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A new choristodere (Reptilia, Choristodera) from an Aptian-Albian coal deposit in China

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Abstract

Choristoderes are a small clade of freshwater aquatic reptiles known from deposits of Jurassic to Miocene age. They show their greatest diversity in the Early Cretaceous of Asia, with seven recorded genera including longirostrine and brevirostine taxa, long- and short-necked taxa, and representatives of both neochoristoderes and non-neochoristoderes. The latter, informal grouping, comprising Monjurosuchus, Philydrosaurus, Hyphalosaurus, Khurendukhosaurus, and, probably, Shokawa, is distinguished by the closure of the lower temporal fenestra. This differentiates them from typically diapsid stem choristoderes like the Jurassic Euramerican Cteniogenys and from all neochoristoderes like Champsosaurus and Simoeodosaurus. The recent description of Coeruleodraco jurassicus from the Callovian/Oxfordian of China provided the first example of an Asian non-neochoristodere with an open lower temporal fenestra. Herein we describe a second, geologically younger, genus and species from the Shahai Formation of Badaohao locality in western Liaoning, considered to be Aptian-Albian in age. This adds the eighth genus of choristoderes to the Early Cretaceous Asian record. The new species shares the diapsid skull morphology of C. jurassicus, demonstrating that a lineage of small, brevirostrine choristoderes with fully diapsid skulls persisted in Asia until the latter part of the Early Cretaceous.

Keywords

Choristodera; China; Coal; Early Cretaceous; CT scan; phylogeny
Introduction

Choristoderes form a small, enigmatic clade of freshwater aquatic reptiles that are recorded from deposits of Middle Jurassic (Evans 1990; Averianov et al. 2006) to Miocene age (Evans & Klembara 2005). They range from the size of a small lizard (e.g. Cteniogenys, Evans 1990) to that of large crocodiles (e.g. Champsosaurus, Brown 1905; Erickson 1972; Simoedosaurus, Sigogneau-Russell & Russell 1978; Erickson 1987), from brevirostrine to longirostrine, and from short-necked to long-necked (see Matsumoto & Evans 2010). Over the last two decades, a series of discoveries have revealed that the group underwent an important radiation in Asia during the Early Cretaceous, with records from Japan, China, Russia (eastern and western Siberia), and Mongolia (Matsumoto & Evans 2010; Zhang & Gao 2013; Skutschas & Vitenko 2017). These Asian genera include the short-necked, brevirostrine Monjurosuchus, total length up to 300 mm (Endo 1940; Endo & Shikama 1940; Gao et al. 2000; Gao & Li, 2007; Matsumoto et al. 2007) and Philydrosaurus (Gao & Fox 2005, Gao et al. 2007, 2013), up to 300 mm; the long-necked brevirostrine Khurendukhosaurus, ~1 m (Sigogneau-Russell & Efimov 1984; Skutschas 2008; Matsumoto et al. 2009, 2019a; Skutschas & Vitenko 2017), Hyphalosaurus, up to 1 m (Gao et al. 1999; Gao & Ksepka 2008) and Shokawa ~ 400 mm (Evans & Manabe 1999); and the longirostrine, short-necked Ikechosaurus ~ 2 m (Sigogneau-Russell 1981; Brinkman & Dong 1993; Liu 2004) and Tchoiria ~ 2 m(Efimov 1975; Ksepka et al. 2005). The latter two are the earliest known members of the Neochoristodera (sensu Evans & Hecht 1993, also including the Cretaceous-Paleogene Champsosaurus and Simoedosaurus). Gao et al. (2005) described and named an additional longirostrine taxon (Liaoxisaurus) from the Lower Cretaceous.
Jiufotang Formation of China. However, the specimen on which the new genus was based is closely similar to *Ikechosaurus pijiagouensis* (Liu 2004) from the same horizon. Matsumoto *et al.* (2015) also reported, but did not name, a longirostrine neochoristodere from the Early Cretaceous of Japan.

Neochoristoderes are consistently recovered as a monophyletic clade in phylogenetic analyses (e.g. Matsumoto *et al.* 2013, 2019a, b). The relationships of the brevirostrine taxa have proved more controversial, but they consistently fall outside Neochoristodera. Significantly, although the earliest known unquestionable choristodere (the Middle-Late Jurassic *Cteniogenys*) is fully diapsid, all other ‘non-neochoristoderes’ for which the skull is known (i.e. *Lazarussuchus* Hecht 1993, *Monjurosuchus, Philydrosaurus, Hyphalosaurus, Khurendukhosaurus*) had completely closed the lower temporal fenestrae by expansion of surrounding bones. This observation raised questions as to the ancestry of the earliest known neochoristoderes (*Ikechosaurus, Tchoiria*) as these classically diapsid taxa are unlikely to have arisen from a lineage with a closed lower fenestra.

More recently, however, we (Matsumoto *et al.* 2019b) described a new brevirostrine choristodere, *Coeruleodraco jurassicus*, from the Late Jurassic of China. This species differs from other Asian brevirostrine species in the presence of an open lower temporal fenestra. Our phylogenetic analysis of *C. jurassicus* placed it, with weak support, as the sister taxon of a clade comprising all Asian brevirostrine choristoderes as well as the European Paleocene-Miocene *Lazarussuchus*.

*Cteniogenys* was consistently placed on the choristoderan stem.

Here we describe new choristoderan material from the Aptian-Albian Shahai Formation of Badaohao locality, Liaoning Province, China. Although only a few bones are visible at the surface of the relevant blocks, CT scans revealed many
other cranial and postcranial elements within the matrix, including a partial skull. These specimens show that, like *Cteniogenys* and *Coeruleodraco jurassicus*, the Badaohao choristodere combined a brevirostrine skull with an open lower temporal fenestra. Thus, a lineage of fully diapsid non-neochoristoderes persisted in Asia until the latter part of the Early Cretaceous.

**Geological Background**

The choristodere specimens reported here, IVPP V 25322, 25323 and 25324 were collected from coaly siltstone in the middle part of the Shahai Formation, at the Badaohao locality, in Heishan County, Liaoning Province, China (Fig. 1). The Shahai Formation is generally considered to overlie the Jiufotang Formation conformably and to be overlain conformably by the Fuxin Formation (Wang 1989; Jin 1996), although there are debates as to the conformity between the Shahai and Jiufotang formations (Chen *et al.* 1988). Moreover, there have been suggestions that the Shahai Formation is a synonym of the Fuxin Formation (based on bivalves), or that the Shahai Formation is equivalent to the Jiufotang Formation (based on pollen) (Jiang *et al.* 2010). The age of Shahai Formation has not been ascertained by either radiometric dating or index fossils, but is considered to be of Aptian-Albian age based on the underlying Jiufotang Formation that has a radiometric age of 120 Ma (He *et al.* 2004; Kusuhashi *et al.* 2009a, b, 2010).
The Fuxin flora, represented by the plant fossils from the Shahai and Fuxin formations, consists of over 300 species, dominated by Filicopsida, Ginkgopsida and Coniferopsida. The flora is divided into three assemblages, of which the Shahai Formation is represented by the *Acanthopteris-Ginkgo coriacea* Assemblage (Deng et al. 2012). The Fuxin flora is considered indicative of a humid, temperate climate, comparable with the Early Cretaceous floras of Siberia and Canada, and the Tetori flora of Japan (Deng et al. 2012).

Several mammals, including eutriconodontans, spalacotheriids, multituberculates, stem zatherian and eutherians (Hu et al. 2005; Li et al. 2005; Kusuhashi et al. 2009a, b, 2010, 2016), have been reported from the Badaohao locality, as well as some dinosaur teeth and eggs (Xu et al. 1998; Zhao & Zhao 1999; Amiot et al. 2010), and fishes (Jin 1996). Other fossil vertebrates, including lizards and frogs, have been recovered from the locality and are currently under study.

**Material and methods**

There are three blocks (IVPP V 25322, 25323, 25324) (Fig. 2), all collected by Dr. Qian Li on the 23rd September, 2003, at the Badaohao locality, and housed in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing, China. The surface of IVPP V 25323 bears the impression of a dentary that is preserved on the surface of IVPP V 25322, and the two blocks fit together showing they were originally one piece. However, based on the embedded elements (see below; one right surangular in IVPP V 25323, and a right and a left surangulaturs in IVPP V 25322), separate catalogue numbers were given to the blocks in case two
different individuals are represented between these blocks. The only elements
exposed on the surface of the blocks are a left dentary on IVPP V 25322, its
impression on IVPP V 25323, and a right jugal on IVPP V 25323.

We scanned the specimens 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. All
three blocks were scanned with a beam energy of 140 kV and a flux of 120 µA, using
a detector resolution of 63.05 µm per pixel for IVPP V 25322, of 61.90 µm per pixel
for IVPP V 25323; and of 63 µm per pixel for IVPP V 25324. A 360° rotation with a
step size of 0.5° and an unfiltered aluminium reflection target was adopted for each
scan. 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 slice data revealed that the blocks
contained many more elements than were visible on the surface (Fig. 2). Each
element from each block was segmented out and visualized using the software Avizo
8.1 and 9.0 to display detailed anatomical information. The cranial elements,
mirrored as necessary, were then 3D printed to assemble into a reconstruction (Fig.
3). The 3D printing was carried out using an Objet 260 Connex3, at three times the
original size. The elements from IVPP V 25322 and 25323 were then scaled with
those on IVPP V 25324 based on the length of squamosal and jugal to give a
uniform scale.
IVPP V 25322 was found to contain several skull bones including a left squamosal, jugal, prefrontal, and lachrymal, a right ectopterygoid, and the right and left dentaries and surangulars. It also bears a scatter of vertebrae (cervical, caudal), ribs, and phalanges, as well as some unidentified elements. IVPP V 25323 contains further vertebrae (cervical, dorsal, caudal), ribs, gastralalia, and phalanges, as well as a clavicle, a possible tibia, a right surangular, and some unidentified bones including what may be fragments of braincase. IVPP V 25324 (Fig. 2E, F) contains the remains of a second individual including a partial skull (left parietal, postorbital, jugal, quadratojugal and squamosal); further disarticulated skull elements including right and left quadrates, a right premaxilla, a right jugal, a left ectopterygoid, a left coronoid, prearticular and splenial, a right palatine, and a few postcranial elements including a rib, a vertebra, phalanges, and possible carpals. We have designated IVPP V 25324 as the holotype due to the partial articulated skull that is certainly from a single individual.

The close similarity in the morphology of bones such as the jugals, squamosals, and prearticulars between the blocks supports the conclusion that the bones on all three blocks represent individuals of a single species.

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, Chinese Academy of Science, 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.

Systematic Palaeontology

Reptilia Linnaeus, 1758
Choristodera Cope, 1884
Genus Heishanosaurus gen.nov.

Etymology. Heishan is the name of the county in which the type locality for the choristoderan material is located.

Type species. Heishanosaurus pygmaeus.

Diagnosis. As for type and only species.

Heishanosaurus pygmaeus sp. nov

(Figs 2, 3, 5–12)
Etymology. Pygmaeus (Latin), meaning dwarf. The species name recognizes the small size of this taxon compared to many other Cretaceous species.

Holotype. IVPP V 25324, partial skull with some disarticulated cranial and postcranial elements (Fig. 2E, F).

Type Locality and horizon. Badaohao locality, Heishan County, Liaoning Province, China. Shahai Formation, of Aptian-Albian (Early Cretaceous) age.

Differential diagnosis. A small choristodere that resembles Cteniogenys and Coeruleodraco, and differs from all other described choristoderes, in combining the possession of a small lower temporal fenestra with a short rostrum, a small lachrymal limited to the orbital margin, separate postfrontal and postorbital bones, and a short mandibular symphysis. It resembles Cteniogenys and differs from Coeruleodraco in having a lachrymal canal that perforates the lachrymal bone (passes between lachrymal and prefrontal in Coeruleodraco). Heishanosaurus differs from Cteniogenys in having a more slender postorbital process of the squamosal; a narrower, more tapered dorsal process of the jugal; a prefrontal that is pentagonal rather than rectangular in dorsal view; a parietal that is more massive in its build with deeper postparietal processes; a coronoid that, although small, has a distinct coronoid process (rounded dorsal margin in Cteniogenys); and a skull outline that is proportionally shorter and wider (narrow and tapering in Cteniogenys). It resembles Coeruleodraco and differs from Cteniogenys in having tubercular sculpture along the posterior margin of the squamosal. Heishanosaurus also resembles Coeruleodraco in having ungual phalanges without a tubercle, but differs in having a squamosal with a postorbital process longer than quadratojugal process (shorter/equal in Coeruleodraco); a square lateral plate of the squamosal (anteroposteriorly elongated in Coeruleodraco); a median parietal suture that is longer than the parietal
squamosal process (shorter/equal in C. jurassicus); distinct dorsal and posterior processes of the jugal (processes short in Coeruleodraco); a sickle-shaped quadratojugal (narrow rectangle in Coeruleodraco); a postorbital with a weakly concave (vs strongly concave) ventral margin; a shorter mandible with fewer dentary teeth (27 in Heishanosaurus pygmaeus vs 37–38 in Coeruleodraco); and caudal transverse processes that are not expanded (expanded caudal ribs are a diagnostic character of Coeruleodraco).

**Referred specimens.** IVPP V 25322 and IVPP 25323 (originally part of a single block), also from Shahai Formation at the type locality.

**Remarks.** This newly discovered small reptile is identified as a choristodere based on the combination of the following characteristic features: paired prefrontals meeting in the midline, forming anterior margin of orbits; a long shallow dentary ramus with labial neurovascular foramina opening into longitudinal grooves; conical subthecodont teeth; well sculptured parietal and squamosal forming cordiform skull. *Heishanosaurus* most closely resembles *Coeruleodraco* in general skull features, but a majority of these are either primitive (short rostrum, lower temporal fenestra, separate postorbital and postfrontal) or common in non-neochoristoderes crownward of *Cteniogenys* (tubercular sculpture). In the phylogenetic analyses run for this work (see below), *Heishanosaurus* and *Coeruleodraco* were not found to be sister taxa and were consistently placed as consecutive or unresolved outgroups to all other choristoderes except *Cteniogenys*. This separate placement could be due to missing data (e.g. for the palate, braincase, and limb skeletons of *Heishanosaurus*) but, given the age difference (Aptian/Albian vs Callovian/Oxfordian), and the striking
differences between *Heishanosaurus* and contemporary Asian choristoderes, it seems preferable to place the Badaohao choristodere in a new genus pending the recovery of further material. To aid comparison, new comparative figures of *Coeruleodraco* are provided in Supplementary data files.

**Description.**

Fig. 3 shows a reconstruction of the skull (Fig. 3A) and lower jaw (Fig. 3B) based on the individual elements on the three blocks, with comparable elements scaled to the same size and 3D printed. Overall skull length is constrained by dentary and surangular length, but we cannot be certain of the shapes or relative proportions of the nasals (absent), prefrontals (possibly breakage), and frontals (absent). The cranial bones and their articular surfaces are fully formed and seem therefore to be those of adult and/or sub-adult individuals. This is supported by the complete closure of the neurocentral sutures, the absence of a patent notochordal canal in the vertebrae, and the ossification of tarsal and carpal elements scattered through the blocks.

[insert Fig. 3 here]

As reconstructed, the skull is dorsoventrally compressed with preorbital and postorbital regions of roughly equal length, although snout length remains somewhat uncertain (as is coded as such in the data matrix). As in all choristoderes, the prefrontals met in the midline between the nasals and frontals, and contributed to the preorbital skull roof, and there is a large, posteriorly expanded upper temporal fenestra. As in neochoristoderes, *Cteniogenys*, and *Coeruleodraco jurassicus* (Fig.
4, and Supplementary Information), there is also a lower temporal fenestra. All median skull bones are paired, and the parietals and squamosals are strongly sculptured with bony tubercles and spikes.

[insert Fig. 4 here]

The skull of IVPP V 25324

The designated holotype (IVPP V 25324) contains the partial left half of a skull with the parietal, squamosal, postorbital, jugal, and quadratojugal in close association (Fig. 3C). Other cranial (right jugal, right prearticular, right coronoid, both quadrates, left ectopterygoid, left palatine, left premaxilla) and postcranial elements (phalanges, possible carpals, a rib, a caudal vertebra) in proximity to the association are probably part of the same individual, based on size and the consistency of morphological features.

The parietals were originally paired (Fig. 5A, B). As preserved, the left parietal is formed by two distinct plates, the dorsal skull table and a posteroventrolaterally expanded squamosal wing, with the former slightly longer than the latter (almost equal in Coeruleodraco). The median parietal suture is relatively shallow for a choristodere, although it deepens slightly at the posterior end. As in all choristoderes, there was no medial parietal foramen (Fig. 5A). The dorsal plate of the parietal is heavily sculptured with a strong lateral crest that runs parallel to the midline and forms the dorsomedial margin of the upper temporal fenestra. The crest separates the horizontal rectangular skull table from a sloping ventrolateral flange that would have accommodated adductor muscles. As delimited by the crests, the skull table is narrower than that of Coeruleodraco. The forked anterior margin of the
skull table bears an interdigitating suture for the frontal. Further laterally, the angled margin of the adductor flange bears a facet for the postorbital. Posterolaterally, the parietal expands into a broad wing that met the squamosal to form the posteromedial margin of the upper temporal fenestra. However, the posterior 20% of this wing lies at a slightly different level to the rest and could be the anterior edge of the squamosal. Clearly, the squamosal has a strong articulation with the parietal. The ventral margin of the posterior wing is damaged, but it probably attached to the opisthotic, whereas the posteromedial edges of the parietal table met the supraoccipital.

The left squamosal on IVPP V 25324 (Fig. 5C, D) is almost complete but it is supplemented by the squamosal on IVPP V 25322 (Fig. 5E–H). The squamosal is formed by lateral and posteromedial plates that meet at 30°, and together formed the posterolateral border of the upper temporal fenestra. The lateral plate is square (roughly equal in length and height), strongly ornamented, and has ventral and posterior margins bearing strong spikes (Fig. 5C, E). The plate bifurcates anteriorly into dorsal and ventral processes. The narrow dorsal process is mediolaterally compressed and is roughly one and a half times the length of the ventral process (almost equal in Coeruleodraco). The dorsal process is damaged at the tip but bears part of a slot facet for the postorbital (Fig. 5E). Together the squamosal and postorbital formed the upper temporal bar, between upper and lower temporal fenestrae. The shorter, ventral process of the lateral plate met the quadratojugal, and bears a sloping facet for that bone at its anteroventral tip. The squamosal thus provided the posterodorsal and posteroventral borders of the small lower temporal fenestra. The medial lamina of the squamosal met the parietal anterodorsally, as described above. Below the parietal facet, the medial lamina bears a deep groove
that expands dorsoventrally and accommodated the dorsolateral margin of the quadrate (Fig. 5D, 5C). At the junction of the parietal and quadrate facets, there is a small notch facet for the neomorph (Fig. 5D, 5F–G).

The associated left jugal on IVPP V 25324 is in two parts, with its suborbital process slightly displaced (reconstructed in Fig. 6A, B). It is supplemented by a disarticulated right jugal on the same block, and by a well-preserved left jugal on IVPP V 25322 (Fig. 6C–E). The jugal is strongly triradiate with anterior, dorsal and posterior processes. The dorsal process is slightly shorter than the posterior process and has a small anterolateral postorbital facet at its tip. The shallow anterior suborbital process is the longest and bears a narrow, ventromedial facet for the maxilla (Fig 6B, D, E). The narrow posterior process bears a distinct posteromedial facet for the quadratojugal (Fig. 6B, D), the two bones forming most of the ventral margin of the open lower temporal fenestra. This slender posterior process is markedly different from the jugal of *Monjurosuchus, Philydrosaurus*, and *Hyphalosaurus*, where the deep posterior flange of the jugal contributes to the closure of the lower temporal fenestra. The medial surface of the jugal is generally smooth, but it bears a facet for the ectopterygoid at the medial junction of the three processes. At its anterior tip, the ectopterygoid facet lies adjacent to the posterior part of the maxillary facet (Fig. 6B, D), and it is possible that these bones were in contact.

The left quadratojugal is preserved only on IVPP V 25324 (Fig. 6F–I). It has a scythe-like shape in lateral view, tapering anteriorly but with a slight dorsal concavity.
The anterior process forms the posterior half of the lower temporal bar. Its anterior tip is somewhat dorsoventrally compressed, and bears a shallow dorsolateral facet for the jugal (Fig. 6F). The thicker posterior end of the bone bears a medial slot facet that accommodated the lateral process of the quadrate (Fig. 6G, I), and a posterodorsal overlap facet for the ventrolateral process of the squamosal (Fig. 6H, I).

The left postorbital completes the associated skull part on IVPP V 25324 (Fig. 6J–N). It is a robust bone with a thick, ornamented, orbital rim that supports the postfrontal facet dorsally and an interlocking jugal facet ventrally. A broad temporal lamina extends posteriorly from the orbital margin, divided into dorsal and ventral parts by a strong ridge that formed the anterolateral margin of the upper temporal fenestra (Fig. 6K). The lamina tapers posteriorly into the ventral squamosal process that bears a mediolaterally compressed, interdigitating facet for the squamosal at its tip (Fig. 6K, M–N). The facet for the postfrontal excavates the dorsal surface of the dorsal temporal lamina anteriorly, whereas the anteromedial border bears an interdigitating surface for articulation with the parietal (Fig. 6K, M–N). As articulated, it seems unlikely that the postfrontal met the parietal, unlike Coeruleodraco where there is a small contact. The posteromedial edge enters the margin of the upper temporal fenestra. The ventrolateral margin of the temporal lamina borders the lower temporal fenestra.

[insert Fig. 6 here]

Both right and left quadrates lie in association with the partial skull on IVPP V 25324 although they are not in articulation (Fig. 7A–F). Each resembles a flattened
triangle, with a narrow dorsal apex, a slightly expanded lateral flange and a more strongly expanded medial one separated by a dorsoventral crest (Fig. 7B, E). This crest, absent in *Coeruleodraco*, supports a small rounded dorsal condyle, and an anteroposteriorly compressed, bilobed, ventral mandibular condyle (Fig. 7F). The anterior surface of the quadrate is slightly concave at the junction between the mandibular condyle and the medial flange (Fig. 7A, D). The lateral margin of the bone bears two facets. The longer, dorsal one is a narrow facet that extends up to the dorsal condyle, and which inserted into the slit on the medial surface of the squamosal. The smaller ventral facet inserted into the shallow groove on the posteromedial margin of the quadratojugal (Fig. 7C). The medial flange of the quadrate is expanded into a pterygoid lappet that has a deep pterygoid facet along the ventral margin (Fig. 7B, E). Dorsal to the pterygoid facet, the medial border of the bone bears an overlapping facet for the opisthotic, whereas a more dorsal facet, close to the apex, may be for a neomorph (Fig. 7B, E).

Three other cranial bones are preserved on IVPP V 25324, a right premaxilla, a right partial palatine, and a left ectopterygoid. Given their proximity to the associated skull region, they probably belong to the same individual.

The premaxilla is small and may not be complete (Fig. 7G–J). The vertical medial margin met the contralateral premaxilla in a short anterior suture. The lateral margin is deeper and notched, possibly for articulation with the maxilla (not preserved on any specimen). From medial to lateral, the anterodorsal margin is curved. No median nasal process is preserved, suggesting the nares may have been confluent, but this is coded as uncertain in the data matrix as the bone may be damaged. Two conical teeth are preserved in situ, with space for an additional tooth
medially (Fig. 7H). On the posterodorsal surface, a shallow depression may represent an articular facet for the vomer (not identified; Fig. 7G).

A small triangular bone lying close to the left jugal seems to be part of the palate, but it may not be complete (Fig. 7K, L). It has processes for the maxilla and vomer (Fig. 7K). The maxillary process is short and broad-based, and seems to have abutted the medial surface of the maxilla (Fig. 7K). The vomerine process may be broken, but its tip has part of a slot facet for the vomer. Between the maxillary and vomerine processes, the concave anterior margin formed the posterior border of the choana. Posterolateral to the vomerine facet, the palatine would have articulated with the pterygoid, but this part of the bone is damaged (Fig. 7K). A single, slightly curved, palatal tooth row extends along the maxillary border, with conical denticles (Fig. 7K). On the dorsal surface, there are several features, including a ridge that crosses the bone parallel to the choanal margin before curving posteriorly (Fig. 7L). Small grooves cross the dorsal surface of the palatine in *Cteniogenys* (Evans, 1990), but it is not clear whether this ridge is a part of a similar groove arrangement, or some other structure. The ridge is flanked posteriorly by what appears to be a facet. However, without either the maxilla or pterygoid, it is difficult to estimate how far anteriorly the palatine was placed and how it was related to the other rostral skull elements.

The ectopterygoid is a small hammer-shaped element, composed of a short, wide lateral head, and a slender, horizontally orientated, pterygoid process (Fig. 7M–O). The lateral head bears a smooth triangular surface (Fig. 7O), apex anterior, that fits into a recess on the medial surface of the jugal. The anteroventral part of this surface has a small, narrow facet for the maxilla (Fig. 7N). The pterygoid process has a slightly expanded medial end that lies at 90° to the jugal surface. The facet for
the pterygoid is probably not complete. A right ectopterygoid is preserved on IVPP V 25322, but provides no additional details.

A coronoid and prearticular associated with IVPP V 25324 are described below with the lower jaw elements.

Additional skull elements on IVPP V 25322 and 25323

The prefrontal is preserved only on IVPP V 25322 (Fig. 8A–E). As in other choristoderes, it comprises a horizontal dorsal lamina, and a ventrolateral lamina that contributed to the orbital margin and the preorbital skull wall (Fig. 3A). The dorsal lamina met the contralateral prefrontal in the midline to form the anterior part of interorbital skull roof and to contribute to the rostrum between the nasals and frontals. The reconstruction in Fig. 3 is based on the assumption that the median suture is fully preserved, but this area is thin and the surface lacks detail. The main body of the bone is trapezoid with a slight ornamentation (Fig. 8A). Its posterodorsal surface bears an anteriorly tapering concavity that represents the frontal facet (Fig. 8A). The ventrolaterally expanded lamina met the lachrymal along the orbital margin. Anterior to the lachrymal facet, the lamina bears a narrow shelf that was overlapped by the maxilla (Fig. 8A, E). On the ventral surface, an L-shaped ridge met the palatine (Fig. 8B). When the skull is reconstructed, the prefrontal as preserved seems to be too short and it is possible that part of the bone is missing anteriorly. The shallow descending lamina also suggests that the rostrum was depressed.

IVPP V 25322 also preserves a small wedge-shaped lachrymal that lay in the orbital margin between the jugal posteroventrally, the maxilla anteroventrally, and the prefrontal anterodorsally (Fig. 8F–J). The concave orbital margin is perforated by a foramen (probably two merged foramina) that would have led into a nasolachrymal
canal, but this canal could not be traced through the bone on the CT scan data due to the difficulty of distinguishing between cracks and canals. The dorsolateral surface of the bone is triangular with a long tapering posterior process and a short curved anterior border (Fig. 8F). The lateral surface is slightly concave, and it is perforated by a small foramen that leads into a recess on the ventromedial surface (Fig. 8G). This foramen is likely to have carried a sensory branch of the maxillary (trigeminal) nerve. The ventral border of the bone bears a deep groove that accommodated the maxilla anteriorly and the jugal posteriorly (Fig. 8G, H). The maxillary facet extends a short distance up the anterior margin of the bone (Fig. 8I). Further dorsally, this anterior margin would also have met the prefrontal but the articular surface is not clearly demarcated on the specimen except at the dorsal tip (Fig. 8F). This may be a resolution problem or due to damage.

Other fragmentary elements on the blocks may be parts of the braincase or rostrum, but we were not able to identify any of these with confidence.

[insert Fig. 8 here]

Lower jaws

Both dentaries are preserved on IVPP V 25322, the right bone exposed on the surface and the left within the block and revealed by CT scan. They are ~ 28 mm in length and show typical choristoderan features including a long shallow dentary ramus with fine lateral striations and two rows of labial neurovascular foramina with many of these foramina opening into longitudinal grooves on the lateral surface (Fig. 9A, E). However, the dentaries differ from those of most choristoderes in being relatively short, and in being significantly deeper (by three times) at the posterior end.
than the symphysial end (twice the depth in *Coeruleodraco*), with a slightly curved ventral margin (Fig. 9B). The bone is bifurcated at its posterior tip, with the upper ramus much longer than the lower one. Seen in medial view (Fig. 9B), the meckelian fossa is open the full length of the bone, and divides the short (3–4 tooth positions) symphysial surface into dorsal and ventral parts (Fig. 9B, C). The subdental ridge and the ventral border of the bone are smooth, so that the presence or absence of a splenial cannot be confirmed (Fig. 9B, D). At the posterior end of the tooth row there is a shallow facet for the small coronoid and, below this, a larger facet for the surangular that slots into the posterior end of the dentary (Fig. 9B). There is no obvious angular facet. The right dentary bears 26 conical homodont teeth with a subthecodont implantation in shallow circular alveoli (Fig. 9C). With 3–4 positions missing the teeth, the total tooth count is around 30. A tooth count is more difficult on the left, but appears to be roughly the same. These teeth are simple and conical throughout the tooth row, with no basal labyrinthine folding and enamel extending only over the upper two-thirds of the crown. The anterior ten teeth are somewhat smaller and narrower than those in the middle and posterior end of the jaw (Fig. 9B). Empty tooth positions suggest that active replacement was ongoing.

[insert Fig. 9 here]

The left and right surangulars are also preserved in IVPP V 25322 (Fig. 10A–E), with the right element more complete (Fig. 10C–E). There is also an additional, partial surangular on IVPP V 25323. The bone is deep posteriorly and tapers anteroventrally. The lateral surface of the surangular shows a similar ornamentation to that seen on the dentary (Fig. 10A, C). The anterior tip inserts into the posterior
end of the Meckelian canal of the dentary, as shown by the deep forked grooves along almost two thirds of the dorsolateral margin (Fig. 3B, 10C). Posterior to the dentary facet, the ventral margin bears a shallow angular facet (Fig. 10A, C). In medial view, the dorsal border of the adductor region is thick and rounded, with an incised facet for the coronoid along the anterior edge (Fig. 10B, D). The ventral border is thinner, especially anteriorly (Fig. 10E). There are no obvious facets for the prearticular, and it is likely that this was supported ventrally by the angular. Posteromedially, a sharp crest separates the adductor chamber from the articular region (Fig. 10B, D). The articular compartment has a roughened surface for the attachment of the articular (Fig. 10B, D), but neither this element, not the angular, are preserved on any of the blocks.

The coronoid is a small, needle-like element preserved on the holotype block (IVPP V 25324; Fig. 11A–D). As seen in medial view, the bone comprises a small coronoid process, a short, thick, posterior surangular process, and a long slender anterior dentary process (Fig. 11A). Just anterior to the coronoid process, the bone also expands medially into a small hook-shaped process that forms the curved anterior margin of the adductor fossa (Fig. 11B). The inferior surface of this medial shelf must have contacted the prearticular, although there is no obvious facet (Fig. 11D).

A prearticular is preserved on IVPP V 25324 (Fig. 11E–G) and IVPP V 25323 (Fig. 11H), both from the left side. The bone on IVPP V 25323 is better preserved (Fig. 11E–G). It forms a smooth, slender plate with a keel running along the
ventromedial margin and delimiting the dorsal margin of a large angular facet. The prearticular expands posteriorly, creating a gently curved dorsal margin (Fig. 11E, H). In lateral view, this dorsal margin appears thick and rounded, forming the medial edge of the adductor fossa (Fig. 11F). The expanded posterior end of the bone is slightly inflated dorsally and ventrally bears a recess that may have supported the articular (Fig. 11F, G).

Although the angular is not preserved, the facets on the surangular and prearticular suggest that it would have been a substantial, trough-like bone forming the posteroverentral margin of the mandible and linking the surangular laterally with the prearticular medially.

**Axial skeleton**

Isolated vertebrae are preserved on each of the blocks. All vertebrae are amphicoelous but with a closed notochordal canal and closed neurocentral sutures (Fig. 12A–T).

A single cervical is preserved on IVPP V 25323 (Fig. 12A–E). It is almost complete, with only slight damage to the slightly tapering neural spine that is set towards the posterior end of the vertebra (Fig. 12B). The centrum is short, its length almost equal to its height (Fig. 12B). The anterior and posterior joint surfaces contain a small notochordal pit (Fig. 12A, C). The centrum bears a strong midventral keel, flanked by concavities on either side of the centrum (Fig. 12A). The transverse process is positioned at the junction of the centrum and neural arch, but the
parapophysis is damaged and not visible (Fig. 12B). The anterior and posterior
zygapophyses are broad (Fig. 12A, C), with the anterior joint surfaces almost
horizontal and the posterior one slightly inclined (~30° to the horizontal).

Three complete dorsal vertebrae are preserved on IVPP V 25322 (Fig. 12F–J)
and V 25323 (Fig. 12K–N). That on IVPP V 25322 has a shorter centrum (1.5 times
longer than high) than those on IVPP 25323 (~twice as long as high; Fig. 12L), and
is probably from a more anterior position along the vertebral column. The centra
have a rounded, rather than sharp, midventral ridge (Fig. 12J, N), and are flanked by
shallower concavities. The neural spine is square in lateral view rather than tapering
(Fig. 12G, L), becoming more rectangular in profile in the more posterior dorsals, and
the dorsal edge of the spine (the spine table) is slightly expanded (Fig. 12F, K).
Unlike those of cervical vertebra, the zygapophyses of the dorsal vertebra are
narrow and lie closer to the midline (Fig. 12F, H, K, M). The zygapophysial surfaces
change in orientation from almost horizontal (anterior; Fig. 12F) to more strongly
inclined dorsally (posterior; Fig. 12K). There is no accessory spinous process below
the posterior zygapophysis (Fig. 12G, L). The transverse processes are posteriorly
inclined at about 20° to the vertical plane, and lie across the level of the neurocentral
junction (Fig. 12G, L). They are dorsoventrally deepest in the more anterodorsal part,
perhaps reflecting the fusion of parapophysis and diapophysis, and they become
narrower posteriorly.

[insert Fig. 12 here]

No sacral vertebrae are preserved, but there are several caudals (2: IVPP V
25322; 4: IVPP V 25323; ?1: IVPP 25324), including elements from the anterior,
middle, and posterior ends of the tail. The caudal centra are cylindrical, amphicoelous, and more than three times longer than high (Fig. 12P). The zygapophyses are small with joint surfaces that are almost vertical (Fig. 12O, Q). In the anterior and middle portions of the tail, the centra bear a midventral groove flanked by paired parallel crests (Fig. 12R, T), but these are missing on the more posterior caudals. Some anterior caudals bear a neural spine, but this is lost in more posterior vertebrae. Anterior caudals also bear caudal ribs that are fused to the centrum. These ribs are mostly slender, with rounded or rectangular ends (Fig. 12R, T). In this respect they differ from the flared caudal ribs of *Coeruleodraco*.

Apart from the vertebrae, the axial skeleton is represented by a few single headed ribs (all blocks; Fig. 13A–B) and by a single, slender, gastral element (IVPP V 25323; Fig. 13C).

[insert Fig. 13 here]

**Appendicular skeleton**

Very little of the appendicular skeleton is preserved across the three blocks, other than scattered metapodials and phalanges (Fig. 13F–H). The exceptions are a right clavicle and a right tibia on IVPP V 25322 (Fig. 13D–E).

The clavicle is an L-shaped element with tapering ventromedial and dorsolateral ends (Fig. 13D–E). The medially extended process is slightly wider than the dorsal one, and bears a groove facet for the interclavicle (Fig. 13E). The dorsal process bears a keel on the dorsal edge (Fig. 13E).

The tibia is 17 mm in length (Fig. 13I). It is robust with a proximal head of roughly twice the width of the distal one (5.5 mm: 3.7 mm), and a midshaft width of
2.1 mm (Fig. 13K–M). The proportions are generally similar to those of *C. jurassicus*, although the proximal head of *Heishanosaurus pygmaeus* is slightly broader relative to the length of the bone.

The length of the tibia by comparison with that of the fully articulated skeleton of *Coeruleodraco* (Matsumoto *et al.* 2019b) allows us to make a rough estimate of the size of *Heishanosaurus pygmaeus* individual(s) on IVPP V 25323 (Fig. 13I–M). The type and only specimen of *Coeruleodraco* has a snout-pelvis length (SPL) of 200 mm. Given a roughly similar tibia, this would yield a SPL of ~162 mm for *Heishanosaurus pygmaeus*.

**Phylogenetic analysis**

*Heishanosaurus pygmaeus* was coded into the data matrix of Matsumoto *et al.* (2019b) and an analysis was run using TNT (version 1; Goloboff *et al.*, 2008) with a New Technology search mode with ratchet (1000 random addition sequences: 50 iterations). The diapsid *Petrolacosaurus* was the designated outgroup taxon but, as done previously (e.g. Matsumoto *et al.* 2019b), several other diapsids were included in the ingroup (stem-diapsids *Youngina* and *Araeoscelis*, the archosauromorphs *Prolacerta* and *Mesosuchus*, the lepidosaur *Gephyrosaurus*, and the sauropterygians *Nothosaurus* and *Keichosaurus*) because the diapsid sister taxon of choristoderes remains uncertain. The resulting trees were then reanalysed using a Traditional search option. The bootstrap tree was analysed with 10,000 replicate resampling.

Matsumoto *et al.* (2019b) found weak support for the placement of the Jurassic *Coeruleodraco* as the sister taxon of non-neochoristodere genera (other than *Cteniogenys*), despite its retention of a lower temporal fenestra. The process of
coding *Heishanosaurus* into the matrix led to a re-assessment of two character state
codings for *Coeruleodraco*: character 87 (dorsal vertebral centrum) from 0
(subcylindrical) to ? (cylindrical or subcylindrical); and character 96 (caudal centrum)
from 1 (amphiplatyan) to ? (amphiplatyan or amphicoelous). These changes, and the
combination of character states found in *Heishanosaurus* moved *Coeruleodraco*
stemward. A strict consensus of 31 most parsimonious trees (Fig. 14A) placed
*Heishanosaurus*, in an unresolved polytomy with *Coeruleodraco*, the
Neochoristodera (strongly supported), and a ´parapsid´ non-neochoristodere clade
made up of those taxa in which the lower temporal fenestra is closed
(*Hyphalosaurus, Monjurosuchus, Philydrosaurus, Khurendukhosaurus, Lazarussuchus*), or likely to be closed (*Shokawa*) based on its phylogenetic position
as sister to *Hyphalosaurus*. This clade has been recovered consistently in recent
analyses (e.g. Matsumoto *et al*. 2019a, b), although it is not supported in the
Bootstrap tree (Fig. 14B) and only weakly by Bremer Support (Fig. 14A).

Discussion

Based on comparisons of tibial length in *Heishanosaurus* and *Coeruleodraco*, we
estimated that the individuals of *Heishanosaurus* were around 160 mm in snout-
pelvis length and perhaps 300 mm in total length, which is similar in size to
*Cteniogenys* (Evans, 1991). This is relatively small for a Cretaceous choristodere;
e.g. long-necked *Hyphalosaurus* (IVPP-V 17705), total length 1036 mm; *Shokawa*,
total length ~400 mm (Evans and Manabe, 1999); short-necked *Monjurosuchus*,
snout-vent length up to 300 mm (Gao et al., 2000); *Philydrosaurus*, total length up to
300 mm (personal observation, RM). Although small size and low tooth count could be juvenile features, the fused neurocentral vertebral sutures suggest the individuals were close to adult size.

These new specimens are significant. They not only represent a new genus and species for the latter part of the Early Cretaceous, but also a distinct morphotype for this period. Although distinct in its details, the skull of *Heishanosaurus* most closely resembles that of the Jurassic *Cteniogenys* and *Coeruleodraco*, which represent the likely ancestral choristoderan skull morphology (e.g. open lower temporal fenestra, short mandibular symphysis). The most complete material of *Cteniogenys* comes from the Jurassic of Euramerica (Evans 1990), but *Cteniogenys*-like vertebrae have been recorded from the Middle Jurassic of Kyrgyzstan (Averianov *et al.* 2006), Western Siberia (Averianov *et al.* 2016), European Russia (Pashchenko *et al.* 2018) and eastern Morocco (Haddoumi *et al.* 2016), and putative choristodere dental remains were reported from the Late Jurassic (Oxfordian) of Xinjiang (Richter *et al.* 2010). The recovery of the complete skeleton of *Coeruleodraco jurassicus* (Matsumoto *et al.* 2019b) confirmed the presence of relatively conservative small choristoderes in eastern Asia during the Jurassic. The revised position for *Coeruleodraco* recovered in our phylogenetic analysis (Fig. 14A), lying stemward of both Neochoristodera and a clade of non-neochoristoderes with closed lower temporal fenestrae, is more consistent with both its anatomy and its stratigraphic position (Callovian-Oxfordian).

The grouping of *Lazarussuchus* (Palaeocene-Miocene, Europe), *Hyphalosaurus, Monjurosuchus*, and *Philydrosaurus* (Early Cretaceous, China), *Shokawa* (Early Cretaceous, Japan), and *Khurendukosaurus* (Early Cretaceous, Mongolia and Transbaikalian Russia) has been recovered in several recent
phylogenetic analyses, but the clade is always weakly supported (e.g. Matsumoto et al. 2013, 2019a, b, this paper). All are brevirostrine with a lower temporal fenestra closed by expansion of the postorbital, squamosal, jugal and quadratojugal. All, with the exception of the more recent Lazarussuchus, are from Asia. To date, we have refrained from erecting a formal name for this specialized clade of small choristoderes, as the support values are consistently low. However, to distinguish this grouping of derived taxa from more conservative non-neochoristoderes (Cteniogenys, Coeruleodraco, Heishanosaurus), we suggest the informal name ‘allochoristoderes’ with the potential of formalizing this name should future material and/or analysis provide more robust support. The prefix allo (Greek) means other or different.

Until now, all Cretaceous choristoderes recovered from Asia have been either longirostrine neochoristoderes (Tchoiria and Ikechosaurus from Mongolia and China) or brevirostrine ‘allochoristoderes’ with a closed lower temporal fenestra. The latter appear too specialized to provide an ancestral stock for Neochoristodera. The recovery of a small choristodere, albeit fragmentary, with an open lower temporal fenestra and a short jaw symphysis, implies the survival of a lineage of small, relatively conservative choristoderes similar to Cteniogenys in Asia from the Jurassic through to the latter part of the Early Cretaceous (Aptian/Albian). To date, Heishanosaurus pygmaeus is the geologically youngest choristodere from China.

The coal-bearing deposit of Shahai Formation is considered to represent a lowland swamp environment, very rich in accumulated vegetation (Deng et al. 2012). Although most of the taxa recovered are terrestrial (dinosaurs, lizards, mammals), fish remains have also been recovered (Jin 1996) as well as freshwater invertebrates (Jiang et al. 2010). In fact, the environment was probably not unlike that of the
swampier facies at Shiramine (Tetori Group, Japan) which has also yielded choriostoderes (Evans & Manabe 1999; Matsumoto et al. 2007; Matsumoto et al. 2015).

Taken in combination with Coeruleodraco jurassicus from the Jurassic of Qinglong, the Heishanosaurus specimens from the Aptian-Albian add to the remarkable diversity of choriostoderes in the Late Jurassic-Early Cretaceous of Asia (China, Japan, Mongolia). Although Choriostera may have originated elsewhere, the waterways of Asia seem to have provided an ideal habitat in which the group thrived and diversified.

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Figure Captions

Figure 1. Location and horizon of *Heishanosaurus pygmaeus* sp. nov. Map showing the location of the new specimen and other choristoderes from this region. 1, Badaohao: *Heishanosaurus pygmaeus* gen. et sp. nov. (IVPP V 25322, IVPP V 25323, IVPP V 25324, this paper); 2, Pijiagou: *Ikechosaurus pijiagouensis* (Holotype, IVPP V 13283, Liu 2004); 3, Shangheshou: *Philydrosaurus proseilus* (Holotype, PKUP V2001, Gao & Fox 2005); 4, Yuanjiawa: *Philydrosaurus proseilus* (LPMC 021, Gao et al. 2007); 5, Luojiagou: *Hyphalosaurus* sp. (Zhang et al. 2012); 6, Niuyingzi: *Monjurosuchus splendens* (Neotype, GMV 2167, Gao et al. 2000). There are three more specimens of *Monjurosuchus* (GMV 2135, 2162, 2166) whose localities Gao et al. (2000) did not record. Based on the rock matrix around these specimens, they probably came from the neotype locality; 7, Dawangzhangzi: *Hyphalosaurus lingyuanensis* (Fanzhangzi, IVPP V 11705, Gao et al. 1999; PKUP V1052, GMC juvenile, Gao & Ksepka 2008, see note below); 8, Danangou: *Monjurosuchus splendens* (Holotype, CNMM 3671, Endo 1940; IVPP V 3673, Endo & Shikama 1942); 9, Jingangshan: *Monjurosuchus splendens* (IVPP V 13761, Wang et al. 2005) (Gao & Fox [2005] thought Caocishan and Jingangshan were the same locality, see text); 10, Baitaigou: *Hyphalosaurus baihaiguensis* (Holotype, CAGS-IG-03-7-02, Ji et al. 2004); 11, Toutai: *Monjurosuchus splendens* (BMNHC V073, Gao et al. 2007); 12, Nanshimen: *Coeruleodraco jurassicus* (IVPP V 23318, Matsumoto et al., 2018). Horizon yielding the type and referred specimens of *Heishanosaurus pygmaeus*, with the stratigraphic distribution of Chinese choristoderes found so far. The stratigraphy is modified from Huang et al. 2015 and Wang 1989.
Figure 2. *Heishanosaurus pygmaeus*, gen. et sp. nov. Specimens IVPP V 25322, IVPP V 25323, and IVPP V 25324 (Holotype). A–B, IVPP V 25322: A. Digital image of the specimen; B. CT model showing the skeletal elements within the block; C–D. IVPP V 25323, C. Digital image of the specimen; D. CT model showing the skeletal elements within the block; E–F. IVPP V 25324 (Holotype), E. Digital image of the specimen; F. CT model showing the skeletal elements within the block. G. Left dentary on the surface of IVPP V 25322; H. Right jugal on the surface of IVPP V 25324 (Holotype). G and H are not to the scale.

Figure 3. Skull and mandible of *Heishanosaurus pygmaeus*, gen. et sp. nov. A, reconstruction of *Heishanosaurus pygmaeus* skull in dorsal view; B, reconstruction of the left lower jaw in medial view; C, three-dimensional reconstruction of the postorbital region in lateral view.

Figure 4. Skull and mandible of *Coeruleodraco jurassicus* IVPP V 23318. A, three-dimensional reconstruction of the postorbital region in lateral view. B–C, left lower jaw in medial (B) and in lateral (C) views. Abbreviations: Ang, angular; Ar, articular; Co, coronoid; D, dentary; J, jugal; Pa, parietal; Pf, postfrontal; Po, postorbital; Pra, prearticular; Qj, quadratojugal; Sq, squamosal; Sur, surangular.

Figure 5. *Heishanosaurus pygmaeus*, gen. et sp. nov. A–B, left parietal (IVPP V 25324) in dorsal (A), and ventral (B) views. C–D, left squamosal (IVPP V 25324) in lateral (C) and medial (D) views. E–H, supplementary left squamosal (IVPP V 25322) in lateral (E), medial (F), anterior (G), and posterior (H) views. Abbreviations: fr,
frontal facet; ne, neomorph facet; pa, parietal facet; po, postorbital facet; q, quadrate facet; qj, quadratojugal facet; soc, supraoccipital facet; sq, squamosal facet.

Figure 6. *Heishanosaurus pygmaeus*, gen. et sp. nov. A–B, F–I, J–N, left jugal, quadratojugal, and postorbital (IVPP V 25324). C–E, supplementary left jugal (IVPP V 25322). A–B, left jugal in lateral (A) and medial (B) views; left jugal in lateral (C), medial (D), and ventral (E) views. F–I, left quadratojugal (IVPP V 25324) in lateral (F), dorsal (G), posterior (H), and medial (I) views. J–N, left postorbital in lateral (J), dorsal (K), anterior (L), ventral (M), and medial (N) views. Abbreviations: ecpt, ectopterygoid facet; fr, frontal facet; j, jugal facet; la, lachrymal facet; mx, maxilla facet; pa, parietal facet; pf, postfrontal facet; po, postorbital facet; q, quadrate facet; qj, quadratojugal facet; sq, squamosal facet.

Figure 7. *Heishanosaurus pygmaeus*, gen. et sp. nov. IVPP V 25322. A–C, right quadrate, in anterior (A), posterior (B), and lateral (C) views. D–F, left quadrate, in anterior (D), posterior (E), and ventral (F) views. G–J, right premaxilla, in dorsal (G), ventral (H), lateral (I), and medial (J) views. K–L, right palatine, in ventral (K) and dorsal (L) views. M–O, right ectopterygoid, in dorsal (M), ventral (N) and lateral (O) views. Abbreviations: ch, choana margin; j, jugal facet; mid, midline facet; mx, maxilla facet; ne, neomorph facet; opi, opisthotic facet; pt, pterygoid facet; qj, quadratojugal facet; sq, squamosal facet; t p, tooth position; v, vomer facet.

Figure 8. *Heishanosaurus pygmaeus*, gen. et sp. nov. IVPP V 25322. A–E, left prefrontal, in dorsal (A), ventral (B), anterior (C), medial (D), and lateral (E) views. F–J, left lachrymal, in dorsolateral (F), ventromedial (G), ventral (H), anterior (I), and
posterior (J) views. Abbreviations: fo, foramen; fr, frontal facet; j, jugal facet; la, lachrymal facet; la f, lachrymal foramen; mid, midline facet; mx, maxilla facet; pal, palatine facet; prf, prefrontal facet.

Figure 9. *Heishanosaurus pygmaeus*, gen. et sp. nov. IVPP V 25322. A–D, right dentary, in lateral (A), medial (B), dorsal (C) and ventral (D) views. E, left dentary in lateral view. Abbreviations: co, coronoid facet; ne f, neurovascular foramina; sur, surangular facet; sym, symphysis.

Figure 10. *Heishanosaurus pygmaeus*, gen. et sp. nov. IVPP V 25322. A–B, right surangular in lateral (A), and medial (B) views. C–E, left surangular in lateral (C), medial (D), and dorsal (E) views. Abbreviations: ang, angular facet; ar, articular facet; co, coronoid facet; d, dentary facet.

Figure 11. *Heishanosaurus pygmaeus*, gen. et sp. nov. A–D, left coronoid (IVPP V 25324) in lateral (A), medial (B), dorsal (C), and ventral (D) views. E–G, right prearticular (IVPP V 25323), in medial (E), lateral (F), and ventral (G) views; H, right prearticular (IVPP V 25324) in medial view. Abbreviations: add f, adductor fossa; ang, angular facet; ar, articular facet; d, dentary facet; sur, surangular facet.

Figure 12. *Heishanosaurus pygmaeus*, gen. et sp. nov. A–E, cervical vertebra (IVPP V 25323), in anterior (A), lateral (B), posterior (C), dorsal (D), and ventral (E) views. F–J, dorsal vertebra 1 (IVPP V 25322), in anterior (F), lateral (G), posterior (H), dorsal (I), and ventral (J) views. K–N, dorsal vertebra 2 (IVPP V 25323), in anterior (K), lateral (L), posterior (M) and ventral (N) views. O–R, caudal vertebra (IVPP V
25323), in anterior (O), lateral (P), posterior (Q), and ventral (R) views. S–T, caudal vertebra (IVPP V 25323), in posterior (S), and ventral (T) views. Abbreviations: gr, groove; sph, synapophysis.

Figure 13. Heishanosaurus pygmaeus, gen. et sp. nov. A–B, left dorsal rib (IVPP V25324) in anterior (A), and posterior (B) views. C, gastric rib (IVPP V 25323) in anterior view. D–E, left clavicle (IVPP V 25323) in ventral (D) and dorsal (E) views. F–H, ungual phalanx (IVPP V 25323) in lateral (F), and posterior (G) views. H, phalanx (IVPP V 25323) in dorsal view. I–M, right tibia (IVPP V 25323) in medial (I), anterior (J), proximal (K), lateral (L), and distal (M) views. Abbreviations: ri, ridge; incl, interclavicle facet.

Figure 14. Phylogenetic relationships of Heishanosaurus pygmaeus, gen. et sp. nov. within Choristodera. A, strict consensus of 31 most parsimonious trees (MPTs) obtained by TNT (tree length = 335). Numbers in brackets indicate Bremer branch supports. B, bootstrap consensus tree with bootstrap values, as examined by a 10,000 replicate resampling analysis.

Supplementary Information

Sup-Data. Data Matrix for the phylogenetic analyses.

Sup-Fig. 1. Skull of Coeruleodraco jurassicus (IVPP V 23318). A, three-dimensional reconstruction of the skull in dorsal (A), and lateral (B) views. Abbreviations: Fr, frontal; J, jugal; La, lachrymal; Mx, maxilla; Pa, parietal; Pf, postfrontal; Pmx,
premaxilla; Po, postorbital; Prf, prefrontal; Q, quadrate; Qj, quadratojugal; Sq, squamosal.

Sup-Fig. 2. *Coeruleodraco jurassicus* (IVPP V 23318). A–B, left parietal in dorsal (A) and ventral (B) views. C–D, left squamosal in lateral (C) and medial (D) views.

Abbreviations: fr, frontal facet; ne, neomorph facet; pa, parietal facet; pf, postfrontal facet; po, postorbital facet; q, quadrate facet; qj, quadratojugal facet; soc, supraoccipital facet.

Sup-Fig. 3. *Coeruleodraco jurassicus* (IVPP V 23318). A–C, left jugal in lateral (A), medial (B), and ventral (C) views. D–F, left postfrontal in dorsal (D), ventral (E), and anterior (F) views. G–J, left quadratojugal in lateral (G), dorsal (H), posterior (I), and medial (J) views. Left postorbital in lateral (K), dorsal (L), anterior (M), ventral (N), and medial (O) views. Abbreviations: ect, ectopterygoid facet; fr, frontal facet; j, jugal facet; mx, maxilla facet; ne, neomorph facet; pa, parietal facet; pf, postfrontal facet; po, postorbital facet; q, quadrate facet; qj, quadratojugal facet; sq, squamosal facet.

Sup-Fig. 4. *Coeruleodraco jurassicus* (IVPP V 23318). A–C, left quadrate, in anterior (A), posterior (B), lateral (C), and ventral (D) views. E–J, left premaxilla, in dorsal (E), lateral (F), anterior (G), ventral (H), medial (I), and posterior (J) views. Abbreviations: mx, maxilla facet; na, nasal facet; opi, opisthotic facet; pt, pterygoid facet; qj, quadratojugal facet; v, vomer facet.
Sup-Fig. 5. *Coeruleodraco jurassicus* (IVPP V 23318). A–D, left prefrontal, in dorsal (A), ventral (B), lateral (C), and medial (D) views. I–L, left maxilla in dorsal (I), lateral (J), medial (K), and ventral (L) views. Abbreviations: fr, frontal facet; j, jugal facet; la, lachrymal facet; la f, lachrymal foramen; mid, midline facet; mx, maxilla facet; na, nasal facet; pal, palatine facet; pmx, premaxilla facet; prf, prefrontal facet; v, vomer facet.