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A neomorphic ossification connecting the braincase, squamosal, and quadrate in choristoderan reptiles: insights from μCT data

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Abstract

Choristoderes are extinct semi-aquatic to aquatic diapsid reptiles, occupying a similar niche as modern crocodilians from the Jurassic to the Miocene. Distinct from other diapsids, choristoderes have a neomorphic ossification between the braincase, squamosal, and quadrate. This neomorphic bone is described as thin and plate-like in long-snouted choristoderes (Neochoristodera), yet little is known about its presence and morphology in short-snouted non-neochoristoderes that are sister groups to Neochoristodera. Using X-ray micro-CT scanning, this study describes in detail the neomorph of two non-neochoristoderes, *Coeruleodraco jurassicus* and *Philydrosaurus proseilus*. The neomorph of both species is found between the parietal, quadrate, and squamosal. The shape of the neomorph resembles a pyramid in three-dimensions, with a triangular dorsal surface and a prominent ventral process. This confirms the neomorph is shared among early and late branching choristoderes; therefore, presence of the neomorph is a potential synapomorphy of Choristodera. In addition, the pterygoquadrate foramen is identified in non-neochoristoderes for the first time, located between the neomorph and quadrate in *C. jurassicus*. In the holotype of *P. proseilus*, the neomorph and quadrate were dislocated, but a possible pterygoquadrate foramen is identified between the two bones. Although the neomorph and pterygoquadrate foramen have been suggested to be homologous with the stapes and stapedial foramen in *Champsosaurus*, more evidences are required to confirm this homology in non-neochoristoderes, because 1) the neomorph is long and plate-like in neochoristoderes, but pyramid-shaped in non-neochoristoderes; 2) in *Champsosaurus*, the neomorph is situated lateral to the prootic and opisthotic; in *C. jurassicus* and *P. proseilus*, articulation between the neomorph and prootic (or opisthotic) cannot be confirmed due to damage to the braincase during preservation. To understand the origin of the neomorph, more intact specimens are needed to assess contact relationships between the neomorph and otic region in non-neochoristoderes.

Key Words

Choristodera, *Coeruleodraco*, micro-CT scan, neomorph, *Philydrosaurus*

1. Introduction

Choristoderes are a group of extinct aquatic-to-semi-aquatic diapsid reptiles, with a fossil record from the Middle Jurassic (Evans 1990) to Early Miocene (Evans and Klembara 2005). They were found across the Laurasia, including North America, Europe, and East Asia (Evans and Hecht 1993, Matsumoto and Evans 2010). Possible choristoderan dentary fragments and vertebral centra were found from the Middle Jurassic of Africa (Haddoumi et al. 2016). In the Cretaceous and Paleogene, several species of choristoderes were large predators, with a long snout and stout body resembling modern crocodilians (Gao 2007, Matsumoto and Evans 2010). These long snouted species form a monophyletic clade, Neochoristodera (Evans and Hecht 1993), including *Champsosaurus* (Cope

1876, Brown 1905, Russell 1956, Erickson 1972, Gao and Fox 1998) and *Simoedosaurus* (Russell-Sigogneau and Russell 1978, Erickson 1987) from North America and Europe. In Asia, neochoristoderes are found from the Lower Cretaceous, including *Ikechosaurus* (Brinkman and Dong 1993), *Tchoiria* (Efimov 1975, Efimov and Storrs 2000, Ksepka et al. 2005), and *Mengshanosaurus* (Yuan et al. 2021). Sister to neochoristoderes are short snouted species collectively called non-neochoristoderes (*sensu* Matsumoto and Evans 2010), including *Cteniogenys* from North America and Europe (Evans 1990, Gao and Fox 1998) and *Lazarussuchus* from Europe (Hecht 1992, Evans and Klembara 2005). In addition, seven genera have been reported from the Lower Cretaceous of East Asia and Siberian Russia, including *Coeruleodraco* (Matsumoto et al. 2019), *Monjurosuchus* (Endo 1940, Gao et al. 1999, 2000), *Philydrosaurus* (Gao and Fox 2005), *Shokawa* (Evans and Manabe 1999), *Hyphalosaurus* (Gao and Ksepka 2008), *Heishanosaurus* (Dong et al. 2020), and *Khurendukhosaurus* (Skutschas 2008, Matsumoto et al. 2009).

Distinct from other diapsids, choristoderes have a neomorphic ossification between the braincase and pterygoquadrate (Fox 1968). In neochoristoderes, descriptions vary about the shape of the neomorph (*sensu* Fox 1968) and its relationship with the pterygoquadrate foramen. Fox (1968) first identified the neomorph in *Champsosaurus lindoei* (UALVP 931) and *C. natator* (NMC 8922) as a triangular bone between the quadrate, squamosal, parietal, prootic, and pterygoid. The pterygoquadrate foramen is surrounded by the neomorph, quadrate, and squamosal. Based on another *C. lindoei* specimen (RTMP 87.36.41), Gao and Fox (1998) identified a large and elongated neomorph forming the pterygoquadrate foramen with the quadrate. Contrary to Gao and Fox (1998), a recent study of *C. lindoei* (CMN 8920) showed the pterygoquadrate foramen was enclosed within the neomorph (Dudgeon et al. 2020). In *C. gigas*, the neomorph was suggested as a part of the parietal (Erickson 1972). In *Simoedosaurus* (Russell-Sigogneau and Russell 1978, Erickson 1987) and *Ikechosaurus sunailinae* (Brinkman and Dong 1993), the neomorph is large and elongate, and the pterygoquadrate foramen is found between the neomorph and quadrate. In *Tchoiria* (Ksepka et al. 2005), the neomorph is present, but the pterygoquadrate foramen has not been identified. In *Mengshanosaurus* (Yuan et al. 2021), the neomorph and pterygoquadrate foramen remain unknown.

In non-neochoristoderes, the neomorph is poorly known, and the pterygoquadrate foramen has not been recognized in published materials. In *Cteniogenys*, the neomorph was inferred to be present according to articulation facets on an isolated quadrate (Evans 1990). Similarly, a facet for the neomorph is recognized on the quadrate of *Monjurosuchus* (Matsumoto et al. 2007) and *Heishanosaurus* (Dong et al. 2020). In *Shokawa* and *Khurendukhosaurus*, their skull elements are poorly known, and presence or absence of their neomorph have not been confirmed (Russell-Sigogneau and Efimov 1984, Evans and Manabe 1999, Skutschas 2008, Matsumoto et al. 2009). Using μCT scanning, the neomorph of *Coeruleodraco* was described as a small plate-like bone, but the pterygoquadrate foramen remains unknown (Matsumoto et al. 2019). In *Hyphalosaurus* (Gao and Ksepka 2008) and *Philydrosaurus* (Gao and Fox 2005), well preserved skulls have been known. It is possible to observe their neomorph and pterygoquadrate foramen by μCT scanning.

In this study, we describe the neomorph in two non-neochoristoderes: *Coeruleodraco jurassicus* and *Philydrosaurus proseilus* (Gao and Fox 2005, Gao et al. 2007, Matsumoto et al. 2019). Skulls of the two species are available to us for high-resolution CT scanning, which required separating the skull from the postcranial skeleton and preparing the skull out of the matrix. The neomorph in the holotype of *C. jurassicus* is crushed (Matsumoto et al. 2019); here we describe this bone in a new specimen with a more intact temporal region (PKUP V2003). The neomorph in the holotype of *P. proseilus* is largely blocked from external view by surrounding bones (Gao and Fox 2005); in this study, we CT-scanned the skull of the holotype (PKUP V2001) to reconstruct the neomorph in three dimensions.

Institutional abbreviations: CMN, Canadian Museum of Nature, Ottawa, Canada; IGM, Geological Institute of the Mongolian Academy of Sciences, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; LPMC, Paleontological Museum of Liaoning, Shenyang, China; PKUP, Peking University Paleontological Collections, Beijing, China; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada. UALVP, Laboratory for Vertebrate Paleontology, Department of Biological Sciences, University of Alberta, Edmonton, Canada.

2. Materials and methods

A new specimen of *Coeruleodraco jurassicus* (PKUP V2003, Fig. 1a, b) and the holotype of *Philydrosaurus proseilus* (PKUP V2001, Fig. 1c) were first prepared out the matrix for μCT scanning. The new specimen of *C. jurassicus* (PKUP V2003) was found from the type locality of the species, Nanshimenzi of Qinglong County, Hebei Province, China. It consists of a nearly complete adult skeleton with a well-preserved skull exposed in ventral view (Fig. 1a). The new specimen is referred to *C. jurassicus* based on a combination of the following characters: short snout, the preorbital region of the skull (17.8 mm) being shorter than the postorbital region (25.3 mm), small lower temporal fenestra, 39 marginal teeth, tubercular posterior projections of the squamosal, and ischiadic plate with a posterodorsal process.

Specimens were scanned using a Nikon XT H 320 LC Industrial CT scanner at China University of Geosciences (Beijing). The skull of *Coeruleodraco jurassicus* (PKUP V2003) is preserved in two blocks divided by a natural crack; therefore, the two blocks were scanned

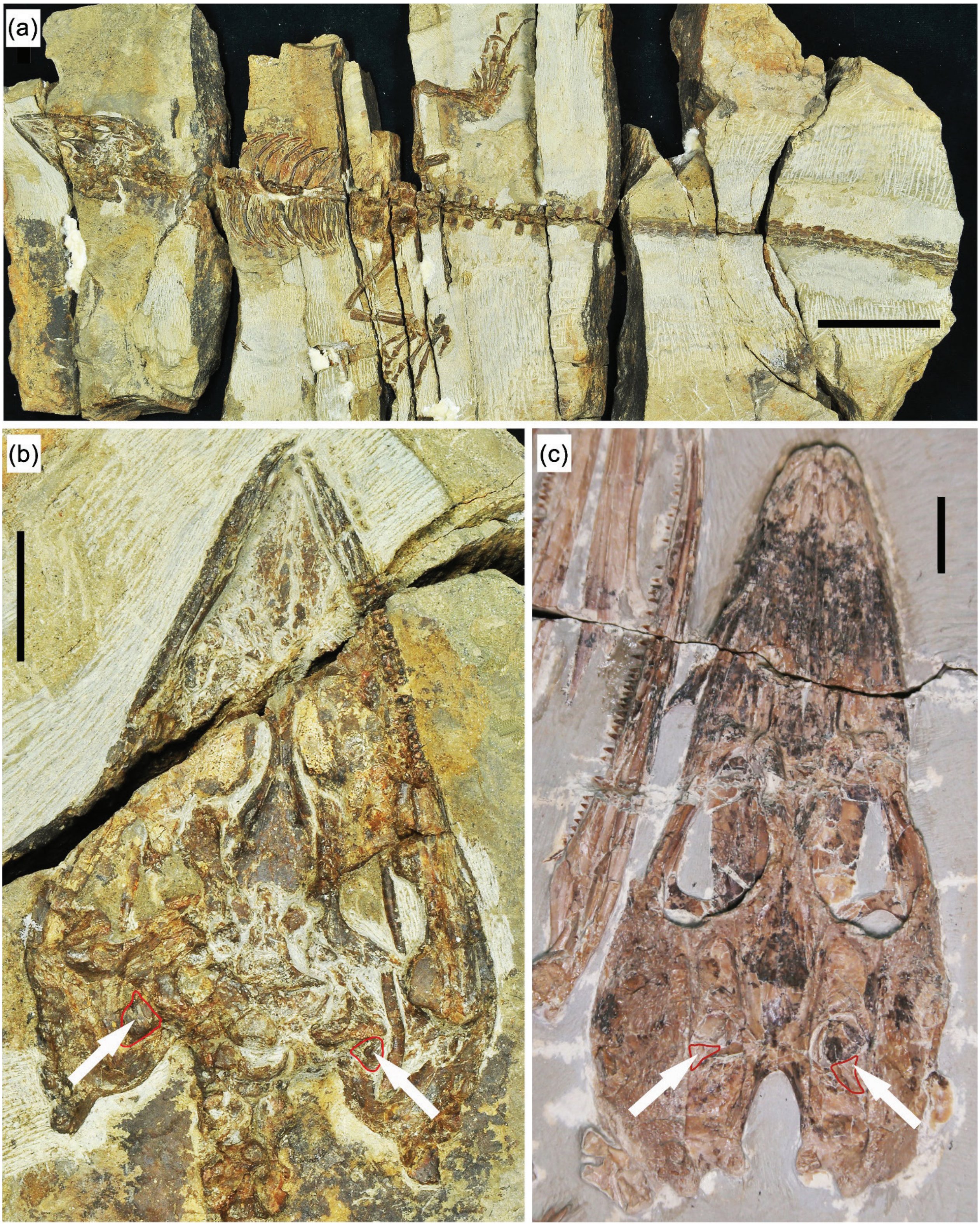

Figure 1. Photographs of the two specimens CT scanned in this study. Arrows and red lines denote the neomorphs. **a.** A new specimen of *Coeruleodraco jurassicus* (PKUP V2003); **b.** The skull of PKUP V2003 in ventral view; **c.** The skull of *Philydrosaurus proseilus* (PKUP V2001) in dorsal view. Scale bars: 50 mm (**a**); 10 mm (**b, c**).

separately using the same spatial resolution and virtually stitched together using VGSTUDIO MAX (Volume Graphics, Heidelberg, Germany). The same procedure applies to *Philydrosaurus proseilus*, as the skull (PKUP V2001) is also preserved in two blocks. Spatial resolution is 44.3220 μm for the *C. jurassicus* skull (PKUP V2003) and 39.5442 μm for the *P. proseilus* skull (PKUP V2001). The CT data were processed using VGSTUDIO MAX,

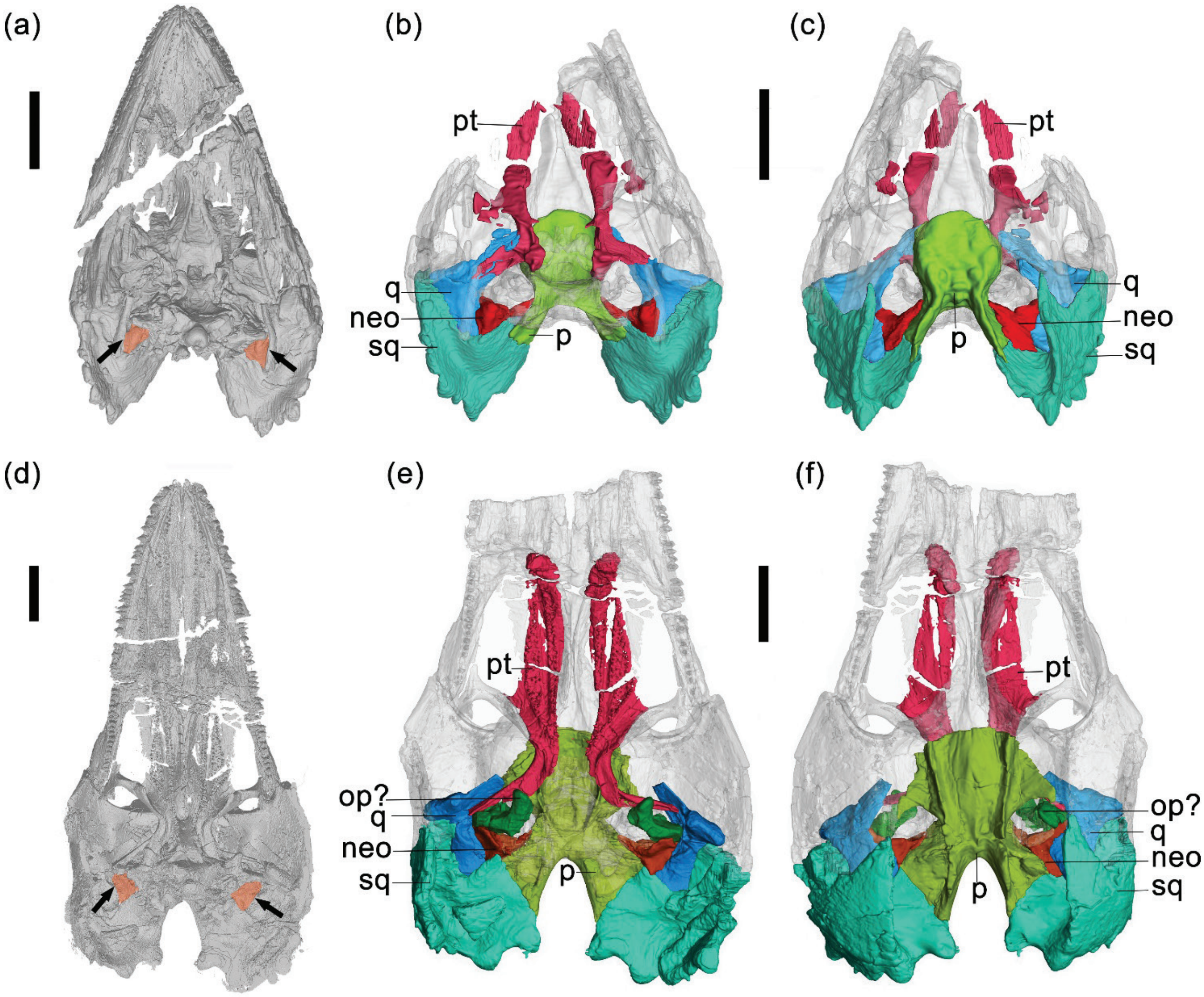

Figure 2. Virtual CT models of the *Coeruleodraco jurassicus* (PKUP V2003) and *Philydrosaurus proseilus* (PKUP V2001) skulls showing the neomorph: **a.** *C. jurassicus* skull in ventral view, arrows denoting the neomorphs (red marked); **b.** *C. jurassicus* skull showing the neomorph and surrounding bones in ventral view; **c.** *C. jurassicus* skull showing the neomorph and surrounding bones in dorsal view; **d.** *P. proseilus* skull in ventral view, arrows denoting the neomorphs (red marked); **e.** *P. proseilus* skull showing the neomorph and surrounding bones in ventral view; **f.** *P. proseilus* skull shows the neomorph and surrounding bones in dorsal view. Abbreviations: neo, neomorph; op, opisthotic; p, parietal; pt, pterygoid; q, quadrate; sq, squamosal. Scale bars: 10 mm.

including three-dimensional reconstruction of the skulls and segmentation of individual bones (parietal, squamosal, pterygoid, quadrate, and neomorph) (Fig. 2).

3. Description

3.1. The neomorph of *Coeruleodraco jurassicus*

The new specimen of *Coeruleodraco jurassicus* (PKUP V2003) consists of a nearly complete skeleton with the skull exposed in ventral view (Fig. 1a). The neomorph is partially exposed; a small ventral process of the neomorph can be observed anterior to the squamosal on both sides of the skull (Figs 1b, 2a). Using CT scanning, the dorsal portion of the neomorph has been virtually reconstructed, following sutures between the neomorph and other bones in the medial wall of the supratemporal fenestra (Fig. 2b, c).

The neomorph has an anteroposteriorly broad lateral process, an elongated medial process extending anteromedially, and a tuber-like ventral process (Fig. 3). The lateral process of the neomorph shares a long suture with the quadrate, and the long medial process articulates with the squamosal and parietal (Fig. 3d). The medial process of the neomorph extends anteriorly along the supratemporal process of the parietal, but it does not contact the pterygoid (Fig. 2b). Unlike in *Champsosaurus lindoei* (Dudgeon et al. 2020: fig. 1), the pterygoid of *Coeruleodraco jurassicus* has a short posterior process that does not extend beyond the parietal table. Ventrally, the neomorph has a distinct projection, but it is unclear whether this ventral process (or the ventral margin) contacts the opisthotic as in *C. lindoei* (Dudgeon et al. 2020: fig. 1). Although fragmentary bones are present surrounding the ventral process of the neomorph, none of the fragments can be identified as the prootic or

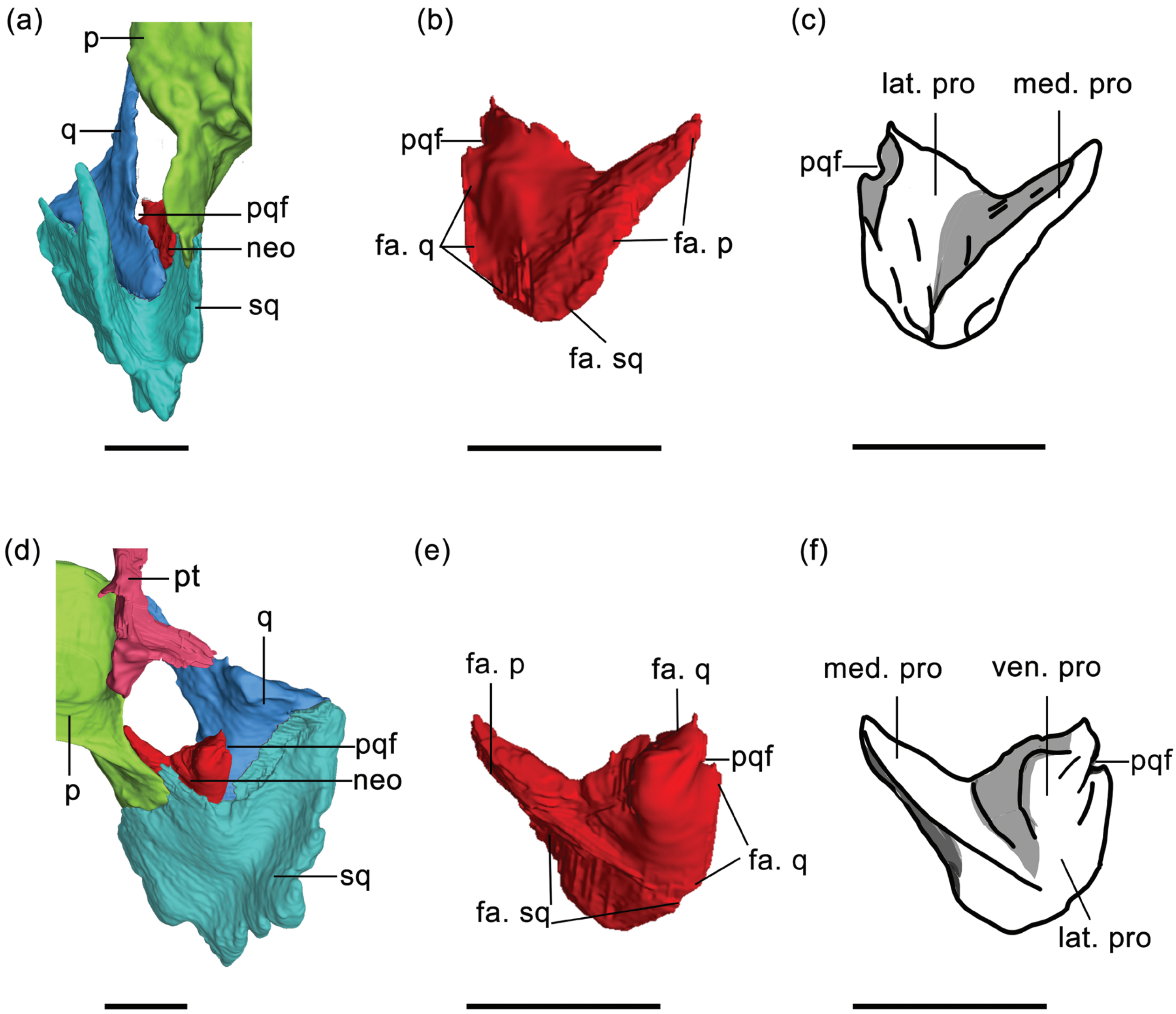

Figure 3. Morphology of the neomorph of *Coeruleodraco jurassicus* (PKUP V2003): **a.** The neomorph in the medial wall of the left supratemporal fenestra in dorsal view, with the pterygoquadrate foramen between the neomorph and quadrate; **b.** The left neomorph in dorsal view; **c.** Line drawing of the left neomorph in dorsal view; **d.** The left neomorph and surrounding bones in ventral view; **e.** The left neomorph in ventral view; **f.** Line drawing of the left neomorph in ventral view. Abbreviations: fa. p, articulation facet with the parietal; fa. q, articulation facet with the quadrate; fa. sq, articulation facet with the squamosal; lat. pro, lateral process of the neomorph; med. pro, medial process of the neomorph; neo, neomorph; p, parietal; pqf, pterygoquadrate foramen; pt, pterygoid; q, quadrate; sq, squamosal; ven. pro, ventral process of the neomorph. Scale bars: 5 mm.

opisthotic due to strong distortions of the braincase on both sides of the skull.

Between the neomorph and quadrate, there is a small foramen that we identify as the pterygoquadrate foramen (Fig. 3a). The neomorph is slightly dislocated due to lateral compression of the skull, but it clearly has a small recess forming the medial and posterior margins of the pterygoquadrate foramen. Unlike the condition in *Champsosaurus* (Fox 1968, Dudgeon et al. 2020), no groove develops near the pterygoquadrate foramen on the neomorph. In *Champsosaurus*, the margin of the pterygoquadrate foramen is either fully enclosed within the neomorph (Dudgeon et al. 2020), or bordered by the neomorph and quadrate as in *Ikechosaurus* (Brinkman and Dong 1993, Gao and Fox 1998). In the new specimen (PKUP V 2003), the anterior margin of the pterygoquadrate foramen shows a small gap between the neomorph and quadrate (Fig. 3a). With the current resolution of the CT data, it could not be determined whether the gap was caused by dislocation of the neomorph and quadrate, or the gap was originally bordered by the prootic or opisthotic. The braincase is damaged, and bones in the otic region cannot be identified (Fig. 2). Future specimens with a better-preserved braincase are required to resolve this question.

3.2. The neomorph of *Philydrosaurus proseilus*

The skull of *Philydrosaurus proseilus* holotype (PKUP V2001) is exposed dorsally. Anterior to the squamosal, the neomorph is visible in the medial wall of both supratemporal fenestrae. Dorsal exposure of the neomorph is limited

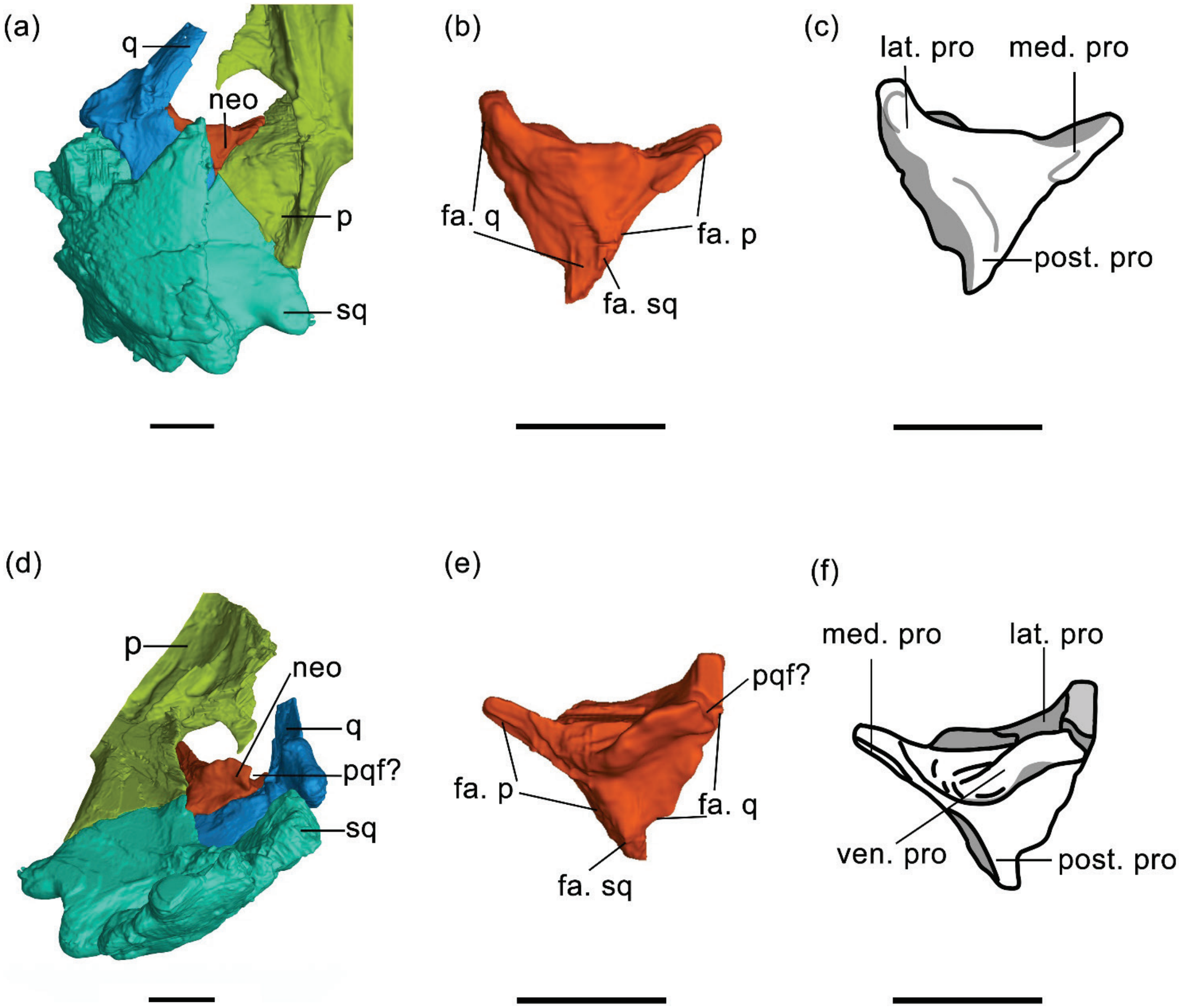

Figure 4. Morphology of the neomorph of *Philydrosaurus proseilus* (PKUP V2001): **a.** The neomorph in the medial wall of the left supratemporal fenestra in dorsal view; **b.** The left neomorph in dorsal view; **c.** Line drawing of the left neomorph in dorsal view; **d.** The left neomorph and surrounding bones in ventrolateral view, with the possible pterygoquadrate foramen between the neomorph and quadrate; **e.** The left neomorph in ventral view; **f.** Line drawing of the left neomorph in ventral view. Abbreviations: fa. p, articulation facet with the parietal; fa. q, articulation facet with the quadrate; fa. sq, articulation facet with the squamosal; lat. pro, lateral process of the neomorph; med. pro, medial process of the neomorph; neo, neomorph; p, parietal; post. pro, posterior process of the neomorph; pqf, pterygoquadrate foramen; q, quadrate; sq, squamosal; ven. pro, ventral process of the neomorph. Scale bars: 5 mm.

(Fig. 1c): on both sides of the skull, the anterior part of the neomorph is covered by several fractured bones, and the lateral part is overhung by the postorbital and squamosal. The fractured bones may be from the otic region, but they are too damaged to be identifiable. With μCT data, the morphology of the whole neomorph is revealed, including its ventral articulation with the quadrate (Fig. 2d–f).

In dorsal view, the neomorph of *Philydrosaurus proseilus* has three processes oriented medially, posteriorly, and laterally (Fig. 4). As in *Coeruleodraco jurassicus*, the medial process extends along the supratemporal process of the parietal. Anterior to the neomorph are a cluster of bone fragments possibly from the lateral wall of the braincase, but they are too crushed to be identified. In ventral view, the neomorph has a large ventral process from which extends a prominent bony ridge to the anteromedial tip of the bone (Fig. 4e, f). Differing from the condition in *Champsosaurus lindoei* (Dudgeon et al. 2020), the neomorph does not contact the pterygoid, and the pterygoid of *P. proseilus* lacks a long posterior process extending to the posterior margin of the parietal table. Anterior to the neomorphs on both sides of the skull, a pair of wing-shaped bones can be segmented in the CT data (Fig. 2e, f). With an expanded medial process and a long lateral process, this bone is identified as the opisthotic. However, the opisthotic has been shifted forward during preservation, making it uncertain with regard to the contact relationship between the opisthotic and neomorph.

The neomorph does not fully enclose a pterygoquadrate foramen. At the anterior tip of its lateral process, the neomorph has a small medially-concaving notch that seems to match a laterally-concaving notch in the quadrate (Fig. 4d). This indicates the pterygoquadrate foramen is probably between the neomorph and quadrate,

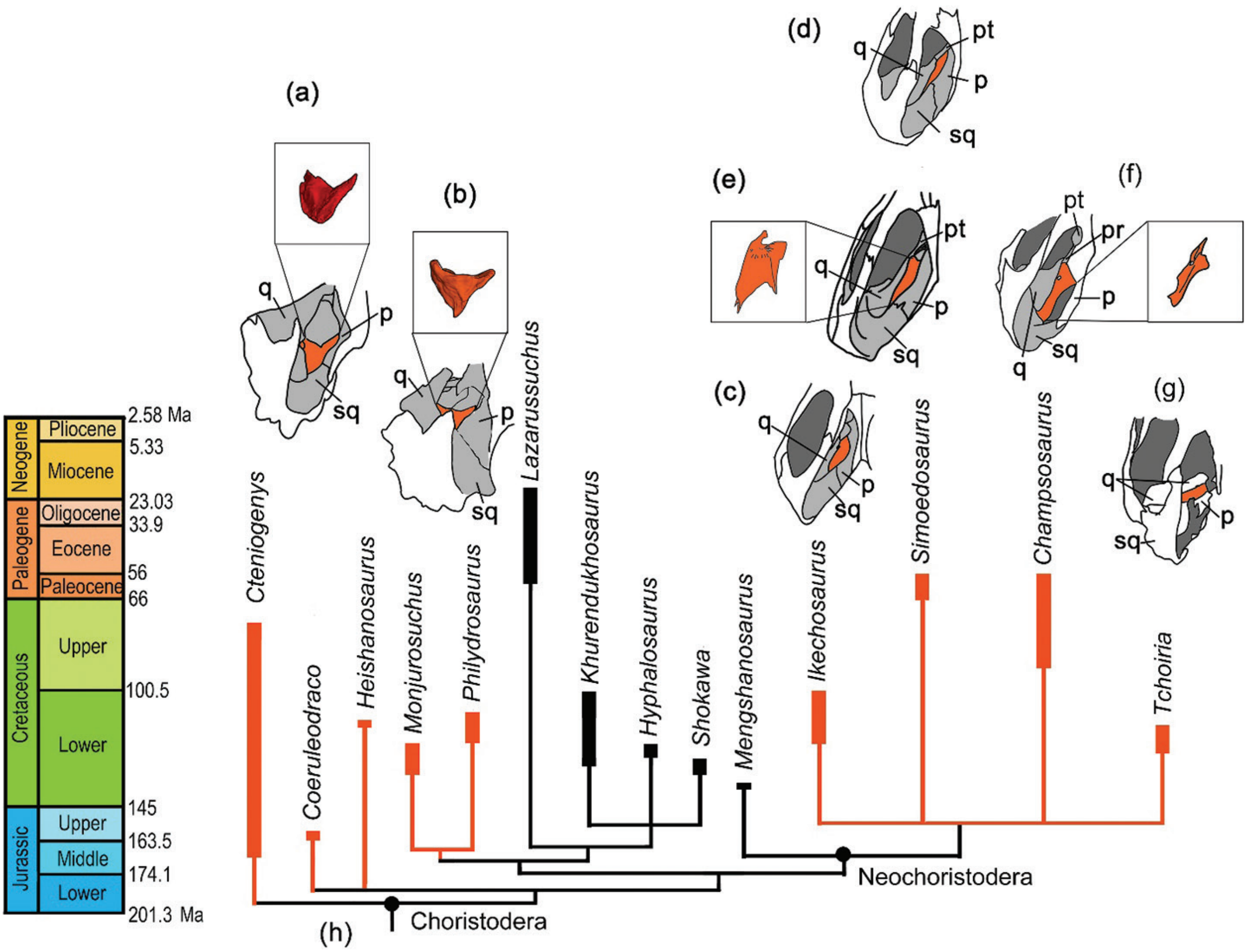

Figure 5. Morphological evolution of the neomorph in Choristodera. Red branches are taxa in which the neomorph is identified. Line drawings are the left supratemporal fenestra of choristoderes in dorsal view, the neomorph highlighted in red: **a.** *Coeruleodraco jurassicus* (PKUP V2003); **b.** *Philydrosaurus proseilus* (PKUP V2001); **c.** *Ikechosaurus sunailinae* (IVPP V9611-3), adapted from Brinkman and Dong (1993); **d.** *Simoedosaurus dakotensis*, adapted from Erickson (1987); **e.** *Simoedosaurus lemoinei*, adapted from Russell-Sigogneau and Russell (1978), the neomorph is in medial view; **f.** *Champsosaurus lindoei* (CMN 8920), adapted from Dudgeon et al. (2020); **g.** *Tchoiria klauseni* (IGM 1/8), adapted from Ksepka et al. (2005); the line drawing is mirrored from the right supratemporal fenestra for comparisons with other species; **h.** Cladogram of Choristodera, composited from Dong et al. (2020) and Yuan et al. (2021). Line drawings not to scale. Abbreviations: p, parietal; pr, prootic; pt, pterygoid; q, quadrate; sq, squamosal.

similar to the condition in *Coeruleodraco jurassicus* (Fig. 3a). However, the neomorph and quadrate are slightly dislocated on both sides of the skull, and it cannot be determined how the notches on the bones contact each other in life. This possible pterygoquadrate foramen needs to be confirmed with more specimens.

4. Discussion

The neomorph was first identified in *Champsosaurus* as a unique ossification connecting the braincase and pterygoquadrate (Fox 1968). This bone was later discovered in other neochoristoderes, including *Simoedosaurus*, *Ikechosaurus*, and *Tchoiria* (Russell-Sigogneau and Russell 1978, Brinkman and Dong 1993, Gao and Fox 1998, Ksepka et al. 2005). Although its presence remains unconfirmed in *Mengshanosaurus* (Yuan et al. 2021), the neomorph possibly represents a synapomorphy of all neochoristoderes.

Among non-neochoristoderes (Fig. 5), the neomorph has been reported in *Cteniogenys*, *Coeruleodraco*, *Monjurosuchus*, and *Heishanosaurus* (Evans 1990, Matsumoto et al. 2007, Matsumoto et al. 2019, Dong et al. 2020), and it was discovered in *Philydrosaurus* in this study. Finding the neomorph in multiple species close to the root of the choristoderan tree implies this unique ossification might be shared among all choristoderes (Fig. 5).

The neomorph of *Coeruleodraco jurassicus* was previously described as a small bone in the temporal region (Matsumoto et al. 2019). This may be a result of distortion of the holotype. In the new specimen, the neomorph forms the medial wall of the supratemporal fenestra and shares extensive sutures with the quadrate and parietal. In addition, the shape of the neomorph differs between short-snouted and long-snouted taxa. The neomorph of the short-snouted *C. jurassicus* and *Philydrosaurus proseilus* resembles a pyramid in three dimensions, with a triangular dorsal surface and a large ventral process. In the long-snouted neochoristoderes, such as *Champsosaurus* and *Simoedosaurus* (Fig. 5), the neomorph is elongate and plate-like, lacking a ventral process (Russell-Sigogneau and Russell 1978, Brinkman and Dong 1993, Ksepka et al. 2005, Dudgeon et al. 2020) (Fig. 5). This shape disparity suggests varying structural roles of the neomorph among choristoderes, as the supratemporal fenestra is much more expanded anteroposteriorly in the long-snouted species than that in short-snouted species.

As in several neochoristoderes (*Champsosaurus* Dudgeon et al., 2020; *Simoedosaurus* Russell-Sigogneau & Russell, 1978; *Ikechosaurus* Brinkman & Dong, 1993), the neomorph cooccurs with the pterygoquadrate foramen in *Coeruleodraco jurassicus* (Fig. 3) and possibly in *Philydrosaurus proseilus* (Fig. 4). In *C. jurassicus*, the pterygoquadrate foramen is between the neomorph and quadrate (Fig. 3). In neochoristoderes, this foramen is either fully enclosed by the neomorph (Dudgeon et al. 2020) or situated between the neomorph and quadrate (Brinkman and Dong 1993, Gao and Fox 1998). Although the pterygoquadrate foramen has been suggested to be homologous with stapedial foramen in *Champsosaurus* (Dudgeon et al. 2020)—and the neomorph being homologous with the stapes—this hypothesis remains to be proven in non-neochoristoderes. The neomorph is long and plate-like in neochoristoderes (Russell-Sigogneau and Russell 1978, Brinkman and Dong 1993, Ksepka et al. 2005, Dudgeon et al. 2020) but pyramid-shaped in non-neochoristoderes (Figs 2–5). The neomorph is situated lateral to the otic region in *Champsosaurus lindoei* (Dudgeon et al. 2020). This condition cannot be confirmed in *Coeruleodraco jurassicus* and *Philydrosaurus proseilus*, as CT scans of available specimens show the braincase is badly crushed by dorsoventral compressions. Previous studies on the *C. jurassicus* holotype noted a possible stapes preserved with the neomorph, although the authors suggested higher-resolution CT scanning to confirm the presence of the stapes (Matsumoto et al. 2019). Little is known about the braincase wall in other non-neochoristoderes. *Monjurosuchus* and *Hyphalosaurus* from the Early Cretaceous Jehol Biota are preserved in articulation and in three dimensions, but their specimens are generally dorsoventrally compressed, hindering the understanding of their lateral braincase wall (Gao and Li 2007, Gao and Ksepka 2008). More intact specimens are needed to assess the contact between the neomorph and the otic region in non-neochoristoderes.

5. Conclusions

This study provides detailed morphological descriptions about the neomorph of two short-snouted choristoderes, *Coeruleodraco jurassicus* and *Philydrosaurus proseilus*. The neomorph connects the braincase (parietal), quadrate, and squamosal. The shape of the neomorph varies in the evolution of Choristodera and shows a greater elongation in neochoristoderes than in non-neochoristoderes. In the two species examined here, the neomorph has a triangular dorsal surface and a prominent ventral process, differing from the plate-like shape in neochoristoderes. The pterygoquadrate foramen is identified in *C. jurassicus*, and it is likely present in *P. proseilus*. More intact specimens are needed to assess the contact between the neomorph and the otic region in non-neochoristoderes.

Data availability

All specimens discussed in this paper are deposited in public museums. The original CT data is available upon request to the authors.

Author contributions

GK and WQ collected and described the fossil material. WQ, HY and GK prepared the figures and wrote the manuscript.

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