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A new Early Cretaceous salamander (*Regalerpeton weichangensis* gen. et sp. nov.) from the Huajiying Formation of northeastern China

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ABSTRACT

Recent discoveries of well-preserved Late Jurassic and Early Cretaceous salamander fossils from China are helping to resolve highly controversial aspects of caudate phylogeny. Here we report on a new Early Cretaceous salamander, *Regalerpeton weichangensis* gen. et sp. nov., from the Huajiying Formation in Hebei Province, China. This specimen is characterized by long, arched vomerine tooth rows running parallel to the maxillary arcade; a long and tapered anterior ramus of the pterygoid that curves anteromedially; an ossified hyobranchium with one pair of hypobranchials and two pairs of ceratobranchials; and scapulocoracoids with greatly expanded, approximately rectangular coracoid components. Phylogenic analysis places *Regalerpeton* as the sister group to a Cryptobranchidae clade including *Chunerpeton*, with *Jeholotriton* and *Pangerpeton* as successive sister taxa.

1. Introduction

Salamanders (Caudata) are one of the three living groups of lissamphibians (Duellman and Trueb, 1986), with some researchers proposing Albanerpetontidae as the fourth member (Fox and Naylor, 1982; McGowan and Evans, 1995; Gardner, 2001). The early evolution of caudates is not well known and is based on relatively few Mesozoic fossils (Estes, 1981; Milner, 1988, 2000). Recent discoveries of well-preserved articulated skeletons from the Early Cretaceous Jehol Biota of China, and associated faunae, have provided important new information relating to the diversification and phylogeny of Mesozoic caudate (Gao and Shubin, 2001, 2003; Wang and Gao, 2003; Wang and Evans, 2006a,b; Wang, 2006; Wang et al., 2008).

To date, six genera and seven species of Mesozoic salamanders have been described from five localities in China, all in the northeastern provinces (Fig. 1). Three of these salamander species are members of the Jehol Biota, which also features feathered dinosaurs and primitive birds (Chang et al., 2003; Zhou et al., 2003). *Liaoxitriton zhongjiani* Dong and Wang, 1998 came from the Yixian/Jiufotang Formation at the Shuikouzi locality, Huludao, Liaoning, and *Laccotriton subsolanus* Gao et al., 1998 and *Sinerpeton fengshanensis* Gao and Shubin, 2001 are both from the Dadianzi/Xiguayuan Formation at the Paozhanggou locality, Fengning, Hebei. The other four species were recovered from the Daohugou Bed, a horizon lower than the Jehol strata, but of uncertain date (estimates range from Middle Jurassic to Early Cretaceous, Ren et al., 2002; Zhang, 2002; Wang et al., 2005). *Jeholotriton paradoxus* Wang, 2000, *Chunerpeton tianyiensis* Gao and Shubin, 2003, and *Liaoxitriton daohugouensis* Wang, 2004a are from the Daohugou locality of Ningcheng, Nei Mongol (Inner Mongolia), and *Pangerpeton sinesis* Wang and Evans, 2006a is from the Wubaiding locality of Lingyuan, Liaoning. Preliminary phylogenetic analysis suggested a basal position for *Pangerpeton* and *Jeholotriton* on the caudate tree (Wang and Evans, 2006a), providing some support for the hypothesis that East Asia was one of the centres for early caudate evolution and adaptive radiation (Gao and Shubin, 2001; Wang, 2006). However, the phylogeny of these Chinese taxa and, indeed, also of living salamanders around the world, have been the subject of sometimes heated debate (Hillis, 1991; Trueb and Cloutier, 1991; Larson and Dimmick, 1993; Hay et al., 1995; Feller and Hedges, 1998; Wiens et al., 2005; Frost et al., 2006). New attempts have been made in recent years with combined molecular and morphological data (Gao and Shubin, 2001) or combined morphological data from fossil and living taxa (Wang and Evans, 2006a), but resulting trees need to be tested by new fossil finds from key geological periods.

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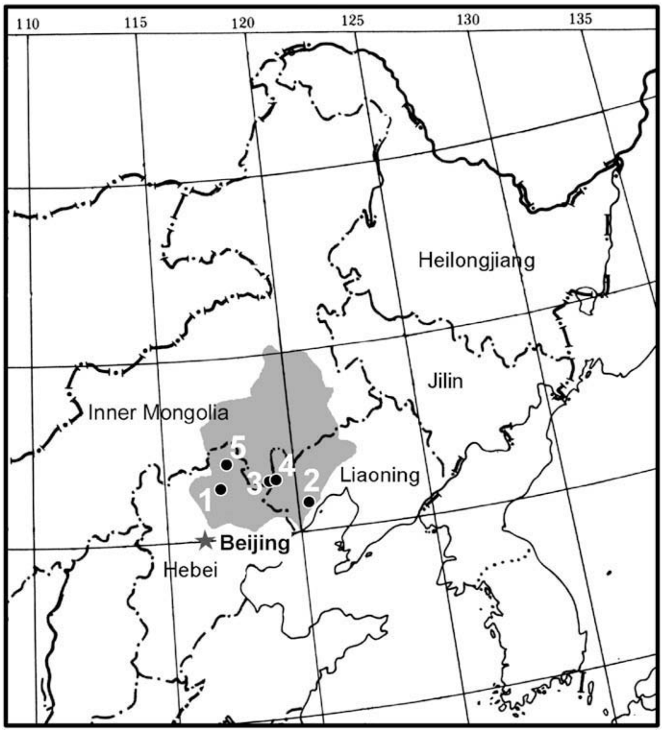

Fig. 1. Locality and geological age of Mesozoic salamanders from China. The shaded area shows the range of the "Jehol Province" of China in the 1920s, after which the "Jehol Fauna" was named. 1, Paozhanggou Locality, Fengning County, Hebei Province: *Laccotriton subsolanus, Sinerpeton fengshanensis*, Dadianzi/Xiguayuan Formation, Early Cretaceous; 2, Shuikouzi Locality, Xintaimen Town, Liaoning Province: *Liaoxitriton zhongjiani*, Yixian/Jiufotang Formation, Early Cretaceous; 3, Daohugou Locality, Ningcheng County, Inner Mongolia Autonomous Region: *Chunerpeton tianyiensis*, *Jeholotriton paradoxus*, *Liaoxitriton daohugouensis*, Daohugou Bed, Late Jurassic/Early Cretaceous; 4, Wubaiding Locality, Lingyuan City, Liaoning Province: *Chunerpeton tianyiensis*, *Pangerpeton sinensis*, Daohugou Bed, Late Jurassic/Early Cretaceous; 5, Daobaziliang Locality, Weichang County, Hebei Province, Huajiying Formation, Early Cretaceous.

An Early Cretaceous salamander from Weichang, Hebei Province, northeastern China, is described in this paper. The fossil-bearing bed is in the second member of the Huajiying Formation, which overlies the Xiguayuan Formation and underlies the Nandian Formation in the Weichang Basin of northern Hebei (Wang et al., 1977). The deposits of the Huajiying Formation are mainly basic to intermediate lavas, inter-bedded by sedimentary layers of mudstone, siltstone, sandstone to conglomerate, with abundant tuffs. The Huajiying Formation in Hebei Province is regarded as a lateral equivalent of the Yixian Formation in Liaoning Province (Wang, 1999; Wang et al., 2000), and the latter has a well-accepted isotopic dating of 125 Ma (Swisher et al., 1999, 2002; Wang et al., 2000). Although invertebrate fossils (e.g., bivalves and conchostracans) are abundant in this formation, the salamander represents the first documented vertebrate from this formation, and the first from the Weichang Basin of Hebei Province.

2. Systematic paleontology

Class: Amphibia Linnaeus, 1758
Subclass: Lissamphibia Haeckel, 1866
Superorder: Caudata Scopoli, 1777 (usage *sensu* Milner, 1988)
Order: Urodela Duméril, 1806
Family indet.
Genus *Regalerpeton* nov.
Type species: *Regalerpeton weichangensis* sp. nov.
Diagnosis.—As for type and only species (see below)

Regalerpeton weichangensis gen. et sp. nov.

Derivation of name. From the Latin, *regalis*, meaning "royal", and the Greek, *herpeton*, a crawling thing. The fossil locality, Weichang (Chinese Pinyin, meaning "encircled field") was once a royal hunting field during the Qing Dynasty.

Holotype. IVPP V14391A, B, an incomplete skeleton with bony impressions preserved as part and counterpart on tuffaceous siltstone. Collections of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing.

Type locality. Daobaziliang, Weichang County, Hebei Province.

Type horizon. Huajiying Formation (equivalent to the Yixian Formation of the Jehol Group).

Diagnosis. An Early Cretaceous salamander differing from other caudates in the following combination of character states: skull wide with round rostrum; alary process of premaxilla moderate in length; parietal with anteromedial extension, about half length of the frontal edge; prefrontal and lacrimal absent; vomerine tooth rows long and parallel to the maxillary arcade; pterygoid with slender, inwardly curved dentate anterior process and a medial process; prearticular/coronoid long, with two processes; angular absent; ossified quadrate present; external gills (including gill rakers) absent; one ossified pair of hypobranchials and two ossified pairs of ceratobranchials present; ribs unicapitate and expanded proximally; transverse process of presacrals half the length of the vertebra; scapulocoracoid greatly expanded proximally; and carpals and tarsals ossified.

Differs from *Chunerpeton* in the absence of ossified gill rakers and the presence of a greatly expanded proximal end to the scapulocoracoid; resembles *Chunerpeton* and differs from *Jeholotriton* and *Liaoxitriton* in having long and arched vomerine tooth rows running parallel to the maxillary arcade (an anterior tooth patch + a posterior longitudinal dentigerous bar in *Jeholotriton*; short and transverse vomerine tooth rows in *Liaoxitriton*). Resembles *Chunerpeton* and differs from *Jeholotriton*, *Liaoxitriton*, *Laccotriton*, *Sinerpeton* and *Pangerpeton* in having a long, curved anterior process of the pterygoid rather than a short one (anteromedially oriented in *Jeholotriton* and anterolaterally oriented in the others); differs from *Jeholotriton*, *Chunerpeton* and *Liaoxitriton* in retaining three pairs of ossified hyobranchial elements including one pair of hypobrachials and two pairs of ceratobranchials (unossified in *Jeholotriton*, two pairs of hypobranchials and one basibranchial ossified in *Chunerpeton*, and one pair of hypobranchials, one pair of ceratobranchials and one ossified basibranchial in *Liaoxitriton*). Further differs from *Chunerpeton*, *Pangerpeton* and *Jeholotriton* in having ossified carpals and tarsals; differs from all other known Mesozoic salamander genera in the presence of *Chunerpeton*-type vomerine tooth rows (parallel to the maxillary arcade) combined with a *Liaoxitriton*-type scapulocoracoid (greatly expanded coracoid end).

2.1. General features

The salamander specimen (IVPP V14391) is preserved in a yellowish tuffaceous siltstone, mainly as impressions of an incomplete articulated skeleton with some fragmentary bones. The skull is generally articulated, but the midline bones are pushed forward relative to the maxillary/mandibular arcade. The vertebral column is incomplete. Some presacrals are displaced from their original position, and some posterior presacrals, the sacral and all the caudals are missing. The pectoral girdle and the forelimbs are better preserved on the left side, as is the hind limb. The pelvic girdle and most of right hind limb are missing. The individual was postmetamorphic as most bone surfaces are finished (except some, e.g., humerus).

Slab A shows mainly the ventral aspect of the skeleton, and Slab B the dorsal aspect. The description that follows is based on both

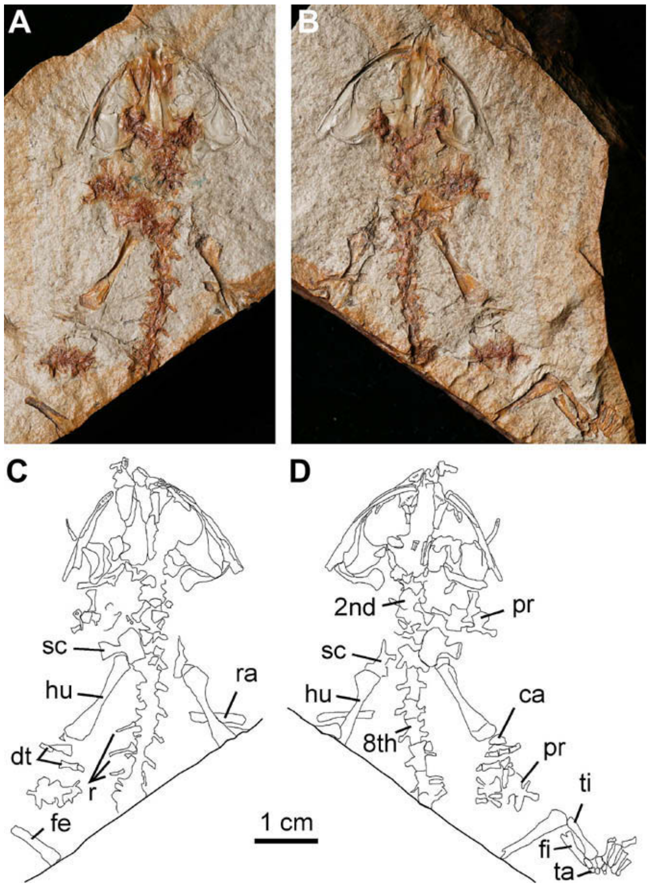

Fig. 2. Photographs and line drawings of the holotype specimen (IVPP V14391) of *Regalerpeton weichangensis*. A and C, Slab A; B and D, Slab B. Abbreviations: 2nd and 8th, second and eighth presacral; ca, carpal; dt, digit, fe, femur; fi, fibula; hu, humerus; pr, presacral; r, rib; ra, radius; sc, scapulocoracoid; ta, tarsal; ti, tibia.

the specimen and on high-fidelity casts taken from the skeletal impressions (Fig. 2).

2.2. Skull and mandibles

The skull has a short, round rostrum, with relatively standard width/length proportions (=1.23, see Table 1). The premaxillae are clearest on Slab A and are slightly displaced and rotated. Each premaxilla has an alary process that is slightly longer than the width of the dental margin, but details of the process and its relationship to the nasal are not clear. The maxilla is on the posterolateral side of the premaxilla; it is not very long, and is approximately half the length of the lower jaw. Impressions of teeth are observed on each side of the maxilla and premaxilla. Whether or not they are pedicellate cannot be determined. See Fig. 3.

The dermal roofing bones (nasals, frontals and parietals), line up along the midline of the skull, and are best shown on Slab B. The nasals are compressed anteriorly and partly overlapped the frontals. Whether each nasal contacts the dorsal process of the premaxilla is not clear because of the displacements of the premaxillae and the nasals. The two frontals are slightly displaced to the right of the midline, with the left frontal inserting posteriorly between the two anterior processes of the parietals. The right frontal lies to the right of the orbitosphenoid and shows no contact with the maxilla. The parietals are notable in being slender and making up nearly half of the skull length. Each parietal has a long, slightly tapering anteromedial process. The squamosal as preserved lies above the posterolateral process of the pterygoid and does not meet the posterolateral edge of the parietal. It has an expanded proximal end and a distinct otic ramus, as shown on the right side. The zygomatic ramus connects to an ossified quadrate, as shown on the left side of the skull.

In ventral view, the palate is dominated by a long parasphenoid that extends almost the whole length of the skull. The cultriform process is parallel-sided, separating the two vomers as preserved. It also overlaps the mid-portion of the square-edged orbitosphenoid which is partially exposed in both ventral and dorsal views of the skull. The lateral ala of the parasphenoid is preserved only on the left side, with a flat broken piece that may belong to the same element. The vomers are located just behind the maxillary arch. The vomerine tooth row is relatively long and runs parallel to the maxillary arcade, with its anterior portion close to the maxilla. The triradiate pterygoids, with an additional distinct anteromedial process, have a short and obtuse otic process and a long and dramatically tapering anterior process that is directed toward the end of maxilla. On both sides, the prootics are preserved abutting the pterygoids. The prootic, exoccipital and opisthotic are apparently separate, though this could result from the breakage of the poorly preserved otic and occipital region.

Lying on the posterior part of the parasphenoid, there are three pairs of ossified hyobranchial elements: one pair of hypobranchials and two pairs of ceratobranchials. As preserved, the hypobranchials overlap part of the ceratobranchials. Behind the skull and in the neck region, there is no trace of external gills which are usually preserved as dark impressions as in *Jeholotriton* and *Chunerpeton*. Ossified gill rakers are also absent.

The lower jaw is composed of the dentary anteriorly and the composite prearticular/coronoid posteriorly. The dentary is narrow and gracile, with the composite prearticular/coronoid bone abutting

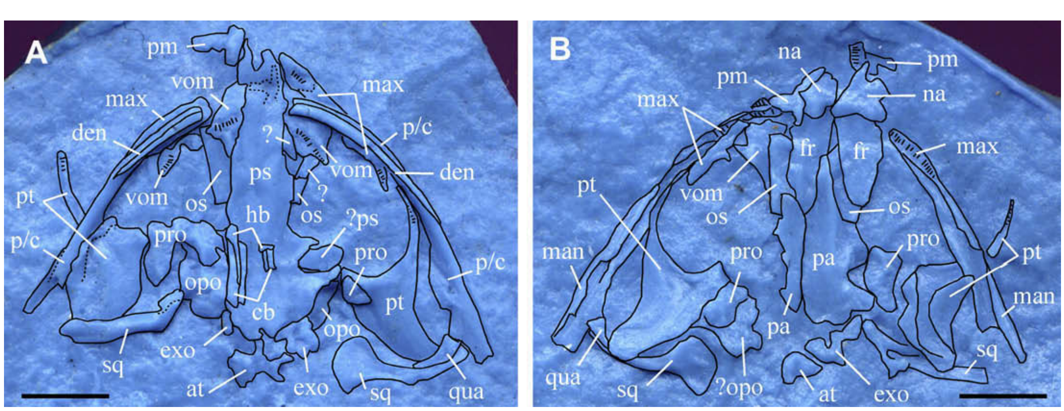

Fig. 3. Outline drawing of the skull of *Regalerpeton weichangensis* superimposed on high fidelity casts, showing ventral (A) and dorsal (B) views. Scales equal to 5 mm. Abbreviations: at, atlas; cb, ceratobranchial; den, dentary; exo, exoccipital; fr, frontal; hb, hypobranchial; man, mandible; max, 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.

its inner surface. Neither preserves teeth. As best shown in ventral view (Fig. 3A), the long prearticular/coronoid has a bilobed posterior flange (i.e., having two processes). This is similar to the posterior flange in *Chunerpeton* and *Liaoxitriton*, but neither process is as well-developed in *Regalerpeton*. The angulars are probably absent.

2.3. Postcranial skeleton

Ten amphicoelous presacrals are preserved behind the head, with Presacral III and IV displaced to the left, in front of the well-preserved left scapulocoracoid (Fig. 2). There is also a dissociated section of vertebral column posterior to the left forelimb with three articulated vertebrae. They may represent Presacrals XI–XIII, but the exact number of presacrals cannot be determined because the sacral and some posterior presacrals are missing. The atlas is roughly the same length as the succeeding vertebrae. The centrum of each vertebra is hour-glass-shaped and the presacral rib-bearers (i.e., the transverse processes) are only about the half length of each vertebra. Ribs are only sporadically preserved, all having an expanded single head.

The pectoral girdle is represented by the paired scapulocoracoids. Each has a greatly expanded, nearly rectangular proximal (coracoid) portion, and a short hatchet-shaped distal (scapular) end.

The humerus (14.06 mm) has expanded proximal and distal heads that are not fully ossified, showing that the animal was a young adult. One displaced bone lying on the right humerus may be the right radius (ca. 9.32 mm), whereas a segment of bone posterior to the radius may represent the broken right ulna. Parts of the left ulna and radius are not preserved. One kidney-shaped element distal to the left humerus may be an ossified carpal. Two right fingers are relatively well-preserved, showing two and three phalanges, respectively. Other elements of the right manus are clustered together posterior to the humerus, but cannot be distinguished so that it is not possible to determine whether or not metacarpal II is expanded as in *Laccotriton, Sinerpeton* and *Liaoxitriton zhongjiani*.

Elements of the pelvic girdle are not preserved, and the hindlimb is only preserved on the left side. The femur is not complete, but a combination of the two slabs provides an estimated femur length of 14.48 mm. The tibia (7.90 mm) is complete, whereas the fibula is broken at the distal end. The tarsals are ossified but their number is not clear due to poor preservation in this area. Four incomplete digits are preserved in the specimen, all on the left pes, but the phalangeal formula is unclear because most of the interphalangeal joints are missing.

The skeletal impression is not surrounded by a soft tissue outline as it is in many Chinese Mesozoic salamanders (e.g., *Pangerpeton, Jeholotriton, Liaoxitriton,* Wang and Evans, 2006a; Wang and Rose, 2005; Wang, 2004a), and the skeleton is incomplete, making it impossible to estimate overall body shape.

3. Discussion and phylogenetic analysis

The Weichang salamander is postmetamorphosed as it shows no trace of external gills. This is apparently different from *Jeholotriton* and *Chunerpeton* which are paedomorphic, retaining external gill in the adult stage (Gao and Shubin, 2003; Wang and Rose, 2005). However, the Weichang salamander is generally similar to *Chunerpeton*, a cryptobranchid caudate (Gao and Shubin, 2003) recovered from the Upper Jurassic/Lower Cretaceous Daohugou fossil bed of Inner Mongolia. The skull structure of the new taxon is *Chunerpeton*-like, with long, curved vomerine tooth rows parallel to the maxillary arcade, and a *Chunerpeton*-type toothed anterior process of the pterygoid that is tapered and curved anteromedially.

The possibility that *Regalerpeton* is a metamorphosed form of *Chunerpeton* should be considered. *Regalerpeton* differs from *Chunerpeton* in the following aspects: 1) the shape of the scapulocoracoid–in *Regalerpeton*, the coracoid portion of the scapulocoracoid is greatly expanded and almost rectangular in shape (Fig. 4G), while in *Chunerpeton* it is only slightly expanded and rhomboid (Fig. 4D). We examined nearly one hundred specimens of *Chunerpeton* in the IVPP collections, with different ontogenetic stages. *Chunerpeton* shows no significant change in the shape of scapulocoracoid through its development, so the difference should be real; 2) the lack of ossification of gill rakers–*Chunerpeton* is characterised by the possession of ossified gill rakers in adult and even juvenile specimens (Gao and Shubin, 2003; personal observation on IVPP collections). This feature has not been observed in any other Chinese Mesozoic caudates; 3) the presence of ossified carpals and tarsals; 4) the lack of prefrontals and distinct angulars, whereas *Chunerpeton* has these elements; 5) the lack of dermal sculptures on the parietals, squamosals, and the dorsal aspect of the pterygoids, contrary to *Chunerepton*. Although characters 1), 2) and 3) can be influence by ontogeny, 4) and 5) cannot. Further proof for the establishment of the two independent taxa comes from their stratigraphic difference: the Huajiying Formation is equivalent to the Yixian Formation (~125 Ma; Swisher et al., 2002), and higher than the Daohugou fossil bed (no earlier than 159–164 Ma; Wang et al., 2005).

The new caudate also shows several similarities to *Liaoxitriton*, (Wang, 2004a; Liu, 2007) such as the greatly expanded coracoid portion of the scapulocoracoid and the presence of ossified carpals and tarsals. The main differences between the two are in the morphology of skull and hyobranchial elements, where *Liaoxitriton* differs in having short transverse vomerine tooth rows, a stout anterolaterally directed anterior process of the pterygoid, as well as ossified pairs of Hypobranchial II and Ceratobranchial II with an anchor-shaped basibranchial.

Regalerpeton differs from *Jeholotriton* and *Pangerpeton* mainly in the morphology of vomerine tooth rows, the pterygoids and the scapulocoracoids. Both *Jeholotriton* and *Pangerpeton* have an anterior tooth patch and a posterior longitudinal toothed bar on the

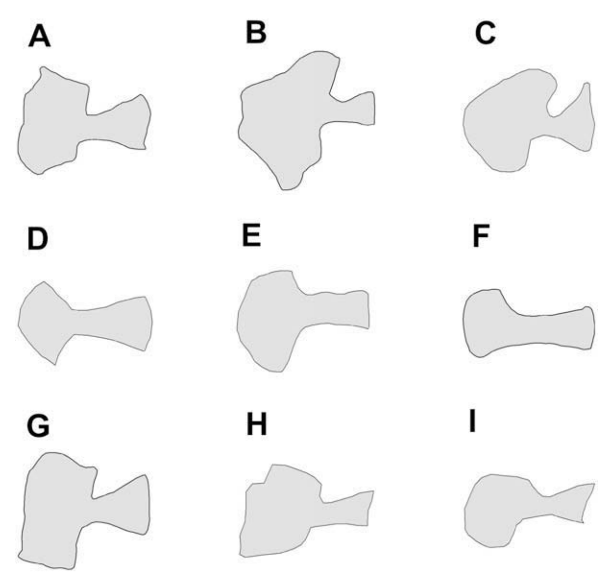

Fig. 4. General morphology of caudate scapulocoracoids. A, *Liaoxitriton zhongjiani* (IVPP V14205); B, *Liaoxitriton daohugouensis* (IVPP V13393, holotype); C, Unnamed taxon from Daohugou (IVPP V14057); D, *Chunerpeton tianyiensis* (CAGS-IG-02051, holotype; drawn from Gao and Shubin, 2003, Fig. 1); E, *Pangerpeton sinensis* (IVPP V14244, holotype); F, *Jeholotriton paradoxus* (IVPP V11984, paratype); G, *Regalerpeton weichangensis* (IVPP V14391, holotype); H, *Laccotriton subsolanus* (GMV 1602, holotype, drawn from Gao and Shubin, 2001, Fig. 3); I, *Sinerpeton fengshanensis* (GMV 1606, holotype, drawn from Gao and Shubin, 2001, Fig. 3). Drawings are based on fossil bones or impressions, and are rescaled to the same width for better comparison.

Table 1
Comparative skeletal measurements (in mm) of *Regalerpeton weichangensis* and five other Chinese Mesozoic salamanders (expanded from Table 1, Wang and Evans, 2006a to include dimension of limbs)

	Pangerpeton	*Jeholotriton*		*Chunerpeton*		*Liaoxitriton zhongjiani*		*Liaoxitriton daohugouensis*		*Regalerpeton*
	V14424 adult	V12623 adult	V11943A juvenile	V14055 adult	V13374 juvenile	V14205 adult	V14076 juvenile	V13393 adult	V14062 juvenile	V14391 adult
Skull W	13.35	23.50	16.25	37.38	14.30	19.14	12.78	20.60	17.25	22.84
Skull L	7.85	18.05	12.85	28.16	15.20	19.54	11.50	17.55	15.15	18.50
Skull W/L	1.69	1.30	1.27	1.33	0.93	0.98	1.11	1.18	1.14	1.23
Average vertebra L	2.03	3.05	2.33	3.35	2.05	3.08	1.72	3.45	3.28	2.70
Skull W/Vertebra L	6.59	7.7	6.99	11.16	6.98	6.21	7.43	5.97	5.28	6.85
Skull L/Vertebra L	3.88	5.9	5.53	8.41	7.5	6.34	6.69	5.08	4.63	8.46
Humerus L	6.32	8.18	4.98	11.52	5.22	9.02	6.34	10.42	9.84	14.06
Radius L	3.86	4.48	2.66	5.02	2.56	6.04	3.00	5.86	5.46	9.32
HumerusL/Radius L	1.64	1.83	1.87	2.29	2.04	1.49	2.11	1.80	1.80	1.51
Femur L	6.52	6.68	4.40	11.28	5.54	9.42	5.84	11.46	10.98	13.5
Tibia L	3.54	3.90	2.36	5.58	2.68	6.24	3.28	6.88	5.58	7.90
Femur L/Tibia L	1.84	1.71	1.86	2.02	2.66	1.51	1.78	1.67	1.97	1.71

L, length; W, width; All specimens in IVPP collection.

vomer (Wang and Rose, 2005; Wang and Evans, 2006a). *Pangerpeton* has a *Liaoxitriton*-like pterygoid, and *Jeholotriton* has an anteromedially oriented process on the pterygoid, both different from that of the Weichang salamander. The general shape of the scapulocoracoid in each of the three salamanders is also different. *Jeholotriton* has a round coracoid portion and a long scapular bar, whereas *Pangerpeton* has a round expanded coracoid plate as shown in Fig. 4. Furthermore, *Pangerpeton* has an unusually short head and short body (presacral number 14) compared to other known Mesozoic salamanders.

In skeletal proportions (Table 1), the new taxon has skull width/length (22.84/18.50) proportions that are similar to *Jeholotriton, Liaoxitriton daohugouensis* and *Chunerperton*, but differ from those of *Liaoxitriton zhongjiani* and *Pangerpeton*. Moreover, by standardizing skull length in comparison to vertebral length, it is clear that *Regalerpeton* has a relatively longer skull than other Chinese Mesozoic salamanders. However, *Regalerpeton* has a relatively short humerus in proportion to radius length, similar to that of adult *Liaoxitriton zhongjiani*. The hindlimb proportions show no distinguished characters.

Two salamanders, *Laccotriton* and *Sinerpeton*, were previously reported from Hebei Province (Gao and Shubin, 2001). The deposits were originally dated as Late Jurassic, but more recent work suggests an Early Cretaceous age (Wang, 2004a, 2006; Wang and Evans, 2006b). These two small salamanders are similar to *Liaoxitriton* in having a short, transverse vomerine tooth row and a stout, anterolaterally directed anterior process of the pterygoid, as well as similar hyobranchial elements and scapulocoracoids (Fig. 4H,I). Wang (2004b) and Wang and Evans (2006b) proposed that *Liaoxitriton* and *Sinerpeton* might both be junior synonyms of *Laccotriton*, but the Weichang salamander is clearly different from all three in its overall skull morphology (vomerine tooth rows, pterygoids, and hyobranchium).

Based on the above comparisons, the new taxon appears to be distinct from all other Chinese Mesozoic caudates. To further investigate the phylogenetic relationships of the new taxon to other caudates, we used the characters and data matrix of Wang and Evans (2006a), and added codings for *Regalerpeton* (Appendix I). The British Middle Jurassic non-urodele *Marmorerpeton* (Middle–Upper Jurassic, Evans et al., 1988) was the designated outgroup taxon, and *Karaurus* (Late Jurassic, Kazakhstan, Ivakhnenko, 1978; Estes, 1981) was included as a second non-urodele. A Branch-and-Bound complete search using PAUP* (Swofford, 2001) resulted in 138 most parsimonious trees (TL = 174, CI = 0.5805, RI = 0.5731).

The strict consensus tree failed to resolve the relationships of most ingroup taxa, except that the monophyly of three groups, (*Chunerpeton*-living Cryptobranchidae-*Regalerpeton*), (Dicamptodon-Rhyacotriton) and (Sirenidae-Proteidae) are always recognized. In the 50% Majority Rule Consensus Tree (TL = 184, Fig. 5), *Regalerpeton* is placed as the sister taxon of Cryptobranchidae (including *Chunerpeton*). Five synapomorphies (see legend of Fig. 5) support this clade. *Jeholotriton* and *Pangerpeton* constitute successive sister groups to this clade with less synapomorphic support. This result is different to that in Wang and Evans (2006a), in which *Jeholotriton* and *Pangerpeton* emerged as sister taxa. This arrangement seems relatively robust for *Regalerpeton* and *Jeholotriton*, but there is less support for the placement of *Pangerpeton*, for the clade comprising all taxa to the exclusion of *Marmorerpeton* and *Karaurus*, or for the clade encompassing *Liaoxitriton*, the North American Late Jurassic *Iridotriton* (Evans et al., 2005) and the living Hynobiidae (monophyletic as regarded by Zhang et al., 2006).

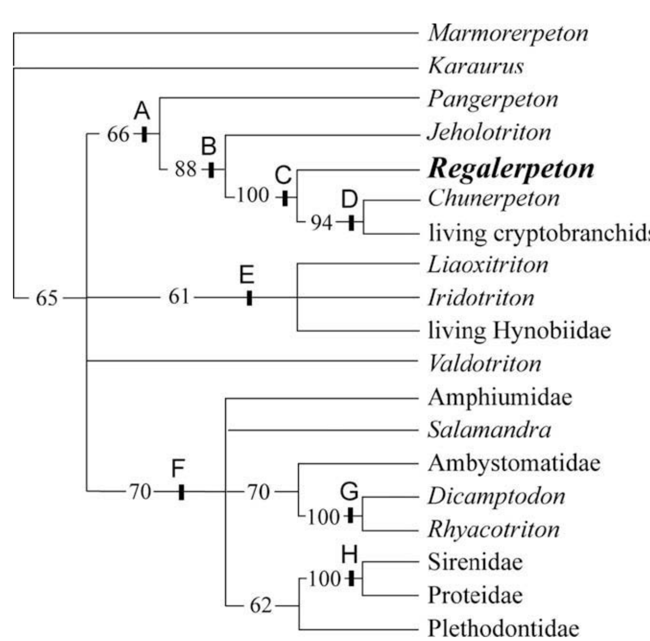

Fig. 5. Fifty Percent Majority Rule Consensus of 138 most parsimonious trees resulting from an analysis using PAUP* version 4.0b10 showing a hypothesised phylogeny of caudates (see text for further explanation). Synapomorphies supporting each clade: Clade A: 22(1), 63(0), 66(2); Clade B: 19(3), 37(0); Clade C: 6(1), 9(1), 34(1), 60(1), 66(1); Clade D (Cryptobranchidae): 13(0), 30(1), 31(1), 32(2); Clade E (Hydobidae): 4(0), 10(1), 22(1), 34(1); Clade F: 2(2), 5(1), 6(1), 17(1), 21(1), 24(3), 26(1), 46(2), 52(1), 54(1), 55(0), 61(2), 66(2), 68(1), 69(1), 70(1), 72(1); Clade G: 6(0), 15(0), 24(2), 65(1); Clade H: 3(2), 9(3), 11(1), 14(0), 19(2), 28(1), 33(2), 34(2), 35(1), 65(1). See codings and character description in Appendices 1 and 2.

The latter clade is palaeobiogeographically interesting, as it would conflict with the long-standing vicariance hypothesis of Milner (1983) that posits a primary dichotomy between Euramerican salamandroids and Asian cryptobranchoids. However, given the relatively weak support, this should be treated with caution until tested by further work. The phylogenetic position of the Early Cretaceous Spanish *Valdotriton* (Evans and Milner, 1996) is essentially unresolved, unlike previous analyses (Gao and Shubin, 2001; Wang and Evans, 2006a).

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Appendix 1. Codings based on character descriptions in Appendix 2:

Liaoxitriton
010?0?1?0? ??11??0000 ?1???????{12} 000{12}0????0 1????????? ?????11110 001??0???? ??
Jeholotriton
011?0?1?20 0??1???130 ?1?00????1 0000000??? ?????????? ??????1110 000??2???? ??
Chunerpeton
010?0?1010 0?01???030 ?1???????1 1201000??? ?????????? ?????11111 000??1???? ??
Valdotriton
010?0?1201 0?111??000 ?0210????2 000001 1??? ?????????? ?????{01}1110 0010?0???? ??
Iridotriton
0000???101 0?01???000 ?1{12}10????2 00??011??? ???1?????? ??????1?1? 10?0?0???? ??
Pangerpeton
010?{01}?1000 ??11??0000 ?1???????? ?0?00????? ?????????? ??????1?1? 100??2???? ??
Sirenidae
04(12)1111031 1210101120 ?023010111 1122100?1? ????111110 00000?110-2?22020000 00
Living Hynobiidae
010000(01)001 00(01)1010000 ?120000002 01010?1?0? ????0000(01)0 10001?1110 ??10(01)(02)0000 00
Cryptobranchidae
0101011021 00011(01)0000 ?120000011 1211000?0? ????000000 10001?1111 2110110000 00
Ambystomatidae
020011120(01) 0011(01)01000 ?02301100(12) 02010(01)1?0? ????221001 11110?1110 ??1{01}(01)01111 11
Salamandra
0301111201 0011001001 1023111012 0100011201 1111220(01)00 1101021110 {01}010020111 01
Dicamptodon
0200001000 0010001000 1022011002 0102001?0? ????221001 11010?1110 2011000111 ?1
Plethodontidae
(01)2(02)(01)(12)11241 (01)2111010(01)1 ?(01)23(01)11002 00(01)0(01)11?1? ????221110 01010?111(01) (012)?2{01}1(02)0111 11
Rhyacotriton
0200201000 0011001000 ?02201100? 000011?0? ????221111 01010?1111 ???0000111 11
Karaurus
010?000?00 0?01???000 00200????0 00000000?? ?????????? ??????1110 0100?0???? ??
Amphiumidae
1201111030 0011101000 ?02101011? 0001000?1? ????220000 01000?1110 2120120011 01
Marmorerpeton
010??????? ???????000 0(01)000????0 ?0???????? ?????????? ????????1? ?0?0?0???? ??
Proteidae
0221211130 12101010{23}0 ?020010112 0222111?1? ????22(01)110 11010?111-2?2{01}010111 11
Regalerpeton
010?011?1? 0?01???030 ?1???????2 01010????? ?????????? ??????111? ?0??1????? ??

Appendix 2. Salamander character list: Amended from Gao and Shubin (2003) and based on Duellman and Trueb (1986), Trueb (1993), Larson and Dimmick (1993). characters 1, 16, 23, 25, 36, 38, 40–45, 53, 56–58, 67 are excluded from real analysis because they are either ambiguous or difficult to code.

1) Premaxillae: separate (0) or fused (1).
2) Dorsal process of premaxilla: absent or poorly defined with only partial contact with nasal bone (0); short but well-defined, separating the tips of the nasals or overlapping them dorsally (1); strong posterior extension separating nasals and contacting frontals (2); extension of dorsal process intervenes deeply between the frontals (3); posterior extension of dorsal process contacts frontal lateral to nasal (4).
3) Maxilla: present in adults as a normal member of the maxillary arcade (0); greatly reduced as a rudimentary element (1); entirely absent and functionally replaced by a modified vomer (2).
4) Septomaxilla: present (0) or absent (1)
5) Nasal ossification: paired nasals present with sutural midline contact or fused (0); nasals separate without midline contact (1); nasal absent (2)
6) Lacrimal: present (0) or absent (1).
7) Quadratojugal: present (0) or absent (1).
8) Prootic-exoccipital-opisthotic fusion: three separate elements (0); prootic-exoccipital fused, separate opisthotic (1); all three elements fused (2)
9) Pterygoid process: triradiate with distinct anterolateral and posterolateral processes (0); with an additional distinct anteromedial process (1); boomerang-shaped with distinct anteromedial and posterolateral processes (2); bar-like/vestigial (3); or absent (4). (Altered from Gao and Shubin with extra states added)
10) Internal carotid foramina: present (0) or absent (1).
11) Prefrontal: present (0) or absent (1).
12) Basilaris complex of inner ear: presence of both recessus basilaris (0); loss of papillae (1); loss of entire basilaris complex (2).
13) Angular: angular distinct from the prearticular (0); no distinct angular (absent or fused to prearticular in adult) (1) [altered from Gao and Shubin].
14) Coronoid: present as a separate element (0); absent in adult stage (1)
15) Articular: present as separate element (0); fused with prearticular (1)
16) First hypobranchial and first ceratobranchial: the two elements separate (0); two elements fused (1).
17) Ceratobranchial II in adults: present (0); absent (1)
18) Premaxillary teeth: present (0); absent (1)
19) Palatine dentition: confined to vomer (0); vomer and parasphenoid (1); vomer and palatine (2); vomer, palatine and pterygoid (3). [altered from Gao and Shubin]
20) Vertebral centrum: amphicoelous (0); opisthocoelous (1)
21) Four facetted articulation of exoccipital and atlas: absent (0), present (1)
22) Postatlantal ribs: bicapitate (0); unicapitate (1)
23) Atlantal spinal nerve foramen: absent (0); notch (1); fully enclosed (2).[Altered from Gao and Shubin]
24) Postatlantal spinal nerve foramina: all postatlantal spinal nerves exit intervertebrally (0); spinal nerve foramina present in some caudal vertebrae (1); foramina present in caudal and sacral vertebrae (2); foramina in trunk, sacral and caudal (3); occasional notch or foramen in posterior presacrals (4) .[Altered from Gao and Shubin]
25) Stapes: present in adult (0); absent in adult (1)
26) Lateral wall of nasal capsule: complete (0); incomplete (1)
27) Lateral narial fenestra: absent (0), present (1)
28) Posterior wall of nasal capsule: complete (0), incomplete (1)
29) Nasolacrimal duct: present (0); absent (1)
30) Dermal sculpture on skull roof: present, coarse (0); present, weak (1); absent (2). [Extended from Gao and Shubin to recognise the difference between the coarse sculpture of karaurids and the very light sculpture of some modern taxa.]
31) Frontal anterior extension: frontal does not extend lateral to nasal bone (0); does extend to lateral border of nasal (1)
32) Medial border of orbit: more than 50% of orbital margin formed by frontal (0); frontal contributes less than 50% of the orbital margin (1); frontal fully excluded from entering orbital margin (2). [Extended from Gao and Shubin.]
33) Frontal/maxillary contact: frontal and maxilla separated by prefrontal (0); frontal contacts dorsal process of maxilla (1); contact absent because of loss of maxilla (2)
34) Anterolateral process of parietal: absent (0); present but forms less than 50% of the total length of the parietal (1); present and makes up more than 50% of total length of parietal (2). [Extended and clarified from Gao and Shubin.]
35) Squamosal orientation in dorsal view: mediolaterally oriented as a transverse bar (0); anteroposteriorly inclined or parallel to skull midline (1)
36) Exposure of prootic-exoccipital-opisthotic complex in dorsal view: the complex largely concealed by parietal or exposed posterior to skull table (0); large exposure extends lateral to parietal table (1)
37) Squamosal contact with the parietal or other roofing elements: contact present (0); absent (1)
38) Origin of m. adductor mandibulae internus superficialis: on dorsolateral surface of parietal (0); origin extends posteriorly to exoccipital (1); origin extends to cervical vertebra (2); origin extends anteriorly towards level of frontal (3).
39) Ypsiloid cartilage: present (0); absent (1)
40) Fusion of distal carpal 1 + 2: fusion absent (0), present (1)
41) Fusion of distal tarsal 1 + 2: fusion absent (0), present (1)
42) Number of centralia in manus or pes: more than one central element (0); or one central element (1)
43) Intermedium and ulnare: intermedium separate (0); fused to ulnare (1)
44) Distal carpal 4 and 5: two elements remain separate (0); fused (1)
45) Haploid chromosome number: more than 20 (0); reduced to 19 (1); further reduced to 14 or fewer (2)
46) Diploid chromosome number: 56 or more (0); 40-55 (1); lower than 40 (2)
47) Microchromosome: present (0); absent (1)
48) Ciliated epithelium of female cloaca: present (0); absent (1). [We have returned to the original character of Larson and Dimmick (1993); Gao and Shubin combined characters.]
49) Extent of epidermis in female cloacal chamber: epidermal lining does not extend to anterior one half of cloacal chamber (0); or does extend into anterior one-half of chamber (1)
50) Male cloacal folds: absent (0); Present (1). [We have used the simpler character of Larson and Dimmick (1993)]

51) Anteroventral glands in female: absent (0); present (1). [We have used the simpler character of Larson and Dimmick (1993)]
52) Spermathecae in cloaca: absent (0) or present (1)
53) Dorsal cloacal glands in female: absent (0); present (1).
54) Posteroventral cloacal glands: absent (0); present (1)
55) Pubotibialis and puboischiotibialis muscles: separate (0) or fused (1)
56) Number of free ribs on anterior caudal vertebrae: more than three pairs (0); two to three pairs (1); free ribs absent (2)
57) Ectopterygoid: present (0) or absent (1)
58) Postfrontal: present (0) or absent (1)
59) Scapulocoracoid ossification: ossified as separate elements (0); fused elements (1)
60) Nasal-prefrontal contact; present (0); absent (1)
61) Number of presacrals: 15 or 16 (0); 14 or fewer (1); more than 16 (2)
62) Shape of atlas centrum in ventral view: roughly equal in length to postatlantals (0), much shorter (1); longer (2)
63) Maximum skull length/width: greater than 1.2 (0); 1.19-0.81 (1); 0.8 or less (2).
64) Marginal dentition: pedicellate, conical (0); pedicellate, compressed (1); non-pedicellate (2)
65) Operculum: separate, ossified operculum and stapes (0); operculum and stapes fused (1); loss of operculum (2)
66) Vomerine dentition: transverse row, medial in the palate (0); marginal, tooth row parallel to premaxilla and maxilla (1); longitudinal row or patch (2) [we used a single coding for longitudinal row or patch because they can be found in different ontogenetic stages of the same individual]
67) Male anteroventral glands in cloaca: absent (0); present (1)
68) Male posteroventral glands in cloaca: absent (0); present (1)
69) Kingsbury's glands in males: absent (0); present (1)
70) Dorsal pelvic glands in males: absent (0); present (1)
71) Lateral pelvic glands: absent in males (0); present (1)
72) Male dorsal or ventral glands: absent (0); present (1)