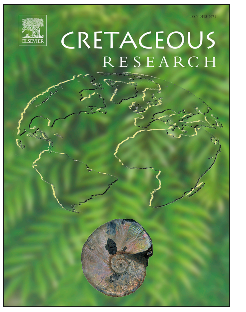
Journal Pre-proof



A new specimen of the Early Cretaceous long-necked choristodere *Hyphalosaurus* from Liaoning, China with exceptionally-preserved integument

Miaoyan Wang, Lida Xing, Kecheng Niu, Qingqing Liang, Susan E. Evans

PII: S0195-6671(22)00315-9

DOI: https://doi.org/10.1016/j.cretres.2022.105451

Reference: YCRES 105451

To appear in: *Cretaceous Research*

Received Date: 30 May 2022

Revised Date: 9 December 2022

Accepted Date: 9 December 2022

Please cite this article as: Wang, M., Xing, L., Niu, K., Liang, Q., Evans, S.E., A new specimen of the Early Cretaceous long-necked choristodere *Hyphalosaurus* from Liaoning, China with exceptionally-preserved integument, *Cretaceous Research*, https://doi.org/10.1016/j.cretres.2022.105451.

A new specimen of the Early Cretaceous long-necked choristodere *Hyphalosaurus* from Liaoning, China with exceptionally-preserved integument

Miaoyan Wang [a], Lida Xing [a, b *], Kecheng Niu [c], Qingqing Liang [a], Susan E. Evans [d *]

[a] School of the Earth Sciences and Resources, China University of Geosciences, Beijing, China;
[b] State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Beijing, China;
[c] Yingliang Stone Nature History Museum, Nan'an, China;
[d] Department of Cell & Developmental Biology, University College London, London, UK

Corresponding author. *E-mail addresses:* xinglida@cugb.edu.cn (L. Xing), s.e.evans@ucl.ac.uk (S. E. Evans).

Abstract

Although the highly specialized long-necked Early Cretaceous choristodere *Hyphalosaurus* is well known from the Jehol Biota of China, the integument of this genus has been only partially described. A new specimen from Liaoning Province, China, attributed to the species *H. lingyuanensis*, reveals additional details. The integumentary remains demonstrate a variety of scale shapes including rhomboid, square, rectangular, polygonal, and round-to-ovoid scales. The latter are arranged in parasagittal rows along the flanks and tail, but not along the neck. These rows of enlarged scales resemble the pattern seen in the contemporaneous short-necked Chinese *Monjurosuchus splendens* and may be a shared derived trait. In addition, carbonaceous films between the phalanges support the view that the manus and pes were partially webbed in *Hyphalosaurus*, as in *Monjurosuchus* and many other aquatic reptiles. The new specimen thus provides further insights into the life appearance of *Hyphalosaurus*.

***Keywords*:** integument; *Hyphalosaurus*; aquatic reptile; Yixian Formation; Lower Cretaceous

1. Introduction

Hyphalosaurus is a specialized fresh-water aquatic reptile with a small, flattened head and long neck, belonging to the Mesozoic–Cenozoic clade, Choristodera. Choristodera was established in

1876 by Cope (1876), and at least fourteen genera have been established to date: *Champsosaurus*, *Coeruleodraco*, *Cteniogenys*, *Heishanosaurus*, *Hyphalosaurus*, *Ikechosaurus*, *Khurendukhosaurus*, *Lazarussuchus*, *Mengshanosaurus*, *Monjurosuchus*, *Philydrosaurus*, *Tchoiria*, *Shokawa* and *Simoedosaurus.* All but *Champsosaurus*, *Cteniogenys*, *Lazarussuchus* and *Simoedosaurus* are from eastern Asia (e.g., Dong et al., 2020; Evans and Manabe, 1999; Gao and Fox, 2005; Gao et al., 1999, 2000; Ksepka et al., 2005; Matsumoto et al., 2019; Sigogneau-Russell, 1981; Sigogneau-Russell and Efimov, 1984; Yuan et al., 2021). The skeletal anatomy of most choristoderan genera is well known, but integumentary structures have been described in only four genera, *Champsosaurus*, *Lazarussuchus*, *Monjurosuchus* and *Hyphalosaurus*. Barnum Brown first mentioned a small area of "reticulations" near the left humerus of a well-preserved specimen of *Champsosaurus laramiensis* from the Upper Cretaceous strata of Hell Creek, USA (Brown, 1905, Pg. 22). More than half a century later, Erickson (1985) reported more general details of scalation from a *Champsosaurus gigas* specimen discovered in Upper Paleocene strata in North Dakota, USA. In 2000, Gao et al. published on the first *Monjurosuchus* specimen with large areas of preserved integument from the Lower Cretaceous of Liaoning Province, northeastern China (Gao et al., 2000), and in 2013 Matsumoto et al. described skin remains on a Palaeocene specimen of the small European choristodere *Lazarussuchus* (Matsumoto et al., 2013).

The fourth choristodere genus for which integumentary structures have been illustrated is *Hyphalosaurus*. Two species of *Hyphalosaurus* have been described, *H. lingyuanensis* and *H. baitaigouensis* (Gao and Ksepka, 2008), differing mainly in neck and body proportions. Both are represented by multiple articulated skeletons from Lower Cretaceous deposits in north-eastern China (Buffetaut et al., 2007; Gao and Ksepka, 2008; Gao et al., 1999, 2000; Ji et al., 2004, 2006, 2010). However, to date, the only previous record of integumentary structures in this taxon was that presented by Gao and Ksepka (2008) for two specimens of *Hyphalosaurus* (PKUP V1052 and GMC V351). Both specimens demonstrate well-preserved integument along the torso and tail.

In this paper, we describe a third specimen of *Hyphalosaurus lingyuanensis* from the Lower Cretaceous Yixian Formation with excellent integumentary remains, and compare it with other choristodere specimens, offering insights as to the life appearance of this specialized aquatic reptile.

2. Materials and Methods

The specimen, YLSNHM00958, was recovered from the lower part of the Yixian Formation in Dawangzhangzi Town, Lingyuan City, Liaoning Province, and deposited in Yingliang Stone Natural History Museum. The specimen described herein was collected by an anonymous citizen from Dawangzhangzi (Fig. 1) around 2000. The locality (Dawangzhangzi Town) is adjacent to Fanzhangzi Village, Songzhangzi Town, the type locality of *Hyphalosaurus lingyuanensis*.

The fossil is preserved in a shale slab that was split into two parts, catalogued as YLSNHM00958(A) and YLSNHM00958(B). Both parts broke into several pieces and were subsequently reassembled using 'super glue' by the museum conservators. Although the original slab was split, it was preserved in a more pristine state when transferred to the museum, thus we are confident that the authenticity of the specimen was not affected by the restoration. Unfortunately, the slab did not split cleanly, leaving partial bones and skin on both parts, making some features difficult to interpret. On YLSNHM00958(B), the skeleton is exposed in ventral view and the integument is revealed more clearly, providing the main basis for the discussion in this paper.

The specimen was photographed using a high-resolution camera (Canon EOS 5D DSLR). Line drawings of the specimen skeleton were then produced in Adobe Photoshop (PS CC), with measurements also made using PS. The measurement data were recorded in Table 1, and then submitted to the modeling artist. The terminology used in this paper follows Schweitzer (2011), Bell (2012) and Pittman et al. (2022). Under the terminology of Bell (2012), the scales that form the main part of the integumentary surface are referred to as "basement-scales" or "basement", with larger scattered "feature-scales"; the tissue separating the scales is termed "interstitial-tissue". A special scale arrangement in sauropod skin, "rosette", is defined as the pattern of having a central scale surrounded by a circle of scales (Pittman et al., 2022), which is relevant in our description.

3. Abbreviations

Institutional: **BDL**, Menat Museum Bord Du Lac; **GMC**, Geological Museum of China, Beijing, China; **GMV**, Geological Museum of China, vertebrate fossil collections, Beijing, China; **PKUP,** Peking University Paleontological Collections, Beijing, China; **SMM**, The Science Museum of Minnesota, St. Paul., America; **YLSNHM**, Yingliang Stone Natural History Museum, Fujian, China.

Anatomical: ca, caudal vertebra; cl, clavicle; cv, cervical vertebra; dv, dorsal vertebra; fem, femur; fi, fibula; hu, humerus; il, ilium; isc, ischium; It, interstitial tissue; mt, metatarsal; or, orbit; pub, pubis; rad, radius; ti, tibia; sv, sacral vertebra; ul, ulna.

4. Description

YLSNHM00958 is an adult individual, preserved in associated with the fish *Lycoptera*, one of the most representative genera of the Jehol Biota. It is attributed to the species *Hyphalosaurus lingyuanensis* based mainly on the possession of 19 cervical vertebrae (vs 24 in *H. baitaigouensis*, Gao and Ksepka, 2008) and 16 dorsal vertebrae (vs 19 in *H. baitagouensis*). The skeleton of YLSNHM00958 has a total body length of ~1.1 m and a snout-pelvis length (SPL, measured from the tip of the snout to the posterior margin of last sacral) of 0.51 m (Table 1). The skeleton is dorsoventrally compressed in general, and several bones (e.g., partial mandible, carpals, and some vertebrae) were lost or damaged during collection and consolidation, but the overall body outline and proportions are clear (Fig. 2). The specimen is distinguished by the preservation of soft tissue (integumental) remains throughout the body (Fig. 3).

4.1. Skeleton

The proportionally small skull is the most severely damaged part of the skeleton (Fig. 4). Nonetheless, it has the short tapering snout and large, round, dorsally oriented orbits that, with the long neck, characterize this genus (Gao and Ksepka, 2008). The postorbital elements have been crushed, but the occipital condyle can be identified on both slab parts.

The vertebral column of YLSNHM00958 is nearly completely preserved, consisting of 19 rather elongated cervicals, 16 dorsals, three sacrals, and at least 56 caudal vertebrae, as in previously reported specimens of *Hyphalosaurus lingyuanensis* (Gao and Ksepka, 2008; Gao et al., 1999). All well-defined vertebrae are platycoelous. The neck is elongate and narrow, with a length of about 0.21 m. The pectoral girdle and dv 1–3 are compressed and poorly preserved. The dorsal vertebrae are shorter than the cervicals and their thick ribs suggest some degree of pachyostosis as in PKUP V1052 and an uncatalogued GMC juvenile specimen reported by Gao and Ksepka (2008). The sacral ribs are apparently longer than the anteriormost caudal ribs.

The appendicular skeleton is relatively well-preserved. The manus and pes both have a phalangeal formula of 2-3-4-4-3, with rather short, curved claws. Metacarpals III and IV are subequal in length and are the longest of the five metacarpals in the well-preserved left manus. The forelimb is shorter than the hindlimb, and the manus is shorter than the pes. These skeletal characteristics are consistent with the diagnosis of *Hyphalosaurus lingyuanensis* (Gao and Ksepka, 2008; Gao et al., 1999). The femur of YLSNHM00958 is significantly longer than the tibia with a proportion of about 157%, close to the value of 158% in PKUP V1052 (Gao and Ksepka, 2008). Based on body length, limb proportions (Gao and Ksepka, 2008 reported distinct changes in limb bone proportions during ontogeny) and well-ossified carpals and tarsals (e.g., Fig. 7), YLSNHM00958 is an adult specimen like PKUP V1052 and the holotype, IVPP V11075, although these latter have smaller SPL values (~0.40 m and 0.48 m, respectively).

4.2. Integument

The carbonaceous films (or compressions) of soft tissue are relatively well-preserved in YLSNHM00958(A) and (B), surrounding the head, neck, shoulder, left forelimb (including manus), both hindlimbs, trunk and tail. In these areas, mineralized remains of integument are also preserved. YLSNHM00958(B) preserves the skin of the ventral body, while YLSNHM00958(A) preserves partial ventral integument and a carbon film with less distinct scales. The ventral integument exhibits five different primary scale shapes: rectangular, square (average length/width ratio of ~1.0–1.1), rhomboid, polygonal, and round-ovoid. The latter are the largest and form a distinct row along the flank. The distribution of the integument is indicated in Figure 3, with the scales in each area described below. Scale sizes are given in Table 2.

4.2.1. Skull and mandible

A small patch of skin measuring 3.4×5.0 mm can be seen through the window exposed on the ventral surface of the head on YLSNHM00958(A). The scales are preserved as permineralized casts, and consists of parallel-arranged rhomboid scales (Fig. 4A), which might form the basement layer. About 0.1 mm of interstitial tissue separate these scales. Unfortunately, this patch is too small to preclude the presence of feature-scales, or any variation.

4.2.2. Cervical region

Rectangular scales form the basement layer in this region, extending longitudinally along the neck, and preserved mainly as carbon films. Where the head meets the neck, the scales appear more mineralized (red box in Fig. 5B). Although a large area of skin is exposed along the lateral margins of the neck, individual scale sizes can only be measured on the anterior part of the neck, on the left side of the mid-neck, and in the posterior region near the shoulder. The scales are strongly rectangular in the anterior neck (with length/width ratio of ~2.3) but gradually shorten along their anteroposterior axis toward the base of the neck where they are almost square (with length/width ratio of ~1.01). Although sections of scalation between each region have been lost, it seems likely that there was a gradual size variation in the scales from anterior to posterior along the neck. The integumentary remains proximal to the vertebral centra are always darker in colour and more distinct in the anterior part of the neck, and the gaps between the dark "shadows" of individual scales suggest 0.14–0.19 mm wide interstitial-tissue bands (Fig. 5B). There is no evidence of feature-scales in this region.

4.2.3. Pectoral girdle and forelimbs

The integument around the pectoral girdle and forelimbs is preserved as thin carbonaceous compressions. The skin patch on the shoulder displays nearly square scales of relatively uniform size, with a length/width ratio of about 1.09 (Fig. 6B, white circle). The integumentary remains extend onto the anterior surface of the brachium and antebrachium, although parts near the joint were damaged by restoration.

The patches preserved anterior to the left humerus and radius (Fig. 6A–C) both consist of a basement of square–rhomboid scales, uniformly distributed in a grid-like arrangement. No feature-scale is present. The basement-scales show a slight decrease in size from proximal to distal forelimb, and are separated by 0.08–0.11 mm wide bands of interstitial tissue. Nevertheless, the integumentary region posterior to the left humerus (Fig. 6D–F) shows a slightly different scalation that includes a basement of irregular polygonal (three- to five-sided) scales and a small number (⩾2) of much larger ovoid feature-scales. Of the latter, the clearest is located level with the midshaft of the left humerus (Fig. 6E, red box) and has a diameter of about 3.58 mm. The feature-scales may have formed a parasagittal row along the brachium. Basement scales are separated by ~0.12 mm wide bands of interstitial tissue. Individual scales around the ulna cannot be distinguished, but probably followed the scale pattern posterior to the humerus.

The manus region (Fig. 7) preserves a ventral covering of polygonal scales adjacent to the carpals and small transversely broad, rectangular scales along the palmar surfaces of the digits. The polygonal scales are smaller than those on the posterior surface of the brachium (Table 2). Additionally, there is some carbonaceous film preserved between the phalanges (containing one proximal phalanx on each digit, and extending to the base of intermediate phalanges), suggesting partial webbing of the manus. The interstitial bands of integument are no more than 0.1 mm wide.

4.2.4. Rib cage

The integument on the left flank is well exposed. The soft tissue of the body wall extends up to 18.7 mm beyond the lateral margin of the ribs on each side. YLSNHM00958(B) preserves the skeleton in a general ventral view, but when the blocks were split, parts of the ventral skeleton were left on YLSNHM00958(A). The split through the skeleton has left more of the ventral integument on the main part (B) whereas YLSNHM00958(A) possesses compressed remains of the ventral integument, which are particularly evident in the rib cage region (Fig. 8).

In YLSNHM00958(B), the integument in the midshaft of the flank is permineralized to some degree, comprising a basement of triangular to heptagonal scales. The polygonal basement scales gradually decrease in size laterally. Feature-scales were also observed along the left flank. There is one longitudinal row of large round-ovoid scales, surrounded by several small, polygonal (⩾5-sided) to nearly round scales, forming a rosette pattern. The scales surrounding the central ovoid scales are larger than the basement-scales. Bands of interstitial material of 0.11–0.21 mm in width separated individual scales from each other.

Unlike its counterpart, YLSNHM00958(A) mainly preserves the carbonaceous compressions, and some mineralized tissues, of the ventral integument. The marginal scales on the middle part of the left flank are preserved as mineralized, three-dimension skin casts, differing from the rock matrix in color and texture. Moreover, the relationship between the smaller scales and the large circular scale (Fig. 8E, yellow halftone dots) suggests that partial dorsal integument was probably superimposed on the ventral feature scale.

4.2.5. Hindlimbs

The anterior region of the hindlimbs shows a basement of compressed preserved, rhomboid to nearly square scales, evenly arranged into a grid pattern as on the forelimbs. The rosette pattern of feature scales also occurs. There is at least one row of polygonal (five- to six-sided) to nearly rounded scales preserved anterior to the left femur (Fig. 9A–C), extending to the lower leg, and regularly interrupted by relatively large, oval scales ~3.8 mm in diameter. The latter is surrounded by the smaller rounded and polygonal scales, which are similar to those arranged into rows in size and morphology. Individual scales are separated by 0.13–0.17 mm interstitial bands. The integument preserved on the posterior surface of the hindlimbs consists of small polygonal (mostly quadrilateral) scales, with unclear boundaries. Those posterior to the right femur on the YLSNHM00958(A) block are better preserved and become slightly smaller from proximal to distal along the femur (Fig. 9D–F), similar to those lying beneath the right lower leg. Scales are separated by 0.09–0.1 mm wide interstitial tissue. The integument on the pes is similar to that on the manus.

4.2.6. Tail

The skin is best preserved in the caudal region where it is preserved as a carbon film that extends laterally up to ~26 mm beyond the caudal vertebrae on each side, about three times the width of the vertebral centra (excluding the transverse process). The integumentary background in the caudal region is divided into two areas (a medial region and a lateral region) by a longitudinal row of uniformly spaced, oval feature-scales (Fig. 10). The medial area, which occurs on either side of the vertebrae was covered in a grid-like arrangement of large square basement-scales, while the lateral area, which lies lateral to the row of feature scales, consists of a basement of apparently smaller square scales in a grid-like pattern. The three types of scales are roughly uniform in size and evenly distributed. The large round feature scales overlap the smaller lateral square scales and can be identified adjacent to the 41st caudal vertebra, suggesting that such scales may have run almost to the tip of the tail. Starting from the 31st caudal vertebra up to the tail tip, the scales become progressively smaller. The integumentary remains disappear completely at the 56th caudal vertebrae. Unlike the large feature-scales along the flanks, the ovoid scales here are more closely arranged and therefore do not show a rosette pattern. Individual basement scales are separated by interstitial tissue ~1.8 mm in width.

5. Discussion

Choristoderes are freshwater aquatic reptiles that range from ~0.3 to 5 m in total length, in skull shape from brevirostrine to longirostrine, and from short- to long-necked (Matsumoto and Evans, 2010). Integumentary remains have been described for four choristodere taxa: *Hyphalosaurus* (Gao and Ksepka, 2008), *Monjurosuchus* (Gao et al., 2000), *Lazarussuchus* (Matsumoto et al., 2013), and *Champsosaurus* (Brown, 1905; Erickson, 1985).

Gao and Ksepka (2008) described two specimens, PKUP V1052 (*Hyphalosaurus lingyuanensis*) and GMC V351 (*Hyphalosaurus* sp.), in which the skin along the flank and tail was clearly preserved as carbonaceous compressions rather than "impressions". As described, the scalation matches that preserved in YLSNHM00958, including a basement of polygonal basement-scales, and parasagittal rows of enlarged round-ovoid feature-scales along the flanks surrounded by smaller polygonal scales. Whereas, the integument of GMC V351 is exposed in dorsal view, revealing more widely spaced feature-scales. Given that the specimen was not identified to the species level, we do not allocate its scale pattern to *H. lingyuanensis*. In PKUP V1052, these large feature-scales run to the base of the tail and, with the surrounding scales, form rosettes as in YLSNHM00958. Gao and Ksepka (2008) referred to these scales as "keeled scutes, implying they were thickened and cornified." Gao and Ksepka (2008) also described a smaller keeled ovoid scale lying anterior to the femur in GMC V351 which they interpreted as representing part of another parasagittal row, either dorsal or ventral to the larger scale row. There are some smaller ovoid scales associated with the limbs in YLSNM00958, arranged into a rosette pattern, confirming that they were part of an additional parasagittal row on each limb. The ventral tail scales in PKUP V1052 were described as regularly arranged “quadrilaterals” (presumably square to rhomboid) and of uniform size, however, the compressions on the left of the tail in YLSNHM00958(B) suggest a parasagittal row of closely-packed round feature-scales, and a size difference in the basement-scales from medial to lateral in the caudal region. Although feature-scales were not identified in PKUP V1052, they can actually be identified in the figure (Gao and Ksepka, 2008, Fig. 7E), which confirm this feature as a characteristic of *H. lingyuanensis*.

Based on its overall anatomy, Gao and Ksepka (2008) concluded that hyphalosaurids were fully aquatic. Neither of their specimens preserved the integument of the manus and pes clearly, although they reported a small patch of scales between proximal pedal phalanges as possibly indicative of webbing. YLSNHM00958 seems to confirm this, at least in the manus, where carbon films between the digits suggests there may have been webbing that extended to the bases of intermediate phalanges. YLSNHM00958 also shows the scalation of the neck region of *Hyphalosaurus* for the first time. Although Gao and Ksepka (2008, Figure 16) reconstructed *H. lingyuanensis* as having a line of the enlarged ovoid scales running along the neck, the new specimen shows no trace of these large scales anterior to the trunk region. Instead, the neck is covered in a basement of elongated rectangular scales that gradually shorten into almost square scales at the base of the neck. YLSNHM00958(A) also provides a glimpse of square–rhomboid scales on the ventral surface of the head.

Of the other choristoderes with preserved integument, *Hyphalosaurus* is most similar to its short-necked Chinese contemporary *Monjurosuchus splendens*. Gao et al. (2000) described a specimen of *Monjurosuchus* (GMV 2135) with well mineralized skin casts that consist of a basement of very small, closely arranged pebble-like scales. Like *Hyphalosaurus*, *Monjurosuchus* has parasagittal rows of enlarged, ovoid feature-scales running along the body and tail. Unlike *Hyphalosaurus*, the large scales also extend along the neck in *Monjurosuchus*. The large feature scales are ovoid in *Monjurosuchus*, and are more prominently keeled than those of *Hyphalosaurus*. They are also more widely spaced and form two distinct rows on each side of the dorsal body. The enlarged scales are surrounded by smaller, rounded (“papilloid”, Gao et al.,

2000) scales, possibly arranged in rosettes as in *Hyphalosaurus*. Scales bearing pustular elevations (like "touch papillae" in crocodilians) also form another kind of regularly-arranged feature-scale in the neck region. GMV 2135 also clearly preserves the skin of the manus and pes, showing that both were webbed, with the webbing extending to include at least the proximal phalanges but not the penultimate ones or the unguals. The webbing may therefore have been a little more extensive in *Monjurosuchus* than *Hyphalosaurus*, in which it seems only to extend to the base of the intermediate phalanges. Like *Hyphalosaurus*, the integument anterior to the limbs is comprised of relatively larger scales than those on the posterior surface, especially in forelimb regions.

The parasagittal rows of enlarged, and probably keeled, feature-scales may be a trait shared between *Hyphalosaurus* and *Monjurosuchu*s. However, integumentary remains have not been recorded for other Chinese Early Cretaceous choristoderes like *Philydrosaurus* (Gao and Fox, 2005) that may be related to *Monjurosuchus*, nor in the Japanese *Shokawa*, the sister taxon of *Hyphalosaurus* (Evans and Manabe, 1999).

Outside China, integumentary traces have been reported in two species of the gavial-like Late Cretaceous *Champsosaurus* from North America. Both Brown (1905, *C. laramiensis*) and Erickson (1985, *C. gigas*) described impressions of small "dorsal" scales and slightly larger "ventral" scales on the limb in *Champsosaurus*, while the variation in size is reversed in the Chinese taxa and even crocodiles. Erickson (1985) reported that the integument of *C. gigas* (SMM P77.33.24) was comprised of polygonal ("pustulate" and "rhomboid") basement-scales along with circular feature-scales (<0.6 mm). However, the latter do not appear to have reached the size and special arrangement of the enlarged feature-scales seen in the Chinese taxa. There is no record of scale impressions on either the manus or pes, therefore no indication as to whether *Champsosaurus* also had webbed feet. Erickson (1985) suggested that the tail of *Champsosaurus gigas* might have borne a fin, but this was based on functional interpretation rather than soft tissue preservation.

The fourth choristodere with skin compressions is *Lazarussuchus*, a small, relatively early branching choristodere known from the Palaeocene to Miocene of Europe. Specimen BDL 1819 was recovered from the Palaeocene locality of Menat, France (Matsumoto et al., 2013). Although individual scales are not visible in this specimen, the skeleton is surrounded by dark carbonaceous films marking the soft-tissue contour of the body. On the manus, the skin outline is not clearly preserved, but on the pes it shows that the digits were fully separated rather than webbed. Above the caudal neural spines, the films have an obvious crenellated margin, indicating the presence of a low caudal crest like that seen in some iguanians and the New Zealand tuatara. This crest may have contributed to tail depth, although the shape of the tail itself (tall neural and haemal spines, lateral compression) was probably more important.

The integumentary remains surrounding the tail of YLSNHM00958 are much broader than those flanking the trunk. The body outline beyond the rib cage is approximately 26% of the maximum width of the rib cage (~27% in PKUP V1052, and ~24% in GMC V351), but in the tail region, the outline extends on each side the caudal vertebra by at least the width of the caudal series (including the transverse processes). This suggests the tail of *Hyphalosaurus* was either very deep or very wide. The caudal neural spines are not visible in YLSNHM00958, but they are tall in *H. baitaigouensis* specimens (Gao and Ksepka, 2008) suggesting the tail may have been deep. In contrast, *Monjurosuchus* has low caudal neural spines, and the integumentary area only extends laterally the equivalent of 66% the width of the caudal series. As in other choristoderes, the trunk of *Hyphalosaurus* was relatively bulky and inflexible, and *Hyphalosaurus* probably mainly used its tail for propulsion in the water, as in extant subcarangiform swimmers (Houssaye, 2009). Figure 11 shows an updated reconstruction of the external appearance of *Hyphalosaurus lingyuanensis* based on the new specimen.

Among all living reptiles, the scale pattern of crocodiles is probably most similar to that of *Hyphalosaurus*. The Chinese *Alligator sinensis* shows: 1) closely-arranged basements of polygonal (most quadrilateral) scales on ventral and dorsal surfaces of head, neck, torso and tail, with most of those on the dorsal surface being carinate; 2) scales on ventral head displaying small papillae; 3) nearly rounded, keeled feature-scales randomly distributed on dorsal surface of the neck; 4) overlapping ovoid scutes on the dorsal and lateral surfaces of the limbs, larger than the ventral polygonal scales which also form a basement; 5) transversely broad scales on the dorsal surface, and polygonal scales on the ventral surface of the manus and pes; 6) relatively small irregular polygonal to nearly rounded scales along the flank (Cong et al., 1998). However, scale rosettes are absent. In addition, the osteoderms underlying the feature-scales in *Alligator* are absent in choristoderes. The two-dimensional scale morphology of *Hyphalosaurus lingyuanensis* is thus similar to crocodile integument.

6. Conclusions

Specimen YLSNHM00958, housed in the Yingliang Stone Natural History Museum of China, provides further information on the external appearance of the specialized aquatic choristodere *Hyphalosaurus lingyuanensis*, both supporting and extending the data from other specimens (Gao and Ksepka, 2008). It demonstrates a diversity of scale types across the body – from rounded or polygonal, to square-rhomboid or rectangular. It confirms that *H. lingyuanensis* had parasagittal rows of enlarged, probably carinate, round-to ovoid feature-scales along the flanks and tail, although it is unclear how many rows were present on each side of the trunk. Rosette scale patterns also occur in this taxon. However, there is no evidence that these enlarged scales extended along the neck. Parasagittal rows of large regularly spaced feature-scales and rosette pattern are also seen in the contemporaneous Chinese taxon *Monjurosuchus*, and might be a shared derived trait, although this needs to be tested by the recovery of specimens of *Philydrosaurus* and *Shokawa* with skin traces preserved. Combined with the bulky stiffened trunk, partially webbed feet, *Hyphalosaurus* probably mainly used the deep tail to propel itself in water, as proposed for other choristoderes.

Acknowledgements

We thank Cheung Chung-tat for his 3D reconstruction of *Hyphalosaurus lingyuanensis*, and thank Prof. Keqin Gao from Peking University for providing the photos of PKUP V1052 to L.X, Wanying Qin for providing morphological suggestions to Q.L. This research was supported by the National Natural Science Foundation of China [No. 41888101, 41790455]. We also thank Dr Phil Bell and Dr Samuel Cooper for their constructive comments and suggestions on an earlier version of the manuscript.

References

Bell, P.R., 2012. Standardized terminology and potential taxonomic utility for hadrosaurid skin impressions: a case study for Saurolophus from Canada and Mongolia. PLoS One 7(2), e31295.

Brown, B., 1905. The osteology of *Champsosaurus* Cope. Memoirs of the AMNH. New York American Museum of Natural History 9, 1–26.

Buffetaut, E., Li, J.J., Tong, H.Y., Zhang, H., 2007. A two-headed reptile from the Cretaceous of China. Biology Letters 3 (1), 81–82.

Cong, L.Y., Hou, L.H., Wu, X.C., Hou, J.F., 1998. The gross anatomy of *Alligator sinensis* Fauvel. Science Press, Beijing, pp. 3–5 (in Chinese).

Cope, E.D., 1876. On some extinct reptiles and Batrachia from the Judith River and Fox Hills beds of Montana. Proceedings of the Academy of Natural Sciences of Philadelphia, 340–359.

Dong, L.P., Matsumoto, R., Kusuhashi, N., Wang, Y.Q., Wang, Y., Evans, S.E., 2020. A new choristodere (Reptilia: Choristodera) from an Aptian-Albian coal deposit in China. Journal of Systematic Palaeontology 18, 1223–1242.

Erickson, B.R., 1985. Aspects of some anatomical structures of *Champsosaurus* (Reptilia: Eosuchia). Journal of Vertebrate Paleontology 5 (2), 111–127.

Evans, S.E., Manabe, M., 1999. A choristoderan reptile from the Lower Cretaceous of Japan. Special Papers in Palaeontology 60, 101–119.

Gao, K.Q., Fox, R.C., 2005. A new choristodere (Reptilia: Diapsida) of western Liaoning Province, China, and phylogenetic relationships of Monjurosuchidae. Zoological Journal of the Linnean Society 145, 427–444.

Gao, K.Q., Ksepka, D.T., 2008. Osteology and taxonomic revision of *Hyphalosaurus* (Diapsida: Choristodera) from the Lower Cretaceous of Liaoning, China. Journal of Anatomy 212 (6), 747–768.

Gao, K.Q., Tang, Z., Wang, X., 1999. A long-necked diapsid reptile from the Upper

Jurassic/Lower Cretaceous of Liaoning Province, northeastern China. Vertebrata PalAsiatica 37, 1–8 (in Chinese).

Gao, K.Q., Evans, S., Ji, Q., Norell, M., Ji, S., 2000. Exceptional fossil material of a semi-aquatic reptile from China: the resolution of an enigma. Journal of Vertebrate Paleontology 20, 417–421.

Houssaye, A., 2009. "Pachyostosis" in aquatic amniotes: a review. Integrative Zoology 4 (4), 325–340.

Ji, Q., Ji, S.A., Cheng, Y.N., You, H.L., Lu, J.C., Yuan, C.X., 2004. The first fossil soft-shell eggs with embryos from Late Mesozoic Jehol Biota of western Liaoning, China. Acta Geoscientica Sin 25, 275–285.

Ji, Q., Ji, S.A., Lu, J.C., You, H.L., Yuan, C.X., 2006. Embryos of Early Cretaceous Choristodera (Reptilia) from the Jehol Biota in western Liaoning, China. Journal of the Paleontological Society of Korea 22 (1), 111–118.

Ji, Q., Wu, X.C., Cheng, Y.N., 2010. Cretaceous choristoderan reptiles gave birth to live young. Naturwissenschaften 97 (4), 423–428.

Ksepka, D.T., Gao, K.Q., Norell, M.A., 2005. A new choristodere from the Cretaceous of Mongolia. American Museum Novitates 2005 (3468), 1–22.

Matsumoto, R., Evans, S.E., 2010. Choristoderes and the freshwater assemblages of Laurasia. Journal of Iberian Geology 36 (2), 253–274.

Matsumoto, R., Buffetaut, E., Escuillie, F., Hervet, S., Evans, S.E., 2013. New material of the choristodere *Lazarussuchus* (Diapsida, Choristodera) from the Paleocene of France. Journal of Vertebrate Paleontology 33 (2), 319–339. https://doi.org/10.1080/02724634.2012.716274

Matsumoto, R., Dong, L.P., Wang, Y., Evans, S.E., 2019. The first record of a nearly complete choristodere (Reptilia: Diapsida) from the Upper Jurassic of Hebei Province, People's Republic of China. Journal of Systematic Palaeontology 17 (12), 1031–1048.

Pittman, M., Enriquez, N.J., Bell, P.R., Kaye, T.G., Upchurch, P., 2022. Newly detected data from *Haestasaurus* and review of sauropod skin morphology suggests Early Jurassic origin of skin papillae. Communications biology 5 (1), 1–8.

Sigogneau-Russell, D., 1981. Presence d' un nouveau champsosauridé dans le Cretace superieur de Chine. Comptes Rendus de l'Académie de Sciences, Paris, Sér III: Sciences de la Vie 292, 1–4.

Sigogneau-Russell, D., Efimov, M.B., 1984. Un Choristodera (Eosuchia?) insolite du Crétacé Inférieur de Mongolie. Paläontologische Zeitschrift 58 (3), 279–294.

Schweitzer, M.H., 2011. Soft tissue preservation in terrestrial Mesozoic vertebrates. Annual Review of Earth and Planetary Sciences 39, 187–216.

Yuan, M., Li, D.Q., Ksepka, D.T., Yi, H.Y., 2021. A juvenile skull of the longirostrine choristodere (Diapsida: Choristodera), *Mengshanosaurus minimus* gen. et sp. nov., with comments on neochoristodere ontogeny. Vertebrata PalAsiatica 59 (3), 213–228.

FIGURE CAPTIONS

Fig. 1 The locality of the new *Hyphalosaurus lingyuanensis* specimen.

Fig. 2 The new *Hyphalosaurus lingyuanensis* specimen, YLSNHM00958(A) and (B).

Fig. 3 Outline drawings of the skeleton and integumentary remains preserved around YLSNHM00958(B). A) The skeleton and possible overall morphology; B) Different regions (Areas A–H) with well-preserved scales: Area A, head; Area B, neck; Area C, pectoral girdle; Area D, brachium and antebrachium; Area E, manus; Area F, flank of rib cage; Area G, hindlimb excluding the pes; Area H, tail. Scale bars equal 100 mm.

Fig. 4 Skulls in YLSNHM00958(A) and (B). The yellow oval boxes indicate the location of occipital condyle. The white box (a) indicates the rhomboid scales of YLSNHM00958(A) in the head region. Scale bars equal 10 mm.

Fig. 5 Close-up and sketch of the skin compressions around the anterior neck. Red box indicates rectangular scales where the head meets the neck, and black arrows point to the border of the carbon films. The relatively intact scales with distinct borders are painted with halftone dots (B and C). Scale bars equal 10 mm.

Fig. 6 Skin patches preserved around the pectoral girdle, brachium and antebrachium regions. A–C) Close-up and sketch of skin compressions around the left shoulder, humerus and radius of YLSNHM00958(B), white circle indicates almost square scales on the shoulder; D–F) Close-up and sketch of skin compressions posterior to the left humerus of YLSNHM00958(A), red box indicates the clearest ovoid feature- scale. Black arrows point to the border of the skin film. Scale bars equal 10 mm.

Fig. 7 Integument on the manus of *Hyphalosaurus lingyuanensis*. A) Carbonaceous compressions around the phalanges in YLSNHM00958(A); B) Individual scales painted with halftone dots, red arrows point to the small scales; C) Sketch of A, red circles indicate the rectangular scales, yellow circle indicates the polygonal scales, and arrows point to the possible borders of the remains of skin compressions. All scale bars equal 10 mm.

Fig. 8 Integumentary remains on the flank. A–C) Close-up and sketch of the scales on the left trunk of YLSNHM00958(B); D–F) Close-up and sketch of the scales at the level of the 5–7th dorsal vertebrae on the left trunk of YLSNHM00958(A), in which the red box indicates the permineralized casts of the ventral scales, and the yellow scales represent the dorsal integument overlapped on the ventral scales. Arrows point to the possible borders of skin compressions.

Scale bars equal 10 mm.

Fig. 9 Integument on hindlimbs of *Hyphalosaurus lingyuanensis*. A–C) Close-up and sketch of the skin lying anterior to the left femur and tibia of YLSNHM00958(B); D–F) Close-up and sketch of the scales posterior to the right femur of YLSNHM00958(A). Red box indicates the *Lycoptera* fish. Arrows point to the possible borders of areas of skin compressions. Scale bars equal 10 mm.

Fig. 10 Close-up and sketch of the skin compressions adjacent to caudal vertebrae 5–15, arrows point to the possible border of the carbon film. Scale bar equals 10 mm.

Fig. 11 Updated life reconstruction of *Hyphalosaurus lingyuanensis*. Artwork by Cheung Chung-tat. A) Overall appearance in ventral, lateral and dorsal views; B) in front and rear views; C) the anterior body; D) the posterior body.

TABLES

Table 1. Primary anatomical measurements of YLSNHM00958 (Unit: mm).

Region	Skull	Postorbital region	Neck	Tail	SPL	Whole body
Length	57	29	211	573	524	1097

Table 2. Shape and size of scales in different body regions (Areas A–H in Figure 2).

Region	**Shape**	**Length range (mm)**	**Width range (mm)**	**Scale area (mm^2)**
Head	rhomboid	1.30~1.38	1.14~1.21	1.47~1.60
Neck	rectangular	1.21~2.74	0.88~1.69	1.49~2.89
Pectoral girdle	square	1.67~1.73	1.54~1.55	2.57~2.68
Forelimb	square–rhomboid	1.00~1.93	0.78~1.85	0.78~3.57
	polygonal	<0.26~1.52	<0.16~1.33	<0.04~1.84
	ovoid	3.58	–	10.07
Manus	rectangular	1.37~1.45	0.72~0.79	1.04~1.10
	polygonal	<0.21~1.40	<0.17~0.67	<0.04~0.87
Rib cage	large ovoid	7.47~9.76	–	43.83~74.82
	small nearly round	1.29~1.49	0.99~1.21	1.28~1.80
	polygonal	<0.20~1.91	<0.16~1.52	<0.032~2.81
Hindlimb	square–rhomboid	1.19~2.22	1.14~2.19	1.35~4.85
	polygonal	–	–	<0.11~1.78
	large ovoid	3.62~4.10	–	10.29~13.20
	small nearly round	2.03~2.41	–	3.23~4.56
Tail	ovoid	3.28~5.63	–	8.45~24.89
	small square	0.90~1.55	0.67~1.52	0.60~<2.36
	large square	1.48~2.82	1.38~2.43	2.13~6.15

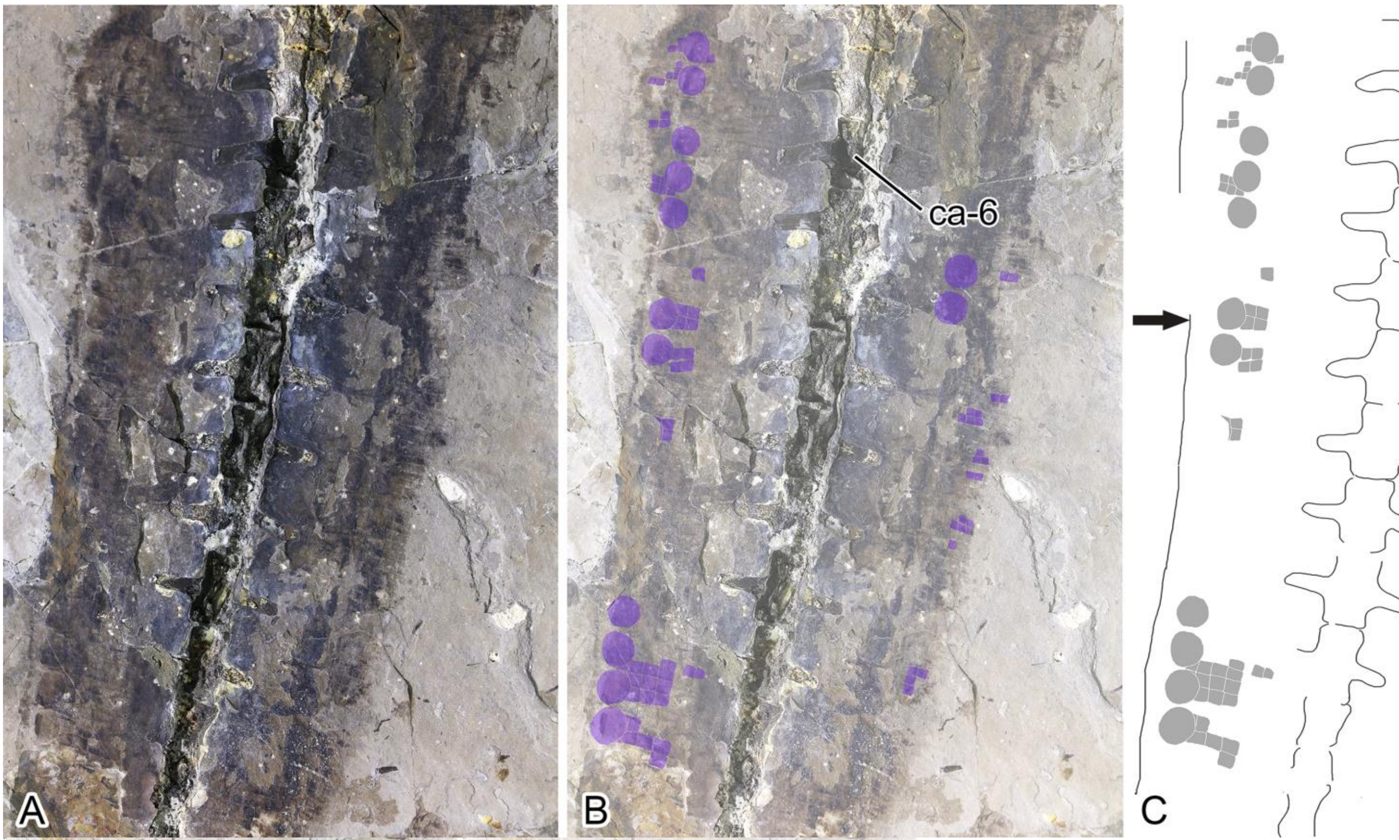
Author Statement

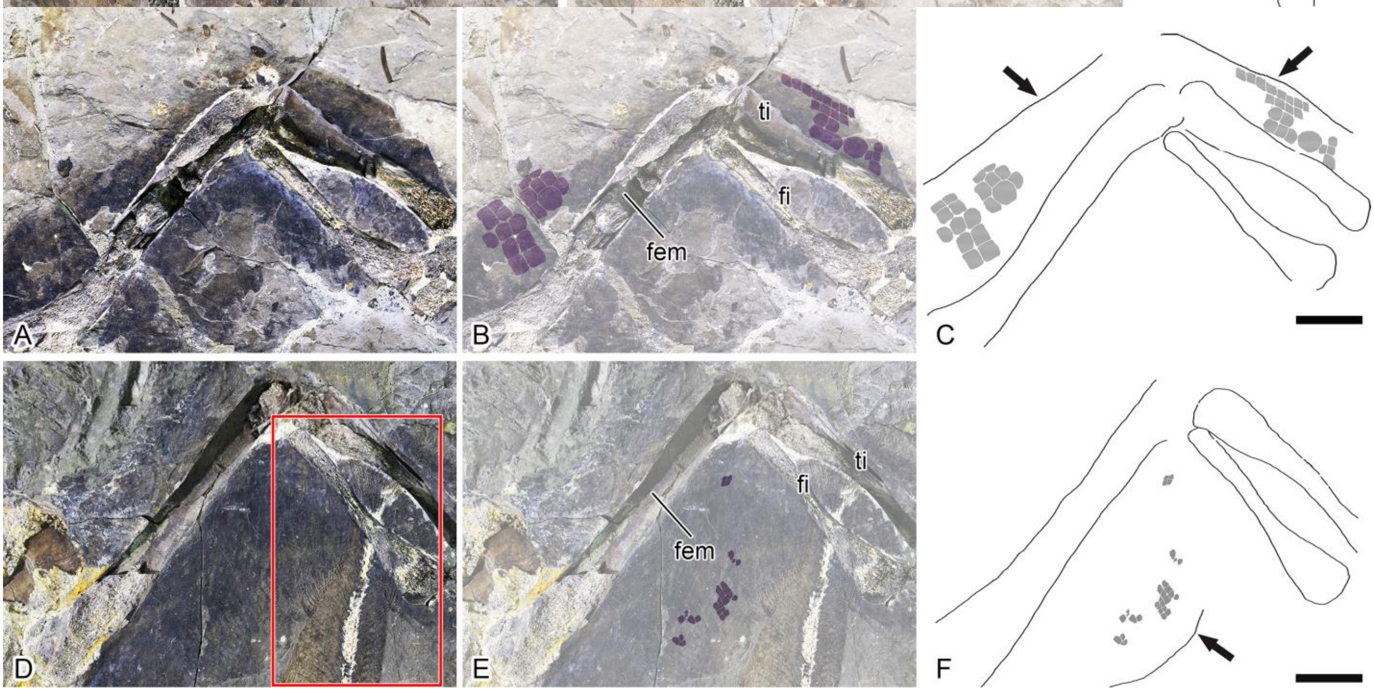
Miaoyan Wang: Analyzed the data, writing- original draft
Lida Xing: Conceived and designed the fieldwork and experiments, Analyzed the data, writing-original draft
Kecheng Niu: geological survey
Qingqing Liang: geological survey, analyzed the data
Susan E. Evans: Conceived and designed the experiments, reviewing and editing

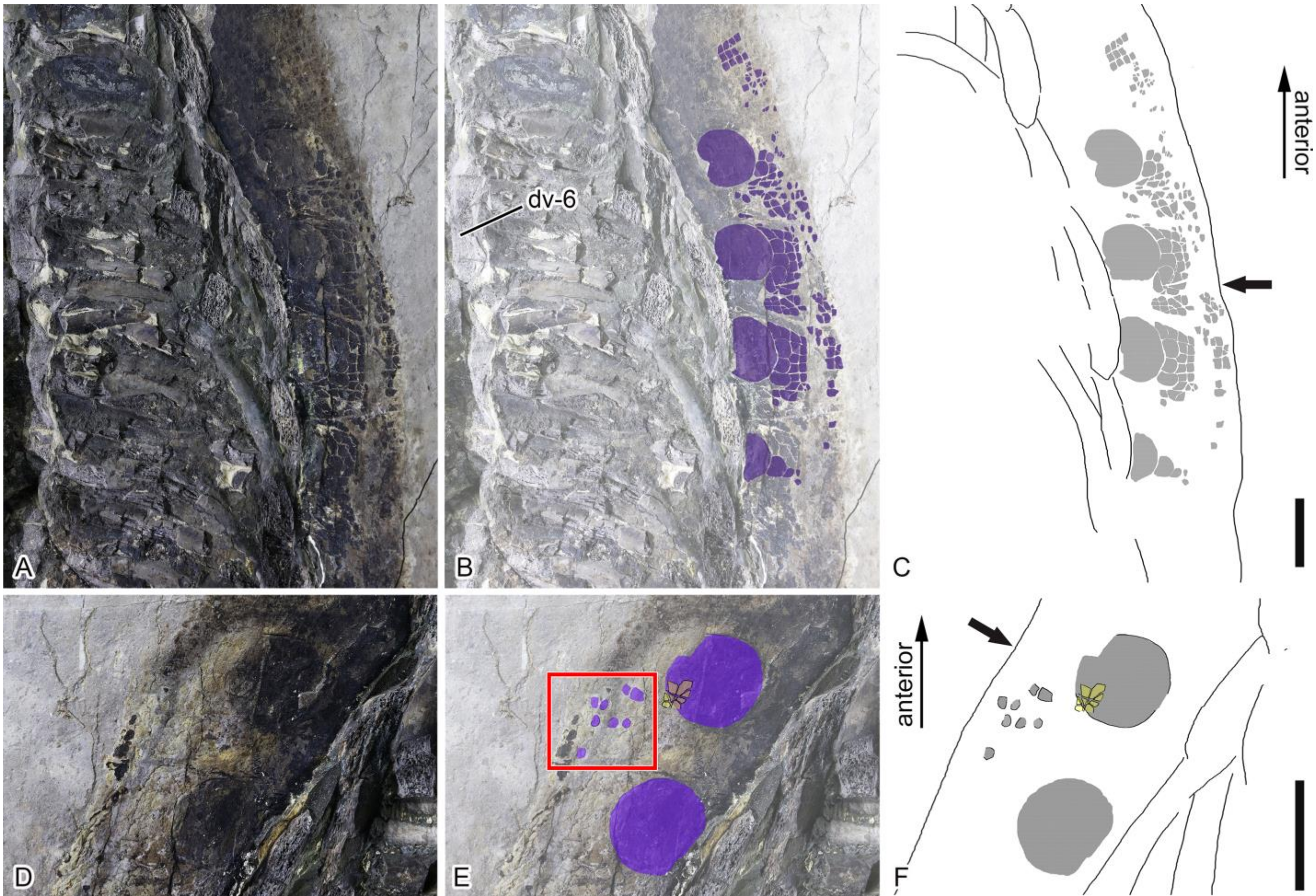
Declaration of interests

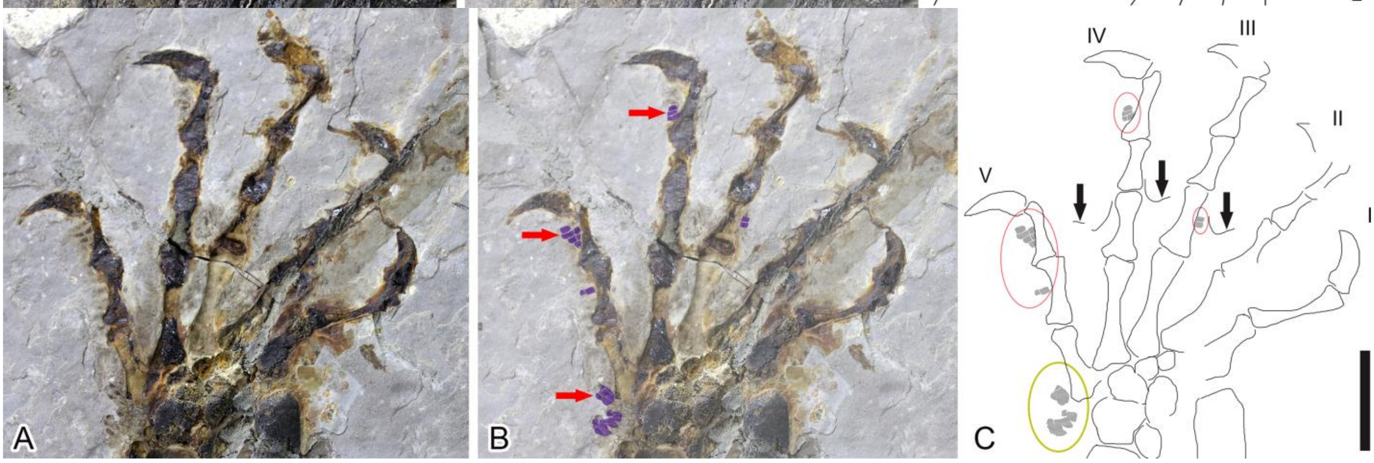
☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

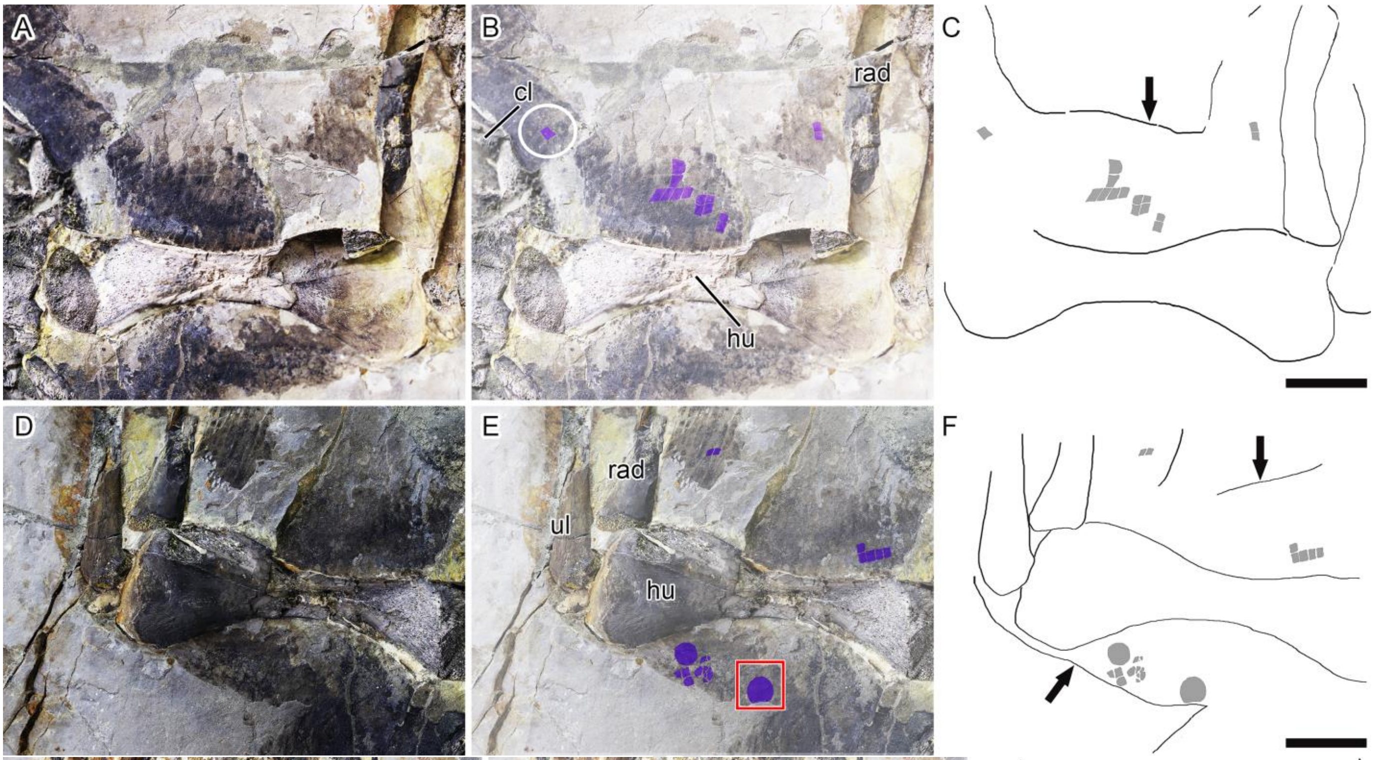
☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

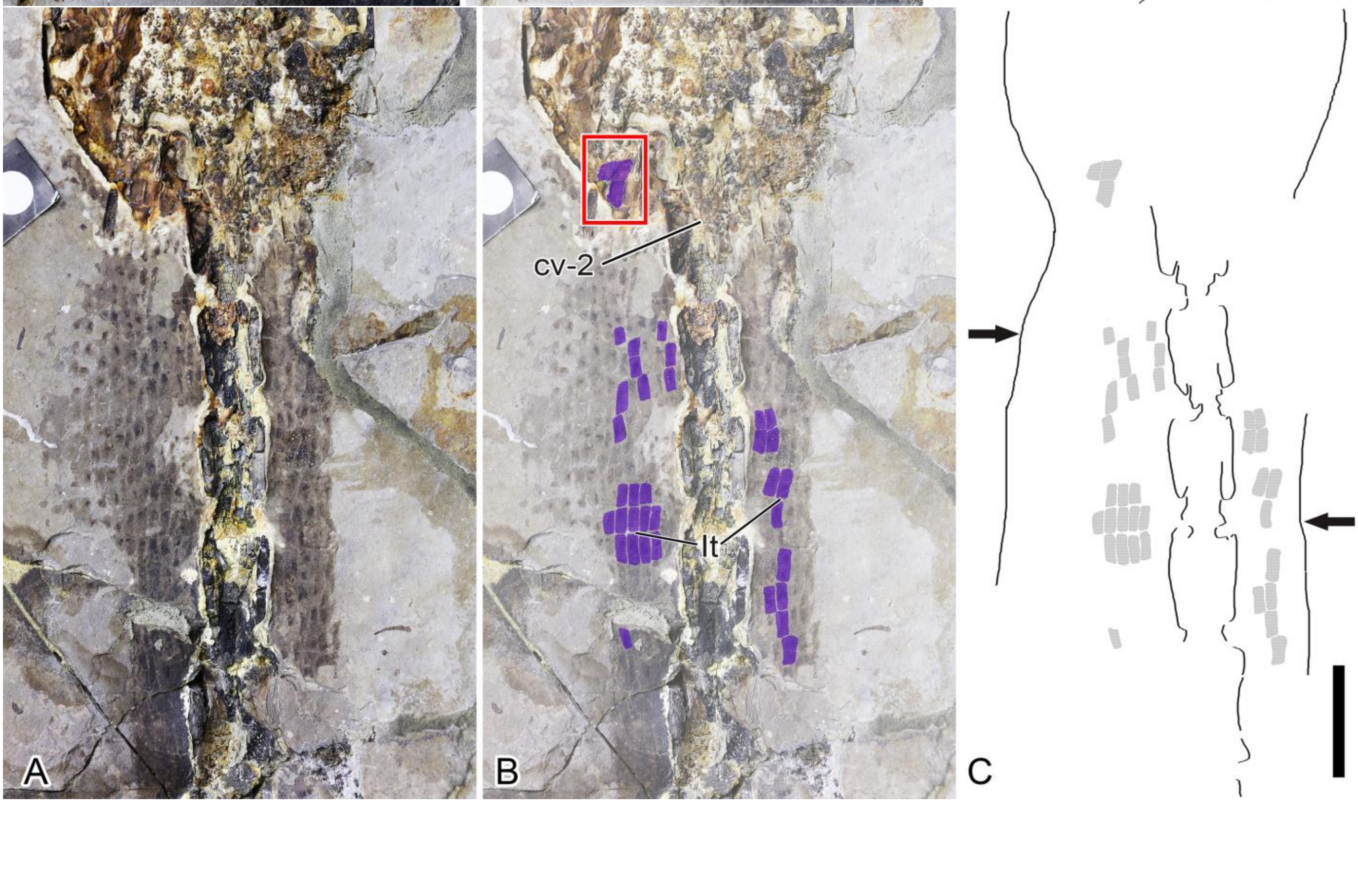

ca-6
A
B
C

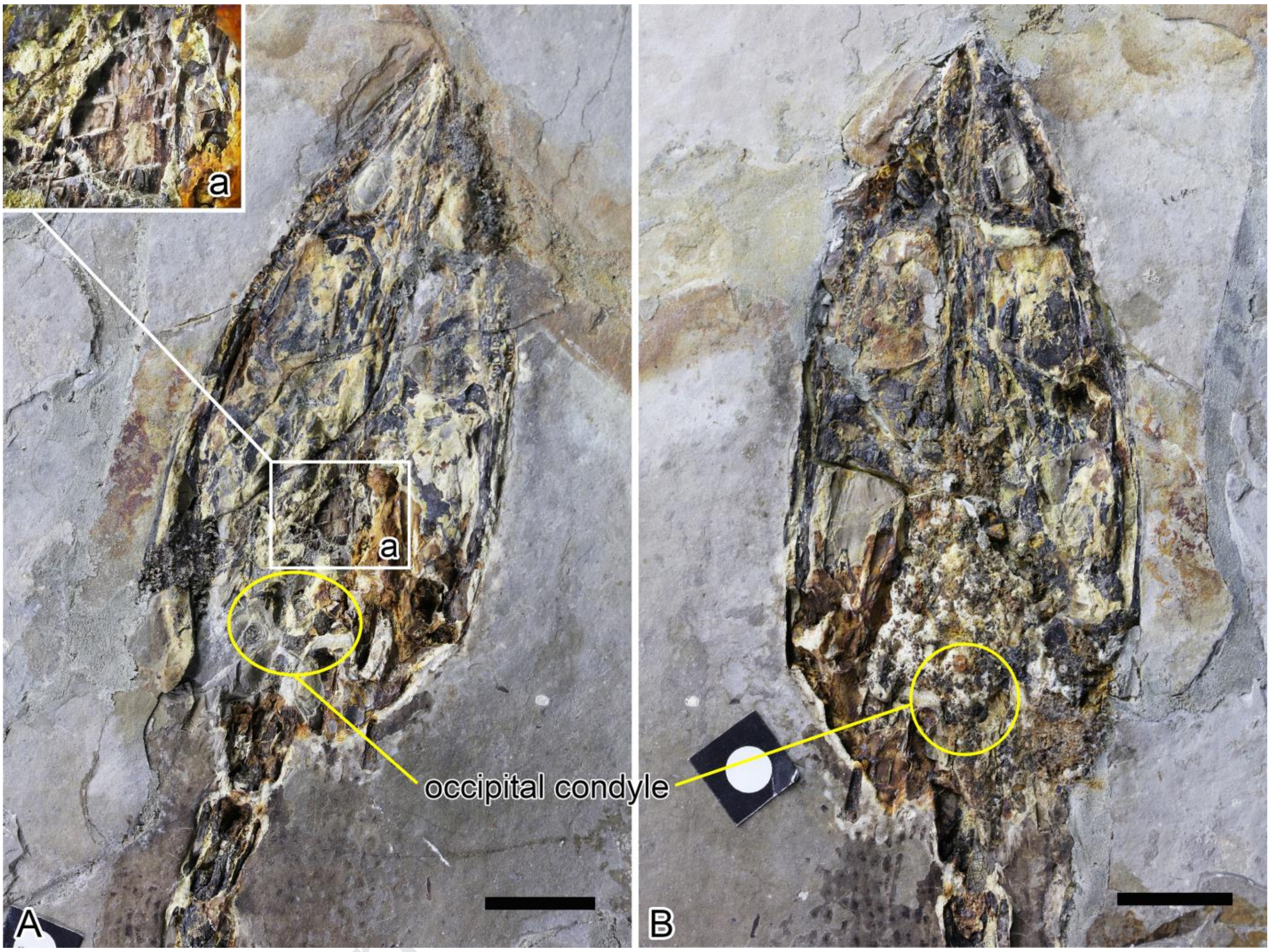

ti
fi
fem
A
B
C
D
E
F

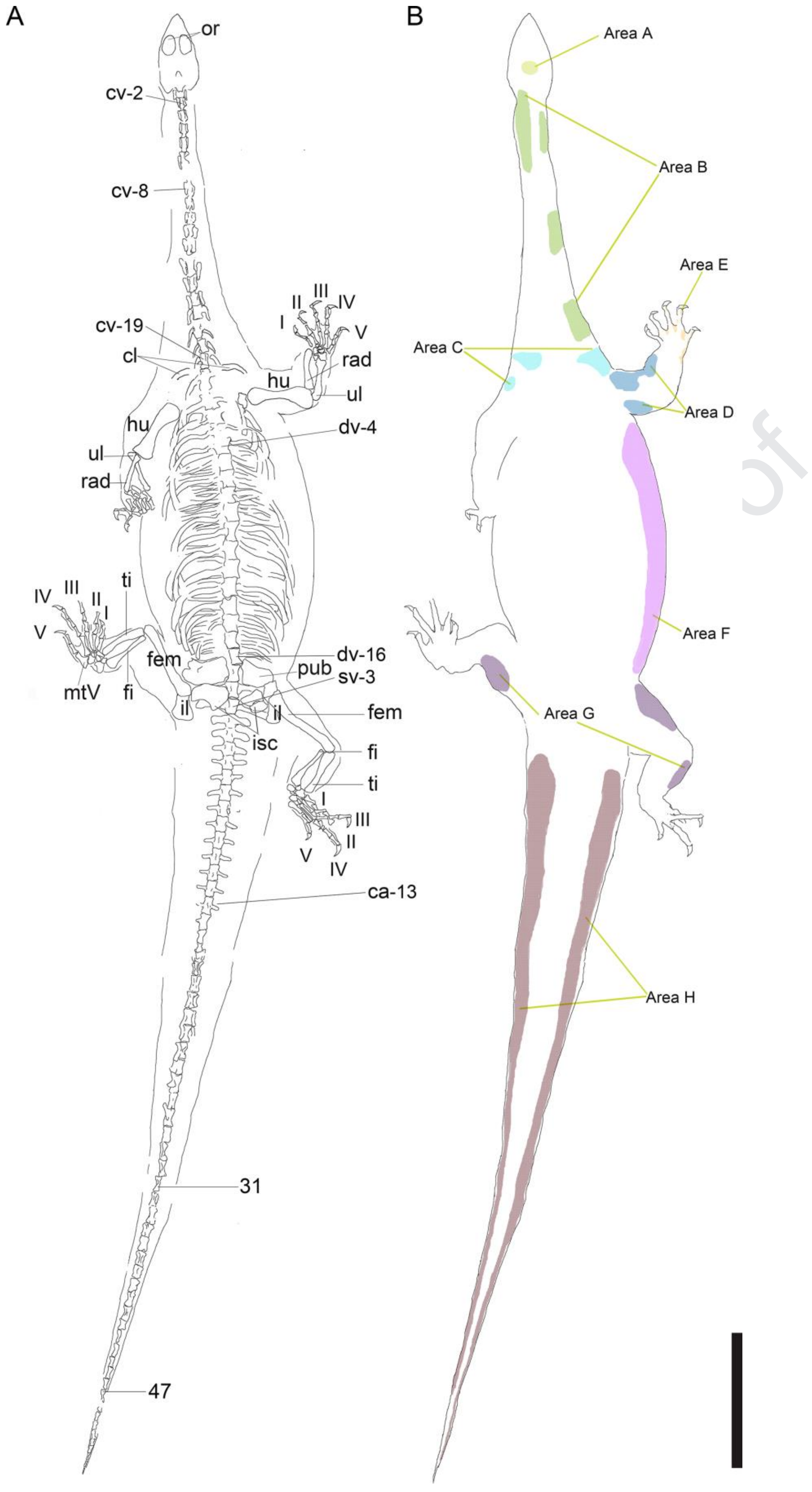

A
B
dv-6
C
anterior
D
E
anterior
F


A
B
C
IV
III
II
V
I

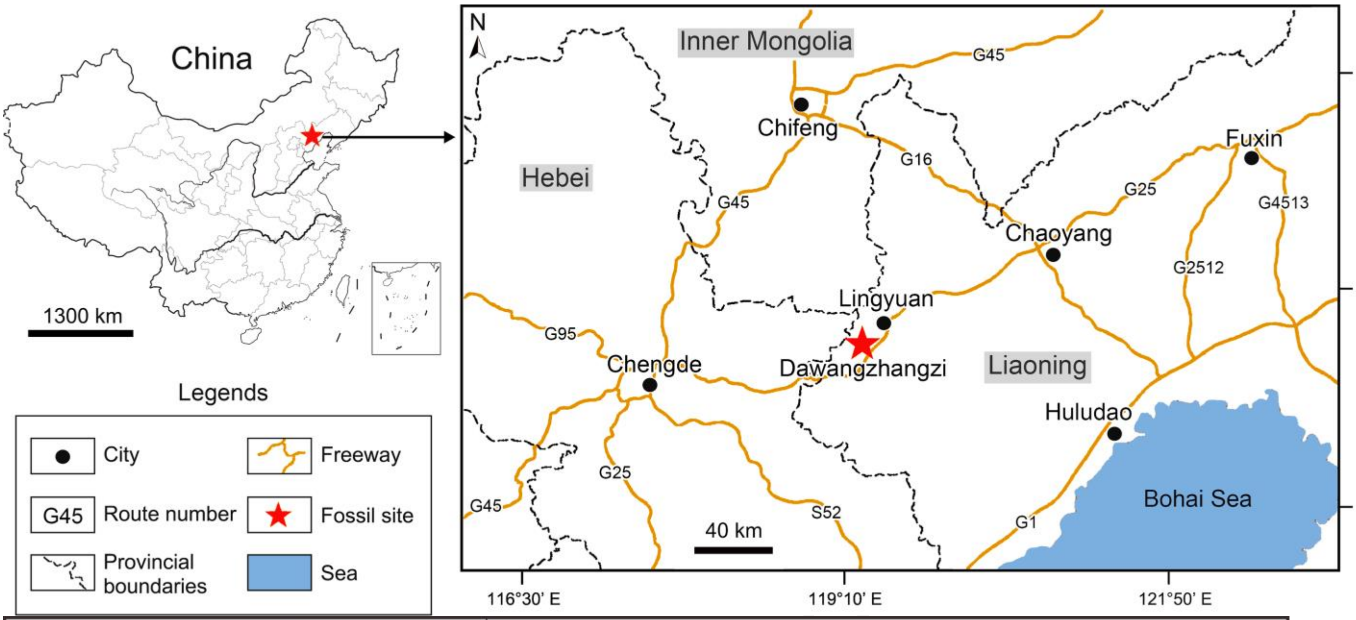

A
B
cl
rad
hu
C
D
E
rad
ul
hu
F

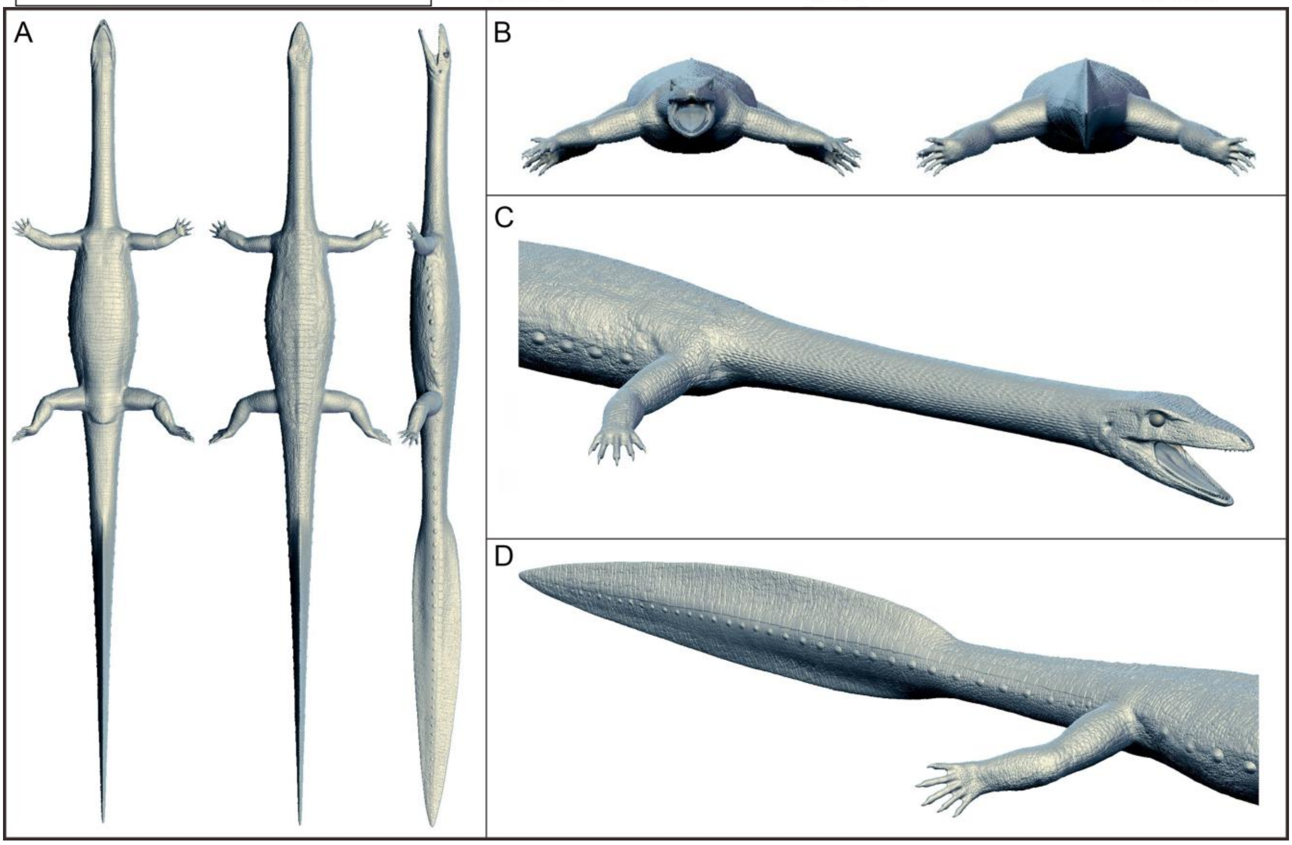

cv-2
lt
A
B
C


a
a
occipital condyle
A
B


A
or
cv-2
cv-8
cv-19
cl
I
II
III
IV
V
rad
hu
ul
hu
dv-4
ul
rad
IV
III
II
I
V
ti
fem
mtV
fi
dv-16
pub
sv-3
il
il
fem
isc
fi
ti
I
III
II
V
IV
ca-13
31
47
B
Area A
Area B
Area E
Area C
Area D
Area F
Area G
Area H


A
B


China
1300 km
Legends
City
Freeway
G45 Route number
Fossil site
Provincial boundaries
Sea
N
Inner Mongolia
Hebei
Liaoning
Chifeng
Fuxin
Chaoyang
Lingyuan
Dawangzhangzi
Chengde
Huludao
Bohai Sea
G45
G16
G25
G4513
G2512
G95
S52
G1
40 km
42°24' N
41°24' N
40°24' N
116°30' E
119°10' E
121°50' E


A
B
C
D