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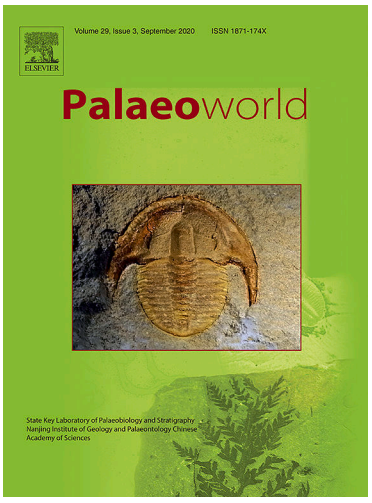

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Revision of *Chunerpeton tianyiense* (Lissamphibia, Caudata): is it a cryptobranchid salamander?

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Abstract

Lacustrine deposits of Juro-Cretaceous age in northeastern China have yielded some of the best-preserved fossils of early crown salamanders. One of those taxa, *Chunerpeton tianyiense*, has been considered as a crown or stem member of the family Cryptobranchidae, significant for implying a long evolutionary history for cryptobranchids and for calibrating the molecular clock of Caudata evolution. Building on the most recent large-scale phylogenetic analysis of relationships among fossil and recent salamanders and utilizing new specimens of *Chunerpeton*, we update the osteological description and diagnosis for *Chunerpeton* and reconsider its phylogenetic relationships. On the basis of recently collected *Chunerpeton* skeletons from the type locality at Daohugou, Inner Mongolia, China and available literature, we update the taxon-character matrix and run phylogenetic analyses with constraints on the relationships among families using a molecular backbone. We redescribe the osteology of *Chunerpeton*, revise and identify some new characters including large anterodorsal fenestra bordered by paired premaxillae, nasals, and frontals; nasals separate and wider than frontal; contact between nasal and prefrontal present; lacrimal present; and contact between pterygoid and parasphenoid absent. Osteological comparisons between *Chunerpeton* and living cryptobranchids reveal a suite of distinct differences in snout shape and in configurations, positions, and contacts of

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certain skull bones. Our phylogenetic analyses consistently place *Chunerpeton* as a stem Caudata outside of Cryptobranchidae and crown salamanders. Exclusion of *Chunerpeton* from Cryptobranchidae will require reconsideration of the origin time for Cryptobranchidae and recalibration of the molecular clock for the whole caudatan tree.

Keywords: *Chunerpeton*; Cryptobranchidae; China; Late Jurassic; Osteology; Phylogeny

1. Introduction

The family Cryptobranchidae includes the world's largest known extant caudates, namely the Chinese and Japanese giant salamanders. Cryptobranchids are represented by two living aquatic genera: *Andrias* and *Cryptobranchus*. *Andrias* contains the exclusively Japanese species *A. japonicus*, as the sister to a clade containing the exclusively Chinese species *A. davidianus*, *A. sligoi*, and an undescribed species, whereas the monospecific *Cryptobranchus*, with the species *C. alleganiensis*, lives in the eastern USA (e.g., Duellman and Trueb, 1994; Turvey et al., 2019). Cryptobranchidae are nested together with their sister family Hynobiidae within the clade of Cryptobranchoidea (e.g., Wiens et al., 2005; Pyron and Wiens, 2011).

Over the past quarter-century, thousands of well-preserved salamander skeletons have been discovered in Jurassic–Cretaceous strata in northeastern China. About a dozen species have been formally named and some have been assigned to living clades. These taxa are important for documenting the early evolutionary diversification and radiation of salamanders (e.g., Gao and Shubin, 2003; Gao et al., 2013; Jia and Gao, 2016a, 2019). One of the geologically oldest species, *Chunerpeton tianyiense*, was described as belonging to the extant family Cryptobranchidae (Gao and Shubin, 2003).

Subsequent phylogenetic analyses typically grouped *Chunerpeton* with the cryptobranchids and placed it as either a crown or stem member (Gao and Shubin, 2003; Wang and Evans, 2006; Jia and Gao, 2016a, 2019; Rong, 2018), but the cryptobranchid affinities of *Chunerpeton* were questioned by Vasilyan et al. (2013). As the presumed earliest cryptobranchid, *Chunerpeton* has been used to calibrate the molecular clock for the split between Cryptobranchidae and Hynobiidae (e.g., San

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Mauro et al., 2005; Bossuyt et al., 2006; Chen et al., 2015; Irisarri et al., 2017). Its position near the base of the salamander tree also makes *Chunerpeton* useful for dating the origin of Caudata (the total group) and the split between Cryptobranchoidea and Salamandroidea.

In the short type description for *Chunerpeton tianyiense* by Gao and Shubin (2003), just four catalogued specimens were listed, only the holotype was figured, and a limited number of osteological characters were listed in the diagnosis. The authors questionably identified a hypohyal (Gao and Shubin, 2003, pp. 425–426, text-figs. 1b, 2b), an element that is not ossified in the hyobranchium of living cryptobranchids. Several subsequent studies on *Chunerpeton* provided revised diagnoses of *Chunerpeton*, suggested that *Chunerpeton* and *Beiyanerpeton* might be synonyms (Sullivan et al., 2014), and reported their prey preferences for the corixid *Yanliaocorixa chinensis* (Dong et al., 2011) and limb abnormalities (Wang et al., 2015). Despite the above-cited work and the fact that *Chunerpeton* is known by hundreds of skeletons from at least six localities (e.g., Sullivan et al., 2014), a detailed understanding of its osteology is still pending. That situation is unfortunate, given that *Chunerpeton* is a key genus for deciphering the early evolutionary history of salamanders. Here we address those deficiencies by using additional skeletons of *C. tianyiense* from the type locality to present an updated diagnosis and a more detailed osteological description for the species and to reevaluate its phylogenetic affinities.

Institutional abbreviations

CAGS: Chinese Academy of Geological Sciences, Beijing, China.

IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

ZFMK: Zoologisches Forschungsmuseum Koenig, Bonn, Germany.

2. Materials and methods

Our study relies on 31 referred fossil skeletons of *Chunerpeton tianyiense*, all collected from the type locality (i.e., Daohugou locality, Ningcheng County, Inner Mongolia, China) and deposited in the collections of IVPP. We examined specimens using a Leica binocular microscope and photographed using NIKON D850 and NIKON D7000 digital cameras. We created the photographic illustrations using

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Photoshop CS6 and the line drawings using Illustrator CS5. Our anatomical nomenclature generally follows Francis (1934), but for specific bones or regions follows Rose (2003) and Vasilyan et al. (2013).

According to Article 34.2 of the 4th Edition of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999), "The ending of a Latin or latinized adjectival or participial species-group name must agree in gender with the generic name with which it is at any time combined [Art. 31.2]; if the gender ending is incorrect it must be changed accordingly (the author and date of the name remain unchanged [Art. 50.3.2])." The Greek word "herpeton" is neuter, meaning the corresponding specific names should also be neuter. Therefore, the following names are corrected for the six species of Chinese Mesozoic salamanders: *Sinerpeton fengshanense* Gao and Shubin, 2001, *Chunerpeton tianyiense* Gao and Shubin, 2003, *Pangerpeton sinense* Wang and Evans, 2006, *Regalerpeton weichangense* Zhang et al., 2009, *Beiyanerpeton jianpingense* Gao and Shubin, 2012, and *Nuominerpeton aquilonare* Jia and Gao, 2016b, and all with neuter -e instead of masculine and feminine -is.

3. Systematic paleontology

Class Amphibia Linnaeus, 1758

Subclass Lissamphibia Haeckel, 1866

Order Caudata Scopoli, 1777

Genus *Chunerpeton* Gao and Shubin, 2003

Type species: *Chunerpeton tianyiense* Gao and Shubin, 2003.

Diagnosis: Same as for the type and only species.

Chunerpeton tianyiense Gao and Shubin, 2003

(Figs. 1–3, 4A–C)

Holotype: CAGS-IG-02051, natural molds of dorsal and ventral aspects of an articulated, subadult skeleton preserving skull and postcranium (Gao and Shubin, 2003, pp. 425–426, text-figs. 1, 2).

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Emended diagnosis (updated from Gao and Shubin, 2003): Ribs unicapitate (Gao and Shubin, 2003); three paired ribs bearing anterior caudal vertebrae (Gao and Shubin, 2003); internal carotid foramina penetrate parasphenoid (Gao and Shubin, 2003); well-developed anterolateral process of parietal extending along lateral border of frontal (Gao and Shubin, 2003); frontal-maxilla contact absent (Gao and Shubin, 2003); parietal-prefrontal contact absent (Gao and Shubin, 2003); anteromedial fenestra present (Gao and Shubin, 2003); pars praenasalis of premaxilla midline contact absent (Gao and Shubin, 2003); vomers without posterior extension (Gao and Shubin, 2003); paired hypobranchial I and II ossified (Gao and Shubin, 2003); basibranchial II arrow-shaped (Gao and Shubin, 2003); 16 presacral vertebrae (Gao and Shubin, 2003); nasals without midline contact (contra lacking midline contact of dorsal processes of premaxillae according to Gao and Shubin, 2003); nasal-prefrontal contact present (contra nasal-prefrontal contact absent according to Gao and Shubin, 2003); nasal wider than frontals (contra nasals narrower than frontals according to Gao and Shubin, 2003); lacrimal present and contributing to external naris, but not to orbit (contra lacrimal absent according to Gao and Shubin, 2003); anterodorsal fenestra formed by premaxilla, nasal and frontal (contra anterodorsal fenestra formed only by premaxilla and nasal according to Jia and Gao, 2019); single vomerine tooth row parallel to premaxillary and maxillary tooth rows (new); pterygoid triradiate with a slender dentate anteromedial process (new); palatine present (new); prootic, exoccipital and opisthotic present as separate bones (new).

Type locality and horizon: Daohugou, Ningcheng County, Inner Mongolia, China; Haifanggou Formation; Late Jurassic, 163 Ma (Liu et al., 2006; Huang, 2015).

Referred material: Part and counterpart slabs are identified with the suffixes "A&B", and single slab is identified without suffix. IVPP V 11976, ventral impression of articulated skeleton lacking most of skull; V 12609, an incomplete dorsal skeleton impression lacking most of skull; V 12611, an incomplete ventral skeleton impression lacking anterior part of skull and posterior part of tail; V 13241A&B, articulated skeleton impression; V 13343A&B, nearly complete skeleton impression with part of tail missing; V 13478, articulated natural molds of bones without skull preserved in lateral view; V 14051A&B, articulated skeleton impression lacking pelvic girdle and tail; V 14052, nearly complete dorsal skeleton impression; V 14054A&B, nearly complete skeleton impression; V 14055A&B, nearly complete

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skeleton impression with part of tail missing; V 14056, incomplete ventral skeleton impression lacking part of tail; V 14058A&B, articulated natural molds of skeleton with part of tail missing; V 14060A&B, nearly completely articulated natural molds of skeleton; V 14063, incomplete natural molds of skull preserved in dorsal view; V 14220A&B, articulated skeleton impression; V 14221A&B, articulated skeleton impression; V 14222A&B, incomplete skeleton impression lacking pelvic girdle and tail; V 14223A&B, incomplete skeleton impression with six presacral vertebrae, pelvic girdle and fifteen caudal vertebrae; V 14224A&B, incomplete skeleton impression lacking part of skull and pelvic girdle and tail; V 14225, incomplete ventral skeleton impression; V 14226A&B, incomplete skeleton impression with the tail missing; V 14227A&B, nearly complete skeleton impression; V 14228A&B, incomplete skull impression; V 14250A&B, incomplete skeleton with part of skull and tail missing; V 14254, incomplete ventral skeleton impression with skull and nine presacral vertebrae; V 14256A&B, incomplete skull and part appendicular skeleton; V 14429A&B, nearly complete natural molds of skeleton with axial skeleton preserved in impression; V 14604A&B, nearly complete skeleton impression; V 14609, ventral skull impression; V 14745, nearly complete dorsal skeleton impression lacking part of the tail; V 15422, incomplete natural molds of skeleton in ventral view.

4. Description

4.1. General features

All studied specimens are preserved in articulation as natural impressions or some with bones on part and counterpart slabs or a single slab. They represent individuals of different size and the snout-pelvic length ranges from 20 mm (IVPP V 13241A&B) to 115 mm (IVPP V 15422). *Chunerpeton* is a neotenic salamander, with a short, broad, and rounded snout. The skull is slightly longer than wide. The preserved soft tissue impressions indicate that *Chunerpeton* had three pairs of densely-branched external gills bearing branchial teeth (Figs. 1, 2A, C, 3A–C). The skull roof has a distinct and large anterodorsal fenestra bordered by the paired premaxillae, nasals, and frontals (Figs. 2A, B, 4A), an observation differing from that of Gao and Shubin (2003, p. 426, text-fig. 2b) which excluded the frontal. A recent study has recognized five patterns of anterodorsal fenestrae for living salamanders

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that shows this feature has taxonomic significance (Jia and Gao, 2019). Thus, the framing of the anterodorsal fenestra of *Chunerpeton* by the paired premaxillae, nasals, and frontals is identified as a diagnostic character. The palate consists of paired vomers, palatines, and pterygoids, and a broad parasphenoid. The vomerine teeth are monostichous and arranged in a single, curved line extending parallel to the premaxillary and maxillary tooth rows. The fore- and hindlimbs are well developed. The tail is laterally compressed, with tall neural and deep haemal arches; for a given caudal vertebra, its haemal arch is slightly longer than its neural arch (Fig. 3I).

4.2. Skull

The paired premaxillae (Figs. 2A, B, 4A) are thin, with moderately-long medial portions where the bones articulate across the skull midline. The premaxilla dorsally bears a small, triangular pars praenasalis that posteriorly overlaps the nasal (Figs. 2A, B, 4A), which contrasts with the original publication where the pars praenasalis was described as large and broad (Gao and Shubin, 2003, p. 426, text-fig. 2b). The lateral portion of the premaxilla for *Chunerpeton* is slightly longer and more slender than its medial portion, and its lateral end articulates with the anterior process of the maxilla. The premaxillary pars dentalis bears about 23 closely arranged pedicellate and monocuspid teeth. The pars palatina is reduced or absent (Figs. 2C, D, 4B).

A complete maxilla preserved as part of IVPP V 14228A&B (Fig. 3E, F) bears a moderately-developed anterior process. About 20 teeth are observable on the pars dentalis. The maxillary posterior process is longer than its anterior one. The maxilla bears a small and triangular facial process that contacts dorsally with the nasal and lacrimal (Figs. 3E, F, 4A). The maxillary pars palatina is reduced (Fig. 3F).

The paired nasals (Figs. 2A, B, 4A) are large, broad, and triangular in contrast to the original publication where the nasals were described as small, narrow, and elongated (Gao and Shubin, 2003, p. 426, text-fig. 2b). The pars praenasalis of the premaxilla covers the anterior process of the nasal. The posterolateral edge of the nasal contacts the prefrontal whereas the original publication states that a nasal-prefrontal contact is absent (Gao and Shubin, 2003, p. 426, text-fig. 2b). The nasal is wider than the frontal in contrast to the original description where the nasal was said to be narrower than the frontal (Gao and Shubin, 2003, p. 426, text-fig. 2b). The posterior process of the nasal overlies the frontal. The nasals are broadly separated

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across the skull midline by a large anterodorsal fenestra (Fig. 4A) in contrast with the original publication where a midline contact of nasals was described as present (Gao and Shubin, 2003, p. 426, text-fig. 2b).

The prefrontal (Figs. 2A, B, 4A) is triangular. Its medial part overlies the frontal, whereas its anteromedial edge contacts the nasal and lacrimal (Fig. 4A). The prefrontal does not articulate with the parietal.

The lacrimal (Fig. 3E, F, 4A) is a small bone that contacts the nasal and prefrontal, and contributes to the external narial margin, whereas the original description described the lacrimal as absent (Gao and Shubin, 2003). We did not observe a septomaxilla in any of our specimens.

The paired frontals (Figs. 2A, B, 4A) are roughly rectangular in shape. The anterior portion of the frontal is covered by the nasal and prefrontal in contrast to the original description where the frontals were said to extend anteriorly to the lateral border of the nasal (Gao and Shubin, 2003). The anterior portion of the frontal is developed into two large, lobe-like anterior processes and, more laterally, a smaller and pointed process. The suture between the frontals is wavy (Fig. 2A, B). The posterior end of the frontal articulates with the anterior portion of the parietal. A distinct median opening surrounded by both frontals and parietals is observable in IVPP V 13343A (Fig. 2A, B). However, that opening is not present in IVPP V 14226A (Fig. 3A) or in the holotype (Gao and Shubin, 2003, p. 426, text-fig. 2).

The parietals (Figs. 2A, B, 4A) are large bones located behind the frontals. The parietal has a wide lateral extension that articulates with the proximal head of the squamosal (Fig. 3B). The parietal bears a long anterolateral process extending along the lateral edge of the frontal, but that process does not extend far enough anteriorly to articulate with the prefrontal (Figs. 2A, B, 3A, 4A). In IVPP V 13343A, the dorsal surface of the parietal is weakly sculpted with irregular, curved low ridges (Fig. 2A), but in IVPP V 14226A the same surface is smooth (Fig. 3A).

The paired squamosals (Figs. 2A, B, 3B, 4A) are elongate bones that form the posterolateral margin of the skull. The squamosal is positioned transversely and inclines slightly anteriorly. The proximal head of the squamosal is triangular and articulates medially with the parietal. The quadrate ramus is gracile and articulates ventrally with the quadrate. Preserved impressions of the squamosal show that the

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external surface of the caput squamosi is weakly sculptured in IVPP V 13343A, but the same surface in IVPP V 14745 is smooth (cf. Fig. 2A versus Fig. 3B).

The paired quadrates (Fig. 2A–D) are triangular bones sandwiched between the squamosal and the lateral process of the pterygoid.

The pterygoid (Figs. 2, 3A, C, 4A, B) is triradiate, consisting of a central portion and the anteromedial, medial, and lateral processes. The anteromedial process is long, slender and curved. Its anterior tip is medially orientated and free of bony contacts. About ten teeth are observable in a single row on the anterior end of the anteromedial process (e.g., IVPP V 13343: Fig. 2C–E). The pterygoid teeth are present even in the largest individuals (skull length = 3 cm) that we examined (e.g., IVPP V 15422: Fig. 3C). The medial process of the pterygoid is small and free of bony contacts (Figs. 2, 3A, 4A). The lateral process of the pterygoid is large, wide and articulates dorsally with both the quadrate and squamosal (Fig. 4A, B). In most adult salamanders, the pterygoid (if present) is toothless (but dentate in *Necturus*) and has various shapes (e.g., Duellman and Trueb, 1994; Rose, 2003). The triradiate pterygoid with a slender dentate anteromedial process is a newly identified feature for *Chunerpeton*.

The paired vomers (Figs. 2C, D, 4B) are located at the anterior portion of the palate. They do not meet the premaxillae and maxillae, but articulate posteriorly with the anterior process of the parasphenoid. The vomers are broadly separated from each other across the skull midline by the anteromedial fenestra. They are long, narrow, and slightly curved. Approximately 28 teeth are present and aligned in a row paralleling the posterior portion of the premaxillary tooth row and the anterior portion of the maxillary tooth row (Fig. 2C). Rare, preserved tooth crowns indicate that the vomerine teeth are pedicellate and monocuspid. In living salamanders, the arrangement and position of the vomerine teeth has ontogenetic and taxonomic significance (e.g., Rose, 2003). Given that the vomerine teeth retain the same shape and position in different size *Chunerpeton*, a single vomerine tooth row parallel to the premaxillary and maxillary tooth row is identified as a new diagnostic character for *Chunerpeton*.

The paired palatines (Figs. 2E) are small bones located behind the vomer. The palatine does not contact any adjacent bones. The palatine tooth row consists of ten teeth. The teeth are similar in structure to those on the vomer and are arranged in a single row paralleling the posterior portion of the maxillary tooth row. Palatine teeth

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are present in all studied individuals, independent of body size; e.g., IVPP V 13343B (Fig. 2E) and IVPP V 15422 (Fig. 3C). The paired, dentate palatines are a newly identified feature which was not mentioned in the original description (Gao and Shubin, 2003, although it is illustrated, but not labeled, in text-fig. 2b).

The parasphenoid (Figs. 2C, D, 4B) is a large bone located along the ventral midline of the skull. It occupies about four-fifths of the total skull length. Two anterior processes are present and separated by a deep, U-shaped notch. Each of the anterior processes articulates with its corresponding vomer. Paired internal carotid foramina (Fig. 2C, D) are present in the lateral extensions of the parasphenoid.

The prootic, opisthotic, and exoccipital (Figs. 2B, 3B, 4A) are neither fused together, nor with other skull bones, even in large-sized individuals (e.g., IVPP V 14745: Fig. 3B). Details of those bones cannot be seen, due to crushing in that region of the skull. Different levels of fusion among prootic, opisthotic, and exoccipital occurs in living salamanders, such as three elements without fusion in proteids, fused exoccipital + opisthotic with separate prootic in most cryptobranchoids, fused prootic + opisthotic with separate exoccipital in sirenids, and all three elements fused in most salamandroids (e.g., Duellman and Trueb, 1994; Rose, 2003). Thus, the presence of a separate prootic, exoccipital, and opisthotic is treated as a new diagnostic character for *Chunerpeton*. The paired orbitosphenoids form the bony lateral wall of braincase in most mature salamanders except proteids (Rose, 2003). We did not observe an orbitosphenoid in any of our specimens.

4.3. Lower jaw

The lower jaw (Fig. 2C, D) consists of the dentary, prearticular, articular, and angular. The dentary and prearticular form, respectively, the majority of the labial and lingual surfaces of the lower jaw (Fig. 2C, D). The dentary bears a row of 50 teeth that are closely packed, narrow, pedicellate, and monocuspid. The angular (Figs. 2C, D, 3C) is a narrow bone sandwiched between the dentary and prearticular. The angular has a pointed anterior end (Fig. 3C) and it does not fuse with the prearticular. The articular is a tiny bone located at the posterior end of the lower jaw, where it articulates with the quadrate to form the skull-jaw joint (Fig. 2A, B).

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4.4. Hyobranchium

The ossified hyobranchial elements consist of paired hypobranchial I and II and a single, median basibranchial II (Figs. 2C, D, 4C). The paired second hypobranchials are located posteromedially to the first hypobranchials, whereas basibranchial II is located directly behind them along the skull midline. Hypobranchial I and II are both rod-shaped and laterally curved. Basibranchial II is arrow-shaped with an elongated and needle-like posterior process.

4.5. Axial skeleton

Chunerpeton has 15 presacral (one atlas and 14 trunk vertebrae), one sacral, and at least 38 caudal vertebrae (Gao and Shubin, 2003, pp. 425–426, text-figs. 1a, 2a; Figs. 1, 3I). The atlas is the same length as the following trunk vertebrae (Fig. 3D). Anteriorly, the atlas bears a small and triangular tuberculum interglenoideum (sensu Evans and Milner, 1996) arising between a pair of broad anterior cotyles, the latter being firmly articulated with the occipital condyles on the skull. No free ribs or transverse processes are observable on the atlas (Fig. 3B, D). The trunk vertebrae are amphicoelous and, on either side, bear a relatively short and unicapitate transverse process that articulates distally with a rib (Fig. 3D). The first three pairs of ribs are more massive than the following ones, and have expanded proximal and distal ends (Fig. 3D), serving as attachment surfaces for the pectoral musculature (Francis, 1934). All trunk ribs are unicapitate and, from the fourth pair back, they gradually reduce in size. The last pair of trunk ribs is triangular (Fig. 1). The sacral ribs, for articulation with the pelvis, are larger than the most anterior trunk ribs (Fig. 3J). IVPP V 14054 (Fig. 3I, J) shows that the first three caudal vertebrae bear ribs. Starting with the fourth caudal vertebra, all remaining caudals lack free ribs, but they bear distinct neural and haemal arches (Fig. 3I). The haemal arch of a given caudal vertebra is longer than its neural arch (Fig. 3I).

4.6. Appendicular skeleton

The pectoral girdle consists of a pair of scapulocoracoids (Figs. 1A, 3D). In each, the coracoid portion is triangular and the scapular portion has an expanded distal end. The proximal end of the humerus is wider than the distal end (Fig. 1A) and its shaft bears a distinct crista ventralis. The radius and ulna are both straight, with the ulna

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slightly longer than the radius. The carpals are not ossified (Fig. 3G). The phalangeal formula is 2-2-3-2 in both IVPP V 13343 (Fig. 1A) and IVPP V 11976 (Fig. 3G).

The pelvic girdle consists of the paired ilia and ischia. The ilium is waisted and slightly curved (Fig. 1A). The ischium in IVPP V 14250 is large and blade-shaped. Both femora are detached from the pelvis in IVPP V 13343 (Fig. 1). The femur has a straight shaft and expanded proximal and distal ends (Figs. 1, 3I). The tibia and fibula are straight bones, both much shorter than the femur (Fig. 1). The tibia is shorter and more robust than the fibula. The tarsals are not ossified (Fig. 3H). In IVPP V 13343A, the phalangeal formula of the left pes is 2-2-2-2-2, and 2-3-3-3-2 for the right pes (Fig. 1). However, the right phalangeal formula is 2-2-3-4-3 in IVPP V 14055 (Fig. 3H).

4.7. Taxonomic identification.

The 31 salamander skeletons we examined can be referred to *Chunerpeton tianyiense* based on the following combination of characters they share with the holotype (see Gao and Shubin, 2003): large anterodorsal fenestra formed by premaxillae, nasals, and frontals; pterygoid bearing a long, slender, curved, and free anteromedial process, and bearing a small, pointed, and free medial process, and bearing a large, wide lateral process; oval vomer, broadly separated across the skull midline, and with their long axis paralleling the premaxillae and maxillae, but not contacting those upper jaw bones; vomerine teeth in single row paralleling the premaxillary and the maxillary teeth; longer parasphenoid occupying posterior four-fifths of head length, and bearing two anterior processes separated by a deep, U-shaped notch; same configuration for hyobranchium consisting of paired hypobranchials I and II, and an arrow-shaped basibranchial II; 15 presacral vertebrae; and scapulocoracoid with triangular coracoid portion.

5. Comments on the skull and hyobranchium of *Chunerpeton*

Gao and Shubin's (2003) type description for *Chunerpeton tianyiense* was limited exclusively to characters they considered diagnostically informative. Our study expands on that original description, by providing a more detailed osteological description for the species. In particular, our study clarifies and reveals new aspects of cranial structure in *Chunerpeton*. We have been able to (1) reinterpret the relative size

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of the anterodorsal fenestra and show that it is bordered by the premaxillae, nasals, and frontals; (2) reinterpret the shapes and contacts of the premaxillae, nasals, and prefrontals; (3) reinterpret the elements identified as the vomer and nasal by Gao and Shubin (2003, p. 426, text-fig. 2b) as, respectively, the nasal and premaxilla; (4) establish that the pterygoid is triradiate with a slender dentate anteromedial process; (5) provide a detailed description of the palatal dentition; (6) confirm that free palatines are present; and (7) establish that the prootic, opisthotic and exoccipital are three separate bones. We are unable, however, to resolve the identity of a pair of prominent, subcircular structures, located to either side of the midline and about midway along the anteroposterior axis in the holotype skull, which were tentatively identified as hypohyals by Gao and Shubin (2003, pp. 425–426, text-figs. 1b, 2b). None of the *Chunerpeton* skeletons we examined preserves comparable structures, meaning that for the time being any discussion of those problematic structures relies on the holotype. In extant neotenic salamanders (e.g., *Amphiuma means*, *Necturus maculosus*, *Ichthyosaura alpestris*), the paired hypohyals lie near the anteromedial end of the hypobranchium and are relatively small and unossified elements (Fig. 4J), but in extant cryptobranchids the hypohyals are unossified and separated into anterior and posterior hypohyals (Fig. 4F), and a small, paired third hypohyal is possibly the result of resorption that detaches the anterior ceratohyal process from the rest of the larval ceratohyal cartilage (Rose, 2003; Heiss and Grell, 2019).

Although the shape and relative size of the problematic elements in the holotype of *Chunerpeton* are reminiscent of the posterior hypohyals in extant cryptobranchids (cf. Gao and Shubin, 2003, p. 425, text-fig. 1b versus Fig. 4F), we note that the shape, size, and position of those problematic elements suggest an alternative interpretation — that they may represent the orbitosphenoids forming the walls of the braincase. Clearly, examination of additional specimens will be required to resolve the identity of that element.

Below we compare *Chunerpeton* to other relevant salamanders and assess its phylogenetic relationships. Because many extinct salamander species are known by isolated and often fragmentary bones (e.g., Gardner and DeMar, 2013; Skutschas, 2013; Vasilyan et al., 2013), we limit our comparisons to species of Mesozoic salamanders (mostly Juro-Cretaceous species from China) known from complete or nearly complete skeletons and to the extant cryptobranchids *Andrias* and

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Cryptobranchus. Our phylogenetic analysis utilizes a broader range of extant salamander species from all living families and a modest selection of Mesozoic species represented by phylogenetically informative fossils, the latter mostly known by articulated skeletons.

6. Discussion

6.1. *Chunerpeton* compared with other Mesozoic taxa

With the possible exception of two paracontemporaneous species discussed in the latter part of this section, *Chunerpeton tianyiense* can be distinguished from all adequately known Mesozoic salamander species. It differs from the stem salamanders *Karaurus* and *Kokartus* (Jurassic, Central Asian) in lacking heavily-sculptured skull bones (Skutschas and Martin, 2011). Compared to crown salamanders, *Chunerpeton* differs from the Chinese Juro-Cretaceous species *Laccotriton subsolanus*, *Liaoxitriton daohugouensis*, *Liaoxitriton zhongjiani*, *Linglongtriton daxishanensis*, *Nuominerpeton aquilonare*, *Pangerpeton sinense*, and *Sinerpeton fengshanense* and the Spanish Cretaceous species *Valdotriton gracilis* in having: (1) pterygoid with a long, slender, and curved anteromedial process versus a shorter anteromedial process in all the listed taxa and (2) unossified tarsals and carpals versus ossified in most of the listed taxa, except *Pangerpeton* and *Valdotriton* (Evans and Milner, 1996; Dong and Wang, 1998; Gao and Shubin, 2001; Wang, 2004; Wang and Evans, 2006; Jia and Gao, 2016b, 2019). *Chunerpeton* further differs from *Pangerpeton*, as follows: (1) posteriorly elongate and narrow vomer versus triangular vomer with posterior extension in *Pangerpeton* and (2) 15 presacral vertebrae versus 14 presacral vertebrae in *Pangerpeton*. *Chunerpeton* further differs from *Valdotriton*, as follows: (1) premaxilla bearing a short pars praenasalis versus long pars dorsalis in *Valdotriton*; (2) unfused prootic, exoccipital, and opisthotic versus fused prootic, exoccipital, and opisthotic in *Valdotriton*; (3) unicapitate ribs versus bicapitate ribs in *Valdotriton*; and (4) single row of vomerine teeth versus two or three rows in *Valdotriton*. *Chunerpeton* can be further distinguished from *Regalerpeton weichangense* (Early Cretaceous, China), as follows: (1) long and narrow vomer with posterolaterally oriented vomerine tooth row versus roughly pentagonal vomer with transversely oriented vomerine tooth row in *Regalerpeton*; (2) separate opisthotic and exoccipital versus fused opisthotic and exoccipital in *Regalerpeton*; and (3) arrow-shaped basibranchial

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II versus triradiate in *Regalerpeton* (Rong, 2018). *Chunerpeton* differs from *Jeholotriton paradoxus* in having monostichous vomerine teeth versus multiple vomerine tooth rows in *Jeholotriton* (Wang and Rose, 2005). Finally, *Chunerpeton* differs from *Iridotriton hechti* (Late Jurassic, USA), as follows: (1) internal carotid foramina penetrating the parasphenoid versus internal carotid foramina absent from parasphenoid in *Iridotriton*; and (2) unfused prootic, exoccipital, and opisthotic versus three elements forming a single unit in *Iridotriton* (Evans et al., 2005).

More detailed comparisons are warranted between *Chunerpeton tianyiense* and two other neotenic and Chinese Jurassic species — *Beiyanerpeton jianpingense* and *Qinglongtriton gangouensis* for two reasons. First, Sullivan et al. (2014) and Wang et al. (2015) questioned whether fossils of *Chunerpeton* and *Beiyanerpeton* might belong to the same taxon, with *Chunerpeton* being the senior synonym. Although not previously expressed in print, similar questions also could be raised regarding the distinctiveness of *Chunerpeton* and *Qinglongtriton*. Second, in addition to being neotenic, all three taxa resemble each other in having (1) similarly shaped pterygoids, vomers, and parasphenoid; (2) the same suite of ossified hyobranchium elements; (3) palatine present in adults; (4) pterygoid bearing teeth; (5) and 15 presacral vertebrae (Gao and Shubin, 2012; Jia and Gao, 2016a). On the other hand, *Chunerpeton* appears to differ from the other two taxa, as follows: (1) unicapitate ribs versus probable bicapitate ribs in *Beiyanerpeton* and *Qinglongtriton* (Gao and Shubin, 2012; Jia and Gao, 2016a) and (2) arrow shaped basibranchial II versus arrow-shaped (juveniles) or anchor-shaped with two additional posterior spikes (adults) in *Qinglongtriton* (Jia and Gao, 2016a) and trident-shaped in *Beiyanerpeton* (Gao and Shubin, 2012). The above-listed two potential differences should be treated with caution. *Beiyanerpeton* and *Qinglongtriton* were reported to have weakly bicapitate ribs. It is important to mention that the proximal ends of some unicapitate ribs are grooved and, when their cartilaginous heads are lost, those ribs may erroneously appear weakly bicapitate. Apparent differences among the species in shapes of the basibranchial II may be at least partially ontogenetic. Although beyond the scope of our current paper, it is evident that more detailed comparisons are needed to resolve the taxonomic distinctiveness of the three species. For the purposes of our study, we accept *C. tianyiense*, *B. jianpingense*, and *Q. gangouensis* as distinct species.

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6.2. *Chunerpeton* compared with living cryptobranchids

Osteological comparisons of *Andrias* (limited to *A. davidianus* and *A. japonicus*) and *Cryptobranchus alleganiensis* indicate that they share four synapomorphies: angular present, and no septomaxilla, lacrimal, or basibranchial II (Rose, 2003). Our observations on *Chunerpeton tianyiense* find that it shares two of those characters (angular present and septomaxilla absent) with living cryptobranchids, but *Chunerpeton* differs in having an ossified lacrimal and a basibranchial II.

During the course of our study, we noted numerous additional differences between *Chunerpeton* and extant cryptobranchids. When viewed in ventral or dorsal aspect, the snout of *Chunerpeton* is narrower than the maximum width of its head (as measured across the skull-mandible joints), whereas in extant cryptobranchids the snout is nearly as wide as the maximum width of the head (Fig. 4A, D, G). *Chunerpeton* further differs from extant cryptobranchids in an extensive suite of features related to the presence/absence, configurations, positions, and articulation of certain bones and hyobranchial bones, as follows: (1) pars praenasalis of premaxilla located in the middle of the bone (Fig. 4A) versus shifted towards the medial end of the bone in cryptobranchids (Fig. 4D, G); (2) large, triangular nasals separated along the skull midline by an anterodorsal fenestra in *Chunerpeton* (Fig. 4A) versus narrow and elongate not separated by an anterodorsal fenestra and, instead, articulating with each other along the skull midline in cryptobranchids (Fig. 4D, G); (3) wide frontal not contacting the maxilla in *Chunerpeton* (Fig. 4A) versus narrow, elongate, and anteriorly curved frontal articulating with the pars facialis of the maxilla in cryptobranchids (Fig. 4D, G); (4) triangular prefrontal not contacting the parietal in *Chunerpeton* (Fig. 4A) versus long, narrow, and curved prefrontal articulating with the anterolateral process of parietal in cryptobranchids (Fig. 4D, G); (5) pterygoid bearing a long, slender, curved, and free anteromedial process and bearing a small, pointed, and free medial process in *Chunerpeton* (Fig. 4A) versus pterygoid bearing a shorter anteromedial process and bearing an enlarged medial process articulating with the orbitosphenoid in cryptobranchids (Fig. 4D, G); (6) broad and posteriorly elongate anterodorsal fenestra bordered by the premaxillae, nasals, and frontals in *Chunerpeton* (Fig. 4A) versus small anterodorsal fenestra located far anteriorly and bordered by the premaxillae and nasals in cryptobranchids (Fig. 4D, G); (7) lacrimal present in *Chunerpeton* (Fig. 4A) versus absent in cryptobranchids (Fig. 4D, G); (8) oval

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vomers, broadly separated across the skull midline, and with their long axis paralleling the premaxillae and maxillae, but not contacting those upper jaw bones in *Chunerpeton* (Fig. 4B) versus larger and triangular vomers articulating medially with each other and anteriorly with the premaxillae and maxillae in cryptobranchids (Fig. 4E, H); (9) large anteromedial fenestra forming by premaxillae, vomers, and parasphenoid in *Chunerpeton* (Fig. 4B) versus reduced anteromedial fenestra entirely enclosed by anterior portions of vomers in cryptobranchids (Fig. 4E, H); (10) single vomerine tooth row present and extending parallel to premaxillary and maxillary tooth rows in all taxa, but located in middle of vomer in *Chunerpeton* (Fig. 4B) versus located along anterolateral edge of vomer in cryptobranchids (Fig. 4E, H); (11) a small and free palatine present in *Chunerpeton* versus absent in extant cryptobranchids (Fig. 4E, H); (12) longer parasphenoid occupying posterior four-fifths of head length in *Chunerpeton* (Fig. 4B) versus shorter parasphenoid occupying posterior two-thirds of head length in cryptobranchids (Fig. 4E, H); (13) overlapping joint between premaxilla and maxilla in *Chunerpeton* (Fig. 4A) versus abutting joint between premaxilla and maxilla in cryptobranchids (Fig. 4D, G); (14) separate opisthotic and exoccipital in *Chunerpeton* (Fig. 4A) versus fused opisthotic and exoccipital in cryptobranchids (Fig. 4D, G); (15) ossified hyobranchium consisting of paired hypobranchials I and II and median basibranchial II in *Chunerpeton* (Fig. 4C) versus ossified hyobranchium consisting of paired hypobranchial II and ceratobranchial II in cryptobranchids (Fig. 4F, I). The presence of orbitosphenoids may be another difference. Ossified orbitosphenoids unequivocally are present in cryptobranchids (Fig. 4D, G), but have not reliably been identified in *Chunerpeton*. However, that difference may not stand if we are correct in our earlier suggestion that the holotype skull of *Chunerpeton* may preserve orbitosphenoids. Regardless of the distribution of the orbitosphenoid, the extensive suite of characters listed here clearly distinguishes *Chunerpeton* from extant cryptobranchids and raises further questions about whether *Chunerpeton* is related to Cryptobranchidae.

6.3. Phylogenetic relationships of *Chunerpeton*

We tested the phylogenetic position of *Chunerpeton* by running five sets of analyses using modified versions of the data matrix provided by Jia and Gao (2019), which consists of 120 characters (see Appendix A, Section 1) and 34 taxa. We ran our

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analyses in TNT version 1.5 (Goloboff and Catalano, 2016), using a traditional search of 100 000 replicates, 30 trees per replication, tree bisection-reconnection. We designated the stem salamander *Karaurus* as the outgroup and set all characters as unordered and equally weighted. Consistent with earlier analyses by Gao and Shubin (2012) and Jia and Gao (2019), we excluded eleven inapplicable characters (11, 18, 28, 47, 50, 72, 73, 92, 93, 103, and 109).

For our first analysis, we modified fourteen codings (Appendix A, Section 3) for *Chunerpeton* in the matrix of Jia and Gao (2019), based on the new fossils we examined. The result of this analysis produced 30 most parsimonious trees (tree length = 314; consistency index = 0.449; retention index = 0.718). The 50% majority consensus tree (Fig. 5A) recovers *Chunerpeton* as the sister to two contemporary Chinese taxa (*Beiyanerpeton* + *Qinglongtriton*). The existence of this clade of *Chunerpeton* + (*Beiyanerpeton* + *Qinglongtriton*) is supported by three synapomorphies: separate nasals without midline contact [character 8(1)]; well-developed anterolateral process of parietal surpassing midlevel of the orbit [character 60(1)]; and anterodorsal fenestra bordered by the premaxilla, nasal and frontal [character 107(1)]. In contrast to previous proposals that *Chunerpeton* is closely related to, or a member of, Cryptobranchidae, our analysis places the clade of *Chunerpeton* + (*Beiyanerpeton* + *Qinglongtriton*) near the base of the tree, as the secondmost basal clade and removed from cryptobranchids. Other Mesozoic salamanders from China and *Iridotriton* fall out between the clade of *Chunerpeton* + (*Beiyanerpeton* + *Qinglongtriton*) and crown salamanders. Placement of *Chunerpeton* well outside of Cryptobranchidae and near the base of the tree is a consistent pattern in all our analyses that include *Chunerpeton*.

For our second analysis, we re-coded 23 characters for *Jeholotriton* and 33 characters for *Iridotriton* (Appendix A, Section 3), based on details in relevant publications (Evans et al., 2005; Wang and Rose, 2005; Carroll and Zheng, 2012), whereas both taxa were excluded in preceding study (Jia and Gao, 2019). Our second analysis produced 51 most parsimonious trees (tree length = 319; consistency index = 0.429; retention index = 0.708). The 50% majority consensus tree (Fig. 5B) retains the sister pair of *Beiyanerpeton* + *Qinglongtriton* in the same basal position, but shifts *Chunerpeton* one node crownward to become the sister to the remaining Mesozoic (except *Karaurus*) and all recent salamanders. Once again, *Chunerpeton* is far

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removed from crown Cryptobranchidae. As for the two re-coded taxa, *Iridotriton* remains in an unresolved polytomy with many Chinese Juro-Cretaceous taxa, whereas *Jeholotriton* shifts crownward to become the sister to a clade containing all non-hynobiid crown salamanders.

Because the family-level relations of living salamanders recovered in our first two analyses are inconsistent with molecular results (cf. Fig. 5A, B versus Fig. 6B), we performed a third analysis in which relationships of recent families were constrained by the molecular tree (Pyron and Wiens, 2011, Fig. 6B) and all fossil taxa are set as 'floaters'. That analysis produced 1211 most parsimonious trees and tree length equals to 344. The 50% majority consensus tree (Fig. 6A) recovers a trichotomy consisting of three groupings: *Chunerpeton* alone; a second clade consisting of *Beiyanerpeton*, *Qinglongtriton*, and salamandroids; and a third clade consisting of *Iridotriton*, the remaining Chinese Juro-Cretaceous salamanders, crown Cryptobranchidae, and a paraphyletic Hynobiidae. There are two differences among families compared to the molecular backbone (Fig. 6B). One is that hynobiids (*Onychodactylus*, *Hynobius*, *Pseudobranchus*, and *Liua*) fail to form a clade and the other is a trichotomy occurring between Proteidae (*Necturus* and *Proteus*), Rhyacotritonidae (*Rhyacotriton*) and Plethodontidae (*Desmognathus* and *Plethodon*) + Amphiumidae (*Amphiuma* and *Proamphiuma*). These differences may result from excessive parsimonious trees caused by problematic taxon or taxa.

In order to improve the resolution, we performed a fourth analysis by re-running our third analysis, but this time using the 'Agreement subtree' option, which aims to find the largest subset of taxa and to measure the similarity of these trees (Goloboff et al., 2008). The resultant agreement subtree (Fig. 6C) includes 17 of 19 recent taxa (the hynobiids *Hynobius* and *Onychodactylus* are excluded) and just three of the fossil taxa (*Karaurus*, *Habrosaurus*, and *Valdotriton*) from our previous analyses. The excluded fossil taxa consist of all the Juro-Cretaceous taxa from China (including *Chunerpeton*), the Jurassic *Iridotriton*, and the Late Cretaceous *Proamphiuma*. The agreement subtree (Fig. 6C) recovers an arrangement of families that exactly matches the molecular analysis presented in Fig. 6B, and *Habrosaurus* and *Valdotriton* are as the sister to crown sirenids and crown ambystomatids, respectively.

For our fifth and final analysis, we re-ran our analysis with the same 17 recent and four fossil taxa recovered in our agreement subtree and added *Chunerpeton* (i.e.,

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essentially our third analysis, minus the problematic extant and fossil taxa). This analysis produced just two most parsimonious trees (tree length = 275; consistency index = 0.498; retention index = 0.779) that differ from one another only in the placement of *Valdotriton*, where one recovers *Valdotriton* as a stem salamandroid and the other as the sister to *Ambystoma*. The strict consensus tree (Fig. 7) recovers *Chunerpeton* as a stem-caudate and the sister of all crown salamanders, but there is no synapomorphy to support the clade of *Chunerpeton* + crown salamanders. Two synapomorphies support the "crown salamander" clade and exclude *Chunerpeton* from membership within that clade: anterior process of the maxilla elongated and extensively overlapped by the premaxilla [character 106(0)], and arrow-shaped basibranchial II [character 116(0)]. Cryptobranchidae is supported by nine autapomorphies: anterodorsal fenestra present [character 6(0)]; nasals greatly reduced and narrower than frontals [character 9(1)]; enlarged pterygoid with distinct anteromedial process suturing with the parasphenoid [character 16(1)]; contact between nasal and prefrontal absent [character 23(1)]; basibranchial II absent [character 35(1)]; articulation between pterygoid and parasphenoid present and along the anterior extension of the parasphenoid [character 44(1)]; articulation between parietal and prefrontal present [character 61(1)]; contact between frontal and maxillary present [character 62(1)]; and anteroventral extension absent from ventral border of the orbitosphenoid [character 111(1)]. These nine characters of cryptobranchids are significantly different from *Chunerpeton* (detailed comparison is given above).

To determine whether the nine characters are constant for Cryptobranchidae, more detailed comparisons are warranted between cryptobranchids and other salamanders outside of this data matrix. A small anterodorsal fenestra formed by the premaxillae and nasals [character 6(0)] occurs in cryptobranchids (Fig. 4D, G), as well as in some salamandrids (Jia and Gao, 2019). A pair of small, elongated nasals narrower than frontals [character 9(1)] occurs in cryptobranchids (Fig. 4D, G), as well as in sirenids (Duellman and Trueb, 1994) and some hynobiids (e.g., *Salamandrella*; see Zhou et al., 2017: fig. 1e). However, there are two different cases: nasals articulating each other along the skull midline in cryptobranchids versus nasals separated along the skull midline in sirenids (Duellman and Trueb, 1994). An enlarged pterygoid with a distinct anteromedial process suturing with the

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parasphenoid [character 16(1)] occurs in cryptobranchids (Fig. 4E, H) and is a unique character for cryptobranchids (Gao and Shubin, 2012). No nasal-prefrontal contact [character 23(1)] occurs in cryptobranchids, as well as in some plethodontids (e.g., *Stereochilus marginatum*), some salamandrids (e.g., *Taricha granulosa*), and amphiumids (Duellman and Trueb, 1994). No basibranchial II [character 35(1)] occurs in cryptobranchids because the element disappears at early larval stages (Rose, 2003), as well as in salamandrids (e.g., *Notophthalmus viridescens*) where it is completely resorbed, and in amphiumids where it is never formed (Rose, 2003). A pterygoid-parasphenoid articulation along anterior extension of parasphenoid [character 44(1)] occurs in cryptobranchids (Fig. 4E, H), as well as in amphiumids, proteids, and *Pseudobranchus* (Gao and Shubin, 2012). A parietal-prefrontal articulation [character 61(1)] occurs in cryptobranchids (Fig. 4D, G), as well as in amphiumids and ambystomatids (Gao and Shubin, 2012). A frontal-maxilla contact [character 62(1)] occurs in cryptobranchids (Fig. 4D, G), as well as in some plethodontids (Duellman and Trueb, 1994). Absence of an anteroventral extension of the ventral border of the orbitosphenoid [character 111(1)] occurs in cryptobranchids, as well as in all known fossil taxa and some living hynobiids (Jia and Gao, 2019).

7. Conclusions

In this study, we restudied one of the earliest salamanders *Chunerpeton tianyiense* on the basis of recently collected fossil skeletons from the type locality. We provided currently the most detailed osteological description for the species, recognized a suite of new taxonomically and phylogenetically informative features (e.g., anterodorsal fenestra present and formed by premaxillae, nasals, and frontals; nasals without midline contact; nasal-prefrontal contact present; nasal wider than frontal; lacrimal present and contributing to external naris, but not to orbit; pterygoid triradiate with a slender dentate anteromedial process; single vomerine tooth row parallel to premaxillary and maxillary tooth rows; palatine present; prootic, exoccipital and opisthotic present as separate bones), and provided a revised diagnosis for the species.

We performed five phylogenetic analyses to reassess the phylogenetic position of *Chunerpeton* and, for the first time, we constrained a phylogenetic analysis that includes extinct salamanders by using a molecular backbone. Our results show that

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Chunerpeton is a stem salamander, consistently placed outside of both recent giant salamanders (Cryptobranchidae) and all crown salamanders. Our finding that the Jurassic *Chunerpeton* is not a cryptobranchid has two significant implications: (1) the origin of crown Cryptobranchidae and even Cryptobranchoidea might have occurred later than originally proposed by Gao and Shubin (2003), and (2) it is unsuitable to directly use *Chunerpeton* to calibrate a molecular clock in molecular studies of salamanders.

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Figure captions

Fig. 1. Photographs of a nearly complete skeleton of *Chunerpeton tianyiense* (IVPP V 13343A&B) from the Jurassic of China. (A) Dorsal view of skeleton on slab IVPP V 13343A. (B) Ventral view of skeleton on slab IVPP V 13343B. Abbreviations: fe, femur; fi, fibula; hu, humerus; il; ilium; isc, ischium; ra, radius; sca, scapulocoracoid; sv, sacral vertebra; ti, tibia; ul, ulna. Photograph source credit: Wei Gao.

Fig. 2. Close-up of the skull of *Chunerpeton tianyiense* (IVPP V 13343A&B) from the Jurassic of China (see Fig. 1 for entire specimen). (A, B) Dorsal impressions of skull on slab IVPP V 13343A, photograph (A) and interpretive line drawing (B). (C, D) Ventral impressions of skull on slab IVPP V 13343B, photograph (C) and interpretive line drawing (D). (E) Close-up of palatal region, denoted by red box in

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(C) showing right palatine and portions of adjacent pterygoid and vomer, in ventral view. For interpretive drawings: dark grey shading denotes mandibles, medium grey shading denotes palatal tooth rows, light grey shading denotes skull bones, and dashed lines on frontals indicate correct anatomical positions for the displaced prefrontals. Abbreviations: adf, anterodorsal fenestra; amf, anteromedial fenestra; an, angular; ar, articular; bb II, basibranchial II; d, dentary; exo, exoccipital; fr, frontal; hb I–II, hypobranchial I–II; in. c. f, internal carotid foramen; lac, lacrimal; m, maxilla; n, nasal; opi, opisthotic; pa, parietal; pal, palatine; pm, premaxilla; pra, prearticular; prf, prefrontal; pro, prootic; ps, parasphenoid; pt, pterygoid; qua, quadrate; sq, squamosal; vo, vomer. Photograph source credit: Wei Gao.

Fig. 3. Photographs of referred skeletons of *Chunerpeton tianyiense* from the Jurassic of China. (A) Dorsal impression of skull on slab IVPP V 14226A. (B) Dorsal impression of the otico-occipital region and anterior trunk on slab IVPP V 14745. (C) Ventral views of skull on slab IVPP V 15422. (D) Ventral view of anterior part of vertebrae on slab IVPP V 14058A. (E, F) Dorsal (E) and ventral (F) impressions of articulated maxilla, lacrimal, and prefrontal on slabs IVPP V 14228A and IVPP V 14228B, respectively. (G, H) Impressions of left manus (G) and left pes (H) on slabs IVPP V 11976 and IVPP V 14055, respectively. (I) Lateral view of the tail, also includes posterior trunk vertebrae and sacrum, pelvic girdle, and hindlimbs on slab IVPP V 14054. (J) Close-up of the anterior caudal region, denoted by black box in (I), showing the first three caudal vertebrae bearing ribs, in lateral view. Abbreviations: an, angular; at, atlas; cv 4, the fourth caudal vertebra; exo, exoccipital; fr, frontal; ha, haemal arch; hu, humerus; lac, lacrimal; m, maxilla; n, nasal; na, neural arch; opi, opisthotic; pal, palatine; prf, prefrontal; pt, pterygoid; sca, scapulocoracoid; sq, squamosal; sv, sacral vertebra; vo, vomer. Photograph source credit: Wei Gao.

Fig. 4. Color-coded line drawings of skulls and hyobranchium of *Chunerpeton tianyiense* and representative living cryptobranchids, plus hyobranchium of paedomorphic *Ichthyosaura alpestris*. Images not to scale. (A–C) Reconstruction of *Ch. tianyiense*, dorsal (A) and ventral (B) views of skull and ventral view (C) of hyobranchium. (D–F) *Cryptobranchus alleganiensis*, dorsal (D) and ventral (E) views of skull and ventral view (F) of hyobranchium. (G–I) *Andrias davidianus* (ZFMK

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90469), dorsal (G) and ventral (H) views of skull and ventral view (I) of hyobranchium. (J) *Ichthyosaura alpestris*, ventral view of hyobranchium. Grey shading denotes unossified hyobranchial elements. (D) and (E) are redrawn from Carroll and Holmes (1980), (F) and (I) from Rose (2003), and (J) from Heiss and Grell (2019). Abbreviations: adf, anterodorsal fenestra; ahh, anterior hypohyal; amf, anteromedial fenestra; an, angular; ar, articular; bb, basibranchial; bh, basihyal; bb II, basibranchial II; cb II, ceratobranchial II; ch, ceratohyal; exo, exoccipital; fr, frontal; hb I–II, hypobranchial I–II; hh, hypohyal; hh3, third hypohyal; lac, lacrimal; m, maxilla; n, nasal; opi, opisthotic; opi+exo, fused opisthotic + exoccipital; pa, parietal; pal, palatine; phh, posterior hypohyal; pm, premaxilla; prf, prefrontal; pro, prootic; ps, parasphenoid; pt, pterygoid; qua, quadrate; sq, squamosal; vo, vomer.

Fig. 5. Majority consensus trees showing positions of *Chunerpeton tianyiense* (in green) and crown Cryptobranchidae (in blue). (A) First analysis, generated using modified codings for *Chunerpeton*. (B) Second analysis, generated using modified codings for *Iridotriton* and *Jeholotriton*. See text for details and tree statistics.

Fig. 6. (A) Majority rule consensus tree from third analysis, showing positions of *Chunerpeton tianyiense* (in green) and crown Cryptobranchidae (in blue). (B) Relationships among extant salamander families from Pyron and Wiens (2011), used as a molecular backbone to constrain the third analysis. (C) Agreement subtree from the fourth analysis, showing the largest subset of taxa (14 extant and three fossil) contained within the third analysis. See text for details and tree statistics.

Fig. 7. Strict consensus tree from the fifth phylogenetic analysis, showing *Chunerpeton tianyiense* (in green) as a stem salamander and sister to crown salamanders, the latter consisting of Cryptobranchoidea (in pink) and Salamandroidea (in yellow). See text for details and tree statistics.

Lacustrine deposits of Juro-Cretaceous age in northeastern China have yielded some of the best-preserved fossils of early crown salamanders. One of those taxa, *Chunerpeton tianyiense*, has been considered as a crown or stem member of the family Cryptobranchidae, significant for implying a long evolutionary history for cryptobranchids and for calibrating the molecular clock of Caudata evolution.

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Building on the most recent large-scale phylogenetic analysis of relationships among fossil and recent salamanders and utilizing new specimens of *Chunerpeton*, we update the osteological description and diagnosis for *Chunerpeton* and reconsider its phylogenetic relationships. On the basis of recently collected *Chunerpeton* skeletons from the type locality at Daohugou, Inner Mongolia, China and available literature, we update the taxon-character matrix and run phylogenetic analyses with constraints on the relationships among families using a molecular backbone. We redescribe the osteology of *Chunerpeton*, revise and identify some new characters including large anterodorsal fenestra bordered by paired premaxillae, nasals, and frontals; nasals separate and wider than frontal; contact between nasal and prefrontal present; lacrimal present; and contact between pterygoid and parasphenoid absent. Osteological comparisons between *Chunerpeton* and living cryptobranchids reveal a suite of distinct differences in snout shape and in configurations, positions, and contacts of certain skull bones. Our phylogenetic analyses consistently place *Chunerpeton* as a stem Caudata outside of Cryptobranchidae and crown salamanders. Exclusion of *Chunerpeton* from Cryptobranchidae will require reconsideration of the origin time for Cryptobranchidae and recalibration of the molecular clock for the whole caudatan tree.

Section 1. Characters used in the phylogenetic analysis. 1–105 are taken from Gao and Shubin (2012), 106–120 from Jia and Gao (2019).

1. Premaxillae (Gao and Shubin, 2012: character 1): separate (0); fused (1).

2. Dorsal process of premaxilla (Gao and Shubin, 2012: character 2): simply contacting or overlapping nasal bone (0); strong posterior extension overlapping frontal and separating nasals (1); posterior extension deeply intervening between frontals (2); posterior extension contacting frontal lateral to nasal (3).

3. Maxilla (Gao and Shubin, 2012: character 3): present in adults as a normal element of maxillary arcade (0); reduced to a rudimentary element or entirely lost and functionally replaced by a modified vomer (1).

4. Maxillary tooth row (Gao and Shubin, 2012: character 4): extending close to the posterior extremity of maxilla (0); terminating far anterior to the posterior extremity (1).

5. Septomaxilla (Gao and Shubin, 2012: character 5): present (0); 1 absent (1).

6. Anterodorsal fenestra (Gao and Shubin, 2012: character 6): present (0); absent (1).

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7. Anteromedial fenestra (= anterior palatal fenestra) between vomers (Gao and Shubin, 2012: character 7): fenestra open (0); fenestra closed by vomers or other palatal elements (1).

8. Nasal ossification (Gao and Shubin, 2012: character 8): present with midline contact (0); separate without midline contact (1); nasal absent (2).

9. Lateral expansion of nasals (Gao and Shubin, 2012: character 9): same width or slightly wider than frontals (0); nasals greatly reduced and narrower than frontals (1).

10. Lacrimal (Gao and Shubin, 2012: character 10): present (0); absent (1).

11. Quadratojugal (Gao and Shubin, 2012: character 11): present (0); absent (1).

12. Prootic/exoccipital/opisthotic complex (Gao and Shubin, 2012: character 12): three elements separate (0); exoccipital/opisthotic fused with free prootic (1); opisthotic/prootic fused with separate exoccipital (2); three elements fused into otic-occipital complex (3).

13. Posterior process of vomer (Gao and Shubin, 2012: character 13): poorly defined or absent (0); well-defined process contacting anterior part of parasphenoid or pterygoid (1); greatly elongated process extending along lateral border of parasphenoid (2).

14. Posterolateral border of vomer (Gao and Shubin, 2012: character 14): not notched (0); slightly concave for choana (1); deeply notched and almost embracing choana (2).

15. Ossification of pterygoid (Gao and Shubin, 2012: character 15): present (0); absent (1).

16. Shape of pterygoid (Gao and Shubin, 2012: character 16): triradiate and boomerang-shaped (0); enlarged with distinct anteromedial process suturing with parasphenoid (1); simple straight bar-shaped (2).

17. Vomer/pterygoid contact (Gao and Shubin, 2012: character 17): absent (0); present (1).

18. Pterygoid/maxillary contact (Gao and Shubin, 2012: character 18): absent (0); present (1).

19. Palatine in adult (Gao and Shubin, 2012: character 19): present as discrete element (0); absent by loss or fusion in adult (1).

20. Anterior extension of parasphenoid between premaxillae (Gao and Shubin, 2012: character 20): absent (0); present (1).

21. Internal carotid foramen penetrating parasphenoid (Gao and Shubin, 2012: character 21): present (0); absent (1).

22. Prefrontal (Gao and Shubin, 2012: character 22): present (0); absent (1).

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23. Nasal/prefrontal contact (Gao and Shubin, 2012: character 23): present (0); absent (1).

24. Prefrontal/maxillary contact (Gao and Shubin, 2012: character 24): present (0); absent (1).

25. Basilaris complex of inner ear (Gao and Shubin, 2012: character 25): presence of both recessus basilaris (0); loss of entire basilaris complex (1).

26. Angular/prearticular fusion (Gao and Shubin, 2012: character 26): angular present as a separate element (0); angular fused to prearticular (1).

27. Coronoid (Gao and Shubin, 2012: character 27): present in adult stage as a separate element (0); absent in adult stage (1).

28. Coronoid teeth in adult (Gao and Shubin, 2012: character 28): absent (0); present (1).

29. Articular (Gao and Shubin, 2012: character 29): present as separate element (0); absent by fusion with prearticular (1).

30. Dentary teeth (Gao and Shubin, 2012: character 30): present (0); absent (1).

31. Sharp deflection of posterior part of dentary (Gao and Shubin, 2012: character 31): absent (0); present (1).

32. Hypobranchial I and ceratobranchial I (Gao and Shubin, 2012: character 32): two elements remain separate (0); two elements fused (1).

33. Ossification of hypobranchial I (Gao and Shubin, 2012: character 33): present (0); absent (1).

34. Ceratobranchial II in adults (Gao and Shubin, 2012: character 34): present (0); absent (1).

35. Basibranchial II (Gao and Shubin, 2012: character 35): present as ossified or cartilaginous (0); absent (1).

36. Premaxillary teeth (Gao and Shubin, 2012: character 36): present (0); absent, replaced by horny beaks (1).

37. Vomerine teeth (Gao and Shubin, 2012: character 37): forming simple anterior arcade parallel to maxillary tooth row (0); forming simple tooth row or patch close to vomerine-parasphenoid suture (1); curved longitudinal tooth row extending to the base of parasphenoid (2); forming complex tooth batteries covering entire surface of the bone (3).

38. Multiple and parallel rows of palatine teeth in adult (Gao and Shubin, 2012: character 38): absent (0); present (1).

39. Pterygoid teeth (Gao and Shubin, 2012: character 39): absent (0); present (1).

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40. Parasphenoid tooth shagreen (Gao and Shubin, 2012: character 40): absent (0); present (1).

41. Marginal teeth (Gao and Shubin, 2012: character 41): nonpedicellate (0); pedicellate (1).

42. Tooth crown (Gao and Shubin, 2012: character 42): monocuspid (0); bicuspid (1).

43. Orbitosphenoid (= sphenethmoid) as a discrete bone (Gao and Shubin, 2012: character 43): present (0); absent (1).

44. Parasphenoid/pterygoid contact (Gao and Shubin, 2012: character 44): contact at the base of parasphenoid (0); contact along anterior extension of parasphenoid (1); contact absent (2).

45. Y-shaped dorsal crest in trunk vertebrae (Gao and Shubin, 2012: character 45): absent (0); present (1).

46. Vertebral centrum (Gao and Shubin, 2012: character 46): amphicoelous (0); opisthocoelous (1).

47. Tuberculum interglenoideum of atlas (Gao and Shubin, 2012: character 47): absent (0); present (1).

48. Head of postatlantal ribs (Gao and Shubin, 2012: character 48): bicapitate (0); unicapitate (1).

49. Postatlantal ribs in association with vertebrae (Gao and Shubin, 2012: character 49): ribs present in association with all trunk and sacral vertebrae (0); ribs only present in association with no more than eight anterior trunk vertebrae (1).

50. Atlantal spinal nerve foramen (Gao and Shubin, 2012: character 50): absent (0); present (1).

51. Postatlantal spinal nerve foramina (Gao and Shubin, 2012: character 51): all postatlantal spinal nerves exit intervertebrally (0); spinal nerve foramina present on posterior caudal vertebrae (1); foramina present on all caudal vertebrae (2); foramina occur in trunk, sacral and caudal series (3).

52. Ossified stapes (Gao and Shubin, 2012: character 52): present in adults (0); absent in adults (1).

53. Operculum (Gao and Shubin, 2012: character 53): ossified and free (0); free operculum absent (1).

54. Lateral wall of nasal capsule (Gao and Shubin, 2012: character 54): complete (0); incomplete (1).

55. Lateral narial fenestra (Gao and Shubin, 2012: character 55): absent (0); present (1).

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56. Posterior wall of nasal capsule (Gao and Shubin, 2012: character 56): complete (0); incomplete (1).

57. Nasolacrimal duct (Gao and Shubin, 2012: character 57): present (0); absent (1).

58. Sculptured dermal skull roof (Gao and Shubin, 2012: character 58): present as heavily sculptured surface covering (0); weakly sculptured or absent (1).

59. Frontal anterior extension (Gao and Shubin, 2012: character 59): frontal does not extend lateral to nasal bone (0); frontal does extend to lateral border of nasal (1).

60. Anterolateral process of parietal (Gao and Shubin, 2012: character 60): poorly defined or absent (0); well-developed process extending to or surpassing midlevel of orbit (1).

61. Parietal/prefrontal contact above orbit (Gao and Shubin, 2012: character 61): contact absent (0); contact present to embrace frontals (1).

62. Frontal/maxillary contact (Gao and Shubin, 2012: character 62): absent (0); present (1).

63. Squamosal orientation in dorsal view (Gao and Shubin, 2012: character 63): squamosal present as simple transverse bar (0); squamosal strongly slanting anteriorly or parallel to skull midline (1).

64. Exposure of otic-occipital complex in dorsolateral view (Gao and Shubin, 2012: character 64): otic-occipital complex largely concealed by parietal (0); mainly exposed posterior to parietal (1); large exposure extends lateral to parietal bone (2).

65. Midline contact of otic-occipital complex over foramen magnum (Gao and Shubin, 2012: character 65): contact absent (0); contact present (1).

66. Medial contact of squamosal with parietal or other roofing element (Gao and Shubin, 2012: character 66): contact present (0); contact absent (1).

67. Origin of muscle adductor mandibulae internus superficialis (Gao and Shubin, 2012: character 67): on dorsolateral surface of parietal (0); origin on side of skull (1); origin extends to exoccipital or to cervical vertebra (2).

68. Ypsiloid cartilage (Gao and Shubin, 2012: character 68): present (0); absent (1).

69. Dorsal and ventral crests of humerus (modified from Gao and Shubin, 2012: character 69): absent (0); present (1).

70. Radial and ulnar condyles of humerus (Gao and Shubin, 2012: character 70): not well separated from one another (0); well-defined condyles separate from one another (1).

71. Femoral trochanter forming a twig-like projection (Gao and Shubin, 2012: character 71): absent (0); well developed as a twig-like process branching off from shaft (1).

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72. Fusion of distal carpal 1+2 into a single basale commune in the carpus (Gao and Shubin, 2012: character 72): fusion absent (0); fusion present (1).

73. Fusion of distal tarsal 1+2 into a basale commune in the tarsus (Gao and Shubin, 2012: character 73): fusion absent (0); fusion present (1).

74. Number of centralia in manus and pes (Gao and Shubin, 2012: character 74): more than one central element (0); one central element (1); no central element (2).

75. Intermedium and ulnare (Gao and Shubin, 2012: character 75): separate intermedium (0); fused to ulnare (1).

76. Distal carpal 4 and distal carpal 5 (Gao and Shubin, 2012: character 76): two elements remain separate (0); two elements fused (1).

77. Haploid chromosome number (Gao and Shubin, 2012: character 77): ranging from 20 to 32 (0); reduced to 19 (1); further reduced to 14 or less (2).

78. Diploid chromosome number (Gao and Shubin, 2012: character 78): 56 or more (0); 40–55 (1); less than 40 (2).

79. Microchromosome (Gao and Shubin, 2012: character 79): present (0); absent (1).

80. Ciliated epithelium of cloaca (Gao and Shubin, 2012: character 80): present in both sexes (0); present in male but absent in female (1); absent in both sexes (2).

81. Extent of epidermis in female cloacal chamber (Gao and Shubin, 2012: character 81): epidermal lining does not extend to anterior one-half of the cloacal chamber (0); does extend into anterior one-half of the chamber (1).

82. Primary and secondary folds in male cloacal tube and associated glands (Gao and Shubin, 2012: character 82): both primary and secondary folds absent (0); both folds present (1).

83. Anteroventral cloacal glands (Gao and Shubin, 2012: character 83): absent in both sexes (0); present in male but not in female (1); present in both sexes (2).

84. Spermathecae in cloaca (Gao and Shubin, 2012: character 84): absent (0); present (1).

85. Dorsal cloacal glands (Gao and Shubin, 2012: character 85): absent in both sexes (0); present in male only (1); present in both sexes (2).

86. Posteroventral cloacal glands (Gao and Shubin, 2012: character 86): absent (0); present (1).

87. Kingsbury's glands and dorsal pelvic glands in male cloaca (Gao and Shubin, 2012: character 87): both Kingsbury's and dorsal pelvic glands absent (0); both groups of glands present (1).

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88. Lateral pelvic glands in male cloaca (Gao and Shubin, 2012: character 88): absent (0); present (1).

89. Pubotibialis and puboischiotibialis muscles (Gao and Shubin, 2012: character 89): separate (0); fused (1).

90. Kidney (Gao and Shubin, 2012: character 90): glomeruli normally well developed (0); anterior glomeruli reduced or absent (1).

91. Number of free ribs on anterior caudal vertebrae (Gao and Shubin, 2012: character 91): more than three pairs (0); two to three pairs (1); free ribs absent (2).

92. Ectopterygoid (modified from Gao and Shubin, 2012: character 92): present (0); absent (1).

93. Postfrontal (modified from Gao and Shubin, 2012: character 93): present (0); absent (1).

94 Scapula-coracoid ossification (Gao and Shubin, 2012: character 94): ossified as separate elements (0); co-ossified as a single element (1).

95. Movable eyelids (modified from Gao and Shubin, 2012: character 95): absent (0); present (1).

96. Nasolabial groove (modified from Gao and Shubin, 2012: character 96): absent (0); present (1).

97. Mode of fertilization (Gao and Shubin, 2012: character 97): external fertilization (0); internal fertilization (1).

98. Lungs (Gao and Shubin, 2012: character 98): normally developed (0); reduced (1); entirely lost (2).

99. Number of presacral vertebrae (Gao and Shubin, 2012: character 99): ranging from 14–30 (0); exceeding 30 (1).

100. Pattern of vertebral development (Gao and Shubin, 2012: character 100): neural arch developed before centrum (0); centrum developed before neural arch (1).

101. Quadrate (Gao and Shubin, 2012: character 101): present (0); absent (1).

102. Frontosquamosal arch (Gao and Shubin, 2012: character 102): absent (0); present (1).

103. Maxillary arcade (Gao and Shubin, 2012: character 103): incomplete (0); complete (1).

104. Columellar process of squamosal (Gao and Shubin, 2012: character 104): absent (0); present (1).

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105. Facial nerve in relation to ligamentum squamoso-columellare (Gao and Shubin, 2012: character 105): facial nerve passes below columellar-squamosal connection (0); facial nerve passes above columellar-squamosal connection (1).

106. Anterior process of the maxilla (Jia and Gao, 2019: character 106): elongated and extensively overlap the premaxilla (0); rudimentary or absent, and has an abutting joint with the premaxilla (1).

107. Anterodorsal fenestra's involvement with adjacent bones (Jia and Gao, 2019: character 107): anterodorsal fenestra is (0) bordered by the premaxilla and nasal; (1) by the premaxilla, nasal and frontal; (2) by the premaxilla and frontal; (3) enclosed within the fused/separated partes dorsalis of the premaxillae.

108. Lacrimal's involvement with naris and orbit: lacrimal (0) enters naris only; (1) enters orbit only; (2) enters neither naris nor orbit; (3) enters both naris and orbit.

109. Position of the trochlear foramen (Jia and Gao, 2019: character 109): penetrates the parietal (0); penetrates the orbitosphenoid (1).

110. Ossification of the ascending process of the palatoquadrate (Jia and Gao, 2019: character 110): absent (0); present (1).

111. Anteroventral extension of the orbitosphenoid on the ventral border (Jia and Gao, 2019: character 111): present (0); absent (1).

112. Position of the optic foramen (Jia and Gao, 2019: character 112): opens at the posterior border of the orbitosphenoid (0); opens within the orbitosphenoid (1).

113. Position of the oculomotor foramen (Jia and Gao, 2019: character 113): opens at the posterior border of the orbitosphenoid (0); opens within the orbitosphenoid (1); penetrates the cartilaginous plate posterior to the orbitosphenoid (2).

114. Stapedial foramen at the base of the stylus of the stapes (Jia and Gao, 2019: character 114): (0) present; (1) absent.

115. Dentary groove on the labial aspect of the dentary (Jia and Gao, 2019: character 115): (0) present; (1) absent.

116. Basibranchial II shape (modified from Jia and Gao, 2019: character 116): (0) arrow shaped; (1) non-arrow shaped.

Comments: Replace "arrow-shape/non-arrow shaped" by "anchor-shaped/non-anchor shaped" to distinguish true anchor-shaped basibranchial II present in *Nuominerpeton aquilonare* (Jia and Gao, 2016, p. 12, text-fig. 5).

117. Ceratohyal ossification (Jia and Gao, 2019: character 117): absent (0); present (1).

118. Distal tarsal 4 and 5 (Jia and Gao, 2019: character 118): separate (0); fused (1).

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119. Frontoparietal fontanelle (Jia and Gao, 2019: character 119): absent (0); present (1).

120. Number of toes (Jia and Gao, 2019: character 120): five (0); four or less (1).

Journal Pre-proofs

Journal Pre-proofs

Section 2. Character-taxon matrix used in this study. The modified characters of the original set of characters are highlighted in bold. Explanations to those changes with indication of their original states are given in Section 3 below. "?" denotes non-preservation and "{}" means one character contains multiple character states.

Karaurus

000?? 00000 0?000 000?0 0000? 0??10 00000 00??0 ???00 01000 ?0??? ??000 0000? 00?00 0???? ????? ????? ????? 0111? ???0? ?00?? 000?0 ???0? 00?00

Cryptobranchus

00001 11011 11110 10010 00100 01?10 0{01}101 00?00 11010 01101 00100 01111 11010 02000 01100 {01}0000 00200 00011 11110 00001 00000 1??00 11111 ?1{01}00

Andrias

00001 11011 11110 10010 00100 01?10 01101 00?00 11010 01101 00100 01111 11010 02000 011{01}0 10000 00200 00011 11110 00001 0000? 1??00 11111 ?0000

Hynobius

000{01}0 {01}0000 11{01}10 00010 {01}00{01}0 01?00 0110{01} 0{12}?00 11000 01101 00000 0010{01} 0001{01} {01}2011 011{01}1 00000 ?0200 00011 11111 00000 0000? 1?{13}?1 00211 10000

Onychodactylus

00000 00000 11110 00010 000{01}0 01?00 0{01}101 01?00 11000 01101 00100 00100 00011 12011 01110 10000 ?0200 00011 11111 0020? 0000? 10000 10211 ?1000

Plethodon

{01}1000 00101 13121 ???10 10001 11?10 00110 01??1 110?0 11001 30111 00100 00{01}21 1211? ?1110 12211 10212 11101 21111 11201 000?0 13??0 ?1011 11100

Desmognathus

11000 00101 13121 ???10 11??1 11?10 00110 01??1 110?0 11001 30111 00100 01021 1211? ?1110 ?2211 102{01}2 11101 21111 11201 000?0 13??0 ?1211 1?000

Amphiuma

12001 11101 13100 20010 10000 11?10 01001 00?00 11010 01011 10110 11{01}01 10121 02100 0112{01} 12210 {01}0111 01001 21110 01011 000?0 1???0 ?1010 ?1?01

Proamphiuma

Journal Pre-proofs

????? ????? ????? ????? ????? ????? ????? ????? ????0 010?1 1???? ????? ?????
????? ????? ????? ????? ????? 2???? ????? ????? ????0 ????? ???0?

Rhyacotriton

01000 00100 11120 00010 00010 11?00 00110 01?00 11020 01001 20111 00101
0002{01} 12100 01111 02211 11111 11101 21111 01101 000?? 13310 00211 11000

Siren

031?1 01111 12000 20001 11??1 101{01}1 10000 13100 00021 01011 30110 11111
?0121 11100 ?1?11 12112 10000 000?0 21100 00011 10000 1???0 ?11?0 11?01

Pseudobranchus

031?1 01111 12000 20001 11??1 10111 10000 13100 10011 01011 31110 11111
?0111 11100 ?1?11 12112 10000 000?0 21100 00011 100?? ????0 ?11?0 1??01

Habrosaurus

0?0?? ????? ??00? ???0? ????? ????0 1???? 001?? 00??1 01??1 3???? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? 1???0 ????0 ?????

Necturus

011?1 102?1 10100 21010 11??1 10110 00100 01?10 10110 01001 00110 111?1
??120 02100 01121 ?1211 10211 11101 21110 01001 00011 ????0 ????1 ?0?01

Proteus

011?1 102?1 10100 21010 11??1 10110 00000 0??10 00110 01001 00110 111?1
??110 02100 01121 ?1211 10211 11101 21110 01011 00011 ????0 ????1 ?1?01

Salamandra

01011 00101 13220 01010 10000 11?00 01110 02?00 11020 11001 31011 00100
00021 12011 11111 12210 00211 11001 21111 01001 000?0 1{13}??0 1{01}0?{01}
10000

Taricha

11011 00101 13210 01010 10000 11?00 00011 02?00 11020 11001 31011 00100
00121 12011 11111 12210 00211 11001 21111 01001 010?? 11??0 011?1 11100

Tylototriton

00011 00001 13210 01{01}10 10000 11?00 00011 02?00 11020 11001 31011 00000
00111 02011 11101 12210 00211 01001 21111 01001 011?? 11??0 ????1 ?1100

Dicamptodon

Journal Pre-proofs

01000 00100 13{01}{02}0 0{01}010 00000 10010 00{01}10 0{01}?{01}0 11000 01001 20011 00101 00021 12011 01110 02210 01211 11101 21111 01001 0000? 130?0 ?1011 11000

Ambystoma

01000 10101 13020 00010 {01}0000 11?{01}0 00110 00?00 11020 01001 30011 00101 10021 12000 01110 02210 01212 11101 2111{01} 01001 000?0 1??00 00211 10000

Valdotriton

0000? 11001 1?000 0??10 100?? 11?10 0?110 00?00 1?020 01001 20??? ??101 ?0021 1??1? 0???? ????? ????? ????? 2111? ???0? ?00?? ????0 ???11 10?00

Jeholotriton

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L. zhongjiani

0000?0 000?1 01100 00101 000?0 1?000 000?0 0?001 ?0000 ?10?? 0???? ?1000 00??0 ??1?0 1100? ????? ????? ????1 111?? ??0?0 000?0 0???? 02??? 0?00

Pangerpeton

000?? 00000 102?0 00010 000?? 01??0 000?0 01?00 110?0 01101 ????? ??100 00011 ???01 1???? ????? ????? ????? 1111? ???0? 000?? 00??1 110?? ???00

Chunerpeton

0000? 00**100** 10000 000?0 00**0**0? 01?00 000?0 00?**1**0 **1012**0 0?10? ?**1**??? ??111 0001**0** 0??00 0???? ????? ????? ????? 1111? ???0? 000**0**? 0**10**?0 ????? 00?00

Beiyanerpeton

00000 00100 10000 00000 1001? 11?10 0?0?0 00010 00000 0?001 ?00?? ??101 1000? 0??00 0???? ????? ????? ????? 1111? 0??0? 0000? 110?0 ???00 00?00

Iridotriton

000?? ?0**1**?? 1**3010 0**??**10 1**0**00**? 01??0 **0**???**0** 0??**00** 1?**0**?0 0?10**1 10**??? ??1**0**0 ?**02**?? **1**??11 **11111** ????? ????? ????? **111**1? ???0? 0**000**? 0???? ????? ?????

Qinglongtriton

00000 00100 10010 00000 0000? 10110 000?0 00010 10100 01001 301?? ?0101 00001 0??00 0???? ????? ????? ????? 1111? 0??0? 0000? 110?0 ???00 10?00

Linglongtriton

Journal Pre-proofs

00000 00100 10110 00010 0000? 01?10 0?100 01?00 110?0 01101 001?? ?0100 00011 0??11 11110 ????? ????? ????? 1111? ???0? 0000? 01000 10210 001?0

Liua

00000 00000 11110 00010 00000 01?{01}0 01100 01?00 11020 01101 001?? ?0100 00011 02011 111{01}0 10000 ?0200 00011 11111 00001 0000? 10000 00211 11000

Pseudohynobius

00000 00100 11110 00010 00000 01?10 01100 01?00 11020 01101 001?? ?0100 00011 02011 111{01}0 10000 ?0200 00011 11111 00001 0000? 1230{01} 00211 10010

Nuominerpeton

00000 00000 11110 00010 0000? 01?00 0?100 01?00 11000 01101 001?? ?0100 00011 0??11 11100 ????? ????? ????? 1111? ???0? 0000? 001?0 10211 00000

Regalerpeton

0000? 00000 11100 00010 0000? ?1??0 000?0 01?10 00020 0110? ?01?? ??100 00011 0??1? ?11{01}0 ????? ????? ????? 1111? ???0? 0000? 00??0 ?0??? 10010

L. daohugouense

0?0?? 00??0 1?110 0?010 ?0??? ?1?00 ??100 01?00 ??0?? 0110? ????? ??1?? ????? ????? ?11?? ????? ????? ????? 1111? ???0? ?00?? ????? ?02?? 00??0

Journal Pre-proofs

Journal Pre-proofs

Section 3. The specific modified character states of *Chunerpeton*, *Jeholotriton* and *Iridotriton* are listed below (character number: previous character state→new character state (**in bold**)). The characters of *Chunerpeton* have been modified based on own observations (this paper), *Jeholotriton* on earlier publications of Wang and Rose (2005) and Carroll and Zheng (2012), *Iridotriton* on earlier publication of Evans et al. (2005).

Chunerpeton

Ch. 8: 0→**1**; Ch. 9: 1→**0**; Ch. 10: 1→**0**; Ch. 23: 1→**0**; Ch. 39: 0→**1**; Ch. 41: ?→**1**; Ch. 42: ?→**0**; Ch. 43: 0→**1**; Ch. 44: ?→**2**; Ch. 52: 0→**1**; Ch. 65: 1→**0**; Ch. 104: ?→**0**; Ch. 107: 0→**1**; Ch. 108: ?→**0**.

Explanations for character changes of *Chunerpeton*.

Ch. 8: Modify original description “nasal ossification present with midline contact (0)” to be “nasal ossification present without midline contact (1)”.

Ch. 9: Modify original description “nasals greatly reduced and narrower than frontals (1)” to be “nasal wider than frontals (0)”.

Ch. 10: Modify original description “lacrimal absent (1)” to be “lacrimal present (0)”.

Ch. 23: Modify original description “nasal/prefrontal contact absent (1)” to be “nasal/prefrontal contact present (0)”.

Ch. 39: Modify original description “pterygoid teeth absent (0)” to be “pterygoid teeth present (0)”.

Ch. 41: Coding “?” to be “marginal teeth pedicellate (1)”.

Ch. 42: Coding “?” to be “tooth crown monocuspid (0)”.

Ch. 43: Modify original description “orbitosphenoid present (0)” to be “orbitosphenoid absent (1)”.

Ch. 44: Coding “?” to be “parasphenoid/pterygoid contact absent (2)”.

Ch. 52: Modify original description “stapes present (0)” to be “stapes absent (1)”.

Ch. 65: Modify original description “midline contact of otic-occipital complex present (1)” to be “midline contact of otic-occipital complex absent (0)”.

Ch. 104: Coding “?” to be “columellar process of squamosal absent (0)”.

Ch. 107: Modify “anterodorsal fenestra formed by premaxilla and nasal (0)” to be “anterodorsal fenestra formed by premaxilla, nasal and frontal (1)”.

Ch. 108: Coding “?” to be “lacrimal involvement with naris (0)”.

Journal Pre-proofs

Jeholotriton

Ch. 4: ?→**0**; Ch. 12: ?→**3**; Ch. 19: ?→**1**; Ch. 21: ?→**0**; Ch. 33: ?→**1**; Ch. 34: ?→**1**; Ch. 37: ?→**3**; Ch. 39: ?→**0**; Ch. 43: ?→**1**; Ch. 47: ?→**1**; Ch. 57: ?→**0**; Ch. 61: 0→**?**; Ch. 104: ?→**0**.

Explanations for character changes of *Jeholotriton*.

Ch. 4: Coding "?" to be "maxillary tooth row extending close to the posterior extremity of maxilla (0)".

Ch. 12: Coding "?" to be "prootic/exoccipital/opisthotic fused into otic-occipital complex (3)".

Ch. 19: Coding "?" to be "palatine absent (1)".

Ch. 21: Coding "?" to be "internal carotid foramen penetrating parasphenoid present (0)".

Ch. 33: Coding "?" to be "ossification of hypobranchial I absent (1)".

Ch. 34: Coding "?" to be "ceratobranchial II absent (1)".

Ch. 37: Coding "?" to be "vomerine teeth forming complex tooth batteries covering entire surface of the bone (3)".

Ch. 39: Coding "?" to be "pterygoid teeth absent (0)".

Ch. 43: Coding "?" to be "orbitosphenoid absent (1)"

Ch. 47: Coding "?" to be "tuberculum interglenoideum of atlas present (1)".

Ch. 57: Coding "?" to be "nasolacrimal duct present (0)".

Ch. 61: Modify "parietal/prefrontal contact above orbit absent (0)" to be "?".

Ch. 104: Coding "?" to be "columellar process of squamosal absent (0)".

Iridotriton

Ch. 8: ?→**1**; Ch. 12: ?→**3**; Ch. 13: ?→**0**; Ch. 14: ?→**1**; Ch. 15: ?→**0**; Ch. 16: ?→**0**; Ch. 19: ?→**1**; Ch. 20: ?→**0**; Ch. 21: ?→**1**; Ch. 23: ?→**0**; Ch. 24: ?→**0**; Ch. 31: ?→**0**; Ch. 35: ?→**0**; Ch. 39: ?→**0**; Ch. 40: ?→**0**; Ch. 43: ?→**0**; Ch. 50: ?→**1**; Ch. 51: ?→**1**; Ch. 52: ?→**0**; Ch. 59: ?→**0**; Ch. 62: ?→**0**; Ch. 63: ?→**2**; Ch. 66: ?→**1**; Ch. 71: ?→**1**; Ch. 72: ?→**1**; Ch. 73: ?→**1**; Ch. 74: ?→**1**; Ch. 75: ?→**1**; Ch. 91: ?→**1**; Ch. 92: ?→**1**; Ch. 93: ?→**1**; Ch. 102: ?→**0**; Ch. 103: ?→**0**; Ch. 104: ?→**0**.

Explanations for character changes of *Iridotriton*.

Ch. 8: Coding "?" to be "nasal separate without midline contact (1)".

Journal Pre-proofs

Ch. 12: Coding "?" to be "prootic/exoccipital/opisthotic fused into otic-occipital complex (3)".

Ch. 13: Coding "?" to be "posterior process of vomer poorly defined or absent (0)"

Ch. 14: Coding "?" to be "posterolateral border of vomer with slightly concave for choana (1)"

Ch. 15: Coding "?" to be "pterygoid present (0)".

Ch. 16: Coding "?" to be "pterygoid triradiate and boomerang-shaped (0)"

Ch. 19: Coding "?" to be "palatine absent (1)".

Ch. 20: Coding "?" to be "anterior extension of parasphenoid between premaxillae absent (0)".

Ch. 21: Coding "?" to be "internal carotid foramen penetrating parasphenoid absent (1)."

Ch. 23: Coding "?" to be "nasal/prefrontal contact present (0)".

Ch. 24: Coding "?" to be "prefrontal/maxillary contact present (0)".

Ch. 31: Coding "?" to be "sharp deflection of posterior part of dentary absent (0)".

Ch. 39: Coding "?" to be "pterygoid teeth absent (0)".

Ch. 40: Coding "?" to be "parasphenoid tooth shagreen absent (0)".

Ch. 43: Coding "?" to be "orbitosphenoid present (0)".

Ch. 50: Coding "?" to be "atlantal spinal nerve foramen present (1)".

Ch. 51: Coding "?" to be "spinal nerve foramina present on posterior caudal vertebrae (1)".

Ch. 52: Coding "?" to be "stapes present (0)".

Ch. 59: Coding "?" to be "frontal does not extend lateral to nasal bone (0)".

Ch. 62: Coding "?" to be "frontal/maxillary contact absent (0)".

Ch. 63: Coding "?" to be "squamosal strongly slanting anteriorly (1)".

Ch. 66: Coding "?" to be "squamosal/parietal contact absent (1)".

Ch. 71: Coding "?" to be "femoral trochanter well developed as a twig-like process branching off from shaft (1)".

Ch. 72: Coding "?" to be "fusion of distal carpal 1+2 into a single basale commune (1)".

Ch. 73: Coding "?" to be "fusion of distal tarsal 1+2 into a single basale commune (1)".

Journal Pre-proofs

Ch. 74: Coding "?" to be "one centralia in manus and pes (1)".

Ch. 75: Coding "?" to be "intermedium and ulnare fused to ulnare (1)".

Ch. 91: Coding "?" to be "three pairs free ribs on anterior caudal vertebrae (1)".

Ch. 92: Coding "?" to be "ectopterygoid absent (1)".

Ch. 93: Coding "?" to be "postfrontal absent (1)"

Ch. 102: Coding "?" to be "frontosquamosal arch absent (0)".

Ch. 103: Coding "?" to be "maxillary arcade incomplete (0)".

Ch. 104: Coding "?" to be "columellar process of squamosal absent (0)".

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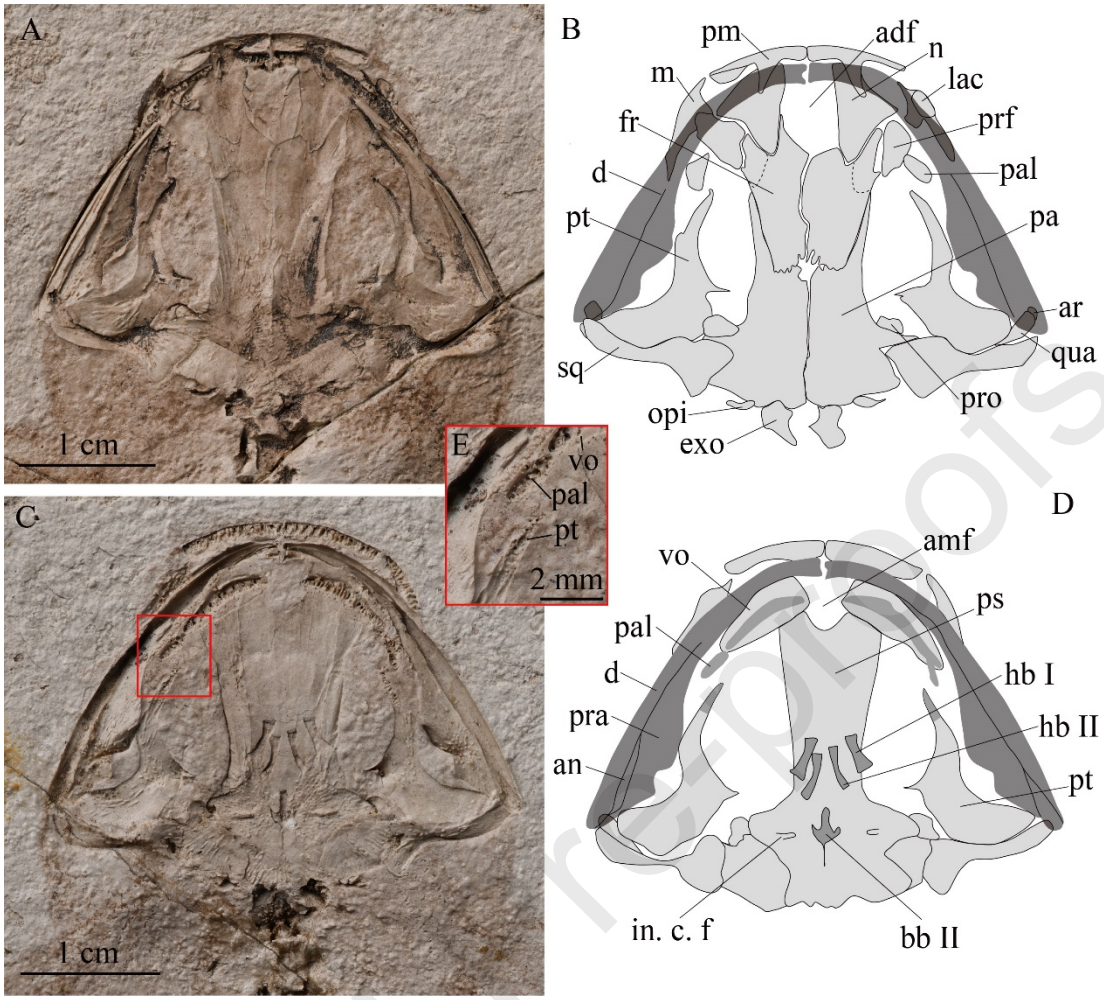

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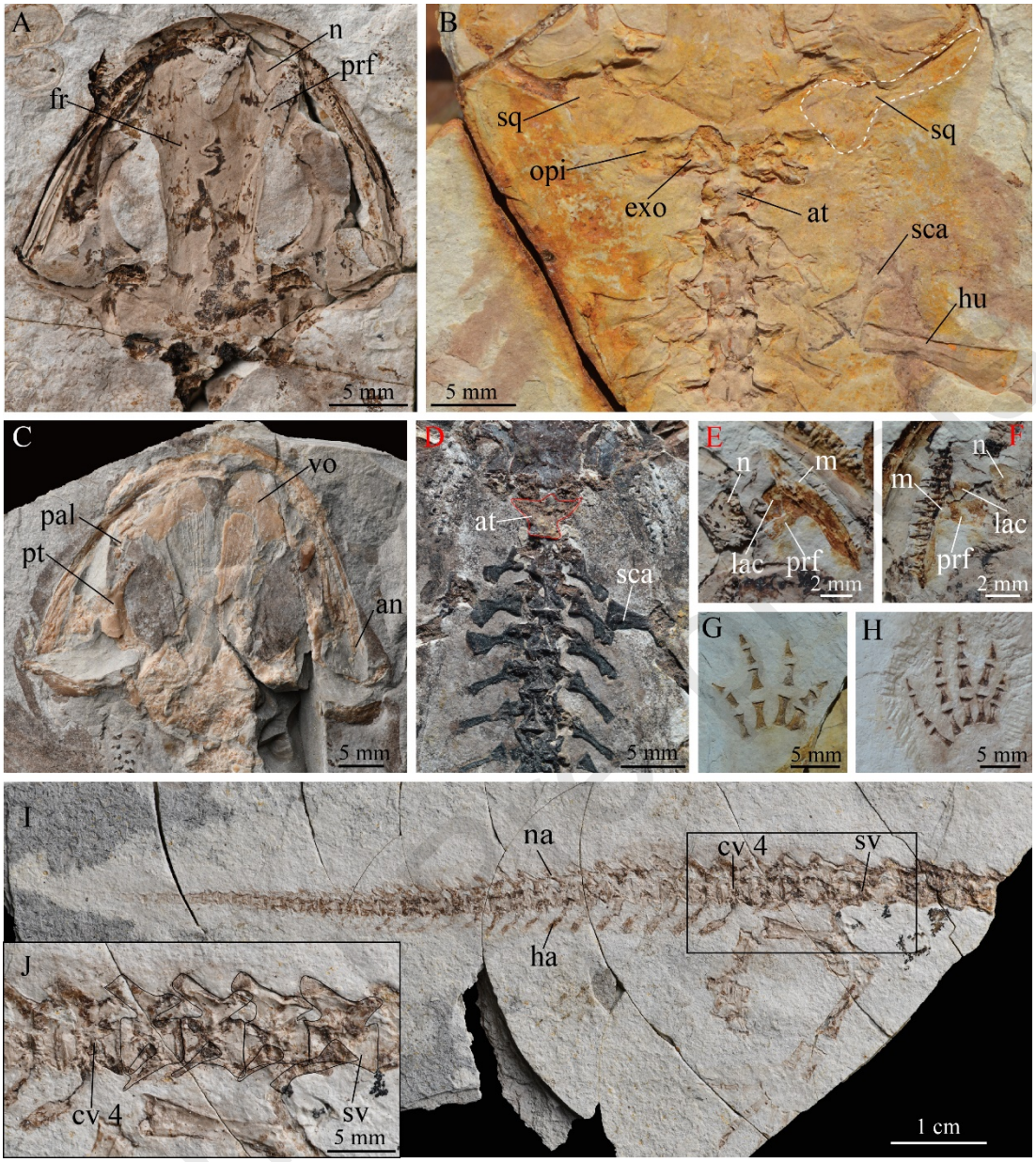
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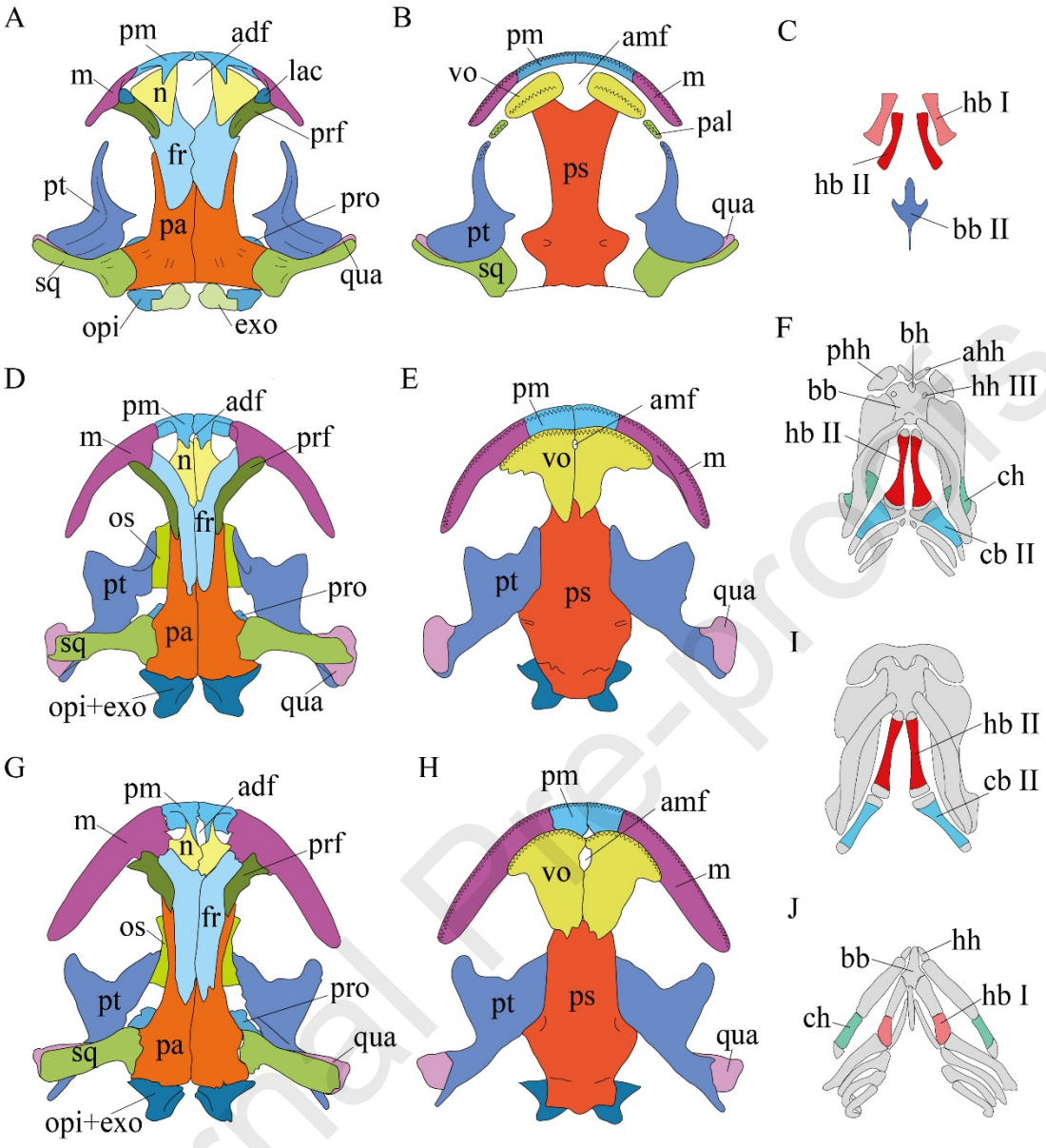

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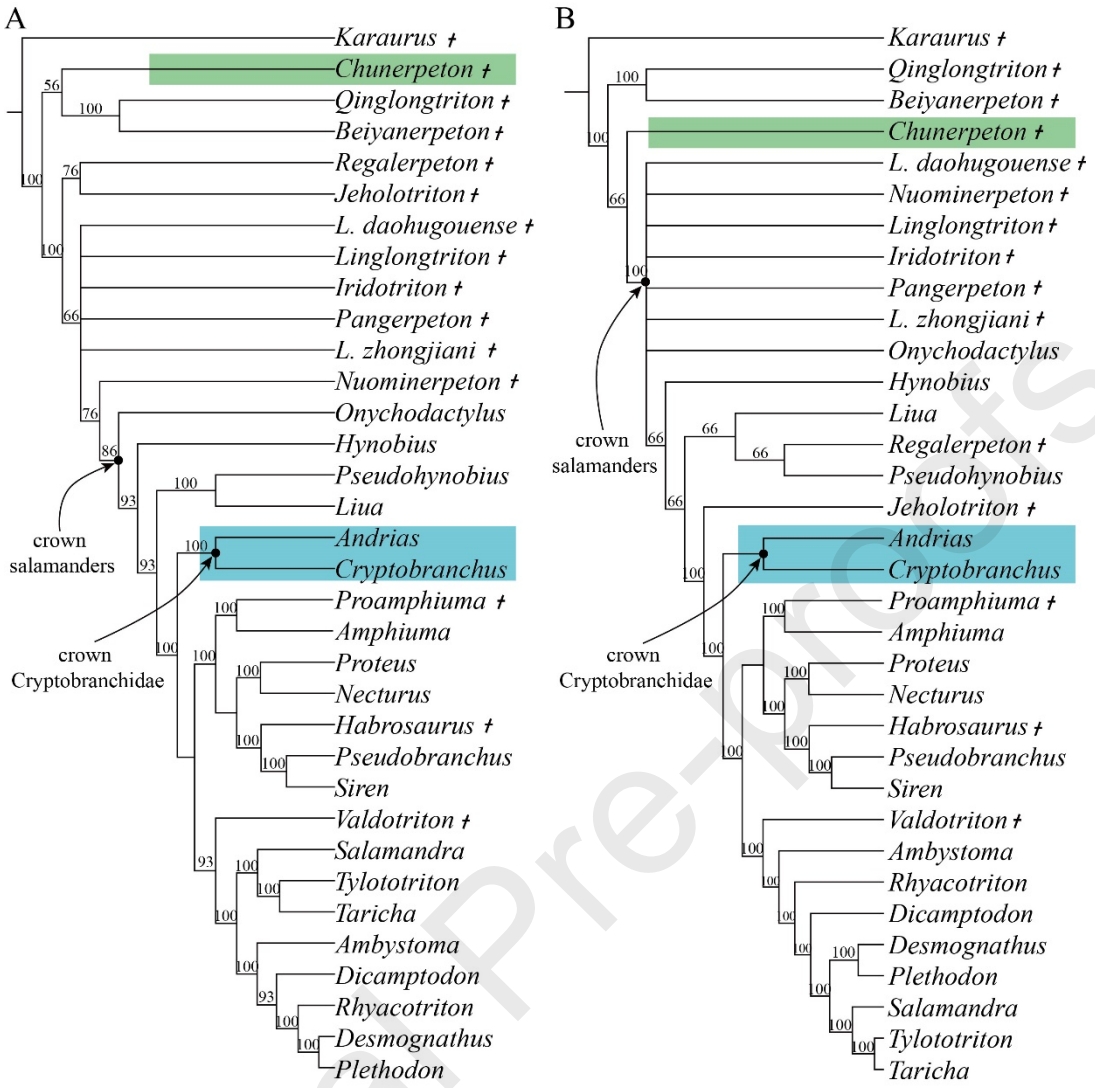

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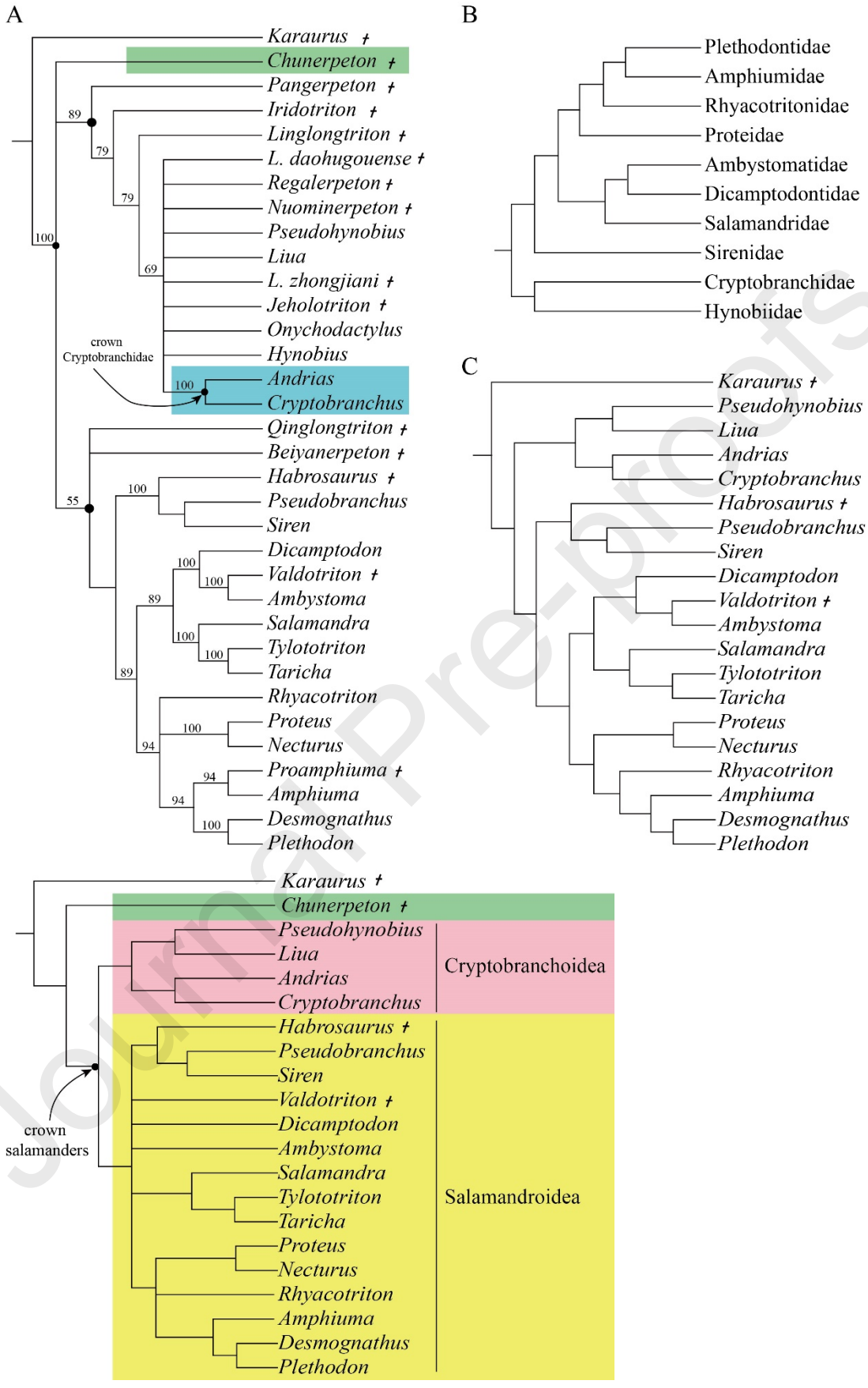
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