The first record of a nearly complete choristodere (Reptilia: Diapsida) from the Upper Jurassic of Hebei Province, People's Republic of China.

Ryoko Matsumoto, Liping Dong, Yuan Wang, Susan E. Evans

Abstract

Choristodera are freshwater aquatic reptiles known from the Middle Jurassic to the Miocene. Their record shows a peak in diversity in the Early Cretaceous of eastern Asia, most notably in the Jehol Biota of China but also in Japan and Mongolia. However, until now, the only Jurassic records from Asia have been rare disarticulated elements from Middle Jurassic microvertebrate sites in Siberia and Transbaikalian, with a possible jaw fragment from the Late Jurassic of Xinjiang, China. Here we describe a new, fully articulated, choristodere skeleton from the Tiaojishan Formation of China, considered to be of Late Jurassic (Oxfordian) age. As such, the new specimen represents the first complete Jurassic choristodere recovered worldwide, as well as providing important information on the pre-Cretaceous history of the group in eastern Asia. In its proportions and postcranial characters, the new taxon resembles previously described Asian taxa such as *Philydrosaurus*, but it is distinct from them in possessing several apparently plesiomorphic characters including a short antorbital region, paired external nares, and an open lower temporal fenestra. Phylogenetic analysis places the new choristodere as the sister taxon of a non-neochoristoderan clade comprising Asian and European taxa, whereas the European Jurassic *Cteniogenys* becomes the sister taxon to all other Choristodera.

Key words: Choristodera; Diapsida; Reptilia; new genus and species; Asia; Jurassic

Introduction

Choristoderes are freshwater aquatic, or semi-aquatic, diapsid reptiles with a fossil record extending from the Middle Jurassic (UK, Kyrgyzstan) through to the Miocene (France, Czech Republic, Germany)(see Matsumoto & Evans 2010 for a review). The group is primarily Laurasian in its distribution, although choristoderes have been reported from the Middle Jurassic of North Africa on the basis of some inconclusive and incomplete jaw elements (Haddoumi *et al*. 2016). Known choristoderes fall into one of two groupings, Neochoristodera (*sensu* Evans & Hecht 1993) and the non-neochoristoderes. Neochoristodera forms a well-supported clade, typified by two relatively large, gavial-like, Euramerican genera of Late Cretaceous-Eocene age, *Champsosaurus* (Cope 1876, 1884; Brown 1905; Parks 1927; Russell 1956; Erickson 1972, 1985) and *Simoedosaurus* (Sigogneau-Russell and Russell 1978; Sigogneau-Russell 1985; Erickson 1987). However, a series of discoveries over the last three decades has shown that many choristoderes, including the earliest, were small and superficially lizard-like in body form. These comprise the non-neochoristoderes, the interrelationships of which are still poorly resolved (e.g. Matsumoto *et al*. 2013).

Recognition of the first choristoderes from the Early Cretaceous of Mongolia (Efimov, 1975, 1979; Sigogneau-Russell & Efimov, 1984), then China (Brinkman & Dong 1993; Gao *et al*. 2000, 2005, 2007; Liu 2004; Gao & Fox 2005; Ksepka *et al*. 2005; Gao & Li 2007; Gao & Ksepka 2008), Japan (Evans & Manabe 1999; Matsumoto *et al*. 2007), and Transbaikalian Russia (Skutschas 2008), opened a new chapter in our understanding of choristoderan history. The Early Cretaceous choristoderes of eastern Asia, especially China, show unexpected taxonomic diversity (7 genera, 12 species) and morphological disparity (in size, snout length, and neck length), suggesting that this region was an important centre for choristoderan evolution. However, with the exception of fragmentary and inconclusive jaw fragments from the Upper Jurassic (Oxfordian age) deposits of the Junggar Basin, Xinjiang (Richter *et al*. 2010), there have been no previous reports of choristoderes from Jurassic deposits in China, and therefore little indication as to when choristoderes began to diversify in this region. Here we describe the first complete choristodere specimen from a Late Jurassic locality

(Nanshimen, Hebei Province). It is also the first complete Jurassic choristodere skeleton recorded from anywhere in the world.

Institutional abbreviations

BMNHC, Beijing Museum of Natural History, Beijing, China; **CAGS-IG**, Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China; **CAS**, Chinese Academy of Sciences; **CNMM**, former Central National Museum of Manchoukuo, in Hsinking (now Changcun); **DR**, Dalian Natural History Museum, Dalian, China; **GMC**, Geological Museum of China, Beijing, China; **GMV**, the Geological Museum of China, vertebrate fossil collections, Beijing, China; **IGM**, Geological Institute of the Mongolian Academy of Sciences, Ulan Bataar, Mongolia; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **LPMC**, Liaoning Paleontological Museum of China, Shenyang, China; **MNHN,** Muséum National d'Histoire Naturelle, Paris, France; **PIN**, Paleontologicheski Institut Rossiiskoi Akademii Nauk, Moscow, Russia; **PKUP**, Peking University Paleontological collections, Beijing, China; **RTMP,** Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **SMM,** The Science Museum Minnesota, St. Paul, Minnesota, U.S.A.

Geology and materials

The new choristodere fossil was recovered from the Nanshimen locality, Gangou Township, Qinglong County, Hebei Province (Fig. 1). It is housed in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences (CAS), Beijing, with the catalogue number IVPP V 23318.

The Nanshimen locality has yielded salamanders (Sullivan *et al*. 2014; Jia & Gao 2016) and mammals (Luo *et al*. 2015), but the contemporaneous neighbouring locality of Mutoudengzi has also yielded pterosaurs (Lü 2009; Lü *et al*. 2012; Lü & Hone 2012; Jiang *et al*. 2015), mammals (Zheng *et al*. 2013), and a non-avian dinosaur (Xu *et al*. 2015). There is a general consensus (Sullivan *et al*.

2014; Luo *et al*. 2015; Jia & Gao 2016) that the fossil beds cropping out at Nanshimen belong to the Tiaojishan (=Lanqi) Formation. Although no datable minerals have been recovered from Nanshimen, stratigraphic correlations with other localities, notably the Daxishan section, Jianchang Basin, Liaoning (Sullivan *et al*. 2014; Luo *et al*. 2015) allow the Nanshimen deposits to be dated to the Late Jurassic (Oxfordian), with U-Pb SHRIMP dates for the horizon at Daxishan given as 160±0.99 Ma. The fauna and flora of these deposits are considered to be components of the Yanliao Biota, which is the antecedent of the Early Cretaceous Jehol Biota.

IVPP V 23318 is the skeleton of a small choristodere, exposed in ventral view on a slab of yellow-grey silty shale (Fig. 2). The skeleton is complete except for the last part of the tail, and is fully articulated except for the anterior 5–6 neck vertebrae, which lie in a small mass behind the head. Despite its small size (total length of ~400 mm), the skeleton appears to be adult or near adult, based on: the closed sutures on the skull and lower jaws; strong ornamentation on the skull roof, especially on the squamosal; closed notochordal canals and fused neurocentral sutures through the vertebral column; fused caudal ribs; fully ossified proximal and distal ends of the limb bones; robust humerus with complete distal condyles; and fully ossified carpals and tarsals.

The skeleton was prepared mechanically. However, to access the dorsal and lateral surfaces of the skull, it was separated from the rest of the skeleton (using the gap between anterior and posterior neck vertebrae). The skull block was then scanned using micro-computerized tomography (developed by the Institute of High Energy Physics, Chinese Academy of Sciences [CAS]) at the Key Laboratory of Vertebrate Evolution and Human Origins, IVPP, CAS, Beijing (beam energy of 130 kV; flux of 120 μA; detector resolution of 45.4810 μm per pixel; 360° rotation with a step size of 0.5°; an unfiltered aluminium reflection target). A total of 720 transmission images were reconstructed in a 2048*2048 matrix of 1536 slices using a two-dimensional reconstruction software developed by the Institute of High Energy Physics, CAS. The software Avizo 8.0, FEI, Hillsboro, Oregon, USA, was used to visualize 3D images of the CT data.

Systematic palaeontology

Class **Reptilia** Linnaeus, 1758

Order **Choristodera** Cope, 1884

Genus ***Coeruleodraco*** gen. nov.

Etymology. From coeruleus (Latin) meaning blue, and draco (Latin) meaning dragon. This is derived from the county name, Qinglong, where Qing=blue; long=dragon.

Range. Upper Jurassic (Oxfordian), the Nanshimen locality, Gangou Township, Qinglong County, Hebei Province, China.

Diagnosis. As for the type and only species

Coeruleodraco jurassicus sp. nov.

(Figs 2–7)

Etymology. To reflect the Jurassic age of the new taxon

Holotype. IVPP V 23318, a nearly complete articulated skeleton of an adult individual (Fig. 2).

Repository. Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences (CAS), Beijing, China.

Type locality and horizon. Nanshimen locality, Gangou Township, Qinglong County, Hebei Province, China; Tiaojishan Formation, Upper Jurassic (Oxfordian).

Diagnosis. Small (snout-vent length ~ 200 mm) choristodere distinguished from all other members of the group by the following combination of characters: paired external narial openings; unossified parasphenoid rostrum; short nasal lacking contact with maxilla; small lower temporal opening that is longer than high; tubercular sculpture along the posterior margin of the squamosal; cervical neural spine tables expanded; well-developed entepicondyle on the humerus with distinct rounded distal tubercle; ischiadic plate with a posterodorsal process; distally expanded fan-like caudal ribs fused to vertebrae.

Differential diagnosis. The new species resembles neochoristoderes (*sensu* Evans & Hecht 1993) and the Euramerican Jurassic *Cteniogenys* (Evans 1990), and differs from the non-neochoristoderes *Monjurosuchus* (Early Cretaceous, China and Japan, Gao *et al*. 2000; Gao & Li 2007; Matsumoto *et al*. 2007), *Philydrosaurus* (Early Cretaceous, China, Gao & Fox 2005; Gao *et al*. 2007), *Khurendukhosaurus* (Skutschas & Vitenko 2017), *Lazarussuchus* (Paleocene-Miocene, Europe: Hecht 1992; Evans & Klembara 2005; Matsumoto *et al*. 2013), and *Hyphalosaurus* (China, Gao *et al*. 1999), in having an open (versus secondarily closed) lower temporal fenestra; further differs from neochoristoderes in having a relatively short preorbital skull, unexpanded upper temporal fenestrae roughly equal in size to the orbits, a short mandibular symphysis limited to a few anterior tooth positions, closed neurocentral sutures, and presacral vertebrae longer than high; resembles *Lazarussuchus* and differs from other known choristoderes, including *Cteniogenys*, in having paired (rather than confluent) nares, but differs from *Lazarussuchus* in lacking an extended premaxillary rostrum; resembles *Cteniogenys* in having separate postorbital and postfrontal bones and a short neck, but differs in having an unossified parasphenoid rostrum, basal tubera with an obtuse angle (~100°) between tubera, a complete humeral ectepicondylar foramen, and closed presacral neurocentral sutures; resembles *Philydrosaurus* in overall postcranial morphology, especially the posterodorsal process on the ischium and the distally expanded fan-like caudal ribs, but differs in having shorter lachrymals and nasals, a shorter parietal plate, and fewer marginal teeth (50–60 in *Philydrosaurus* sp.; 38 in *Coeruleodraco*); differs from the Early Cretaceous Asian *Hyphalosaurus* and *Shokawa* (Japan, Evans & Manabe 1999) in having a short rather than elongated neck; and differs from the incompletely known Early Cretaceous Siberian and Mongolian *Khurendukhosaurus* (Sigogneau-Russell & Efimov 1984; Skutschas 2008; Matsumoto *et al*. 2009; Skutschas & Vitenko 2015, 2017) in having cervical neural spines that are square, nearly equal in height and length, and have swollen neural spine tables, and in having a humeral entepicondyle that is well-developed with a rounded distal tubercle.

Description

IVPP 23318 is the skeleton of a small lizard-like choristodere, preserved in ventral view (Fig. 2). It is complete, except for the tip of the tail, and is almost fully articulated, except for the anterior cervical vertebrae that lie in a mass behind the skull. The skeleton is 203 mm in snout-pelvis length (SPL, anterior tip of premaxilla to posterior edge of last sacral; SPL is roughly equivalent to snout-vent length [SVL] in a living animal), with a total length of around 400 mm when the tail is included. The skull is 54 mm long; the forelimb is 70 mm long (humerus, 25 mm; radius, 17 mm; manus, 28 mm); and the hind limb is 95 mm long (femur, 30 mm; tibia, 21 mm; pes, 44 mm).

In the description that follows, the account of the skull is based on both the original specimen (ventral surface) and the µCT scans, whereas the account of the postcranial skeleton is based on the specimen as exposed in ventral view.

Skull

The rostrum is pointed, but is not elongated and the preorbital skull is shorter than the postorbital one (preorbital skull 18 mm, orbit 12 mm, postorbital skull 24 mm). The premaxillae were paired, as shown by the left premaxilla with four teeth that is exposed under the anterior tip of the left dentary (Fig. 3). Each premaxilla is a small triangular element, the pointed anterior tip of which forms a sharp edge to the snout. The premaxilla has two distinct processes, one dorsal and one lateral. The narrow dorsal process bears a dorsoventrally inclined facet for the nasal. The lateral process meets the anterodorsal margin of the maxilla.

Paired external narial openings are located at the anterior end of the snout, bordered anteriorly by the premaxilla and posteriorly by the small nasal and the anterior tip of the prefrontal. The contribution of the prefrontal to the narial opening distinguishes *Coeruleodraco* from *Philydrosaurus* in which the nasal meets the prefrontal in the mid-portion of the rostrum.

The maxillae are complete. The dorsal flange of the maxilla is inflected medially to form the dorsoventrally flattened snout that is characteristic for all choristoderes. The maxilla fails to contact the nasal and has an elongated articulation with the prefrontal along most of its dorsomedial border. Further posteriorly, the maxilla contacts the lachrymal and, along the ventral orbital margin, the short tapering orbital process has a shallow articulation with the jugal. In ventral view, the maxillary dentition is exposed most clearly on the right side and shows 33 tooth positions. The tooth row ends slightly anterior to the level of the posterior orbital margin.

The prefrontals are in midline contact for about three-quarters of their length and form most of the antorbital skull roof, unlike *Philydrosaurus* where the prefrontals are relatively much shorter. Each prefrontal is widest at the anterior margin of the orbit, but then narrows at the contact with the frontal. Together, the prefrontal and lachrymal form a strong anterior orbital rim.

The lachrymals are restricted to the anterior margin of the orbits and have no contact with the nasals. In dorsal view each lachrymal presents as a relatively small triangular element with a tapering anterior process that intervenes for a short distance between the maxilla and prefrontal, and a posterior process that extends ventrolaterally to meet the jugal at the midpoint of the orbital margin. The lachrymal foramen is enclosed between the lachrymal and prefrontal bones in the anterior wall of the orbit, unlike *Philydrosaurus* where the lachrymal fully encloses the foramen.

The paired frontals are narrow and contribute roughly one third of the dorsal orbital rim between the prefrontals and postfrontals. They extend to the level of the posterior margin of the orbit, but roughly half of their lateral margin is occupied by a facet for the postfrontal. Each frontal tapers posterolaterally, creating a V-shaped central recess into which the anterior margin of the parietal wedges. The frontals bear tubercular dorsal sculpture that is particularly well developed in the interorbital region. The frontal plate is visible in ventral view and has descending flanges (cristae crania, sub-olfactory processes) that appear to meet in the midline anteriorly. This would strengthen the interorbital region of the skull.

The parietals are paired, as in other choristoderes, and there is no parietal foramen. Each bone has two distinct parts, a dorsal parietal table and a posterolaterally directed squamosal process. Anteriorly, the parietal table meets the frontals close to the level of the posterior orbital margin. Laterally, the parietal table meets the postfrontals and postorbitals, whereas posteriorly it forms the anterior and medial margins of the upper temporal fenestra. The anterior width and overall length of the parietal table are roughly equal, but the posterolateral margins angle medially so that the bases of the squamosal processes lie close together on either side of the midline. From this point, the processes diverge posteriorly and meet the squamosals in the posteromedial margins of the upper temporal fenestrae. Each squamosal process is roughly equal in length to the midline suture of the parietal table, a morphology similar to that in *Monjurosuchus* but different from *Philydrosaurus* in which the parietal table is longer than wide, and longer than the squamosal process.

The postfrontal and postorbital are separate, as in *Cteniogenys, Philydrosaurus*, and the neochoristoderes *Champsosaurus* and *Ikechosaurus.* In other choristoderes the two bones are fused into a large postorbitofrontal complex that forms the posterior orbital margin (e.g. Erickson 1987; Evans & Klembara 2005; Gao & Ksepka 2008; Ksepka *et al*. 2005). The postfrontal is a small triangular plate that contacts both the frontal and parietal medially and the postorbital laterally. This postfrontal of *Coeruleodraco* resembles that of *Cteniogenys* in being excluded from the upper temporal fenestra (unlike *Philydrosaurus*, *Ikechosaurus* and *Champsosaurus*). The postorbital is larger than the postfrontal and it is composed of dorsal and lateral plates positioned at an angle to one another. This line of angulation creates a strong keel that is continuous with the dorsal edge of the squamosal and forms the lateral margin of the upper temporal fenestra. The large dorsal plate of the postorbital enters the margins of both the orbit and the upper temporal fenestra, contacting the postfrontal and the parietal medially. Posteriorly, the dorsal plate tapers and overlaps the squamosal. The lateral postorbital plate is narrower and triangular, and forms the anterodorsal margin of the small lower temporal fenestra. A short ventral process provides a strong flange that articulates with jugal in the orbital rim. This suture between the postorbital and jugal is also visible in medial view, where a long narrow orbital process of the postorbital limits the entry of the jugal into the orbital margin.

The jugal is a slender triradiate bone. The anterior process forms the ventral orbital rim in conjunction with the posterior process of the lachrymal. Posteriorly, the jugal bifurcates into dorsal and posteroventral branches that form the anteroventral margins of the lower temporal fenestra. The dorsal process is short (roughly half the length of the posterior process) and bears an anteroposteriorly wide facet for the postorbital. The posterior process overlaps the quadratojugal half way along the ventral margin of the lower temporal fenestra. The lower temporal opening is longer than it is high, and is roughly half the size of the upper temporal fenestra.

As seen in lateral view, the quadratojugal is a small rectangular element with a sculptured surface. The posterior end of the quadratojugal attaches to the anterior margin of the squamosal. The squamosal facet forms a thin plate and a slightly concave quadrate facet accommodates the quadrate. The dorsal margin of the quadratojugal is straight and forms the posteroventral rim of the lower temporal fenestra.

The squamosal is formed by two plates (lateral and posteromedial) that meet at roughly 45 degrees and together form the posterior margins of the upper temporal fenestra. The lateral plate is strongly sculptured, especially along the ventral margin where the sculpture is developed into spikes.

The lateral plate also forms the posterior border of the lower temporal fenestra. It bifurcates anteriorly into roughly equal dorsal and ventral processes. The dorsal process meets the postorbital in a vertical articulation and the narrower ventral process contacts the quadratojugal. The deep medial plate meets the squamosal process of the parietal in the posteromedial margin of the upper temporal fenestra. Ventromedially, the squamosal bears a large facet for the quadrate.

The quadrate is shaped like an isosceles triangle in posterior view and is well exposed in ventral view, partially in articulation with the lower jaw. The ventrolateral margin of the quadrate attaches to the quadratojugal. The dorsal process of the quadrate is slightly inclined posteriorly, and its dorsolateral margin articulates with the squamosal. The ventral condyle is mediolaterally expanded and hourglass-shaped, with the medial portion of the condyle thicker than the lateral part. This condyle, and thus the jaw joint, is located slightly anterior to the level of the occipital condyle. The medial margin is obscured in dorsal view due to the overlapping postorbital (Fig. 3), but the CT slice images show that this margin attaches to the pterygoid and opisthotic. However, the quadrate is not in direct contact with the neomorph because the opisthotic intervenes between the two. This differs from the condition in other choristoderes where the neomorph is known (e.g. *Simoedosaurus*, Sigogneau-Russell 1981).

The neomorph is a thin plate-like bone that lies in the lateral wall of the choristoderan braincase between the parietal, squamosal, quadrate, prootic and pterygoid (Fox 1968; Gao & Fox 1998), and seems to be a choristoderan characteristic. The bone is present in *Coeruleodraco* but it is much smaller than that of the neochoristoderes *Simoeodosaurus* (Sigogneau-Russell 1981), *Ikechosaurus* (pers. ob. RM: IVPP V9611-3), and *Champsosaurus* (e.g. Fox 1968). A pterygoid foramen lies between the neomorph and squamosal in *Champsosaurus*, but is not confirmed in *Coeruleodraco*.

Palate and braincase (Fig. 4)

These regions are not well preserved in the original specimen but due to the presence of the braincase, the posterior part of the skull is somewhat less compressed than the anterior part.

The vomer and palatines are not visible. The central portion of the pterygoid, at the junction of its palatal plate and quadrate process, is preserved on both sides but is more complete on the right. There is a low ridge running along the quadrate process. There are no obvious teeth on the preserved portion of the pterygoid.

The right ectopterygoid is exposed within the orbit in the dorsal view of the skull (Fig. 3B). As preserved, the bone is T-shaped, with a lateral maxillary process that tapers at both ends. The slender medial process is orientated horizontally and bears deep plug-in facet for the pterygoid on the dorsal surface. The ectopterygoid of *Coeruleodraco* differs from that of *Cteniogenys* and *Champsosaurus* in the absence of a neck at the stem of the pterygoid process and in the deeper pterygoid facet. *Simoedosaurus* more closely resembles *Coeruleodraco* in these two features, but the element is shorter and forms a robust triangular plate.

The basisphenoid is exposed between the pterygoids at the posterior end of the interpterygoid vacuity (Fig. 4A). It appears to have short basipterygoid processes that are sutured to the pterygoids (clearest on the right). The anterior end of the bone is bifurcate, with short processes delimiting a narrow U-shaped embayment. The basisphenoid expands posterolaterally, with the edge of the dermal parasphenoid creating a distinct ventrolateral crest along the edge of the bone. No teeth are visible on the parasphenoid.

The posterior part of the skull has been deformed postmortem and the braincase seems to have twisted slightly about its long axis, so that the left edge lies more ventrally than the right, and the basioccipital appears rather asymmetric, with the kidney-shaped occipital condyle offset to the right. The basal tubera are expanded ventrolaterally and are similar to those of the *Khurendukhosaurus* (Skutschas 2008). The degree of expansion is roughly intermediate between the well-developed tubera of *Champsosaurus* and the poorly developed tubera of *Simoedosaurus*.

Immediately to the left of the occipital condyle is a smaller condyle. This could be part of an exoccipital but is probably the base of one of the atlantal arches. The otic capsule is dorsoventrally compressed and higher resolution CT scans would be required to understand its detailed structure, but a slender rod lying in a groove on the occipital surface may be a stapes.

Mandible

Both mandibles are preserved, the right is mainly exposed in labial view and the left in lingual view (Fig. 4A,B). The labial view shows the characteristic choristoderan dentary morphology: long and shallow, with linear striations and multiple foramina, although fracturing of the surface precludes confirmation a distinct double row of foramina. The lingual view shows the symphysis to be short (a few teeth only). There is a strong subdental ridge above a Meckelian fossa that is open medially for much of its length, although fragments of a splenial in the posterior part of the fossa suggest that the fossa was partially closed by this bone. There are 37–38 teeth in the dentary. These are subthecodont in their implantation, sitting in shallow rounded alveoli. The teeth are conical and relatively homodont, although the anterior teeth are more slender than the posterior ones. There is no trace of the labyrinthine infolding that is found at the bases of the teeth in all neochoristoderes except *Ikechosaurus* (Matsumoto *et al*. 2014), but almost all tooth crowns are either broken off or split and therefore the extent of the enamel covering (complete or crown only), and the presence or absence of crown striations, cannot be determined. The dentary tooth row extends almost to the posterior margin of the orbit. The postdentary jaw is exposed on the left side, though damaged. It is short and forms less than one third of the total mandibular length. A long prearticular is exposed, supporting a medially open adductor fossa. The coronoid is not preserved and the articular lacks any development of a retroarticular process.

A single pair of elongated hyoid elements (first ceratobranchials) is exposed on the ventral surface of the skull, extending from the posterior orbital margin into the anterior neck. Each ceratobranchial is a straight rod that tapers gradually from a thickened anterior end to a more slender posterior tip. Similar elements have been described in other choristoderes including *Champsosaurus* (Erickson 1985) and *Ikechosaurus* (Brinkman & Dong 1993; Liu 2004).

Axial skeleton

The vertebral centra are amphicoelous to amphiplatyan (i.e. the cotyles are shallow) but not notochordal (and shown by broken vertebrae), and the neural arches and centra are fused throughout the column. The neck is the only part of the skeleton that is disarticulated, and a cluster of 5-6 cervical vertebrae (including the axis and possibly atlantal elements) lies behind the head (Fig. 3). One additional posterior cervical vertebra is in articulation with the dorsal series (Fig. 2). The cervical centra are short (4 mm) and keeled, but they are longer than they are deep. As exposed on the specimen, the preservation is not good enough to show whether they have facets for a double headed rib, although there is one element overlying them that could be a rib of that type. However, the µCT data has revealed details of the neural spines and zygapophyses. The neural spine tables are slightly swollen, and the zygapophyses in the posterior cervical vertebrae lie at an angle of roughly 40 degrees to the horizontal. Although we cannot be certain whether or not some cervical vertebrae were lost between the anterior and posterior series, it is clear that the neck was comparatively short (like *Lazarussuchus* and *Monjurosuchus*, but not *Hyphalosaurus, Khurendhukosaurus* or *Shokawa*). There are 16 dorsal vertebrae that are significantly longer than the cervicals but become gradually shorter toward sacrum (7.5 mm anterior dorsal vertebral length, 7 mm posterior dorsal vertebral length), and are cylindrical or subcylindrical in shape, without sharp ventral keels. All dorsal vertebrae bear ribs, although these are shorter on the posterior dorsals. In the sacral region, there appear to be three sacrals (sacral 1 centrum, 5.87 mm long, 3.82 mm wide). The rib of the second sacral is visible through a break in the overlying pelvic plate and this shows the sacral ribs to be sutured, not fused, to the centrum. The tail is at least as long as the trunk and may have been longer, allowing for the missing tip. The anterior caudal vertebrae bear broad, flange-like transverse processes. That of the first caudal is broad-based and angles slightly anteriorly, but in subsequent caudals, the transverse processes are relatively narrow at their bases and flare out distally. In this feature, *Coeruleodraco* most closely resembles *Philydrosaurus* (Gao & Fox 2005; Gao *et al*. 2007). The flaring of the processes is most marked in caudals 2–9, after which (caudals 11–16, caudal 10 is damaged) it decreases until the processes are almost parallel-sided. Whether the processes are fully fused to the centra or are sutured is not clear. Posterior to caudal 16, there is then a short break in the specimen (2–3 vertebra lengths), after which there are a further eight caudals that are cylindrical and without processes. This is unlikely to be the tip of the tail, however, as the centra are still quite large. Caudal vertebra 20 has been rotated on to its side, revealing vertical zygapophyses and a neural spine with a base that extends over the posterior two thirds of the neural arch. The neural spine is twice as long as high. It lacks an expanded spine table but the intact posterior edge is crenellated. With the exception of the first three caudals (presumably underlying the cloacal vent), all the caudal centra bear a midline groove for caudal blood vessels flanked by paired parallel crests. These crests are relatively low on caudal vertebra 3, but have developed into deep flanges by caudal vertebra 4 and this morphology extends the full length of the tail as preserved. No haemal arches are evident.

A few short ribs are visible in the cervical region (Fig. 5, cr). One, mentioned above, has a bicipital head but the morphology of the remainder (unicipital or bicipital) is unclear. The trunk ribs are single headed, broad, with strong keels for the intercostal muscle attachments, and expanded surfaces. Together, they form a robust, inflexible trunk region like that in other choristoderes. This is further supported ventrally by gastralia. The full gastral series has been disrupted, but some of these elements are present between the ribs. The median elements are the thickest, roughly half the diameter of the rib head. This contrasts with both the very slender gastralia of, for example, *Lazarussuchus*, and those of some neochoristoderes where they are similar in width to the ribs themselves.

Pectoral girdle and forelimb (Figs 5 and 6)

The scapulocoracoids are both preserved and the scapula and coracoid appear to have been coossified. The scapula is quite long and parallel-sided; the coracoid forms a large plate, but its borders are damaged medially and therefore the shape is unclear. The glenoid fossa is deep and with prominent ‘lips’. Little of the ventral dermal girdle is preserved. The anterior part of the interclavicle remains in position, but its stem is not preserved. The clavicles are thick and completely preserved on both sides.

The forelimb is well ossified (Fig. 6). The humerus is preserved on the right. It is relatively short (25 mm, 75% femur length) and robust, with a thick shaft (5 mm) and wide distal end (10 mm). Proximal and distal ends are twisted in relation to one another, at an angle of around 60 degrees. The proximal head has a wide continuous articular surface and a strong deltopectoral crest. The distal end is broader. The ectepicondyle is small and is perforated by a small foramen. It is flanked medially by a large capitellum for the radius. The entepicondyle is well developed and bears a distinct rounded tubercle at its distal tip. Proximal to it, also along the edge of the distal end, is a larger, but more irregular rugosity. These rugosities imply the presence of strong flexor musculature. In this view, however, there is no evidence of an entepicondylar foramen or groove. The radius (17 mm) has a well-formed cotyle for the humerus and a long, relatively gracile shaft terminating in a distal head without obvious expansion. The proximal end of the right ulna is obscured by the overlying radius, but it is exposed on the left side and seems to have a distinct olecranon process. The shaft is similar in width to that of the radius although it is slightly more expanded distally. The carpus is preserved only on the right side, but the elements are rather jumbled and some have been transposed by the pronation of the manus. A large element distal to the ulna head is presumably the ulnare, whereas a narrower element lying between the radius and ulna may be a displaced radiale. Further distally are at least six more carpals, presumably a mixture of centralia and distal carpals (at least three). The manus is preserved on both sides. It is longer than the humerus (28 mm) with robust metacarpals and phalanges, and a phalangeal formula of 2:3:4:4:2+. Metacarpals 3 and 4, of similar length, are the longest, followed in length order by MC2, MC1 and MC5. The ungual phalanges are long and strong, with a gradual curvature and no obvious flexor tubercle.

Pelvic girdle and hind limb (Fig. 7)

The ilium is not visible in ventral view. The pubo-ischiadic plate is broad and unfenestrated, although crushing has pressed a sacral rib through the centre of the plate creating a pseudofenestra (Fig. 7A, B). The pubis is a simple broad plate, longer than wide, and perforated close to its proximal end by an oval obturator (pubic) foramen. There is a weak pectineal tubercle lying in the same plane as the body of the bone. The ischium is flask-like and wide, and it has a distinct posterodorsal process. This is broken close to the base on the left and appears bifid on the right, although this may be due to damage.

The hind limb is longer than the forelimb (95 mm, 137% forelimb) and is also strongly ossified. The femoral head and internal trochanter are separated by a deep intertrochanteric fossa, with the trochanter lying a short way distal to the femoral head. The shaft is long and sigmoid, but it is narrower at its midpoint (3 mm) than that of the humerus. The distal end forms a single articular surface, without any separation of medial and lateral condyles. The tibia and fibula are of the same length (21 mm). The tibia is the more robust bone, with a thick proximal head that is triangular in cross-section and a long shaft. The fibula has a small proximal head (2.4 mm in width) that is the same width as the shaft. The fibular shaft is gracile for more of its length but it expands to more than twice the original thickness close to the distal end, as in most choristoderes. In the ankle, the astragalus and calcaneum are not fused, and the latter has a prominent calcaneal tuber. Further distally, there are two or three distal tarsals of which the largest (DT4) is flanked by a smaller DT3 and, probably, a small DT2. The pedal metatarsals and phalanges, like those of the manus, are strongly ossified with well-formed joint surfaces and tubercles for muscle and ligament attachments. As in the manus, MT3 and MT4 are of similar length, followed by MT2, and then MT1 and MT5. MT1 is conspicuously broadened and MT5 has an expanded proximal head, with a medial articular surface for DT4 and a square outer process. It lacks plantar tubercles, but the distal head is set at almost 90 degrees to the proximal one, so that the shaft is distinctly twisted. It is thus ‘hooked’ to at least the same degree as that of rhynchocephalians, turtles, and many basal archosauromorphs (Evans 1988). The pedal phalangeal formula is 2:3:4:4:3 and, as in the hand, the ungual phalanges are long and robust.

Phylogenetic analysis

We coded *Coeruleodraco* into a recent data matrix for Choristodera (Matsumoto *et al*. 2013), having added two further choristodere specimens (*Monjurosuchus splendens* [BMNHC 073] and *Ikechosaurus pijiagouensis* [IVPP V 13283]) based on new observations by one of us (RM), and having updated the coding of *Khurendukhosaurus* based on the recent paper of Skutschas & Vitenko (2017). Two characters in the Matsumoto *et al*. (2013) matrix were amended: character 26 (to correct a description error in states 1 and 2) and character 83 (to recognize a new character state):

(26) Parietal skull table (parietal midline suture length/parietal table width): length of parietal midline suture equal to or greater than transverse width of parietal plate 0–100% (0); parietal midline suture length up to twice (100–200%) transverse parietal width (1); parietal midline suture length much greater (200–350%) than transverse width (2). States in the intermediate zone 95–105% are coded as (0/1) and in the zone 195–205% as (1/2).

(83) Cervical zygapophyses: almost horizontal (0–25˚) (0); project dorsolaterally (30–45˚) (1); project dorsolaterally (30–45˚) in anterior neck (C3–5) but are almost horizontal in posterior neck (2).

We ran the analysis using TNT (version 1; Goloboff e*t al*. 2008) in New Technology search mode with the Ratchet option (1000 random addition sequences: 50 iterations) followed by a Traditional search of trees in RAM for additional topologies. The Bootstrap tree was analyzed with 10000 replicate resampling. In addition to *Coeruleodraco*, the ingroup comprised 11 choristoderan genera and 21 species, *Champsosaurus* (2 sp.), *Simoedosaurus* (2 sp.), *Ikechosaurus* (2 sp.), *Tchoiria*

(2 sp.), *Cteniogenys* (1 sp.), *Philydrosaurus* (2 sp.), *Khurendukhosaurus* (1 sp.)*, Monjurosuchus* (2 sp.), *Hyphalosaurus* (2 sp.), and *Shokawa* (1 sp.). *Irenosaurus* (Efimov 1988) and *Pachystropheus* (Storrs & Gower 1993) were excluded in this analysis due to uncertainty as to their morphology and relationship to Choristodera (e.g. Matsumoto *et al*. 2009; Matsumoto *et al*. 2013), while *Liaoxisaurus* (Gao *et al*. 2005) is omitted as it is almost certainly congeneric with *Ikechosaurus* from the same locality. Outgroup choice is problematic for Choristodera, because the position of the group within Diapsida remains uncertain: on the stem of Archosauromorpha + Lepidosauromorpha (e.g. Evans 1988, Dilkes 1998; Gao & Fox 1998); as stem/early archosauromorphs (e.g. Evans 1988, Gauthier *et al*. 1988; De Braga & Rieppel 1997); or as sauropterygian relatives (Müller 2004). Our previous work (Matsumoto *et al*. 2009; Matsumoto 2011) has demonstrated that the selection and combination of outgroups affect ingroup relationships within Choristodera. As TNT only permits a single outgroup rather than several, we designated the Late Carboniferous diapsid *Petrolacosaurus* (Reisz 1981) as outgroup, but included seven additional taxa (representing different hypotheses of relationship for Choristodera) in the ingroup, namely: *Youngina* and *Araeoscelis* (diapsid stem), *Mesosuchus* and *Prolacerta* (archosauromorphs), *Nothosaurus* and *Keichousaurus* (sauropterygians), and *Gephyrosaurus* (Lepidosauria). A second series of analyses was run using the Permian *Araeoscelis* (Reisz *et al*. 1984: which lacks a lower temporal fenestra) as the outgroup taxon.

The two sets of analyses (with *Petrolacosaurus* or *Araeoscelis* as outgroups) both yielded ten MPTs (L= 329), and although there were small differences in the positions of some non-neochoristoderes (e.g. *Monjurosuchus*) and neochoristoderes (e.g. *Ikechosaurus* and *Tchoiria*) in some of the trees, the choice of *Petrolacosaurus* or *Araeoscelis* had no significant effect on the topology of either the strict consensus (Fig. 8A) or bootstrap trees (Fig. 8B). Both analyses supported the monophyly of Choristodera and of Neochoristodera, and both supported the placement of the Middle Jurassic *Cteniogenys* as the sister taxon of all other choristoderes. The main difference between the Strict Consensus and Bootstrap trees is that the latter leaves the non-neochoristodere taxa in an unresolved polytomy (with weak support for long-necked hyphalosaur and short-necked monjurosuchid clades [*sensu* Gao & Li, 2007]), whereas the strict consensus tree places the non-neochoristoderan taxa (other than *Cteniogenys*) in a second clade of which *Coeruleodraco* is the sister taxon. The possible implications of this are discussed below.

Discussion

Coeruleodraco jurassicus is clearly a choristodere, based on the presence of a median contact of the elongated prefrontals, separating nasals from frontals; dorsal flange of the maxilla inflected medially; absence of a parietal foramen; squamosal expanded posterior to the occipital condyle; conical subthecodont teeth; a slender dentary with anteroposterioly elongated grooves on the labial surface; additional sacral vertebrae; expanded spine tables on the vertebrae; and amphiplatyan vertebral centra. This attribution is confirmed by the results of the phylogenetic analyses.

As outlined in the introduction, the known genera of choristoderes fall into two groups, one formal, one informal. Neochoristodera (*sensu* Evans & Hecht 1993) forms a well-supported clade of long-snouted, gavial-like reptiles comprising the Cretaceous-Eocene Euramerican genera *Champsosaurus* and *Simoedosaurus* (e.g. Erickson 1972, 1987; Sigogneau-Russell & Russell 1978; Sigogneau-Russell & de Heinzelin 1979), and the Early Cretaceous Asian *Tchoiria* (Efimov 1975, 1979) and *Ikechosaurus* (e.g. Brinkman & Dong 1993). *Coeruleodraco* lacks the diagnostic features of Neochoristodera (e.g. confluent nares, elongated rostrum, expanded upper and lower temporal fenestrae, extended mandibular symphysis, open neurocentral sutures) and thus falls into the non-neochoristodere grouping. Apart from *Coeruleodraco*, this informal group includes the Middle-Late Jurassic Euramerican *Cteniogenys (*Evans 1989, 1990; Chure & Evans 1998*)*, the Early Cretaceous Asian *Monjurosuchus* (Endo 1940, Endo & Shikama 1942, Gao *et al*. 2000; Matsumoto *et al*. 2007), *Philydrosaurus* (Gao & Fox 2005), *Hyphalosaurus* (e.g. Gao & Ksepka 2008), *Shokawa* (Evans & Manabe 1999) and *Khurendukhosaurus* (Sigogneau-Russell 1981, Skutschas 2008; Matsumoto *et al*.

2009; Skutschas & Vitenko 2015, 1017) and the Palaeocene-Miocene Euramerican *Lazarussuchus* (Hecht 1992; Vejvalka 1997; Böhme 2008; Matsumoto *et al*. 2013). In the past (Evans & Hecht 1993; Gao & Fox 1998; Evans & Manabe 1999; Ksepka *et al*. 2005; Matsumoto 2011; Matsumoto *et al*. 2013), there has been a lack of consensus as to whether *Cteniogenys* or *Lazarussuchus* was the more stemward taxon, with Gao & Fox (1998) actually placing *Lazarussuchus* outside Choristodera.

The results of the phylogenetic analysis suggest that the addition of *Coeruleodraco* to the choristoderan record may have helped to stabilise the ingroup relationships, in confirming the placement of *Cteniogenys* as the sister taxon of all other choristoderes (including *Lazarussuchus*). Matsumoto *et al*. (2013) found the same arrangement. If the topology provided by the Strict Consensus tree (Fig. 8A) is correct, then reduction of the lower temporal fenestra (as in *Coeruleodraco*), followed by closure of the fenestra in younger taxa, could be step-wise changes in the evolution of a non-neochoristoderan clade that evolved in Asia during the Jurassic and diversified in the Early Cretaceous. This may have relevance in relation to the rather puzzling European record of small choristoderes (Fig. 9). *Cteniogenys* is known from the Middle Jurassic of England and Scotland, UK (Evans 1989, 1990), the Upper Jurassic (Oxfordian) of Portugal (Guimarota lignites, Evans 1989) and the Upper Jurassic (Tithonian) of North America (Morrison Formation, Chure & Evans 1998). There are also *Cteniogenys*-like vertebrae recorded from Middle Jurassic microsites in Kyrgyzstan (Averianov *et al*. 2006). However, there is then a hiatus in the European small choristodere record until the first appearance of *Lazarussuchus* in the Palaeocene (Matsumoto *et al*. 2013), but note that this excludes fragmentary choristodere records from western and eastern Siberia (Skutschas & Vitenko 2015, 2017). Either the ancestors of *Lazarussuchus* were present in Europe throughout the Cretaceous, but have not been recovered, or they dispersed back into Europe at some point before the early Palaeogene, after the extinction of earlier primitive choristoderan lineages. For the first alternative, the absence of choristodere remains from the well-studied microvertebrate assemblages of the UK (e.g. the Berriasian Purbeck Limestone Group, Wealden deposits of the Isle of Wight) or rich wetland deposits, like those in Spain (e.g. Las Hoyas), is problematic. These European localities yield faunal assemblages that contain salamanders, frogs, small crocodiles, and turtles, with which choristoderes are found in the European Jurassic and in the Early Cretaceous of Asia (Matsumoto & Evans 2010; Skutschas & Vitenko 2017). However, if *Lazarussuchus* has its origins in a non-neochoristoderan clade that arose in Asia (as suggested by the Strict Consensus tree in Fig. 8A), and later dispersed into Europe, then the European record would make more sense (Fig. 9). Nonetheless, this hypothesis remains speculative and much more needs to be known of the Jurassic and Cretaceous history of small choristoderes throughout Laurasia.

Conclusions

Over the last few decades, the Lower Cretaceous deposits of Asia have yielded an exceptional and unexpected diversity of choristoderan genera with a range of different sizes and body plans. However, until now, there has been little information on the earlier history of the group in the same geographical region. The discovery of a complete choristodere skeleton from the Late Jurassic (Oxfordian) of China therefore helps to fill a significant gap in the record. Phylogenetic analysis suggests the new taxon may have been an early member of a diverse non-neochoristoderan Asian clade from which the Palaeocene-Miocene European *Lazarussuchus* may have been derived.

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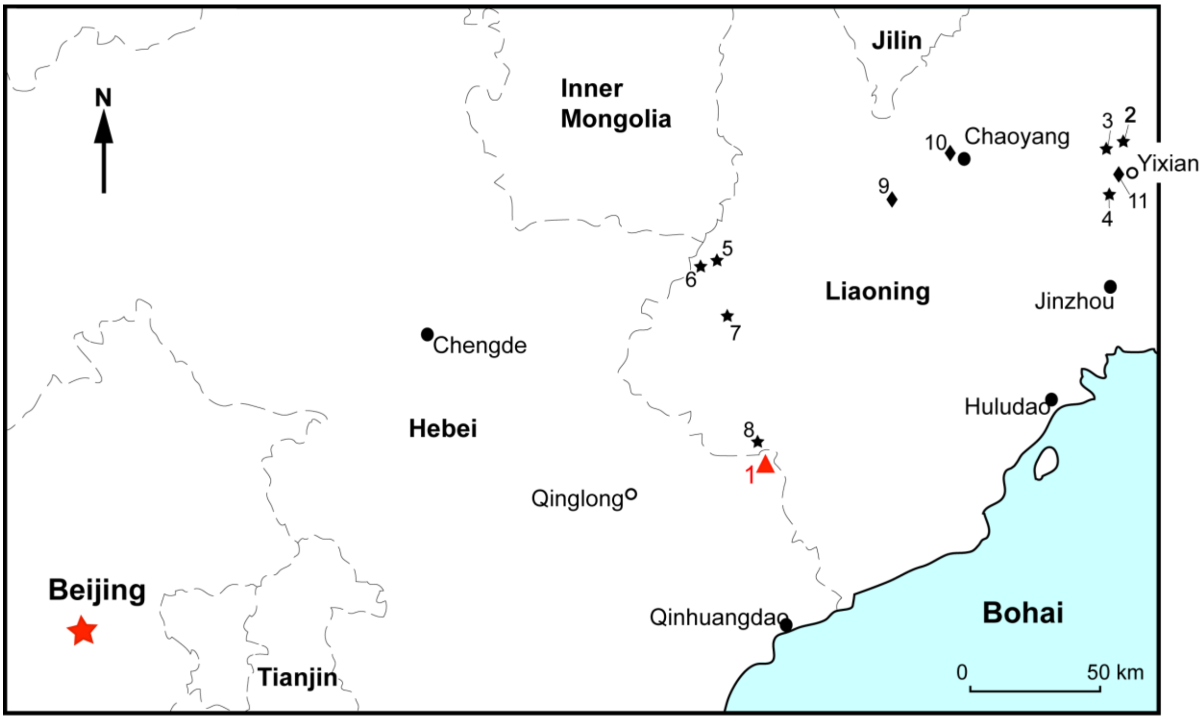

Figure 1: Eleven published choristodere-bearing localities in western Liaoning, with one from the Middle-Upper Tiaojishan Formation (Oxfordian locality 1, triangle), seven from the Yixian Formation (Barremian-Aptian localities 2–8, stars), and three from the Jiufotang Formation (Aptian localities 9–11, diamonds).

1, **Nanshimen**: *Coeruleodraco jurassicus* gen. et sp. nov. (IVPP V 23318, this paper); 2, **Toutai**: *Monjurosuchus splendens* (BMNHC V073, Gao *et al*. 2007); 3, **Baitaigou**: *Hyphalosaurus baitaigouensis* (Holotype, CAGS-IG-03-7-02, Ji *et al*. 2004); 4, **Jingangshan**: *Monjurosuchus splendens* (IVPP V 13761, Wang *et al*. 2005) (Gao & Fox [2005] thought Caocishan and Jingangshan were the same locality, see text); 5, **Danangou**: *Monjurosuchus splendens* (Holotype, CNMM 3671, Endo 1940; IVPP V 3673, Endo & Shikama 1942); 6, **Dawangzhangzi**: *Hyphalosaurus lingyuanensis* (Fanzhangzi, IVPP V 11705, Gao *et al*. 1999; PKUP V1052, GMC juvenile, Gao & Ksepka 2008, see note below); 7, **Niuyingzi**: *Monjurosuchus splendens* (Neotype, GMV 2167, Gao *et al*. 2000). There are three more specimens (GMV 2135, 2162, 2166) whose localities Gao *et al*. (2000) did not record. Based on the matrix of these specimens, they probably came from the neotype locality; 8, **Luojiagou**: *Hyphalosaurus* sp. (Zhang *et al*. 2012); 9, **Yuanjiawa**: *Philydrosaurus proseilus* (LPMC 021, Gao *et al*. 2007); 10, **Shangheshou**: *Philydrosaurus proseilus* (Holotype, PKUP V2001, Gao & Fox 2005); 11, **Pijiagou**: *Ikechosaurus pijiagouensis* (Holotype, IVPP V 13283, Liu 2004).
Note: Gao & Ksepka (2008) mentioned many catalogued (PKUP V1056-1058, BMNHC V014- 053, LPMC R-00052, LPMC R-00065-00066) and uncatalogued specimens (BMNHC, IVPP, LPMC and PKUP) of *Hyphalosaurus baitaigouensis*, but they did not provide locality information.

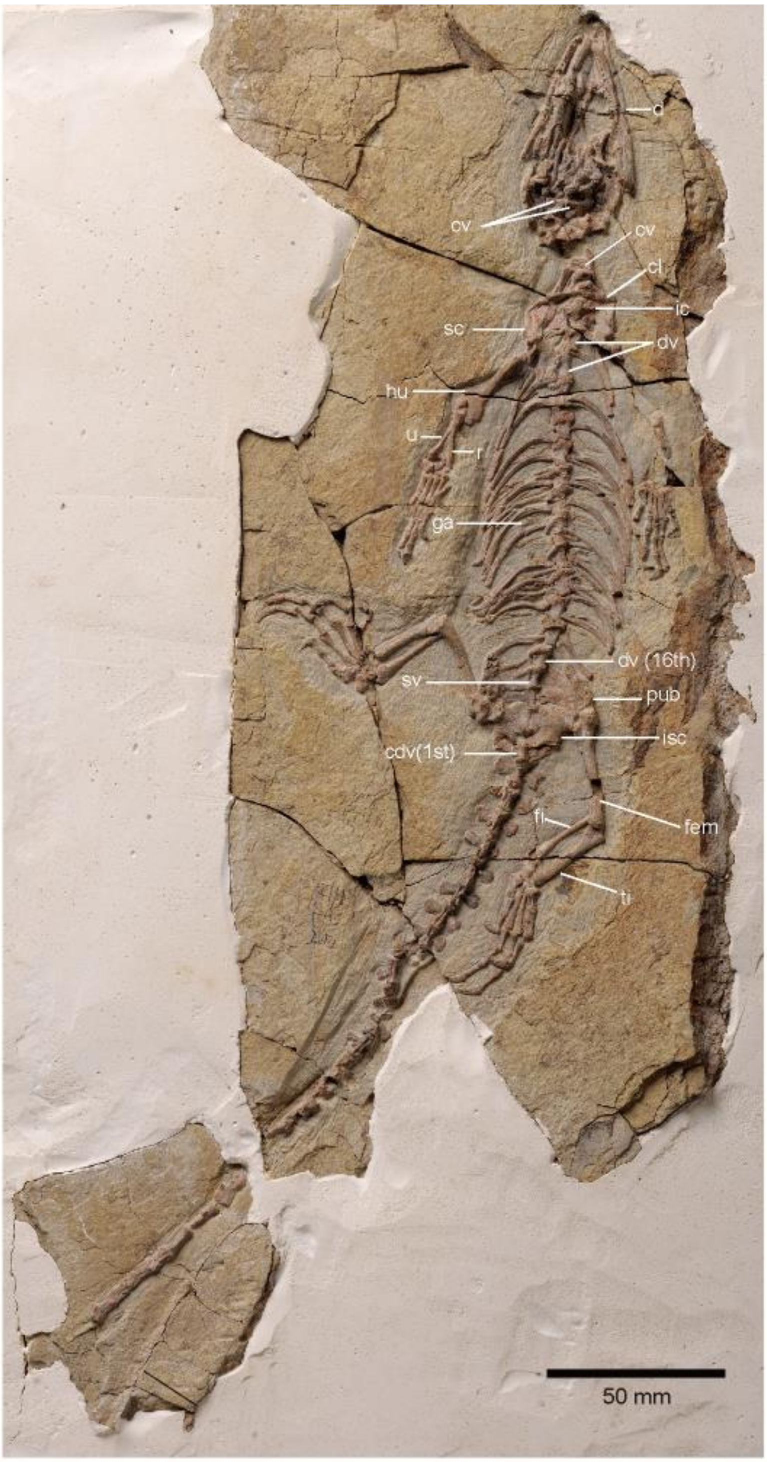

Figure 2. *Coeruleodraco jurassicus* gen. et sp. nov. Holotype (IVPP V 23318) from the Nanshimen locality, Gangou Township, Qinglong County, Hebei Province; Upper Jurassic. Skeleton as preserved in ventral view. Abbreviations: cdv, caudal vertebra; cl, clavicle; cv, cervical vertebra; d, dentary; dv, dorsal vertebra; fem femur; fi fibula; ga, gastralia; hu humerus; ic, interclavicle; isc, ischium; pub, pubis; r, radius; sc, scapulocoracoid; sv, sacral vertebra; ti, tibia; u, ulna.

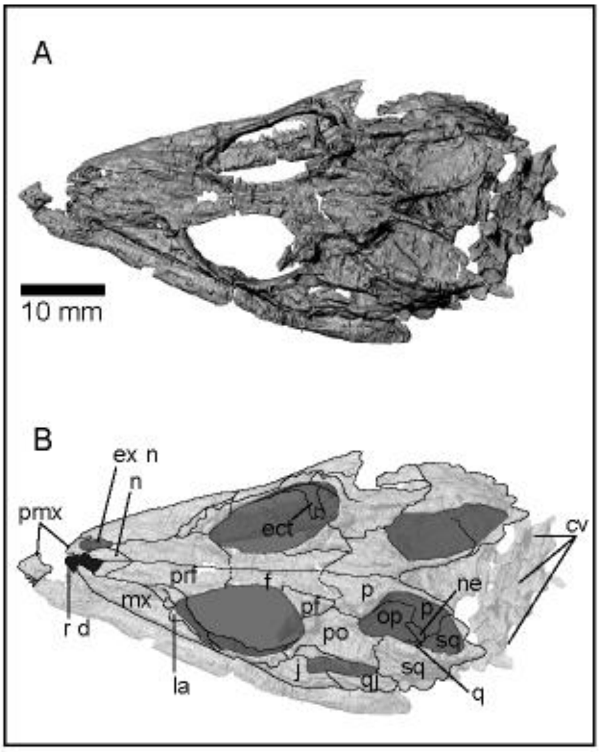

Figure 3. *Coeruleodraco jurassicus* gen. et sp. nov. µCT reconstruction of the dorsal side of the skull and cervical vertebrae (IVPP V 23318): A, dorsal view; B, line drawing of A. Abbreviations: cv, cervical vertebra; ect, ectopterygoid; ex n, external narial opening; f, frontal; j, jugal; la, lachrymal; mx, maxilla; ne, neomorph; op, opisthotic; p, parietal; pf, postfrontal; pmx, premaxilla; po, postorbital; prf, prefrontal; q, quadrate; qj, quadratojugal; r d, right dentary; sq squamosal.

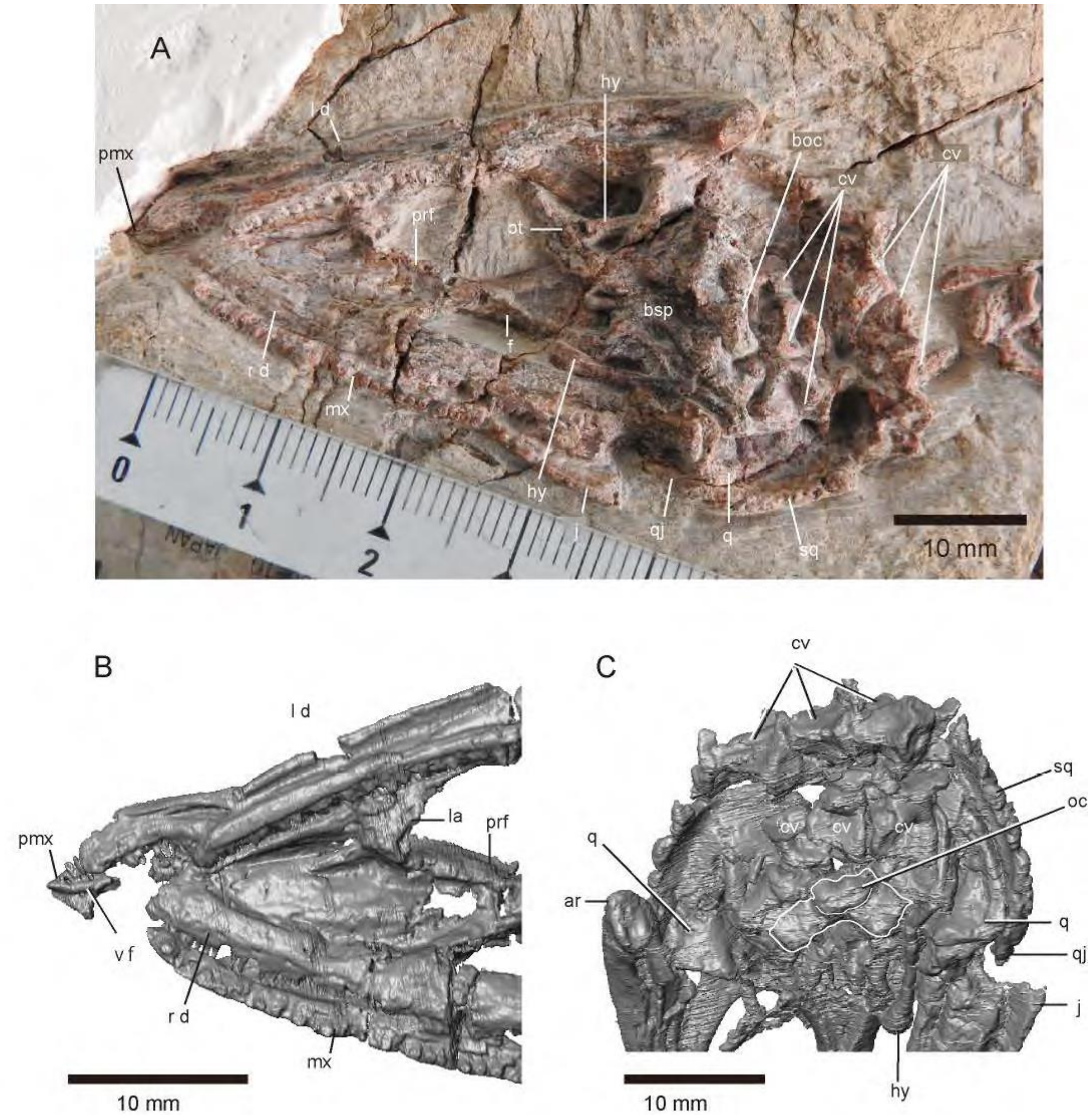

Figure 4. *Coeruleodraco jurassicus* gen. et sp. nov. The ventral side of the skull and cervical vertebrae (IVPP V 23318): A, photograph; B, µCT reconstruction of anterior snout region in ventral view; C, the back of the skull in posteroventral view. Abbreviations: ar, articular; boc, basioccipital; bsp, basipterygoid; cv, cervical vertebra; f, frontal; hy, hyoid; j, jugal; la, lachrymal; l d, left dentary; mx, maxilla; n, nasal; oc, occipital condyle; p, parietal; pf, postfrontal; pmx, premaxilla; prf, prefrontal; psh, parasphenoid; q, quadrate; qj, quadratojugal; r d, right dentary; sq squamosal; v f, vomer facet.

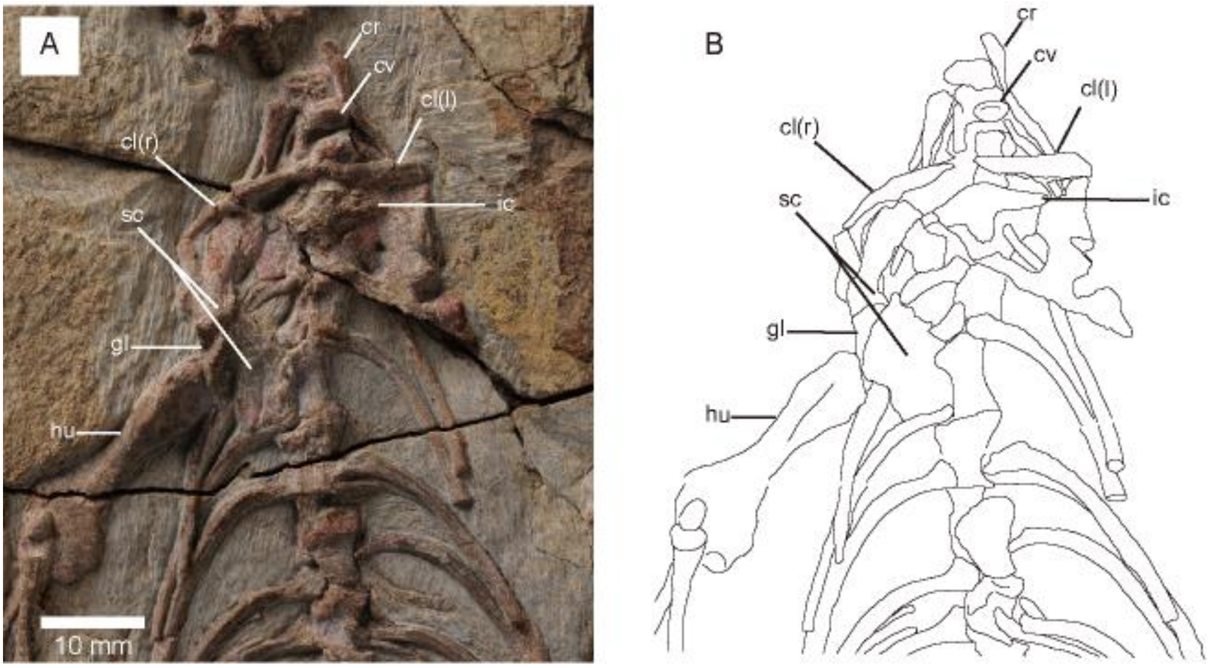

Figure 5. *Coeruleodraco jurassicus* gen. et sp. nov. A, B, pectoral girdle in ventral view (A, photo; B, line drawing). Abbreviations: cl(r) right clavicle; cl(l) left clavicle; cr, cervical rib; gl, glenoid; hu, humerus; ic, interclavicle; sc, scapulocoracoid.

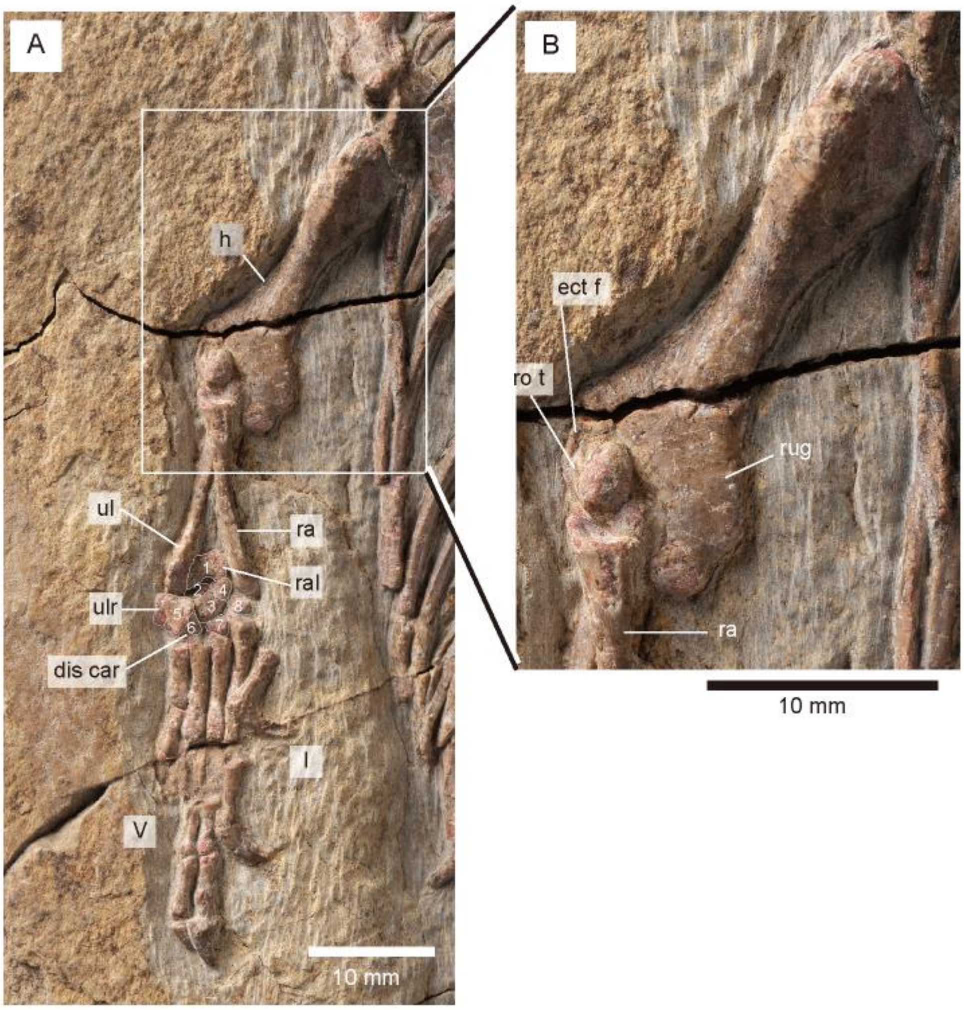

Figure 6. *Coeruleodraco jurassicus* gen. et sp. nov. A, left forelimb; B enlarged image of the area outlined in A. Abbreviations: dis car, distal carpals; ect f, ectepicondylar foramen; hu, humerus; ra, radius; ral, radiale; ro t, rounded tubercle; rug, rugosity; ul, ulna; ulr, ulnare; I, V, digit numbers. Numbered elements are carpals

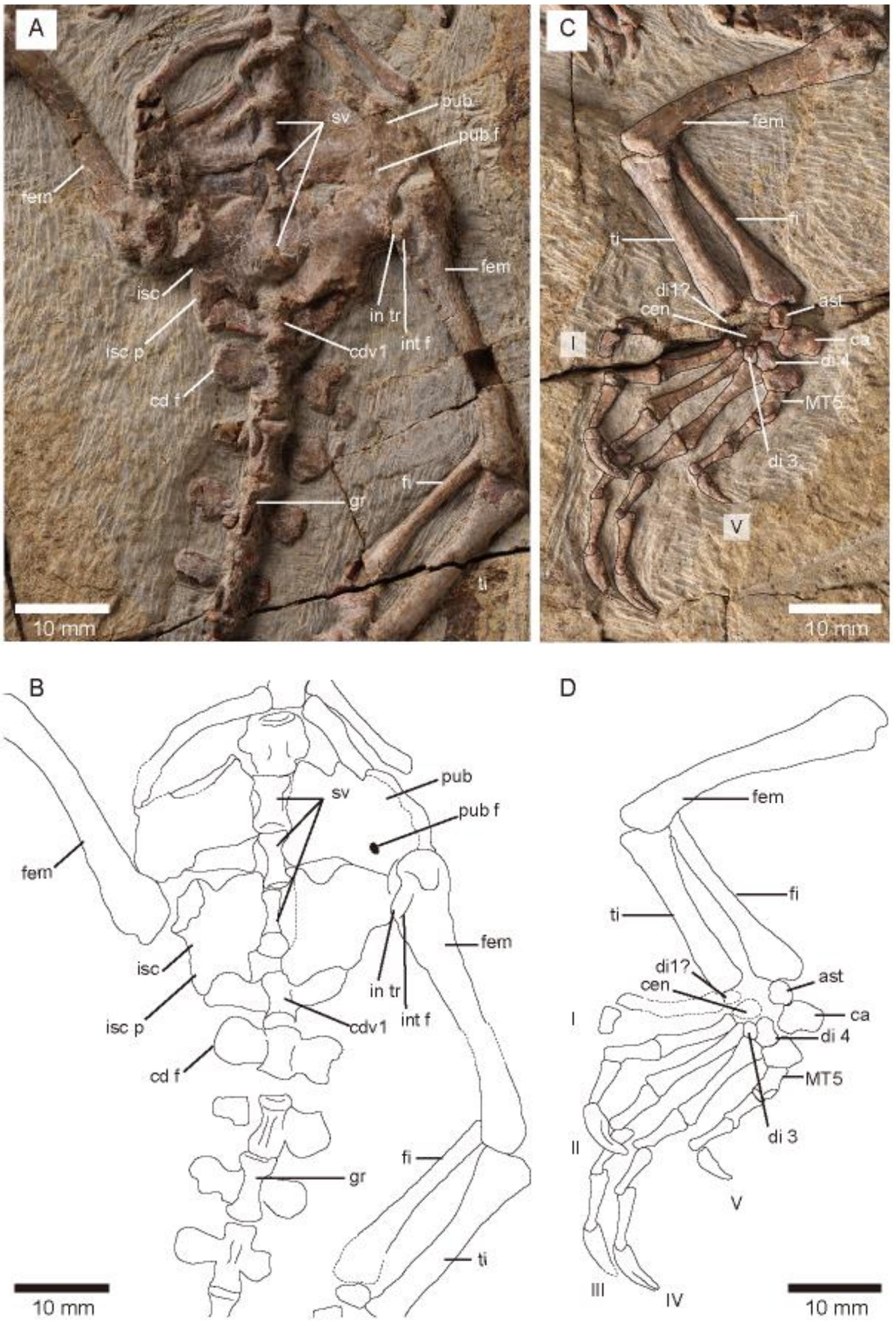

Figure 7. *Coeruleodraco jurassicus* gen. et sp. nov. A, B, pelvic girdle, sacral and anterior caudal vertebrae in ventral view (A, photo; B line drawing); C, D, left hind limb in ventral view (C, photo; D, line drawing). Abbreviations: ast, astragalus; ca, calcaneum; cd f, caudal flange; cdv1, 1st caudal vertebra; cen, centrale; di, distal tarsal; fem, femur; fi, fibula; gr, blood vessel groove; in tr, internal trochanter; int f, intertrochanteric fossa; isc, ischium; isc p, ischiadic process; MT5, 5th metatarsal; pub, pubis; pub f, pubic foramen; sv, sacral vertebra; ti, tibia. I, V, digit numbers.

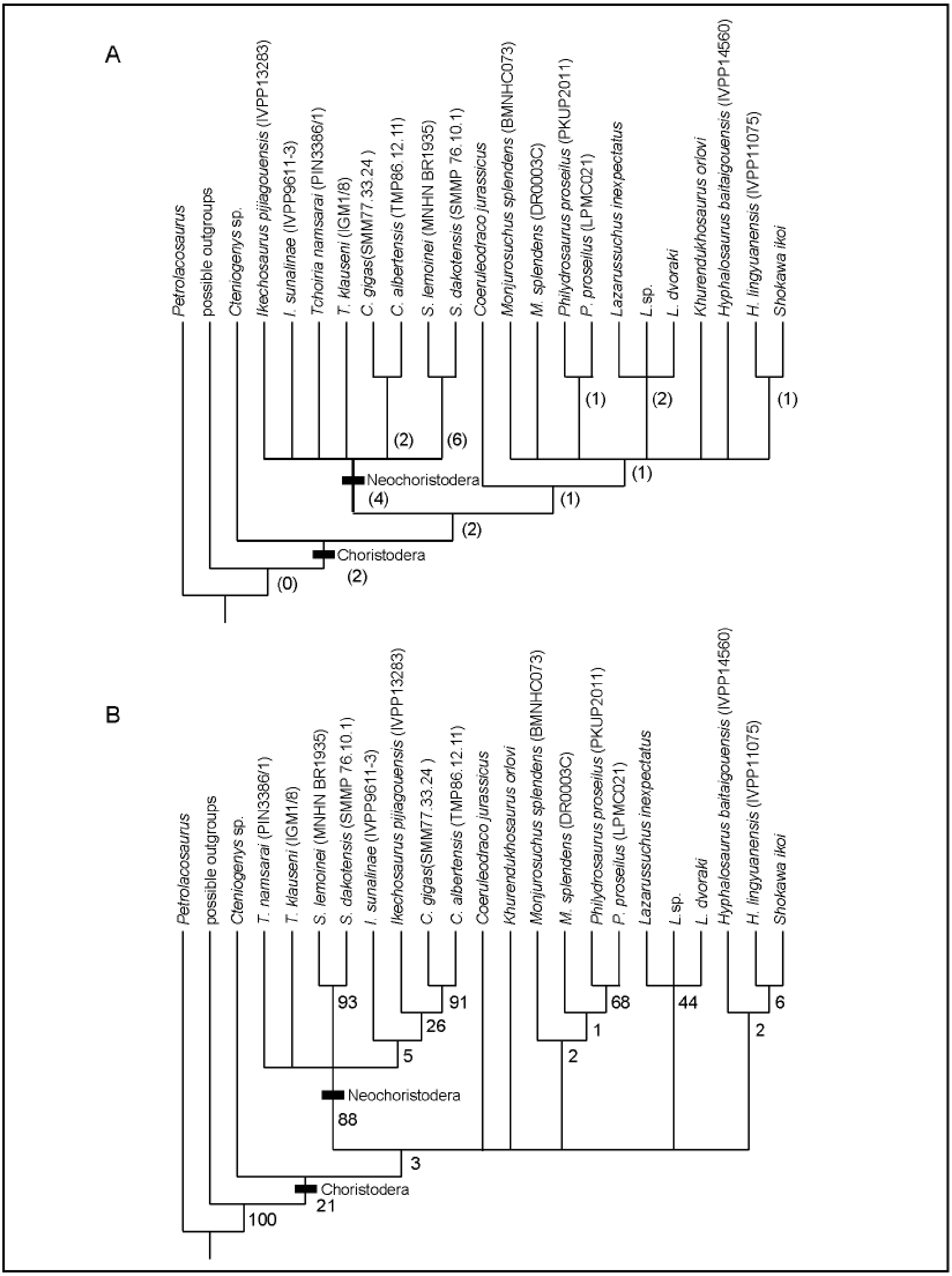

Figure 8. Phylogenetic relationships of *Coeruleodraco jurassicus* gen. et sp. nov. within Choristodera. A, strict consensus of 10 most parsimonious trees (MPTs) obtained by TNT analysis (tree length [L] = 329); B, bootstrap consensus tree, examined by 10000-replicated resampling analysis. Numbers in brackets on the tree A indicate Bremer branch supports, and numbers on the tree B indicate Bootstrap value.

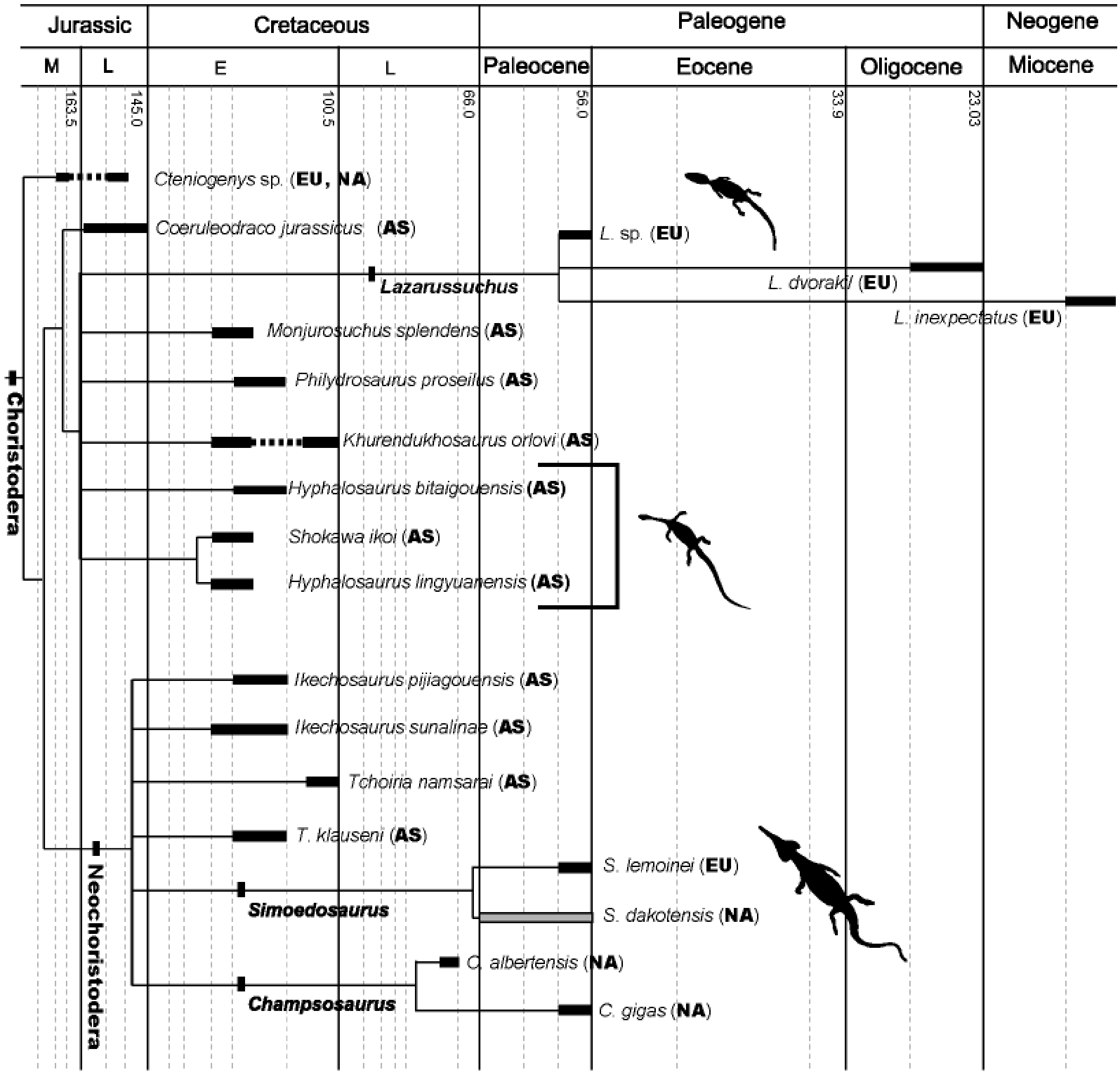

Figure 9. A phylogram of the strict consensus topology with a global chronostratigraphic timescale. Dotted vertical lines represent stage-level time, thick black lines are used when the age of the locality is identified only to stage level, and thick dotted black lines indicate the estimated range of the species. Abbreviations: AS, Asia; EU, Europe; NA, North America