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Restudy of *Regalerpeton weichangensis* (Amphibia: Urodela) from the Lower Cretaceous of Hebei, China

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Abstract *Regalerpeton weichangensis* was established in 2009 on an incomplete skeleton preserved mainly as an impression from the Lower Cretaceous of Hebei, China. However, several anatomical characters were misinterpreted due to distortion of the holotype, and its taxonomic position has been in debate. In this paper, *R. weichangensis* is redescribed based on eight new specimens and its diagnosis and phylogenetic position are re-examined. This work shows that *R. weichangensis* was a neotenic form with ossified carpals and tarsals. It has a series of unique combination of characteristics including the vomer with a transverse vomerine tooth row, anterior end of the cultriform process of the parasphenoid indented, basibranchial II triradiate, a long tail exceeded the snout-pelvis length and scapulocoracoid with a rectangular coracoid end. Phylogenetic analysis suggests *Regalerpeton*, *Jeholotriton* and *Pangerpeton* should be placed in the suborder Salamandroidea with three synapomorphies. Moreover, they also share unicapitate ribs with Cryptobranchoidea, which indicates that they represent an important stage of evolution in the Cryptobranchoidea-Salamandroidea split.

Key words Weichang, Hebei; Lower Cretaceous; Salamandroidea, *Regalerpeton weichangensis*; morphology; phylogeny

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1 Introduction

Since the late 1990s, a large number of salamander fossils have successively been unearthed from Jurassic and Cretaceous strata in northeastern China, and eleven taxa have been established: *Laccotriton subsolanus* Gao et al., 1998, *Liaoxitriton zhongjiani* Dong &Wang, 1998, *Jeholotriton paradoxus* Wang, 2000, *Sinerpeton fengshanensis* Gao & Shubin, 2001, *Chunerpeton tianyiensis* Gao & Shubin, 2003, *Liaoxitriton daohugouensis* Wang, 2004, *Pangerpeton sinensis* Wang & Evans, 2006, *Regalerpeton weichangensis* Zhang et al., 2009, *Beiyanerpeton jianpingensis* Gao & Shubin, 2012, and *Qinglongtriton gangouensis* Jia &

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Gao, 2016a, *Nuominerpeton aquilonaris* Jia & Gao, 2016b. These taxa provide a rich source of information on primitive salamanders, and are significant in understanding the origin of modern salamander clades. Among these taxa, *R. weichangensis* was erected on an incomplete skeleton preserved mainly as impression. This preservation limited our understanding of its morphology and phylogeny. In the original paper, *Regalerpeton* was placed as the sister taxon of *Chunerpeton* plus living cryptobranchids (Zhang et al., 2009), whereas Skutschas and Gubin (2012) suggested it as a sister taxon of Hynobiidae.

In this paper, eight new specimens which can be referred to *R. weichangensis* are described from northern Hebei Province of China. These better preserved materials permit a revised diagnosis of the taxon and allow a new phylogenetic analysis to be conducted that includes most of the fossil taxa from China.

Abbreviations ac, acetabulum; ad. f, anterodorsal fenestra; am. f, anteromedial fenestra; at, atlas; bb I–II, basibranchial I–II; c, centrale; cb I–II, ceratobranchial I–II; cr vent, crista ventralis; d, dentary; dc, distal carpal; dt 1–3, distal tarsal 1–3; d 1–5, digit 1–5; e+o, exoccipital+opisthotic; fe, femur; fi, fibula; fib, fibulare; fo. i. den, inferior dental foramen; fr, frontal; gf, gill filament; gr, gill raker; hb I–II, hypobranchial I–II; hu, humerus; i, intermedium; il, ilium; in. c. a, internal carotid artery; isc, ischium; lac, lacrimal; m, maxilla; n, nasal; os, orbitosphenoid; p+c, prearticular+coronoid; pa, parietal; ph 2–5, phalanx 2–5; pm, premaxilla; pm. apr, ascending process of the premaxilla; prf, prefrontal; pro, prootic; ps, parasphenoid; pt, pterygoid; qua, quadrate; ra, radius; rad, radiale; sa, sacral; sca, scapulocoracoid; sq, squamosal; st, stapes; ti, tibia; tib, tibiale; ul, ulna, uln; ulnare; vo, vomer; vot, vomerine tooth row.

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2 Systematic paleontology

Class Amphibia Linnaeus, 1758
Subclass Lissamphibia Haeckel, 1866
Superorder Caudate Scopoli, 1777
Order Urodela Duméril, 1806
Family Salamandroidea Dunn, 1922
Genus *Regalerpeton* Zhang et al., 2009

Type species *Regalerpeton weichangensis* Zhang et al., 2009.

Holotype IVPP V 14391A, B, an incomplete skeleton impression preserved as part and counterpart on slabs of siltstone.

Referred specimens IVPP V 15677, an incomplete skeleton impression with a nearly complete skull in dorsal view. V 16776A, B, an incomplete skeleton with a nearly complete skull and partial postcranial skeleton that shows well-developed anterodorsal and anteromedial fenestrae. V 16790A, B, an incomplete skeleton with disarticulated bones of the skull that shows the morphology of the premaxilla, vomer, pterygoid, squamosal and dentary. V 16798A, B, an incomplete skeleton impression with impression of the external gills and ossified carpals. V 17989, a nearly complete skeletal impression with a well-preserved skull in ventral view. V 16802A, B, an incomplete skeletal impression with ossified carpals. V 23342A, B, an incomplete skeletal impression lacking part of the tail, with some bones displaced from their original positions due to lateral compression. V 23343A, B, an incomplete skeleton with disarticulated bones of the skull that shows the morphology of the premaxilla, maxilla, prearticular+coronoid, parasphenoid and ilium.

Revised diagnosis *Regalerpeton weichangensis*, a neotenic salamander, is diagnosed by the following unique combination of characters: premaxilla with a distinct ascending process and bearing approximately 25 teeth; slender maxilla without the facial process and bearing approximately 28 teeth; dentary bearing approximately 40 teeth; nasals without midline contact; anterodorsal and anteromedial fenestrae present; lacrimal and prefrontal present; parietal-prefrontal contact absent; squamosal with two proximal expansions; quadrate ossification present; roughly pentagonal vomer with transversely oriented vomerine tooth row; parasphenoid inverted arrow-shaped with an indented anterior end of the cultriform process; internal carotid foramina penetrating parasphenoid; pterygoid triradiate with a vimineous dentate anterior ramus; paired hypobranchial I and II ossified; basibranchial II triradiate; prearticular and coronoid fused with two processes; opisthotic and exoccipital fused; stapes present; three pairs of external gills present with ossified or calcified gill rakers; 16 presacral vertebrae; atlas with bifid interglenoid tuberosity; trunk vertebrae amphicoelous and ribs unicapitate; three pairs of free postsacral ribs; a long tail exceeded the snout-pelvis length; coracoid portion of scapulocoracoid rectangular; ilium spoon-shaped; humerus with crista ventralis; carpals and tarsals ossified; digit 2 in manus and digit 1 in pes short; phalangeal formulae 2-2-3-2 in manus and 2-2-3-3-2 in pes.

Locality and horizon The specimens of *Regalerpeton weichangensis* are from three different localities: Daobaziliang, Weichang County, Hebei Province, China (the holotype); Xishunjing village, Weichang County (V 15677, V 16776A, B, V 16790A, B, V 16798A, B, V 16802A, B, V 17989, V 23342A, B), and Yulinzi village, Weichang County (V 23343A, B). Dabeigou Formation, Lower Cretaceous (Gao et al., 2013).

Remarks Because of incomplete preservation and distortion of the holotype, several morphological characteristics are absent and misinterpreted. Further, series of reliable characteristics can be concluded as below: the pterygoid is triradiate, with a vimineous dentate anterior ramus. Although the original article is described as two pairs of ceratobranchials due to poor preservation, it is reinterpreted as two pairs of hypobranchials. The coracoid portion of scapulocoracoid is rectangular. In the original article, a detailed discussion about the shape of coracoid portion shows that scapulocoracoid is the identification of the characteristics of *Regalerpeton*. The study of new specimens also agrees that conclusion is reliable. The vomerine tooth row is transversely oriented and vomer is pentagonal. The primitive interpretation of the orientation is parallel to the maxillary arcade because of distortion of the parasphenoid. New study on the holotype indicates that vomer should be roughly pentagonal. The parasphenoid has prominent cultriform process. The angular is absent in the mandible. The tarsals are ossified. Based on the comparison of the above characteristics combination, the new specimen are referred to *R. weichangensis.*

3 Description

Among the eight new specimens, V 23342 (Figs. 1, 2) is the best preserved. The following description is based on it unless otherwise noted.

Skull roof The skull roof is composed of the paired nasals, lacrimals, prefrontals, frontals and parietals, showing no dermal sculpture.

The nasal (Fig. 3A) is a large triangular bone. It contacts the ascending process of the maxilla anteriorly, frontal posteriorly and prefrontal laterally. It is not connected to the lacrimal. The nasals are separated by a large anterodorsal fenestra (Fig. 3A, C).

The lacrimal is a small quadrilateral bone (V 16798) that forms the posterior edge of the narial fenestra and the anterior edge of the orbit. The nasolacrimal ducts are not observed due to poor preservation.

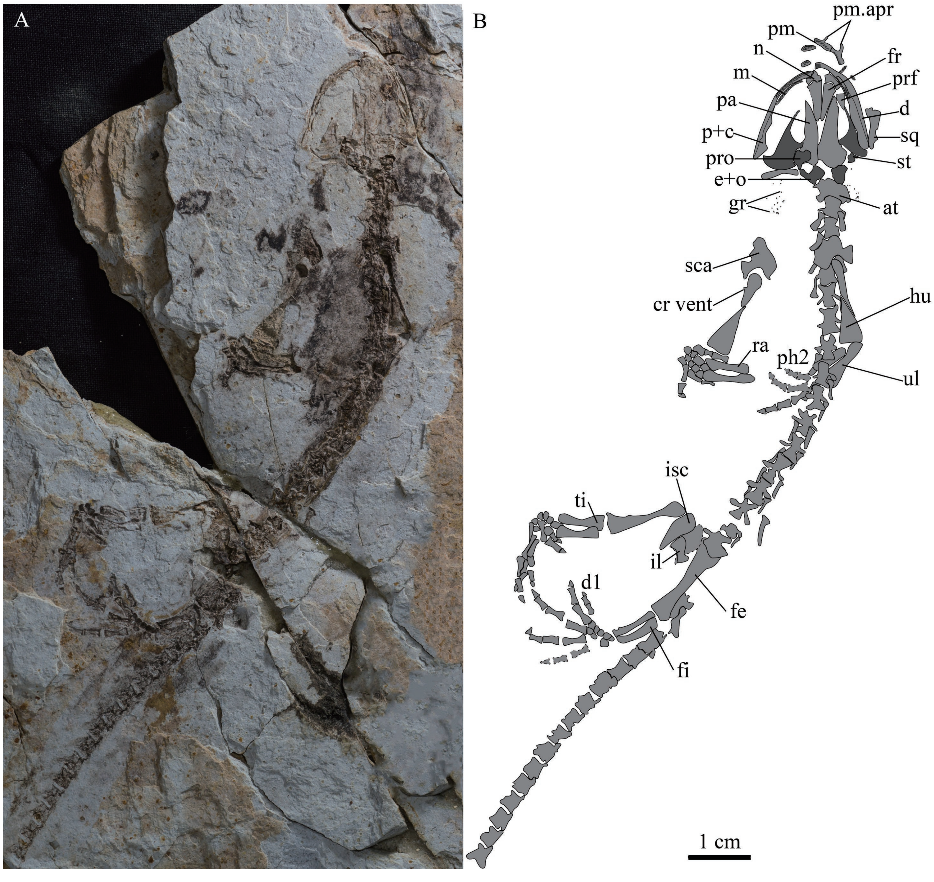

Fig. 1 Photograph (A) and line drawing (B) of *Regalerpeton weichangensis* (IVPP V 23342A) in dorsal view

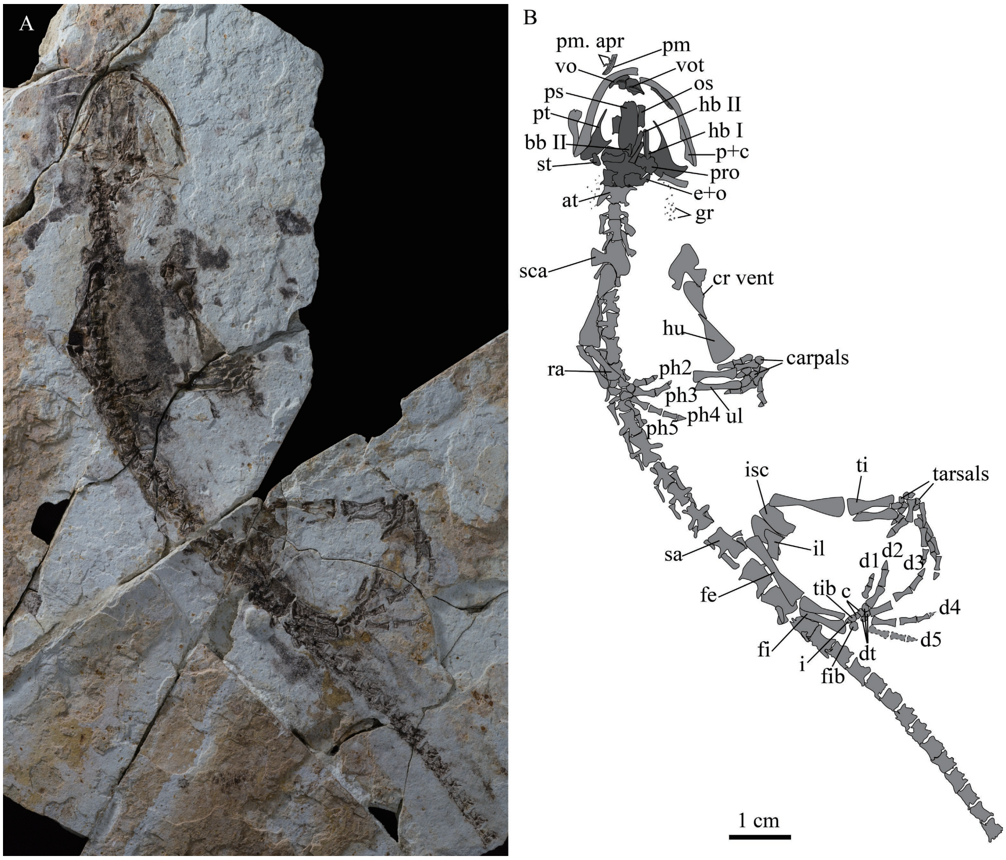

Fig. 2 Photograph (A) and line drawing (B) of *Regalerpeton weichangensis* (IVPP V 23342B) in ventral view

The prefrontal (Fig. 3) is a cuneate bone. Its anterior border has inverted V-shape, with the anteromedial side suturing with the nasal and the posterolateral side with the lacrimal. Medially, it contacts the frontal, but not the parietal.

The frontal (Figs. 1, 3A) is a longitudinal bone with a small anterolateral extension. Its anterior border completely contacts nasal. Posteriorly, the frontal overlies the parietal extensively.

The parietal (Figs. 1, 3A) is also a longitudinal bone. It is slightly shorter than frontal and lies posterior to the frontal. The parietal is sutured along the posterior midline, but separated anteriorly by an anteromedial fenestra (Fig. 3A, C). The parietal has a well-developed anterolateral extension along the posterolateral margin of the frontal, but it fails to extent to the prefrontal. Posteriorly, parietal has an obvious lateral extension that articulates with squamosal (Fig. 3A). In lateral view, the parietal is seen to articulate with the orbitosphenoid ventrally.

Palate The floor of the skull consists of two completely separated vomers anteriorly and one parasphenoid posteriorly.

The vomer (Figs. 3B, 4B) is roughly pen-tagonal with a prominent extension laterally. Poster-olateral border of vomer has a slightly notch for the choana. There are about 20 teeth

(V 17989) in the vomer, they are monostichous and nonpedicellate. The vomerine tooth row (Figs. 3B, 4B) is transversely oriented and runs from the midline towards extension laterally.

The parasphenoid (Fig. 4D) is a large arrow-shape bone. The anterior end of the parasphenoid is serrated including four processes, the medial two of which are cuspidal and the lateral two long and obtuse. The lateral margins of the serrated part have facets for the vomers. Posteriorly, the parasphenoid broadens obviously and has a recognized conule of the both side, for articulating with orbitosphenoids. There is a groove on each side of the parasphenoid wing, along which the internal carotid artery runs. The orbitosphenoid (sphenethmoid) (Fig. 3B) is approximately cuboid and they ossified to form the lateral side of the neurocranium.

Suspensorium The suspensorium consists of the paired pterygoids, squamosals and quadrates.

The pterygoid (Figs. 2, 3) is triradiate, with a vimineous anteromedial process which is free and curving and has ten teeth. Its posterolateral process articulates with squamosal and quadrate. It has a shorter medial process that points to parasphenoid. There is no contact between the pterygoid and the parasphenoid.

The squamosal (Fig. 3) is a slightly curving lamellate of bone and presents as a transverse bar in the posterior skull. It has two proximal expansions, anterior one smaller than the posterior one. Ventrally, the squamosal articulates with the pterygoid and the quadrate (Fig. 3B).

The quadrate (Fig. 3A, B) is a roughly triangular bone that lies in the ventral surface of the squamosal.

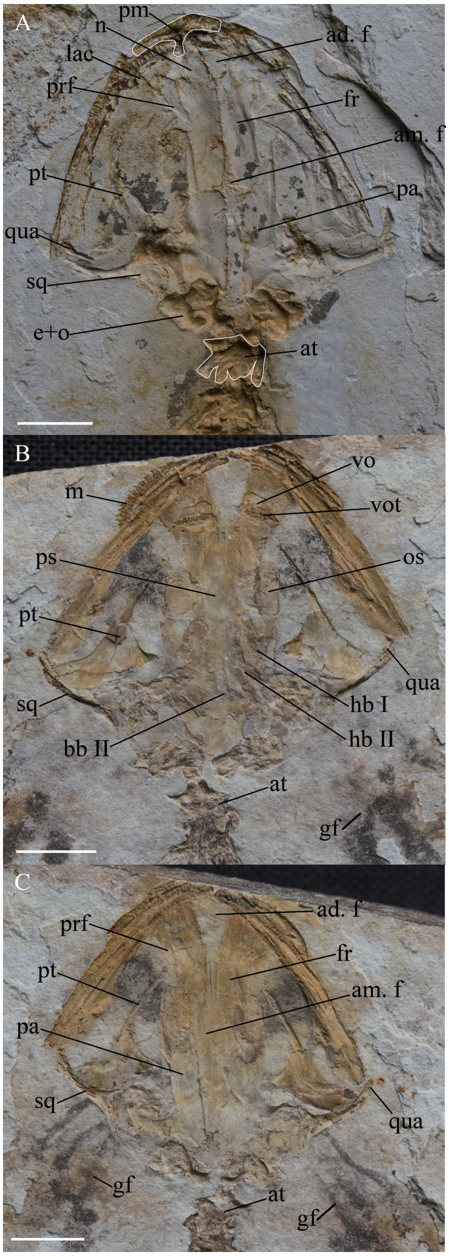

Fig. 3 Photograph of the impression of the skull roof of *Regalerpeton weichangensis*
A. IVPP V 15677; B. V 16776 A; C. V 16776B. Scale bars equal 5 mm

Otico-occipital region The otico-occipital region of *Regalerpeton* consists of three endochondral bones: the prootic, a compound containing opisthotic and exoccipital, and stapes (columella). Both prootic and opisthotic form the anterior and posterior walls of the otic capsule respectively. The stapes (Fig. 2) is nail-shaped, with the head forming the round

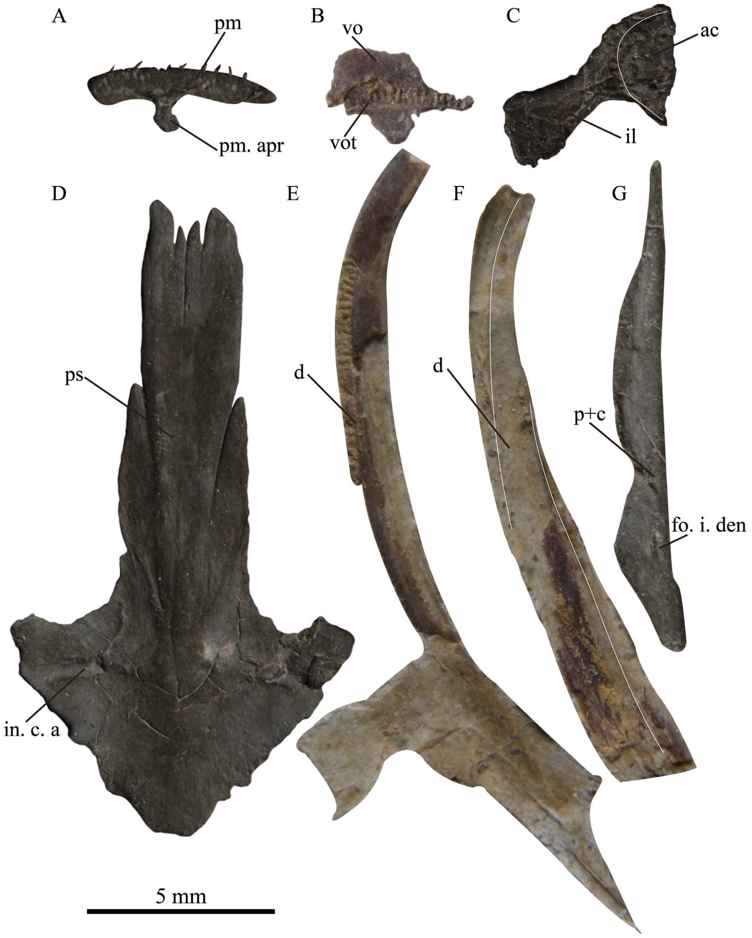

Fig. 4 Skeletons and impressions of *Regalerpeton weichangensis*
Impressions of right premaxilla (A), left ilium (C), parasphenoid (D), left dentary showing articular surface for prearticular+coronoid (F) and left prearticular+coronoid (G); skeletons of right vomer (B), right dentary (E)
A, C, D from IVPP V 23343A; B, E, F from V 16790B; G from V 23343B

footplate and its shaft forming a short stylus. Its footplate covers the lateral wall of the otic capsule. In *Regalerpeton*, opisthotic and exoccipital form a compound which expose completely in the parietal end (Fig. 3A). The opisthotic portion seems to have an obvious expansion on account of deep impression preserved in V 15677 (Fig. 3A). However, more information from otico-occipital region is not observed because most specimens are preserved as impression.

Upper and lower jaws The upper jaw is formed by two dermal bones on each side: the paired dentate premaxillae medially and the paired dentate maxillae posteriorly.

The premaxilla (Figs. 1, 2, 4A) has a distinct ascending process extending along about one-third of the premaxilla near the midline, which contacts the anterior part of the nasal (Fig. 3A). The premaxilla bears approximately 25 teeth that are gracile, pointed and nonpedicellate.

The maxilla (Fig. 3B) is a slender bone that articulates with the premaxilla anteriorly. A distinct facial process is easily observable. The maxilla is slightly longer than the premaxilla and bears approximately 28 teeth which are similar to the premaxillary teeth.

The mandible consists of two distinct dermal bones: the dentary and a compound bone comprising the prearticular and the coronoid. They surround Meckel's cartilage.

The dentary (Fig. 4E) bears approximately 40 teeth on the lingual surface of the lower jaw. The teeth are small, closely packed and nonpedicellate.

The compound of prearticular+coronoid possesses two processes (Figs. 1, 2, 4G). It has a slender extension that runs along the lingual surface of the lower jaw (Fig. 4G). The inferior dental foramen (Fig. 4G) is a conspicuous feature near the posterior of the compound bone and it carried the ramus alveolaris of facial nerve and the alveolar artery (Francis, 1934). The articular and the angular are not visible.

Hyobranchium The hyobranchium consists of three ossified elements: hypobranchial I, hypobranchial II and basibranchial II (os thyroideum) (Figs. 2, 3B). Hypobranchials I and II are paired, parallel to each other, and each of them is a slightly curved strip. The azygous midline basibranchial II is positioned posterior to other hyobranchial elements and it is triradiate.

Axial skeleton The vertebral column consists of 16 presacrals including the atlas and 15 trunk vertebrae, one sacral, and about 40 caudal vertebrae.

The atlas lacks free ribs and is shorter than the trunk vertebrae. It has two relatively elongated transverse processes (Fig. 3A) and a bifid interglenoid tuberosity (Figs. 3B, C) that articulate with the exoccipitals. All the trunk vertebrae are amphicoelous and all the ribs are unicapitate. The sacral vertebra is larger than the trunk vertebrae, and its ribs are long, thick and expanded proximally. *Regalerpeton* has a very long tail that exceeds the snout-pelvis length. The first three caudosacrals bear free ribs. The remaining caudal vertebrae lack free ribs, but bear elongate transverse processes, and distinct neural and haemal arches.

Appendicular skeleton The pectoral girdle lies roughly at the level of the 3rd to 4th trunk vertebrae. It consists of only one ossified bone: the scapulocoracoid. The coracoid portion is almost rectangular, and the scapular portion is cuneate.

The humerus is claviform, with expanded proximal and distal portions. In V 23342, the epiphysis of the humerus is wholly ossified and a crista ventralis is present (Figs. 1, 2, 5). The radius is a slender and claviform bone, although the distal portion is inflated. The ulna, which is parallel to the radius, is a slightly curved bone that is longer than the radius (Figs. 1, 2, 5). The carpals are ossified and consist of a radiale, ulnare, intermedium, one centrale, three distal carpals (Fig. 6). There are four digits in the manus and phalanx 2 is very short (V 16776A, B; V 17989). The phalangeal formula is 2-2-3-2.

The pelvic girdle has two ossified elements: a pair of ischia ventrally and a pair of ilia laterally. Each ischium is approximately blade-shaped and the anterior portion is wider than the posterior one. The ischium joins the cartilagious pubis anteriorly and the ilium laterally to form the acetabulum for the articulation of the femur. The ilium is a spoon-shaped bone (Fig.

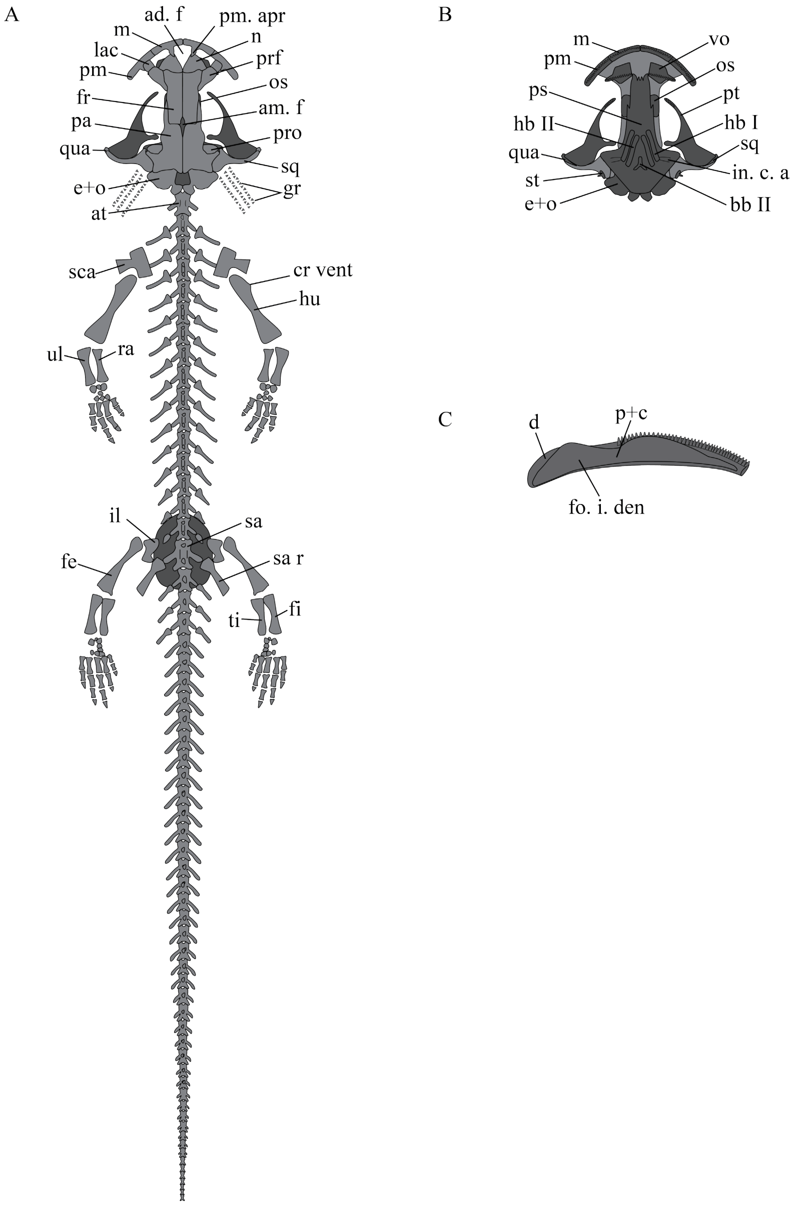

Fig. 5 Reconstruction of the skeleton of *Regalerpeton weichangensis*
A. skeleton in dorsal view; B. skull in ventral view; C. mandible in lingual view. Not to scale

4C). Its proximal portion is expanded and forms part of the acetabulum, while the posterior dorsal portion is slightly curved, and articulates with the sacral rib to attach the pelvic girdle.

The femur (Figs. 1, 2) is a long, straight claviform bone, with the proximal end narrower than the distal one. The tibia and fibula are relative short and straight (Figs. 1, 2). The proximal portion of the tibia is more expanded than the distal end, whereas the fibula is slight curved and its distal portion is relatively inflated. There are seven ossified elements in the ankle (Fig. 2). These consist of the tibiale and fibulare proximally, intermedium, two centralia, and three distal tarsals. There are five digits in the pes. Digit 1 is relatively short (Fig. 1) and the phalangeal formula is 2-2-3-3-2. (Fig. 1, 2)

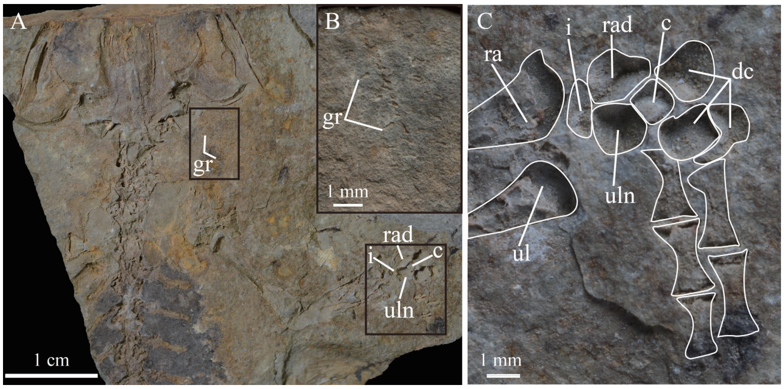

Fig. 6 *Regalerpeton weichangensis* (IVPP V 16802B)
A. photograph of an incomplete skeletal impression; B. the details of gill rakers; C. the details of ossified carpals

4 Comparison and discussion

4.1 Vomer and vomerine tooth row

The vomer is one of the important dentate elements on the palate for salamanders. The vomerine teeth has played important role in the systematics of salamanders (Regal, 1966; Rose, 2003; Fei and Ye, 2017). In the Cryptobranchidae the vomerine teeth is parallel to the maxillary arcade (Qiu and Yang, 1986; Rose, 2003). In the Hynobiidae the vomerine teeth varies in length, shape, location and orientation in different genus-species (Fei and Ye, 2017). In the Salamandroidea the vomerine teeth have more complex types such as transverse row along posterior border of the vomer in the Ambystomatidae, teeth covered the posterior extension of the vomer in the Salamandridae and Plethodontidae, vomerine teeth row paralleled to the maxillary arcade in the Proteidae and Amphiumidae (Regal, 1966; Rose, 2003; Darda and Wake, 2015; Gregory et al., 2016).

The vomer of the *Regalerpeton* is roughly pentagonal and the vomerine tooth row is transversely oriented. Compared with other fossil salamanders (Fig. 7), the vomers do not meet each other in the midline, as in *Pangerpeton*, *Seminobatrachus*, *Chunerpeton*, *Jeholotriton* and *Qinglongtriton*. In contrast, a midline contact of the vomers is present in *Liaoxitriton*, *Valdotriton* and *Beiyanerpeton.* Moreover, the pentagonal shape of the vomers is unique in *Regalerpeton.*

In *Chunerpeton*, *Beiyanerpeton*, *Qinglongtriton*, *Seminobatrachus*, and *Valdotriton*, the vomerine tooth row is parallel to the maxillary arcade. In *Jeholotriton paradoxus*, the vomer overgrows the vomerine teeth and has a gracile posterior palatal extension. In *Liaoxitriton*

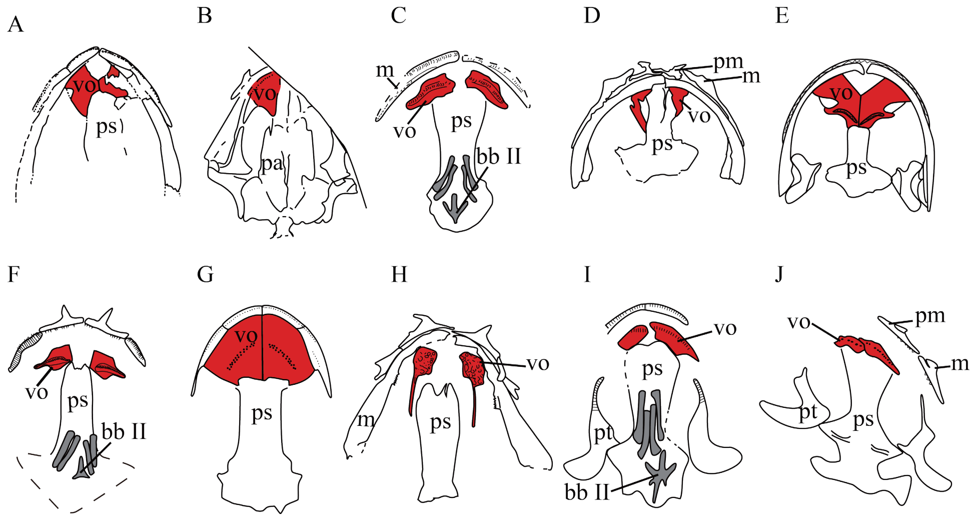

Fig. 7 Comparison of vomer and vomerine tooth row of the fossil salamanders

A. *Liaoxitriton zhongjiani* (Dong and Wang, 1998); B. *Seminobatrachus boltyschkensis* (Skutschas and Gubin, 2012); C. *Chunerpeton tianyiensis* (Gao and Shubin, 2003); D. *Pangerpeton sinensis* (Wang and Evans, 2006); E. *Liaoxitriton daohugouensis* (Wang, 2004); F. *Regalerpeton weichangensis* (IVPP V 17989); G. *Valdotriton* (reconstruction) (Evans and Milner, 1996); H. *Jeholotriton paradoxus* (Wang, 2000); I. *Qinglongtriton gangouensis* (Jia and Gao, 2016a); J. *Beiyanerpeton jianpingensis* (Gao and Shubin, 2012) Not to scale

daohugouensis, like *Regalerpeton*, the vomerine teeth row is transverse and medially placed in the palate, but the vomers are larger and of a different shape (Fig. 7). The *Nuominerpeton aquilonaris* (Jia and Gao, 2016b) from the Lower Cretaceous Guanghua Formation of Nei Mongol, China, differs from *Regalerpeton* in having a *Liaoxitriton*-like vomer with short multiple rows of vomerine teeth.

4.2 Parasphenoid

In most salamanders, the shape of anterior border of the parasphenoid cannot be well displayed because it is covered with vomers (Regal, 1966; Rose, 2003; Darda and Wake, 2015; Gregory et al., 2016; Fei and Ye, 2017). In *Regalerpeton*, parasphenoid is fully exposed in the palate of the skull on account of separated vomer. It is clearly shown that *Regalerpeton* has an arrow-shaped parasphenoid with an indented anterior end. Other than this taxon, this type is only known in *Liaoxitriton daohugouensis* (Fig. 7), which has a relatively shorter anterior process. Besides, it is unique that parasphenoid has an indented anterior end of the cultriform process. The special morphology of the parasphenoid can be used as the identification feature of *Regalerpeton*.

4.3 Hyobranchium

The hyobranchium lies in the floor of the mouth and supports the tongue. It varies in its configuration in different species (Table 1). In *Chunerpeton*, *Beiyanerpeton*, *Qinglongtriton*, and *Regalerpeton*, the hyobranchium consists of ossified hypobranchial I, hypobranchial II and basibranchial II, but the shape of basibranchial II differs among these taxa (Fig. 7). It is triradiate in *Regalerpeton*. However, in *Beiyanerpeton,* basibranchial I and II are co-ossified to form a trident-shaped element with slender arms extending anteriorly and anterolaterally (Gao and Shubin, 2012). In *Chunerpeton*, basibranchial II is trident-shaped (Gao and Shubin, 2003), whereas in *Qinglongtriton*, it is more complex in shape, with paired anterolateral and posterolateral processes fused to a median rod (Jia and Gao, 2016a). In modern salamanders, the paired ossified hypobranchial I and hypobranchial II and paralleled to each other, this occurs in the larval and neotenic salamanders like *Siren intermedia*, *Pachyhynobius shangchengensis*, *Batrachuperus mustersi*, *Pseudobranchus striatus*, *Proteus anguinus*, *Amphiuma means*, *Desmognathus aeneus* (Deban and Wake, 2000; Rose, 2003; Xiong et al., 2013). Accordingly, pairs of hypobranchial I and hypobranchial II present in fossil taxon are considered larval hyobranchium.

Table 1 The ossified elements of the hyobranchium in different fossil taxa

Taxa	Ceratobranchial	Hypobranchial	Basibranchial
Kokartus honorarius$^{1)}$	0	hb I, hb II	0
Laccotriton subsolanus$^{2)}$	?	?	bb II
Liaoxitriton zhongjiani$^{3)}$	cb I	?	?
Jeholotriton paradoxus$^{4)}$	0 ?	0?	0?
Sinerpeton fengshanensis$^{5)}$	cb II	?	?
Chunerpeton tianyiensis$^{6)}$	0	hb I, hb II	bb II
Liaoxitriton daohugouensis$^{7)}$	cb I	hb I	bb II
Pangerpeton sinensis$^{8)}$	cb I, cb II	0	0
Regalerpeton weichangensis	0	hb I, hb II	bb II
Beiyanerpeton jianpingensis$^{9)}$	0	hb I, hb II	bb I + bb II
Qinglongtriton gangouensis$^{10)}$	0	hb I, hb II	bb II
Nuominerpeton aquilonaris$^{11)}$	cb II	hb II	bb II

Based on: 1) Skutschas and Martin, 2011; 2) Gao et al., 1998; 3) Dong and Wang, 1998; 4) Wang, 2000; 5) Gao and Shubin, 2001; 6) Gao and Shubin, 2003; 7) Wang, 2004; 8) Wang and Evans, 2006; 9) Gao and Shubin, 2012; 10) Jia and Gao, 2016a; 11) Jia and Gao, 2016b.

4.4 Neoteny

In salamanders, neoteny is a phenomenon in which an animal retains the larval configuration while attaining reproductive maturity (Pierce and Smith, 1979; Shaffer, 2013). There are gill filament impressions (three pairs) (Fig. 3B, C) and ossified or calcified gill rakers (Figs. 1, 2, 6) present in our newly discovered specimens. As in modern relatives, the gill filaments or rakers are indicative of external gills. *Regalerpeton* must therefore have been neotenic, as the adult individuals have 1) external gills; 2) larval-shaped pterygoids; 3) a larval hyobranchium. *Regalerpeton* therefore resembles *Chunerpeton* (Gao and Shubin, 2003), *Beiyanerpeton* (Gao and Shubin, 2012) and *Qinglongtriton* (Jia and Gao, 2016a). However, *Regalerpeton* differs from the other three taxa in having the carpals and tarsals fully ossified in the adult stage. It is implied that *Regalerpeton* has the ability to support the body.

5 Phylogenetic analysis

In order to determine the phylogenetic position of *Regalerpeton*, it is added into the latest data matrix of caudates as show in Jia and Gao (2016a). The character states of *Jeholotriton* were also added based on descriptions in Wang (2000), Wang and Rose (2005) and Carroll et al. (2012). Some character states of *Pangerpeton* were modified by reexamination of the holotype (see Appendix 1). *Karaurus* was the designated outgroup taxon, and all the characters were unordered and unweighted as in Jia and Gao (2016a).

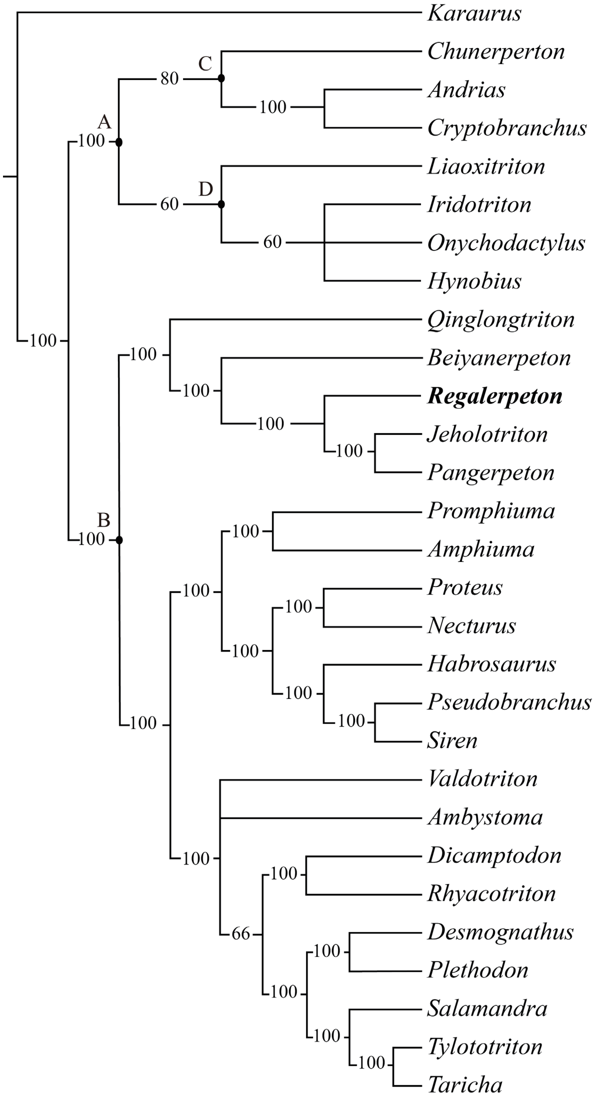

Fig. 8 50% majority rule consensus tree of the most parsimonious trees obtained in TNT (Goloboff and Catalano, 2016) for caudate phylogeny
Clade A. Cryptobranchoidea; B. Salamandroidea; C. Cryptobranchidae; D. Hynobiidae

The implicit enumeration search algorithm using TNT (Goloboff and Catalano, 2016) resulted in fifteen most parsimonious trees (tree length = 263 steps, consistency index = 0.464, retention index = 0.702). 50% majority rule consensus of 15 most parsimonious trees (Fig. 8) suggests that *Jeholotriton* and *Pangerpeton* are sister taxa with three synapomorphies: vomer with greatly elongated process extending along lateral border of parasphenoid [character state 13(2)]; ossified hypobranchial I absent [character state 33(1)]; pterygoid without teeth [character state 39(0)]. *Regalerpeton* forms a sister taxon to the "*Jeholotriton* + *Pangerpeton*" clade. The analysis also reveals that *Regalerpeton*, *Jeholotriton*, *Pangerpeton*, *Qinglongtriton* and *Beiyanerpeton* together form a clade that is sister-taxon to the rest of Salamandroidea. This sister clade is supported by three synapomorphies: ossified nasal without midline contact [character state 8(1)]; angular fused to prearticular [character state 26(1)]; articular absent or by fusion with prearticular [character state 29(1)]. Besides, *Regalerpeton*, *Jeholotriton* and *Pangerpeton* (from the Early Cretaceous of Hebei, Middle/Late Jurassic of Nei Mongol and Liaoning, respectively) share unicapitate ribs with the suborder Cryptobranchoidea. This is in accordance with their transitional position between Cryptobranchoidea and Salamandroidea, which indicates that the two groups may have started to split in the Middle to Late Jurassic. There is also mitochondrial genomes evidence showing the Cryptobranchoidea-Salamandroidea split in the Mid-Jurassic (~171 Ma) (Zhang and Wake, 2009). Therefore, *Regalerpeton*, *Jeholotriton* and *Pangerpeton* represent an important stage of evolution in the history of salamanders.

6 Conclusions

The following conclusions can be drawn from this study:

(1) *R. weichangensis* differs from other salamanders mainly in the following characteristics: it is a neotenic salamander with ossified carpals and tarsals; roughly pentagonal vomer with transversely oriented vomerine tooth row; presence of triradiate basibranchial II; parasphenoid inverted arrow-shaped with an indented anterior end of the cultriform process; a long tail exceeded the snout-pelvis length coracoid portion of scapulocoracoid rectangular. These features support the generic distinction of *Regalerpeton*.

(2) New phylogenetic analysis places *Regalerpeton*, *Jeholotriton* and *Pangerpeton* into the suborder Salamandroidea. They also share unicapitate ribs with Cryptobranchoidea, so the three taxa *Regalerpeton, Jeholotriton* and *Pangerpeton* represent an important transitional stage in the evolution of salamanders.

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河北围场下白垩统围场皇家螈(*Regalerpeton weichangensis*)(两栖类：有尾类)的再研究

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摘要：围场皇家螈(*Regalerpeton weichangensis*)于2009年基于一件产自河北围场下白垩统不完整的骨骼印痕标本命名。然而由于标本变形导致皇家螈的部分解剖学特征被曲解，系统

发育位置也存在争论。本文基于8件新标本对该蝾螈的鉴定特征和系统发育位置进行了修订。研究显示，皇家螈是一种腕骨和跗骨骨化的幼态持续型蝾螈，具有独特的特征组合，包括犁骨齿列横向排列、副蝶骨前端呈齿状、基鳃骨II呈三射型，尾长超过吻臀距以及肩胛乌喙骨的乌喙端呈矩形。新的系统发育分析根据三个近裔共性将围场皇家螈、热河螈和胖螈归入蝾螈亚目。此外，它们还与隐鳃鲵亚目共有“肋骨单关节头”这一特征，显示这三种蝾螈可能代表了隐鳃鲵亚目与蝾螈亚目分离时期这一重要演化阶段。

关键词：河北围场，下白垩统，蝾螈亚目，围场皇家螈，形态学，系统发育学

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Appendix 1 Additions and changes to the date matrix (Jia and Gao, 2016a) used in the phylogenetic analysis

Regalerpeton weichangensis	0000100100	1201000010	0001?11?10	000?001?10	0002?0110?	?01??0?101
	000100??10	0??100????	??????????	1111????0?	000??	
Jeholotriton paradoxus	0000100000	1320000010	?111??1??0	0?1??01?00	0012?0?10?	?01???0100
	000100??10	0??100????	??????????	1111????0?	000??	
Pangerpeton sinensis	0000??1???	1020000010	0????11???	0010001000	?00?00110?	???????1??
	????1???00	0?????????	??????????	?111????0?	?00??	