A new pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of southwestern China and its phylogenetic and biogeographic implications

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Abstract

After the devastating Permo-Triassic Mass Extinction, several new groups of large reptilian predators invaded the sea in the early part of the Triassic. Among these predators, sauropterygians, consisting of placodonts, pachypleurosaurs, nothosaurs and pistosaurs (including the iconic plesiosaurs), displayed the greatest diversity at both the generic and species levels, and persisted from the Early Triassic to the Late Cretaceous. Here we report a new species of Pachypleurosauria, *Dianmeisaurus mutaensis* sp. nov., from a recently discovered Lagerstätte in the Upper Member of the Anisian Guanling Formation. The only known specimen of the new species was collected from a quarry near Muta village, Luxi County, Yunnan Province, South China. Our new phylogenetic analysis based on a novel data matrix recovered the new taxon as a sister group to *Dianmeisaurus gracilis* – a small pachypleurosaur from the Middle Triassic Luoping biota. The new phylogenetic analysis also collapsed the

monophyly of the traditionally recognized Eusauropterygia. Pistosauroidea, *Majiashanosaurus*, and *Hanosaurus* comprise the consecutive sister groups to a new clade including Pachypleurosauria and Nothosauroidea. A monophyletic Pachypleurosauria, within which the clade consisting of *Dianmeisaurus* and *Panzhousaurus* occupies the basal-most position, is recovered by this study. The clade consisting of *Dawazisaurus* and *Dianopachysaurus* forms the sister group to the remaining pachypleurosaurs included in this study. Since *Dianmeisaurus*, *Panzhousaurus*, *Dawazisaurus*, and *Dianopachysaurus* are all exclusively known from South China, our study provides further evidence to the hypothesis that pachypleurosaurs had a palaeobiogeographic origin in the eastern Tethys.

Keywords: marine reptiles, Pachypleurosauria, *Dianmeisaurus*, phylogeny, palaeobiogeographic origin

Introduction

The Sauropterygia is the most flourishing clade among Mesozoic marine reptiles in terms of species diversity, and includes the iconic Plesiosauria from the Jurassic and Cretaceous and the stem-group Placodontia and Eosauropterygia from the Triassic (Kelley et al., 2014; Li & Liu, 2020; Motani, 2009; Rieppel, 2000; Stubbs & Benton, 2016). Eosauropterygians were traditionally divided into three groups, the Pachypleurosauria, the Nothosauroidea, and the Pistosauroidea (Rieppel, 2000). This traditional view holds that a monophyletic Pachypleurosauria comprises the sister

group to the clade Eusauropterygia consisting of Nothosauroidea and Pistosauroidea (Lin et al., 2021; Liu et al., 2011; Neenan et al., 2013; Rieppel, 2000).

Since the review by Rieppel (2000), many new genera of basal eosauropterygians have been described from the Triassic of China and Europe (Cheng et al., 2006; Cheng et al., 2012; Cheng et al., 2016; Dalla Vecchia, 2006; de Miguel Chaves et al., 2018; Jiang et al., 2019; Jiang et al., 2008; Klein et al., 2022; Liu et al., 2011; Ma et al., 2015; Marquez-Aliaga et al., 2019; Renesto et al., 2014; Shang et al., 2020; Shang & Li, 2015; Shang et al., 2011; Xu et al., 2022; Xu et al., 2023), which has complicated eosauropterygian interrelationships. Holmes et al. (2008) restudied *Keichousaurus hui* and questioned the monophyly of Pachypleurosauria for the first time, which has been supported by several later studies (e.g., Cheng et al., 2012; Cheng et al., 2016; Jiang et al., 2014; Marquez-Aliaga et al., 2019; Shang et al., 2011; Shang & Li, 2015; Shang et al., 2017; Wu et al., 2011). Their results also showed the collapse of a monophyletic Eusauropterygia clade, which was supported by some independent studies (e.g., Li & Liu, 2020; Liu et al., 2021; Neenan et al., 2013; Xu et al., 2022, 2023), although these studies recognized a monophyletic Pachypleurosauria. The study by Ma et al. (2015) supported the collapse of a monophyletic Pachypleurosauria, but still recognized a monophyletic Eusauropterygia clade instead. This finding was also supported by some other studies (e.g., Liu et al., 2015; Shang et al., 2020; Jiang et al., 2019).

Although the above-mentioned new Triassic basal eosauropterygian taxa have been well described, the phylogenetic analysis associated with the description of these new taxa primarily relied on slightly expanded data matrices that originated from Rieppel et al. (2002). Thus, the morphological information provided by comparative studies of these new materials of basal eosauropterygians still needs to be incorporated to examine the phylogenetic interrelationships of eosauropterygians. Additionally, the palaeobiogeographic origin of Pachypleurosauria is still controversial (Klein et al., 2022; Liu et al., 2011; Renesto et al., 2014; Rieppel, 1999a; Rieppel & Lin, 1995; Xu et al., 2023). Pachypleurosaurs have been reported in both the western Tethys (the Germanic Basin, Alpine Triassic, and Iberian Peninsula) (e.g., Čerňanský et al., 2018; de Miguel Chaves et al., 2020; Klein et al., 2022; Renesto et al., 2014; Rieppel, 1989; Sander, 1989; Sues & Carroll, 1985) and the eastern Tethys (South China and Myanmar) (e.g., Liu et al., 2011; San et al., 2019; Shang & Li, 2015; Jiang et al., 2019). Rieppel and Lin (1995) proposed an eastern Tethys origin of pachypleurosaurs based on the phylogenetic result that shows *Keichousaurus* from China forms the sister group of all European pachypleurosaurs. This hypothesis was supported by Liu et al. (2011) and Renesto et al. (2014). However, the earliest known pachypleurosaur is *Dactylosaurus* from the early Anisian of the Germanic Basin (Rieppel & Hagdorn, 1997). Thus, the palaeobiogeographic origin of pachypleurosaurs is more complex than previously believed and needs to be reassessed (Klein et al., 2022).

In this paper, we report a new species of Pachypleurosauria from Yunnan Province, China, represented by the part and counterpart of a single individual. The new specimen shares several synapomorphies with *Dianmeisaurus gracilis*, but also presents several unique characteristics meriting the status of a new species. In addition to describing the new species in detail, we also aim to clarify the phylogenetic interrelationships of eosauropterygians by incorporating the morphological information from the recently described basal eosauropterygian taxa and discuss the palaeobiogeographic origin of pachypleurosaurs.

Materials and methods

The new specimen described here was collected from the Upper Member of the Anisian Guanling Formation in an abandoned quarry that is about one km northwest of Muta village, Luxi County, Yunnan Province (Fig. 1). The skeleton was split into two parts during collection and prepared with pneumatic tools and needles in the palaeontological lab of HFUT. The data matrix for the phylogenetic analysis was produced using the software Mesquite Version 3.6. The data matrix comprises 203 characters, of which 179 are from Li and Liu (2020), 17 from Lin et al. (2021), three from Klein et al. (2022), and four are new characters. Published character codings were carefully checked, and several errors were corrected (the character list and data matrix are given in Supplementary Data 1 and 2, respectively). Cladistic analysis was performed using the software PAUP Version 4.0a169 for Windows (Swofford, 2021).

Heuristic search (ADDSEQ = RANDOM, NREPS = 1000, HOLD = 100, with other settings default) was performed to acquire the most parsimonious trees. Bootstrap support values were estimated by 1000 replicates and other settings were default. Measurements were collected using digital callipers and are provided in Table 1.

Figure 1. The geologic map showing the quarry where *Dianmeisaurus mutaensis* sp. nov. (HFUT MT-21-08-001) was discovered (updated after Hu & Liu, 2022). Abbreviations: E, Palaeogene; $T_{2\text{-}3}$f, Falang Formation, Ladinian-Carnian, Middle-Late Triassic; T_2y, Yangliujing Formation, Anisian-Ladinian, Middle Triassic; T_2g^2, Upper Member of Guanling Formation, Anisian, Middle Triassic; T_2g^1, Lower Member of Guanling Formation, Anisian, Middle Triassic; T_1, Lower Triassic.

Systematic palaeontology

Sauropterygia Owen, 1860

Eosauropterygia Rieppel, 1994

Pachypleurosauria Nopcsa, 1928

Dianmeisaurus Shang & Li, 2015

Revised diagnosis

Postfrontal with a distinct constriction behind the orbit (also present in *Anarosaurus*, *Honghesaurus*, and *Prosantosaurus*); distal end of sacral ribs distinctly expanded (also present in *Diandongosaurus* and *Qianxisaurus*); interorbital septum extremely narrowed and distinctly shorter than the distance between external nares (a synapomorphy of *Dianmeisaurus*); skull table with deeply concave posterior margin (also present in *Dawazisaurus* and *Diandongosaurus*).

***Dianmeisaurus mutaensis* sp. nov.**

Holotype

HFUT MT-21-08-001, a complete and articulated skeleton exposed in dorsal view (part and counterpart).

Ontogenetic evaluation

There are currently three known specimens of *Dianmeisaurus*, among which HFUT MT-21-08-001 represents the smallest individual with a total body length of 99.2 mm. It is much smaller than the two published specimens of *Dianmeisaurus gracilis* (315 mm for the holotype, see Shang & Li, 2015; 250 mm for IVPP V 17054, see Shang et al., 2017). Several morphological characters indicate that HFUT MT-21-08-001 is skeletally immature. First, the skull is poorly ossified. The skull has fontanelles, which generally indicates that the individual is at an early ontogenetic stage (Lin & Rieppel, 1998; Piñeiro et al., 2012; Rieppel, 1992a, 1992b; Rieppel, 1993a; Wise et al., 2009). Secondly, the distal end of the humeri is incompletely ossified since the entepicondylar groove is still present. The entepicondylar groove starts close and turns into a foramen when the individual becomes more mature (Currie & Carroll, 1984; Sander, 1989). Thirdly, among the carpals and tarsals of HFUT MT-21-08-001, only the astragalus is ossified, also indicating an early ontogenetic stage of the individual (Fröbisch, 2008; Rieppel, 1992b; Sander, 1989). All these lines of evidence strongly support the conclusion that HFUT MT-21-08-001 is skeletally immature.

Type Locality

Muta Village, Luxi County, Yunnan Province, China.

Type Horizon

Upper Member of Guanling Formation, Anisian, Middle Triassic.

Etymology

Named after Muta village where the holotype was collected.

Diagnosis

A pachypleurosaur with following autapomorphies among pachypleurosaurs: 23 cervical vertebrae, 20 dorsal vertebrae, and two sacral vertebrae; postfrontal extending posteriorly to a level beyond the middle of parietal; last dorsal rib stout and shorter than the first sacral rib; phalangeal formula of manus and pes 2-3-4-4-2 and 1-2-3-4-3 respectively. In addition to the above mentioned autapomorphies, *Dianmeisaurus mutaensis* also differs from *D. gracilis* in the following morphological characters: maxilla enters the external naris; anterior process of the frontal does not extend beyond the anterior margin of the orbit; postfrontal excluded from the upper temporal fenestra; coronoid process absent.

Figure 2. The holotype of *Dianmeisaurus mutaensis* sp. nov. (HFUT MT-21-08-001). A. the skeleton in dorsal view; B, the counterpart of A (natural mold). Scale bars equal 1 cm.

Description

The skeleton, embedded in the dark-grey micritic limestone, consists of a part and its counterpart. The specimen is well-preserved, with a total length of 99.2 mm. Adjacent to the specimen, there are scattered limb and rib bones from other individual(s), but the limited information available prevents further identification.

Skull

The skull of HFUT MT-21-08-001 is dorsoventrally compressed and slightly distorted (Fig. 3). The surface of the dermatocranial bones shows weak sculpturing. The preorbital region of the skull is slightly shorter than the postorbital region. The snout is very short and round anteriorly. The occipital portion is plate-like without an occipital crest.

Figure 3. The skull of *Dianmeisaurus mutaensis* sp. nov. (HFUT MT-21-08-001). A. photo; B, interpreted drawing. Abbreviations: an, angular; ar, articular; ata, atlas arch; atc, atlas centrum; axc, axial centrum; bo, basioccipital; c3, 3rd cervical centrum; d, dentary; eo-op, exoccipital-opisthotic complex; f, frontal; fo, fontanelle; j, jugal; m, maxilla; n, nasal; p, parietal; par, prearticular; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; q, quadrate; r3, 3rd cervical rib; sa, surangular; so, supraoccipital; sq, squamosal. The red arrow marks the pit on the premaxilla-maxilla suture. Scale bars equal 1 mm.

Table 1. Measurements of *Dianmeisaurus mutaensis* sp. nov. (HFUT MT-21-08-001).

MEASUREMENT	VALUE (MM)
Body length	99.2
Condylobasal skull length	10.7
Length of skull (to posterior margin of the parietal	9.3

Maximum width of the skull	8.2
Diameter of right external naris (longitudinal×transverse)	0.5×0.8
Minimum width between external nares	0.5
Diameter of right orbit (longitudinal×transverse)	3.8×3.3
Minimum width between orbits	0.3
Diameter of pineal foramen	0.3
Distance from snout tip to anterior margin of external naris	0.9
Distance from snout tip to anterior margin of orbit (preorbital region)	3.0
Minimum distance between external naris and orbit (length from the posterior margin of the external naris to the anterior margin of the orbit)	1.6
Distance from snout tip to anterior margin of upper temporal fenestra	7.0
Minimum distance between orbit and upper temporal fenestra (minimum width of the postorbital arch)	0.4
Distance from posterior margin of orbit to the posterolateral end of the squamosal (postorbital region)	3.4
Length of right humerus	4.7
Proximal width of right humerus	1.4
Distal width of right humerus	1.5
Minimal width of right humerus	0.9
Length of left ulna	2.6
Length of left radius	3.0
Proximal width of left ulna	0.7
Distal width of left ulna	0.6
Proximal width of left radius	0.8
Distal width of left radius	0.5
Length of left femur	6.6
Proximal width of left femur	1.6
Distal length of left femur	1.1
Minimal width of left femur	0.9
Length of right tibia	3.2

Minimal width of right tibia	0.5
Length of right fibula	3.0
Minimal width of right tibia	1.0

The paired premaxillae constitute the short snout in front of the external nares and the anterior margin of the external nares. The posterodorsal processes of the premaxilla extend backward along the midline, separating the anterior part of the nasal. Each posterolateral process of the premaxilla contacts the maxilla around the lateral margin of the external naris, where the snout constriction is absent as in most pachypleurosaurs (Rieppel, 2000), but a depression is developed.

The maxilla forms the anterolateral margin of the orbit. The anterior process of the maxilla runs into the lateral corner of the external naris where it contacts the premaxilla. Dorsally, the ascending process of the maxilla is wedged between the nasal anteromedially and the prefrontal posteromedially. It almost reaches the level of the midpoint of the anterior margin of the orbit. A small pit is located at the maxilla-prefrontal suture, which is close to the anterolateral corner of the orbit. The posterior process of the maxilla abuts the lateral margin of the jugal and reaches the posterior margin of the orbit.

The external naris is located anteriorly, quite close to the tip of the snout, as is also the case in *Dianmeisaurus gracilis* and *Panzhousaurus* (Jiang et al., 2019). The length from the tip of the snout to the anterior margin of the external naris divided by the condylobasal skull length is 0.08. The longitudinal diameter of the external naris is

less than its transverse diameter and the longitudinal diameter of the orbit. The lateral corner of the external naris shows an acute angle.

A pair of roughly triangular nasal bones meet along the midline, with the contact length comprising 3/4 of the total nasal length. Anteriorly, the nasal forms the posterior and part of the dorsal margin of the external naris. Anterodorsally, the paired nasals embrace the posterior processes of the premaxillae. Anterolaterally, the nasals are not well ossified, leaving an open gap with the maxilla and prefrontal. This gap is interpreted as a morphological feature related to the early ontogenetic stage of the specimen, i.e. a fontanelle. The posterior processes of the nasal separate the posterior processes of the prefrontal and taper backward to overlie the frontal, almost reaching the midpoint of the medial margin of the orbit, which is an autapomorphy of the species. The surface of the nasal shows a few deep pits.

The circular orbit is large, about twice longer than the upper temporal fenestra. The interorbital septum is extremely narrow. The minimum width of the interorbital septum is distinctly shorter than the minimum distance between the external nares, a synapomorphy of *Dianmeisaurus*. The prefrontal forms the anterodorsal margin of the orbit. Laterally, the prefrontal contacts the maxilla. The posterior process of the prefrontal meets the frontal. The paired frontals form the dorsal margin of the orbit. The anterior process of the frontal almost extends to the midpoint of the medial margin of the orbit, which is convergently present in *Dianopachysaurus* among

pachypleurosaurs (Liu et al., 2011). The anterior process of the frontal in other pachypleurosaurs extends very close to or beyond the anterior margin of the orbit (e.g., Cheng et al., 2016; Klein et al., 2022; Shang et al., 2011; Jiang et al., 2019; Xu et al., 2022). The well-developed posterolateral processes of the frontals are widely separated from the upper temporal fenestra and enter between the postfrontal and parietal.

The postfrontal forms the posterodorsal margin of the orbit. It has a roughly triradiate shape. The lateral margin of the postfrontal is distinctly constricted, which is also present in *Dianmeisaurus gracilis*, *Anarosaurus*, *Honghesaurus*, and *Prosantosaurus* among pachypleurosaurs (Klein, 2009; Klein et al., 2022; Shang et al., 2017; Xu et al., 2022). The postfrontal is separated from the upper temporal fenestra by the postorbital and parietal, which is otherwise only seen in *Honghesaurus* (Xu et al., 2022) among pachypleurosaurs. The posterior process of the postfrontal is embraced by the parietal and extends beyond the midpoint of the skull table, a synapomorphy shared with *Panzhousaurus* (Jiang et al., 2019) among pachypleurosaurs.

The postorbital defines the lateral and the entire anterior margin of the upper temporal fenestra. The lateral process of the postorbital contacts the jugal. The dorsal process of the postorbital narrowly meets the parietal, separating the postfrontal from the upper temporal fenestra. The posterior process of the postorbital contacts the squamosal with an interdigitated suture.

The boomerang-shaped jugal constitutes the posterolateral corner of the orbit. The ventral margin of the jugal contacts the maxilla. The posterodorsal process of the jugal covers the postorbital, being separated from the squamosal by the postorbital.

The parietals are partly fused. A distinct suture is present in front of the pineal foramen, dividing the paired parietals, but the parietal is fully fused behind the pineal foramen. The parietal is very broad. Anteriorly, the interdigitated parietal-frontal suture is located anterior to the posterior margin of the orbit. A large unossified gap between the frontal and parietal indicates the existence of another fontanelle. Laterally, the parietal constitutes the posterodorsal margin of the upper temporal fenestra. Posteriorly, the parietal contacts the squamosal and the supraoccipital. The circular pineal foramen is in the middle of the parietal table.

Due to the postmortem alteration, the right upper temporal fenestra is completely covered by the right squamosal, and the left fenestra is incomplete. Even so, it is conclusive that the upper temporal fenestra is distinctly shorter than the orbit.

The large squamosal is irregular in shape due to its postmortem alteration. The forked anterior process of the squamosal forms half of the supratemporal arch. The lateral process of the squamosal caps the quadrate. Medially, the squamosal contacts the dorsal margin of the supraoccipital.

The quadrate is partially covered by the squamosal. The condylar portion of the left quadrate is exposed in lateral view. The quadrate shows a concave region on the right side of the skull.

The supraoccipital is exposed horizontally without a medial crest. The supraoccipital contacts the parietal anteriorly with a V-shaped suture and the squamosal laterally. Posteriorly, it meets the exoccipital-opisthotic complex. The basioccipital is located at the same level as the mandibular articulations.

The relationships between bones of the lower jaw are indeterminate due to the poor preservation of the exposed surface. However, a coronoid process is certainly absent, which is different when compared to *Dianmeisaurus gracilis*, *Diandongosaurus* and *Keichousaurus* (Holmes et al., 2008; Shang et al., 2011; Shang et al., 2017). The dentary extends posteriorly to the midpoint of the orbit and contacts the angular. Medially, the angular meets the surangular. Both of them contribute to the lateral and dorsal margins of the lower jaw. The articular shows a distinct trough in dorsal view, forming the dorsal part of the well-develop retroarticular process. The prearticular is disarticulated from the articular and constitutes the floor of the retroarticular process.

The dentition of the right side is better preserved than the dentition of the left side. Thus, the following description is based on the dentition of the right side. All teeth have a pointed apex. Two premaxillary teeth are visible and are similar in size. No premaxillary and maxillary fangs are present. Five maxillary teeth are visible, of which the second is distinctly smaller than the others, likely because it represents a replacement tooth.

Postcranial skeleton

Vertebrae

HFUT MT-21-08-001 comprises 23 cervical vertebrae, 20 dorsal vertebrae, only two sacral vertebrae, and at least 40 caudal vertebrae (Fig. 2). All zygapophyses are pachyostotic and no intercentra are present. The atlas is dislocated and covered by the basioccipital. Two triangular atlas arches are disarticulated and well exposed (Fig. 3). The cervical vertebrae have low neural spines. The neural spines of the dorsal region are also low, and there is no elongated transverse process on the dorsal region. The caudal vertebrae become smaller posteriorly.

Ribs

The ribs are slender (Fig. 2). The distal end of the dorsal rib becomes flat and slightly expanded. The first dorsal rib is almost twice as long as the last cervical rib. The last (20^{th}) dorsal rib is short and robust. It is shorter than the sacral ribs and all other dorsal ribs, which represents an autapomorphy of the species among Pachypleurosauria. The distal end of last dorsal rib shows an expansion that is slightly more obvious than the distal expansion of other dorsal ribs. However, the last dorsal ribs are too short to articulate with the ilium and do not extend toward the ilium. Additionally, there is no evidence of dislocation for the last dorsal ribs (Fig. 6). So they can not be sacral ribs, but at the best be called transitional ribs (Romer, 1956). The left side of the sacral ribs are completely exposed (Fig. 6). The distal end of the sacral ribs is slightly expanded. The slender caudal ribs all taper to a point. The first

caudal rib extends perpendicularly to the body axis. The third caudal rib is the longest among all caudal ribs. From the third caudal rib to the sixth, the length of the caudal rib is reducing gradually. The 1st-6th caudal ribs of this specimen are prominent. In *Dianmeisaurus gracilis*, the 1st-9th caudal ribs are prominent, while in *Panzhousaurus*, prominent caudal ribs are present on 1st-11th caudal vertebrae.

Pectoral girdle

Among the pectoral girdle elements (Fig. 4), the interclavicle and coracoid are completely covered by ribs and vertebrae. The left scapula is exposed in the lateral view, while the right scapula is exposed in the medial view. As in all other sauropterygians (Klein et al., 2022; Rieppel, 2000), the posterior margin of the clavicle is connected to the medial surface of scapula, a synapomorphy of sauropterygians. The posteriorly directed dorsal wing of the scapula is rod-like and tapers to a blunt tip, a synapomorphy of eosauropterygians (Rieppel, 2000).

Figure 4. Pectoral region of *Dianmeisaurus mutaensis* sp. nov. (HFUT MT-21-08-001). A. photo; B, interpreted drawing. Abbreviations: cl, clavicle; cv23, 23rd cervical vertebra; dv1, 1st dorsal vertebra; h, humerus; sc, scapula. Scale bars equal 1 mm.

Forelimb

The right forelimb is preserved completely (Fig. 5). The humerus is curved as in all sauropterygians. Owing to the weakly developed deltopectoral crest, the preaxial margin of the humerus is slightly angulated. The distal end of the humerus is slightly broadened. Due to its early ontogenetic stage, an entepicondylar groove can be seen in

this specimen, instead of the entepicondylar foramen (Sander, 1989). The ulna is shorter than the radius. The preaxial margin of the ulna is smoothly concave. Both ends of the ulna are slightly expanded. The radius is straight, with its proximal part slightly wider than the distal end. The proximal end and mid-shaft of the radius are approximately as broad as those of the ulna.

No carpal element is ossified. Metacarpal 1 is distinctly shorter and stouter than metacarpals 2- 4, of which metacarpal 3 is the longest. The phalangeal elements are tightly connected. The phalangeal formula of the manus is 2-3-4-4-2.

Figure 5. Right forelimb of *Dianmeisaurus mutaensis* sp. nov. (HFUT MT-21-08-001). A. photo; B, interpreted drawing. Abbreviations: d, digit; eng, entepicondylar groove; h, humerus; r, radius; sc, scapula; u, ulna. Scale bars equal 1 mm.

Pelvic girdle

The pelvic girdle is partially exposed in dorsal view (Fig. 6). The dorsal blade of the ilium is reduced to a simple stub. The pubis and ischium are flat bones, thickened dorsoventrally at the lateral margin. The ischium shows the concave postaxial margin.

Figure 6. Sacral region of *Dianmeisaurus mutaensis* sp. nov. (HFUT MT-21-08-001). A. photo; B, interpreted drawing. Abbreviations: cav, caudal vertebra; dr, dorsal rib; dv, dorsal vertebra; fi, fibula; il, ilium; is, ischium; pu, pubis; sr, sacral rib; sv, sacral vertebra. Scale bars equal 1 mm.

Hindlimb

The hind limb is well preserved except for the distal portion of the left femur (Fig. 2). The femur is long and sigmoidally curved, and the ratio of femur length divided by humerus length is 1.39. The anterior and posterior femoral condyles are subequally extended. The internal trochanter is absent. The fibula and tibia are equal in length, but the flat tibia is much more broadened than the fibula. The small round astragalus is the only ossified tarsal bone. Metatarsal 1 is the shortest and stoutest element of the metatarsals, while others are long and slender. Metatarsals 3 and 4 are approximately the same length, slightly longer than metatarsals 2 and 5. The phalangeal formula of the pes is 1-2-3-4-3.

Figure 7. Right hindlimb of *Dianmeisaurus mutaensis* sp. nov. (HFUT MT-21-08-001). A. photo; B, interpreted drawing. Abbreviations: as, astragalus; d, digit; f, femur; fi, fibula; il, ilium; ti, tibia. Scale bars equal 1 mm.

Phylogenetic analysis

Figure 8. Strict consensus tree showing phylogenetic relationships of eosauropterygians. Bootstrap values over 50% (with 1000 replicates) are indicated in the tree.

To assess the phylogenetic position of *Dianmeisaurus mutaensis* among eosauropterygians, we compiled a new data matrix consisting of 203 characters, among which 182 are informative, for 43 taxa. The matrix was based on a revised version of the one presented by Li and Liu (2020), and many new characters were

added through a comparative study. We also coded several new taxa of eosauropterygians discovered in recent years, including *Qianxisaurus* (Cheng et al., 2012), *Odoiporosaurus* (Renesto et al., 2014), *Dianmeisaurus* (Shang & Li, 2015; Shang et al., 2017), *Dawazisaurus* (Cheng et al., 2016), *Panzhousaurus* (Jiang et al., 2019; Lin et al., 2021), *Honghesaurus* (Xu et al., 2022), and *Prosantosaurus* (Klein et al., 2022). In our phylogenetic analysis, Araeoscelidia, Younginiformes, Archosauromorpha, and *Placodus* were still selected as outgroups taxa as in Li and Liu (2020).

Heuristic searches of the new data matrix found five most parsimonious trees (tree length = 811, consistency index = 0.3169, retention index = 0.6139). *Dianmeisaurus mutaensis* forms the sister group to *D. gracilis*. The strict consensus tree recovered *Dianmeisaurus* as the sister group to *Panzhousaurus*. The clade consisting of *Dianmeisaurus* and *Panzhousaurus* occupies the basal-most position of Pachypleurosauria (Fig. 8). Meanwhile, the monophyly of Eusauropterygia is collapsed. Pistosauroidea, *Majiashanosaurus*, and *Hanosaurus* constitute the consecutive sister group to a monophyletic clade including Pachypleurosauria and Nothosauroidea. Our phylogenetic analysis recovered a monophyletic Pachypleurosauria clade, which is supported by six unambiguous synapomorphies: bones in the dermatocranium relatively smooth (character 1: 1); the ratio of longitudinal diameter of upper temporal divided by that of orbit is between 0.5-1 (character 45: 2); presence of a trough on the dorsal surface of retroarticular process

(character 82: 1); anterolaterally expanded corners of clavicles present (character 128: 1); anterior preaxial margin of shaft of radius rather straight (character 190: 2); pes ungual phalanges extremely expanded (character 194: 1).

Discussion

Comparison with Dianmeisaurus gracilis

HFUT MT-21-08-001 is identified as a pachypleurosaur because of the presence of the following characteristics: the upper temporal fenestra distinctly smaller than the orbit, an anteriorly extended jugal that enters the ventral margin of the orbit, a distinct trough on the dorsal surface of the retroarticular process, pachyostotic pre- and postzygapophyses, and the reduced dorsal iliac blade. HFUT MT-21-08-001 also shares several derived characters with *Dianmeisaurus gracilis*: the postfrontal with distinct constriction behind the orbit; the width of interorbital septum distinctly shorter than the minimum length between external naris; the posterior margin of skull table deeply concave; the distal head of sacral ribs expanded.

Nevertheless, HFUT MT-21-08-001 shows many differences when compared with *Dianmeisaurus gracilis*. In *Dianmeisaurus gracilis*, the postnarial process of the premaxilla excludes the maxilla from the external naris, whereas in HFUT MT-21-08-001, the maxilla enters the external naris, which is similar to all other pachypleurosaurs (Rieppel., 2000; Cheng et al., 2012; Klein et al., 2022; Renesto et al,, 2014; Liu et al., 2011; Shang et al., 2011; Cheng et al., 2016). Also, the

postfrontal extends backward beyond the frontal to a level close to the middle of the skull table in HFUT MT-21-08-001, a unique morphology among pachypleurosaurs, while it just reaches the posterior end of the frontal in *Dianmeisaurus gracilis*. Also, the postfrontal is excluded from the margin of the upper temporal fenestra in HFUT MT-21-08-001, but the postfrontal of *Dianmeisaurus gracilis* enters the upper temporal fenestra. Contrary to the presence of a distinct coronoid process in *Dianmeisaurus gracilis*, the coronoid process in HFUT MT-21-08-001 is absent.

There are even more differences in the postcranial morphology between HFUT MT-21-08-001and *Dianmeisaurus gracilis*. In contrast to the long and slender last dorsal rib in *Dianmeisaurus gracilis*, HFUT MT-21-08-001 has a stout last dorsal rib that is shorter than the first sacral rib. The most significant difference is the number of sacral vertebrae, which is four in *Dianmeisaurus gracilis* but only two in HFUT MT-21-08-001. The phalangeal formula of the manus of HFUT MT-21-08-001 is 2-3-4-4-2 and that of the pes is 1-2-3-4-3, which are both less than the number of phalanges in *Dianmeisaurus gracilis* (manus: 2-3-5-5-3(?), pes: 2-3-4-5-5(?)).

Although HFUT MT-21-08-001 is a juvenile, these differences do not change during the development of the individual among reptiles, as far as we know (Currie, 1981; Currie & Carroll, 1984; Delfino & Sanchez-Villagra, 2010; Fröbisch, 2008; Griffin et al., 2021; Lin & Rieppel, 1998; Rieppel, 1992b; Rieppel, 1993a; Rieppel, 1993b; Rieppel, 1994; Sander, 1989). Therefore, we erected a new species for HFUT MT-08-001, i.e., *Dianmeisaurus mutaensis* sp. nov..

Phylogenetic implications to the interrelationships of eosauropterygians

Many eosauropterygian phylogenies were published after the comprehensive review of sauropterygians by Rieppel (2000). These phylogenetic analyses accompanied the description of *Dawazisaurus* (Cheng et al., 2016), *Diandongosaurus* (Liu et al., 2021; Liu et al., 2015; Sato et al., 2014a; Shang et al., 2011), *Dianmeisaurus* (Shang & Li, 2015; Shang et al., 2017), *Dianopachysaurus* (Liu et al., 2011), *Honghesaurus* (Xu et al., 2022), *Luopingsaurus* (Xu et al., 2023), *Majiashanosaurus* (Jiang et al., 2014), *Odoiporosaurus* (Renesto et al., 2014), *Panzhousaurus* (Jiang et al., 2019; Lin et al., 2021), *Prosantosaurus* (Klein et al., 2022), *Qianxisaurus* (Cheng et al., 2012), and *Yunguisaurus* (Cheng et al., 2006; Lu et al., 2021; Sato et al., 2010, 2014b; Shang et al., 2016; Wang et al., 2019; Zhao et al., 2008). But most of these phylogenetic analyses relied on the data matrix of Rieppel et al. (2002) or slightly modified versions. Recently, some novel data matrices for analyzing the interrelationship of eosauropterygians have been constructed to incorporate the morphological information available from new Chinese eosauropterygians (Li & Liu, 2020; Lin et al., 2021; Xu et al., 2023). In Li and Liu (2020), the monophyly of Eusauropterygia collapsed, and Pachypleurosauria and Nothosauroidea constituted an unnamed clade. Our new phylogenetic analysis here also shows the collapse of the monophyly of Eusauropterygia, as in Li and Liu (2020), and suggests a new monophyletic clade comprising Pachypleurosauria and Nothosauroidea. Pistosauroidea,

Majiashanosaurus, and *Hanosaurus* comprise the consecutive sister groups of the new clade. These results are consistent with those of Li and Liu (2020). However, the Early Triassic *Corosaurus* occupies the basal-most position of the Pistosauroidea in this study, as traditionally recognized (Rieppel 2000). This is in contrast to the phylogenetic result of Li and Liu (2020), which shows *Corosaurus* as the most basal member of Eosauropterygia. *Hanosaurus* is recovered in a relatively basal position within Eosauropterygia as in some previous analyses (e.g., Jiang et al., 2019; Li & Liu, 2020; Liu et al., 2015; Ma et al., 2015; Shang et al., 2017; Xu et al., 2022), rather than in a lineage leading to the Nothosauroidea (e.g., Cheng et al., 2012; Jiang et al., 2014; Sato et al., 2014a; Shang & Li, 2015), as a basal pachypleurosaur (e.g., Neenan et al., 2015), or even outside of the Sauropterygia clade (e.g., Cheng et al., 2016; Klein & Scheyer, 2014; Marquez-Aliaga et al., 2019; Neenan et al., 2013).

Monophyly and the palaeobiogeographic origin of Pachypleurosauria

The first cladistic analysis to test the monophyly of Pachypleurosauria was conducted by Storrs (1991). The monophyly of Pachypleurosauria was subsequently confirmed by a series of independent studies (reviewed in Rieppel, 2000). However, Holmes et al. (2008) restudied *Keichousaurus hui* and questioned the monophyly of Pachypleurosauria for the first time, which has been supported by several subsequent studies (e.g., Cheng et al., 2016; Jiang et al., 2014; Marquez-Aliaga et al., 2019;

Shang et al., 2011; Wu et al., 2011). Nevertheless, some other studies still support the traditional view that Pachypleurosauria is monophyletic (e.g., Liu et al., 2011; Neenan et al., 2013).

A monophyletic Pachypleurosauria is also recovered here, as in several recent studies (Li & Liu, 2020; Lin et al., 2021; Liu et al., 2021). However, different from the traditional topology where *Dianmeisaurus* forms the sister group of *Diandongosaurus*, *Dianmeisaurus* forms the sister group of *Panzhousaurus*, and together they occupy the basal-most position of Pachypleurosauria in this study. *Dianopachysaurus* forms a monophyletic clade with *Dawazisaurus*, which comprises the sister group to all remaining pachypleurosaurs. *Keichousaurus* and *Diandongosaurus* form a monophyletic clade, comprising the sister group to a clade consisting of all European pachypleurosaurs. Our result further indicates that two middle Anisian pachypleurosaurs from South China, *Qianxisaurus* and *Honghesaurus*, are deeply nested in the European pachypleurosaurs, similar to the results of Xu et al. (2022, 2023). Compared with other Chinese pachypleurosaurs, *Qianxisaurus* and *Honghesaurus* exhibit some derived characters: the snout is elongated; the ratio of the longitudinal diameters of the upper temporal divided by that of the orbit is less than 0.5; the deltopectoral crest is well-developed; the posterior process of the postfrontal is close to the middle of the skull table.

Our phylogenetic analysis indicates that Chinese pachypleurosaurs, with the exception of *Qianxisaurus* and *Honghesaurus*, comprise the consecutive sister

groups to all European pachypleurosaurs, supporting a hypothesis that Pachypleurosauria originated in the eastern Tethys (Liu et al., 2011; Renesto et al., 2014; Rieppel & Lin, 1995). However, the earliest known pachypleurosaur, *Dactylosaurus*, is from the early Anisian of the Germanic Basin (Rieppel & Hagdorn, 1997), which implies the existence of a ghost lineage in the eastern Tethys. The two unnamed pachypleurosaur skeletons from Myanmar (San et al., 2019), which could potentially be the oldest known pachypleurosaur, could falsify the existence of a ghost lineage. However, the geological age in the region where the Myanmar pachypleurosaur was collected still requires further study.

Conclusion

Dianmeisaurus mutaensis sp. nov. is established based on a newly discovered specimen from Muta village, Luxi county, Yunnan Province, China. *Dianmeisaurus mutaensis* exhibits several automorphic features, including the postfrontal extending posteriorly to the middle of the parietal table and being excluded from upper temporal fenestra, a stout last dorsal rib shorter than the first sacral rib, and two sacral vertebrae.

In addition, a novel data matrix was compiled to re-evaluate the interrelationships of eosauropterygians. Phylogenetic analysis shows the collapse of the monophyly of Eusauropterygia. Pistosauroidea, *Majiashanosaurus*, and *Hanosaurus* constitute the consecutive sister groups to a monophyletic clade comprising Pachypleurosauria and

Nothosauroidea. Furthermore, the monophyly of Pachypleurosauria is supported by six synapomorphies. Our phylogenetic results provide further evidence to the eastern Tethys origin of pachypleurosaurs. However, early Anisian pachypleurosaurs from the eastern Tethys region are required to test the biogeographic hypothesis.

Institutional Abbreviations

HFUT, Hefei University of Technology, Hefei, Anhui, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences in Beijing, China.

Declarations

Availability of data and materials

All data generated or analyzed during this study are included in the Supplementary Data of this published article. HFUT MT-21-08-001 is stored at the Geological Museum of HFUT, Hefei, China, and publically accessed.

Competing interests

The authors declare that they have no competing financial interests.

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Author's contributions

JL designed the research. YWH prepared all figures and tables. QL and YWH compiled the new data matrix, and YWH performed phylogenetic analyses. YWH and JL were the major contributors to writing the manuscript. All authors read and approved the final manuscript.

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Figure 1

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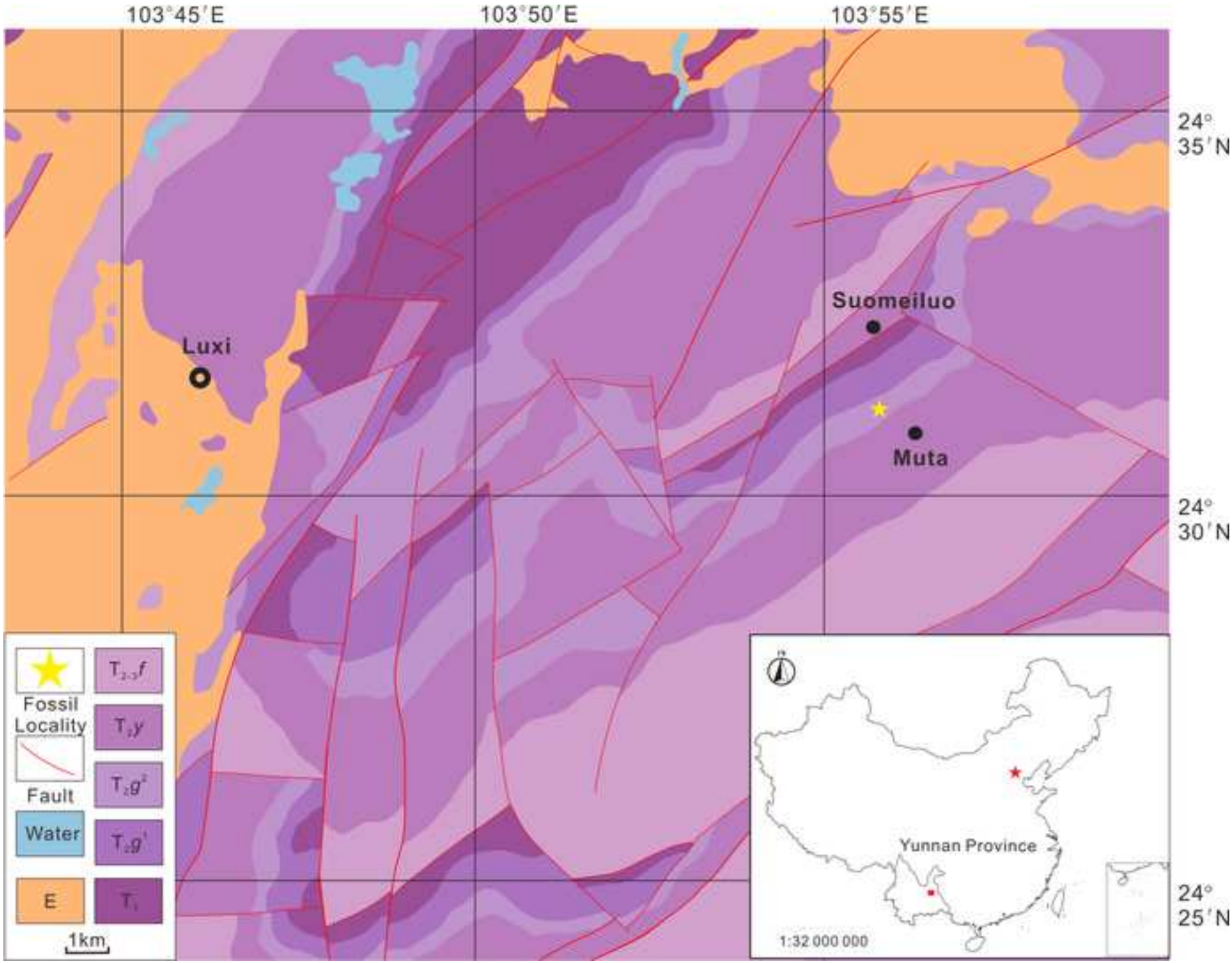

Figure 2

Figure 3

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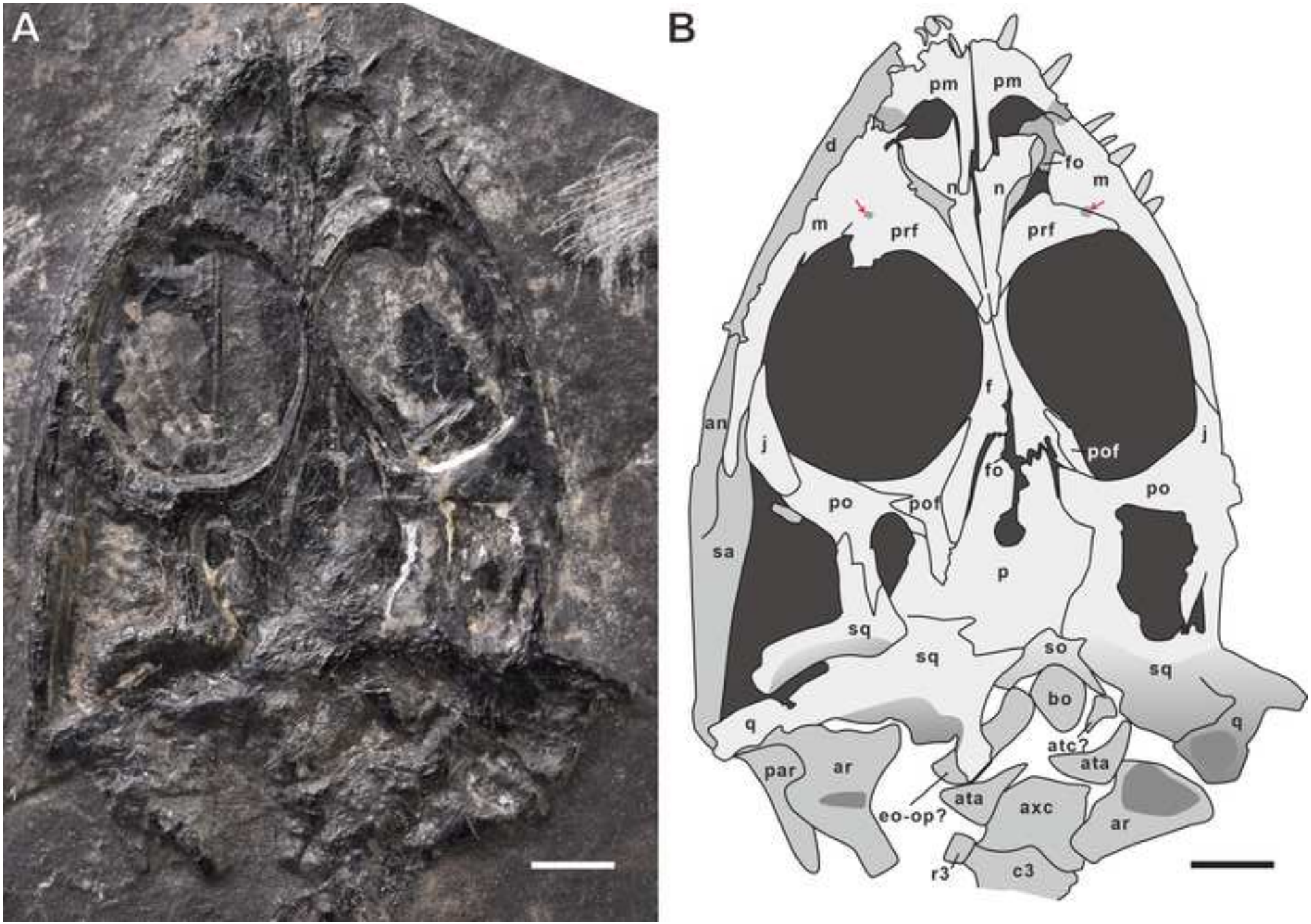

Figure 4

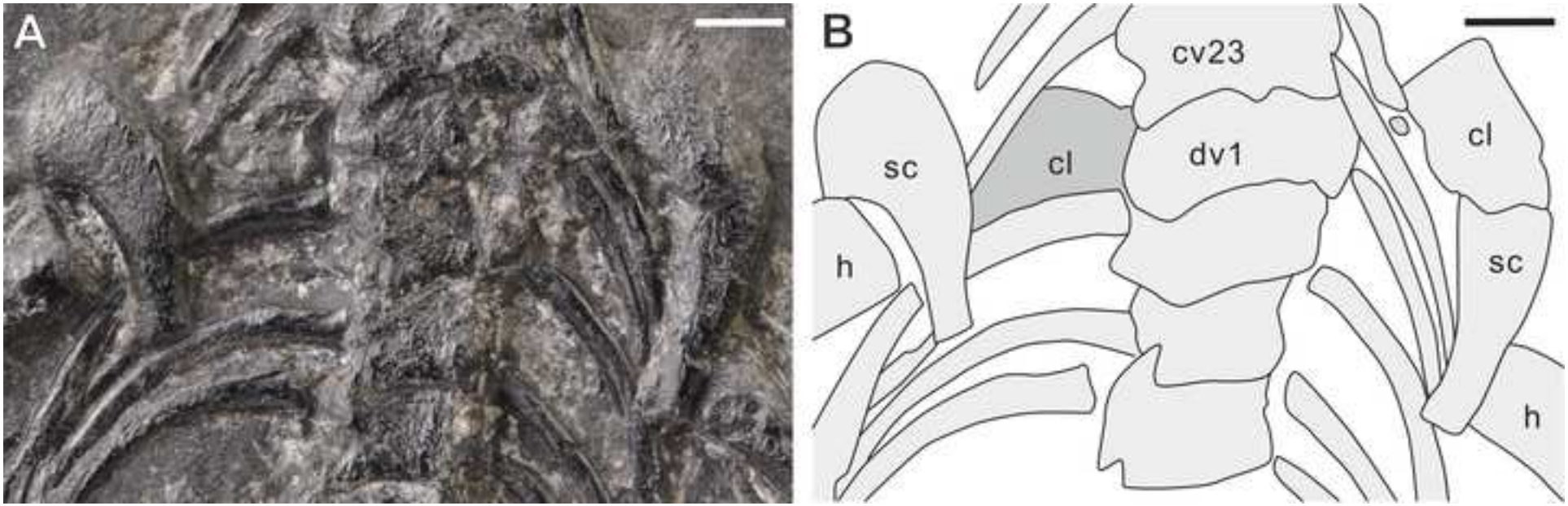

Figure 5

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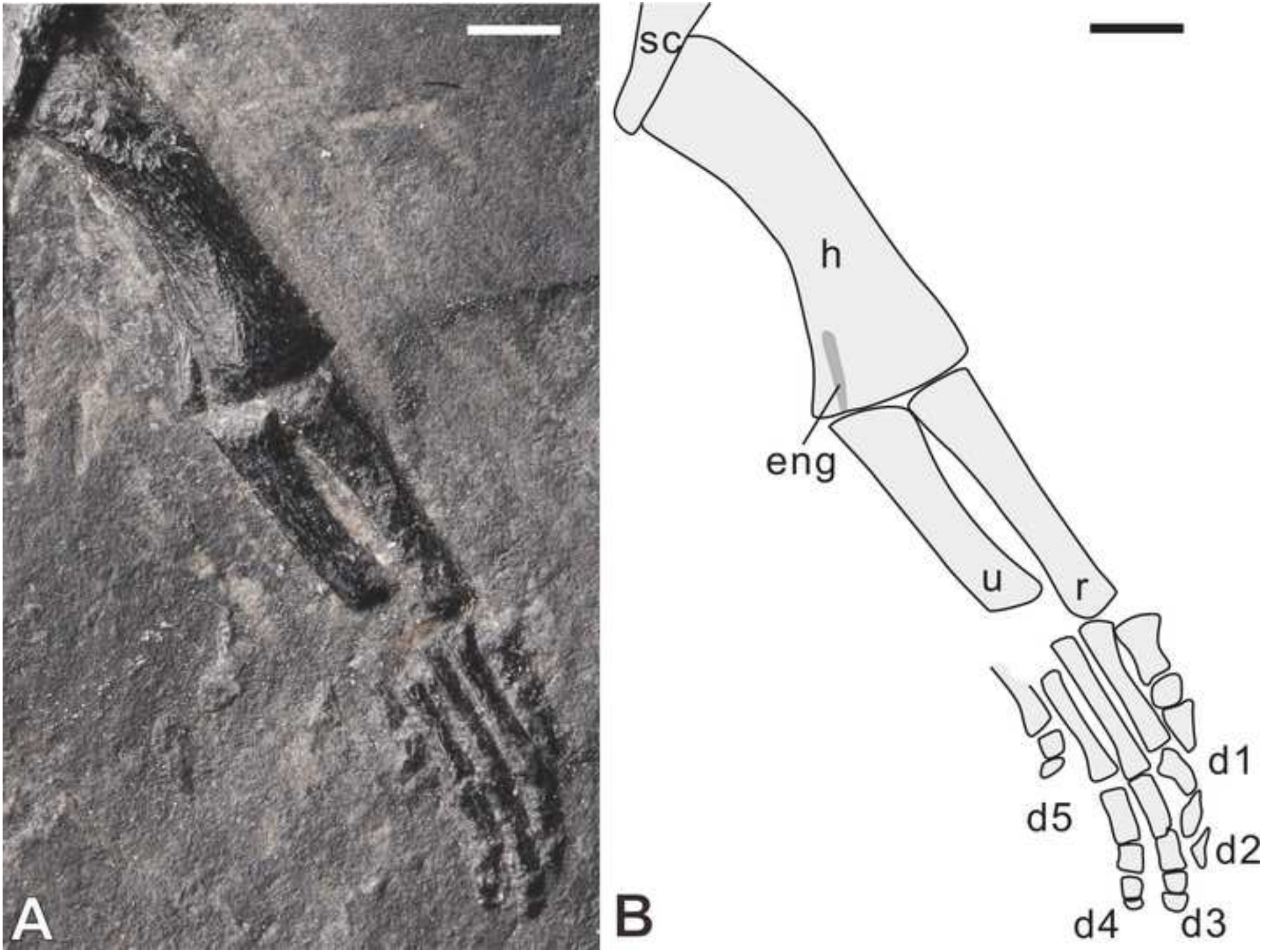

Figure 6

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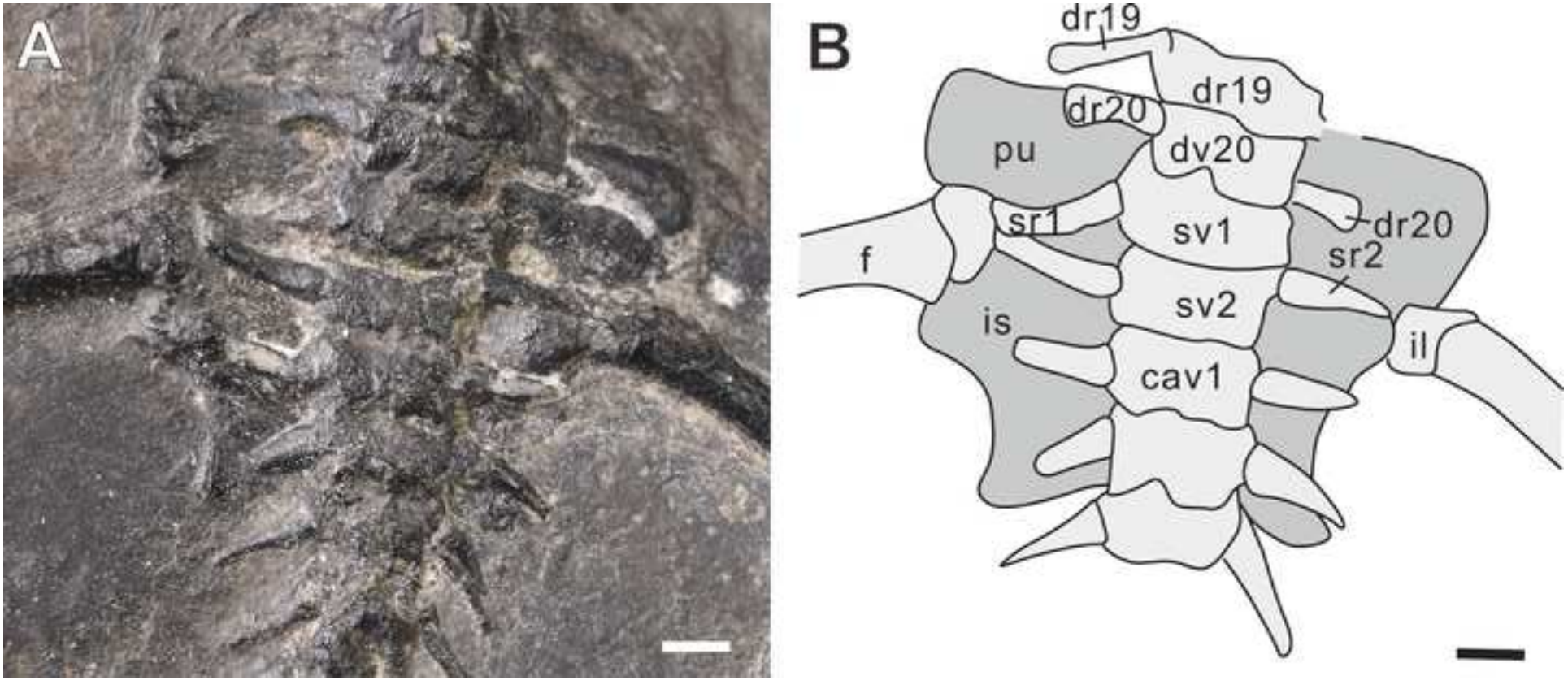

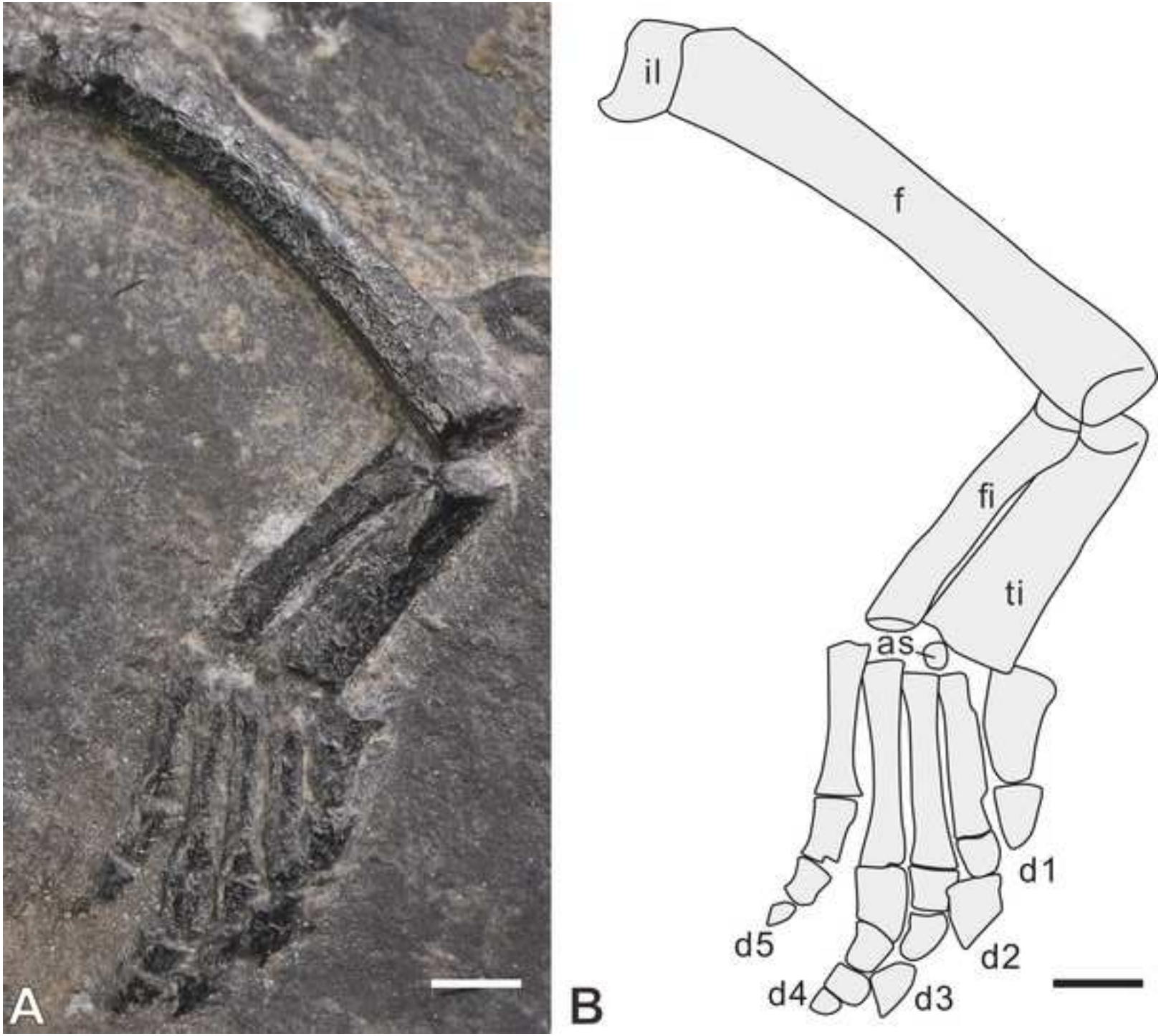

Figure 8