, pedicellate teeth, and a vomerine dentition in which there is an arch of teeth that runs parallel with the marginal dentition (Evans & Milner, 1996). All of these characteristics separate it from a close relationship to *Jeholotriton*. Otherwise, the relationship between *Valdetrion* and modern salamanders remains enigmatic.

Among the modern salamander families, *Jeholotriton* shows no significant similarities to the Proteidae or the Amphiumidae. The amphiumids have fully developed maxillae and a very small pterygoid (Carroll & Holmes, 1980). These salamanders have lost their gills as adults, and they lack a coronoid



bone in the mandible. *Jeholotriton* also differs from proteids, which have no angular, no maxilla, and their pterygoid bone is extremely reduced (Carroll & Holmes, 1980).

None of the salamander families or genera mentioned above bear any significant similarities to *J. paradoxus*. However, there are three additional taxa within the Caudata: *D. tenebrosus*, sirenids, and the genera *Ranodon* and *Hynobius* (within the hynobiids), as well as one group just outside the Caudata, *Kokartus*, which shares some similarities with *Jeholotriton*.

Sirenids are large salamanders that have lost their hindlimbs and retain external gills (Carroll, 2009). They differ from *Jeholotriton* by having extremely reduced pterygoids and maxillae and no premaxillae whatsoever; the function of the upper jaw is replaced by a keratinized beak. In contrast, they have ossified carpals and tarsals (Wang & Rose, 2005). However, the palatine dentition does resemble those in larval *Jeholotriton* in having tooth plates on both the vomers and the palatines. Despite the similar palatine dentition, it is unlikely that *Jeholotriton* is closely related to sirenids because of their many other differences.

*Dicamptodontidae tenebrosus* (Rose, 2003) seems to share many similar features with *Jeholotriton*. Specimens (CAS 210347, CAS 210348, and CAS 93958) of *D. tenebrosus*, on loan from the collection of Department of Herpetology (California Academy of Sciences), were used for comparison. The orientation of the pterygoid in *D. tenebrosus* is very similar to that of *Jeholotriton* because of the neotenic condition of both species. In addition, both of these species lack nasal bones, and have maxillae that are not fully developed (Rose, 2003). *Dicamptodontidae tenebrosus* also retains its coronoid bone, although it remains toothless. It also has a fontanelle between the premaxillae, similar to that of *Jeholotriton*. *Dicamptodontidae tenebrosus* has a phalangeal formula of 2-2-3-2 in the manus and 2-2-3-4-2 in the pes. The phalangeal formulae do differ relative to those in *Jeholotriton* (2-3-3-2 in the manus and 2-2-3-3-2 in the pes). Dicamptodontids are a sister group of ambystomatids, but they are also closely related to sirenids, proteids, and plethodontids (Fig. 4). As *Jeholotriton* is so different from these other groups, it is probable that the similarities that *Jeholotriton* and *D. tenebrosus* share are simply a result of their neotenic condition.

Hynobiids are the most primitive of modern salamander families. They are similar to *Jeholotriton* in that some species (e.g. *Ranodon sibiricus* and *Hynobius maculosus*) develop their vertebrae via a primitive sequence in which arches are ossified before the centra (Boisvert, 2008). Hynobiids are the only members of the modern salamander families that

possess this characteristic. Boisvert argued that this was sufficient evidence to classify the hynobiids as the most basal clade among the modern salamanders. It is significant that *Jeholotriton* shares this primitive characteristic with certain hynobiids, suggesting that hynobiids might be as old as *Jeholotriton*, or maybe even older. Boisvert suggested in her paper that the switch from the primitive vertebral condition to the derived one (ossification of centra before arches) occurred between the Triassic and mid-Jurassic in Asia. Her estimated timeline fits with the estimated age of *Jeholotriton* (middle to late Jurassic). However, modern hynobiid skulls do have some differences relative to *Jeholotriton*. The vomers of hynobiids lack denticles and they have a long and fully developed maxilla. They also retain a prefrontal (Carroll, 2009).

*Kokartus* is a member of the family Karauridae (from Russia), which is classified as a sister taxa of the Urodele (Ivakhnenko, 1978). It is from the Middle–Late Jurassic period, and specimens were found in Central Asia (Skutschas & Martin, 2011). This genus shows some similarities to *Jeholotriton*, including being neotenic and therefore, having a very similar pterygoid orientation to that of *Jeholotriton*. In addition, both have widely separated vomers with very similar vomerine dentition and orientation of the squamosal (Ivakhnenko, 1978). *Kokartus* has denticles on the pterygoid, palatine, and parasphenoid (Skutschas & Martin, 2011). Furthermore, it is characterized by large frontals and parietals with lateral extensions at the posterior end similar to those of *Jeholotriton*. *Kokartus* is a sister group to the genus *Karaurus* and both are outgroups of the urodeles (Skutschas & Martin, 2011). This suggests a plausible sister group related with *Jeholotriton* at the base of urodele salamander radiation.

## CONCLUSION

The uniqueness of *Jeholotriton* and the difficulty in determining its relationship relative to other salamanders stems from the fact that *Jeholotriton* species possess a combination of adult and larval features. *Jeholotriton* is not very similar to any of the other Inner Mongolia salamanders, nor does it fit into any of the modern salamander families. However, striking similarities between *Jeholotriton* and certain hynobiids suggest possible affinities or marked convergence between the two species early in the Mesozoic. This suggests a plausible sister-taxon relationship with *Jeholotriton* at the base of the Urodele radiation.

## ACKNOWLEDGEMENTS

We wish to thank Dr Qing-Long Shao, Director, Inner Mongolia Autonomous Region Museum, Huhehaote,

for the invitation to study and publish descriptions of the fossil salamanders in the museum's collection from the Jurassic Daohugou Fossil Beds. Long Li, Head of Natural Sciences of the museum also contributed greatly in providing access to this extensive collection and arranging for their study and photography. The technical staff of the museum also contributed significantly in making latex casts of the numerous specimens that had been preserved as natural casts. This research could not have been carried out without the prior help of Dr Xiao-chun Wu, Earth Science Section, Canadian Museum of Nature, Ottawa, who initiated the contact between the Inner Mongolia Autonomous Region Museum, Huhehaote, and the Redpath Museum, McGill University, Canada.

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