Mesozoic 003 (2): 196–206
https://www.mapress.com/mz/

Article

ISSN 3021-1859 (print edition)
MESOZOIC
ISSN 3021-1867 (online edition)

https://doi.org/10.11646/mesozoic.3.2.6

http://zoobank.org/urn:lsid:zoobank.org:pub:E799BD15-CB65-41CE-A846-A9DAA2AABD0A

Pteronisculus luopingensis sp. nov., a new stem actinopterygian fish from the Middle Triassic (Anisian) of Luoping, Yunnan, China

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Abstract

The extinct genus *Pteronisculus* represents a stem lineage of marine actinopterygians from the Early to Middle Triassic and is characterized by a toothed lacrimal contributing to the oral margin. To date, 13 species have been referred to *Pteronisculus*; most lived in the Early Triassic, except for two species from the Middle Triassic Luoping biota in Yunnan Province, China. Here, we report a new species of this genus, *P. luopingensis* **sp. nov.**, based on five well-preserved specimens from the Luoping biota, documenting the third species of *Pteronisculus* recovered from the Middle Triassic. The new species possesses diagnostic features of *Pteronisculus* but is easily distinguished from other species of the genus by several autapomorphies of the skull, scales, and fins (*e.g.*, a dermosphenotic shorter than the intertemporal, 89–90 lateral-line scales, and ~40 principal rays in each pelvic fin). The new finding enriches our understanding of the taxonomic diversity of Middle Triassic actinopterygians from the Yangtze Sea and further supports the area as a refuge for the survival of *Pteronisculus* during this epoch.

Keywords: osteology, taxonomy, Actinopterygii, *Pteronisculus*, Luoping biota, Triassic

Introduction

Actinopterygii (ray-finned fishes) is the most diverse clade of extant vertebrates and has a fossil record spanning more than 400 million years (Gardiner, 1984; Long, 1988; Coates, 1999; Hurley *et al*., 2006; Mickle & Bader, 2009; Sallan, 2014). Over 100 genera of primitive actinopterygians were traditionally assigned to the paraphyletic 'Palaeonisciformes' (Gardiner & Schaeffer, 1989; Xu *et al*., 2014a; Friedman, 2015). *Pteronisculus* White, 1933 is an extinct genus whose precise relationships with other early actinopterygians remain unclear. To date, 13 species have been referred to the genus; in addition to the type species *P. cicatrosus* from the Early Triassic of Madagascar, other well-studied species based on relatively complete specimens include *P. stensioi*, *P. magnus,* and *P. gunnari* from the Early Triassic of Greenland, and *P. nielseni* and *P. changae* from the Middle Triassic (Anisian) of Yunnan, China (Stensiö, 1921, 1932; White, 1933; Nielsen, 1936, 1942; Lehman, 1952; Uyeno, 1978; Véran, 1988; Xu *et al*., 2014b; Ren & Xu, 2021; Cavicchini *et al*., 2025). Recent analyses generally place *Pteronisculus* on the actinopterygian stem without reference to a particular family or order (Argyriou *et al*., 2018, 2022; Giles *et al*., 2017; Ren & Xu, 2021; Wilson *et al*., 2018).

Here, we report the discovery of a new species of *Pteronisculus* on the basis of five well-preserved specimens from the Second Member of the Guanling Formation in Luoping County, Yunnan Province, China. The new finding documents the third species of *Pteronisculus* from the Luoping biota and provides an important addition to our understanding of the taxonomic diversity of actinopterygians from the Middle Triassic of China. Along with *Pteronisculus*, other macrofossils from the same fossiliferous horizons at the Luoping localities include plants, invertebrates, marine reptiles, and several other kinds of fishes (see review of Benton *et al*., 2013; Sun *et al*., 2009; Wu *et al*., 2009; Tintori *et al*., 2010; Wen *et al*., 2012; Xu & Wu, 2012; Xu *et al*., 2014b, 2023). The fossil beds are composed of thinly laminated micritic limestone alternating with silty limestone, indicating a semi-enclosed intraplatform depositional environment (Hu *et al*., 2011). The age of the fossil beds (Anisian, ~244

 Submitted: 12 Jun. 2026; accepted by D.-Y. Huang: 25 Jun. 2026; published: 30 Jun. 2026

Ma) is well constrained by conodont analysis (Zhang *et al*., 2009).

Material and methods

The studied specimens are curated in the fossil collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP), Beijing, China. They were mechanically prepared with sharp steel needles under a stereomicroscope. Line drawings were drafted digitally and finalized using Adobe Photoshop. Scale counts and the topological placement of fins follow the standard conventions of Westoll (1944), in which the letters D, P, A, and C are followed by a numerical value denoting the number of vertical scale rows between the first complete row behind the pectoral girdle and the insertion of the dorsal (D), pelvic (P), anal (A), and caudal (C) fins, respectively. The letter T denotes the total number of scale rows between the pectoral girdle and the caudal inversion. General anatomical nomenclature for actinopterygians follows Ren & Xu (2021).

Anatomical abbreviations: an, anterior nostril; ang, angular; ao, antorbital; aop, antopercle; asp, ascending process of parasphenoid; bf, basal fulcra; bpt, basipterygoid process of parasphenoid; br, branchiostegal rays; cl, cleithrum; cla, clavicle; co, coronoid; den, dentary; dhy, dermohyal; dpl, dermopalatine; dsp, dermosphenotic; epl, epichordal lobe; ff, fringing fulcra; fr, frontal; hm, hyomandibular; ih, interhyal; it, intertemporal; ju, jugal; lac, lacrimal; les, lateral extrascapular; lgu, lateral gular; mes, medial extrascapular; na, nasal; op, opercle; pa, parietal; pas, parasphenoid; pcl, postcleithrum; pcr, procurrent ray; pio, postinfraorbital; pl-a, anterior pit line; pl-m, median pit line; pl-p, posterior pit line; pn, posterior nostril; pop, preopercle; pq, palatoquadrate; pr.1, first accessory process of palatoquadrate; pr.2, second accessory process of palatoquadrate; pr.b, basal process of palatoquadrate; prr, principal ray; pt, posttemporal; qj, quadratojugal; r, rostral; san, surangular; sbo, suborbital; scl, supracleithrum; scr, sclerotic ring; sop, subopercle; st, supratemporal.

Systematic palaeontology

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Cope, 1887
Genus *Pteronisculus* White, 1933

***Pteronisculus luopingensis* sp. nov.**

Material. Holotype. IVPP V 24388, a nearly complete, laterally compressed skeleton preserved in right lateral view.

Paratypes. IVPP V20490, V24337, V25616, and V30888.

Etymology. The species name refers to Luoping County, Yunnan Province, the type locality that yielded all known specimens of the new species.

Diagnosis. A large-sized species of *Pteronisculus* distinguished from other members of the genus by the following combination of features: dermosphenotic shorter than the intertemporal; absence of dermosphenotic/nasal contact; presence of three suborbitals; two postinfraorbitals; 53 principal rays in the anal fin; ~40 principal rays in each pelvic fin; pterygial formula of D54/P16–17, A44–46, C80–81/T89–90.

Locality and horizon. Luoping, Yunnan Province; Second (Upper) Member of the Guanling Formation, Pelsonian (~244 Ma), Anisian, Middle Triassic (Zhang *et al*., 2009).

Description. *General morphology and size*. Similar to other species of the genus, *Pteronisculus luopingensis* **sp. nov.** has a blunt snout, an elongate fusiform body, and a heterocercal caudal fin with a deeply cleft profile (Figs 1–6). The holotype (Fig. 1) has a total length of 185 mm, a standard length of 132.5 mm, a head length of 40.5 mm, and a body depth of 46.5 mm. The largest known specimen (IVPP V25616) has a standard length of ~200 mm and a total length of ~260 mm.

Snout. The snout region comprises a median rostral and a pair of nasals and antorbitals (Figs 1–4). The surfaces of these bones are strongly ornamented with tubercles and ridges. No premaxillae are discernible, and they are probably absent, as in many other species of the genus (except *Pteronisculus gunnari* and *P. stensioi*; Nielsen, 1942; Cavicchini *et al*., 2025). The rostral is a large, shield-like bone with lateral margins notched for the anterior nostrils (Fig. 3D; IVPP V30888). No obvious small pores were observed for the ethmoid commissure in the rostral because of the dense ornamentation on the external surface of this bone.

The nasal is elongate, approximately as deep as the rostral (Fig. 3D). It contacts the rostral medially, the frontal dorsally, the antorbital ventrally, and the intertemporal posteriorly. The medial and lateral margins each have a notch for the anterior and posterior nostril, respectively (Fig. 1C). The supraorbital sensory canal in the nasal is indicated by a longitudinal line of small pores in this bone. The antorbital is trapezoidal and relatively small; it contacts the lacrimal posteroventrally and forms a short anterior portion of the oral margin. A tripartite junction of the infraorbital canal and the ethmoid commissure is enclosed in the antorbital (Fig. 4C).

Skull roof. The skull roof comprises a pair of frontals, parietals, intertemporals, supratemporals, and

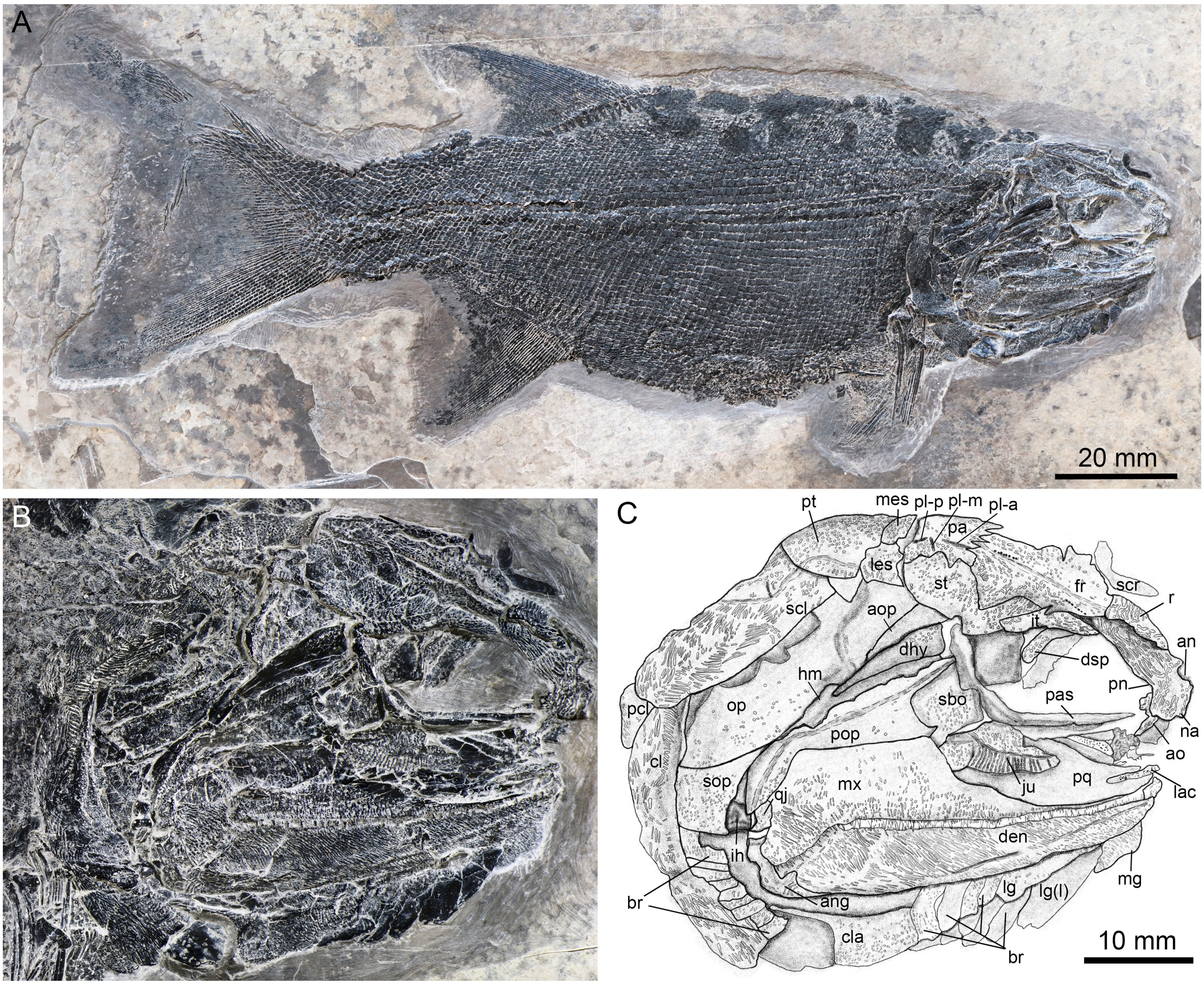

FIGURE 1. Holotype of *Pteronisculus luopingensis* **sp. nov.**, IVPP V24388. **A**, Complete specimen. **B**, Photograph of the skull and pectoral girdle. **C**, Line drawing of the skull and pectoral girdle.

two pairs of extrascapulars (Fig. 3D). All these elements are strongly ornamented with ganoin ridges and tubercles. The elongate frontal is the largest element of the skull roof, approximately twice as long as the parietal. The median suture between the frontals is zigzag-shaped. The frontal has a prominent anterolateral process that inserts between the rostral and the nasal. Posteriorly, the frontal contacts the parietal via a zigzag suture. The parietals are nearly rectangular, bearing a posterolateral extension. The supraorbital sensory canal extends longitudinally through the frontal and enters the parietal posteriorly. Three pit lines are present on the external surface of the parietal. The anterior pit line originates from the middle part of the parietal and extends anteriorly for a short distance. The middle pit line extends anterolaterally for a certain distance. The posterior pit line is short and oriented posterolaterally (Figs 1C, 2C).

The intertemporal is roughly triangular, half the length of the frontal (Fig. 1C). The supratemporal is large and irregular in shape, nearly as long as the frontal, and bears a slender, medially directed anterior process. It contacts the frontal and parietal medially via an S-shaped suture. The supratemporal sensory canal extends from the intertemporal into the supratemporal and runs longitudinally through the bone parallel to its lateral margin.

Two trapezoidal extrascapulars are present on each side of the skull (Figs 1C, 3D). The lateral extrascapular is approximately 1.5 times as wide as the medial one. The supratemporal commissure runs transversely through the middle portion of the extrascapulars.

Circumorbital series and cheek. The circumorbital series comprises a lacrimal, a jugal, two postinfraorbitals, and a dermosphenotic. The lacrimal is narrow and elongate, one-third the length of the maxilla. As a characteristic feature of *Pteronisculus*, the ventral margin of the anterior half of the lacrimal bears conical teeth and contributes to the oral margin. The jugal is relatively large

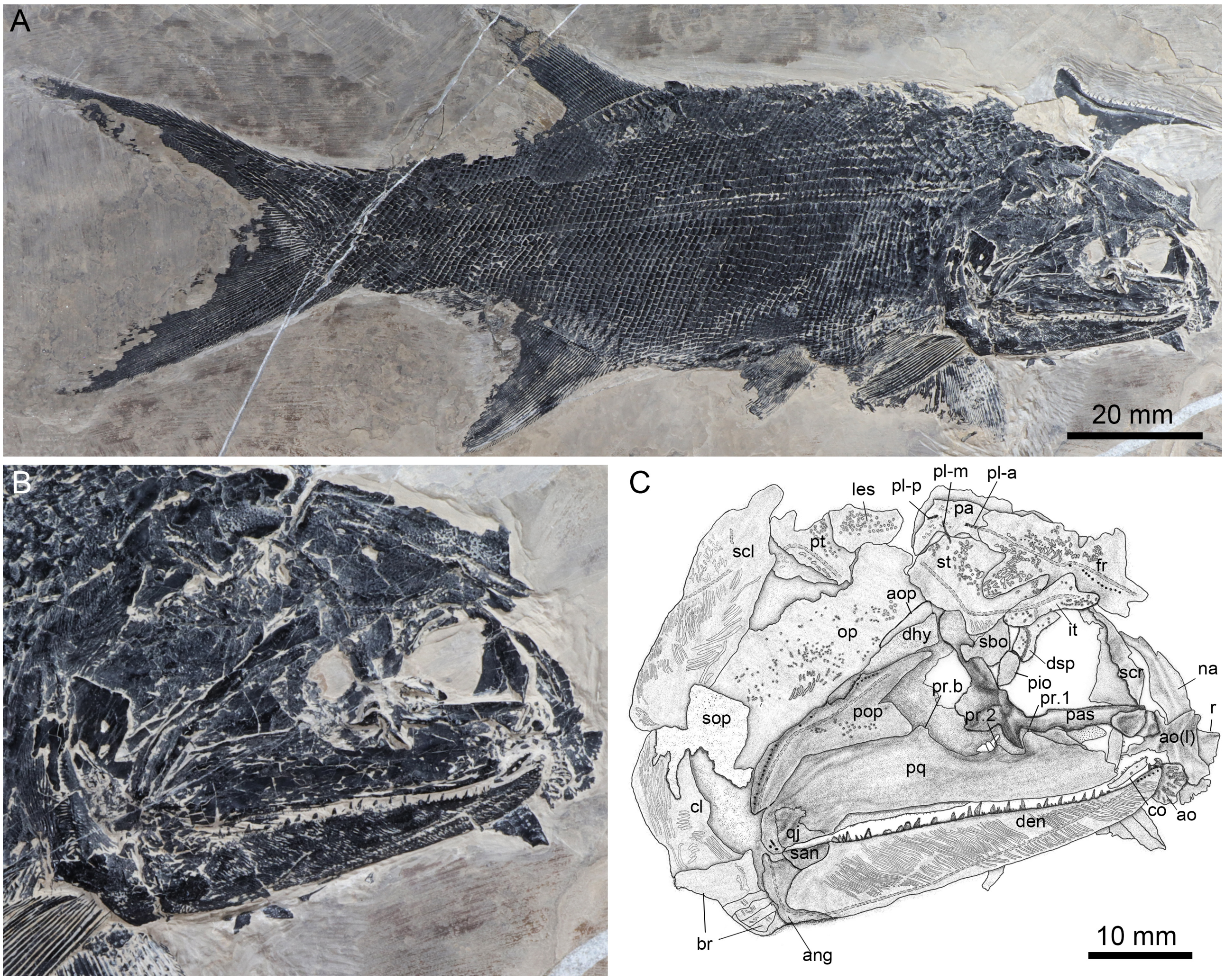

FIGURE 2. Specimen of *Pteronisculus luopingensis* **sp. nov.**, IVPP V24337. **A**, Complete specimen. **B**, Photograph of the skull and pectoral girdle. **C**, Line drawing of the skull and pectoral girdle.

and pentagonal, nearly equal to the lacrimal in length. The infraorbital canal extends from the lacrimal into the jugal, where the canal gives off numerous rami. Two postinfraorbitals are arranged dorsoventrally, defining the posterior margin of the orbit (Fig. 3B); the lower is approximately square, and the upper is trapezoidal. The dermosphenotic is triangular, half the intertemporal length, forming the posterodorsal rim of the orbit. The sclerotic ring comprises curved bones near the orbital rim (Fig. 3B).

Three suborbitals are present between the infraorbitals and the preopercle (Fig. 3B). The upper is small and nearly rectangular, contacting the dermosphenotic anteriorly; the middle and lower are large and roughly triangular, and contact the preopercle posteriorly and the postinfraorbitals anteriorly.

The maxilla consists of an elongate infraorbital portion and a dorsoventrally expanded postorbital portion with a pronounced posteroventral process laterally covering the posterior portion of the lower jaw (Figs 1, 3). The infraorbital portion is nearly equal in length to the postorbital portion. The dentition of the maxilla consists of numerous minute teeth along the outer edge and an inner row of larger conical teeth. The quadratojugal is small and plate-like, contacting the posterior margin of the maxilla anteriorly (Figs 1C, 2C).

The preopercle is hatchet-shaped, consisting of a narrow ventral stem and an enlarged anterodorsal limb (Figs 1C, 2C, 3B). The angle between the posterior margin of the anterodorsal limb of the preopercle and the tooth-bearing margin of the maxilla is about 35°, which corresponds to the suspensorium angle (Gardiner *et al.*, 2005). The preopercular canal is indicated by a series of small pores along the posterior margin of the preopercle.

The dermohyal is a deep and triangular bone that contacts the preopercle anteroventrally. The depth of the dermohyal is approximately half of that of the preopercle. In addition, there is a small triangular anteropercle inserting between the dermohyal and the opercle. All these elements are ornamented with short ridges and tubercles.

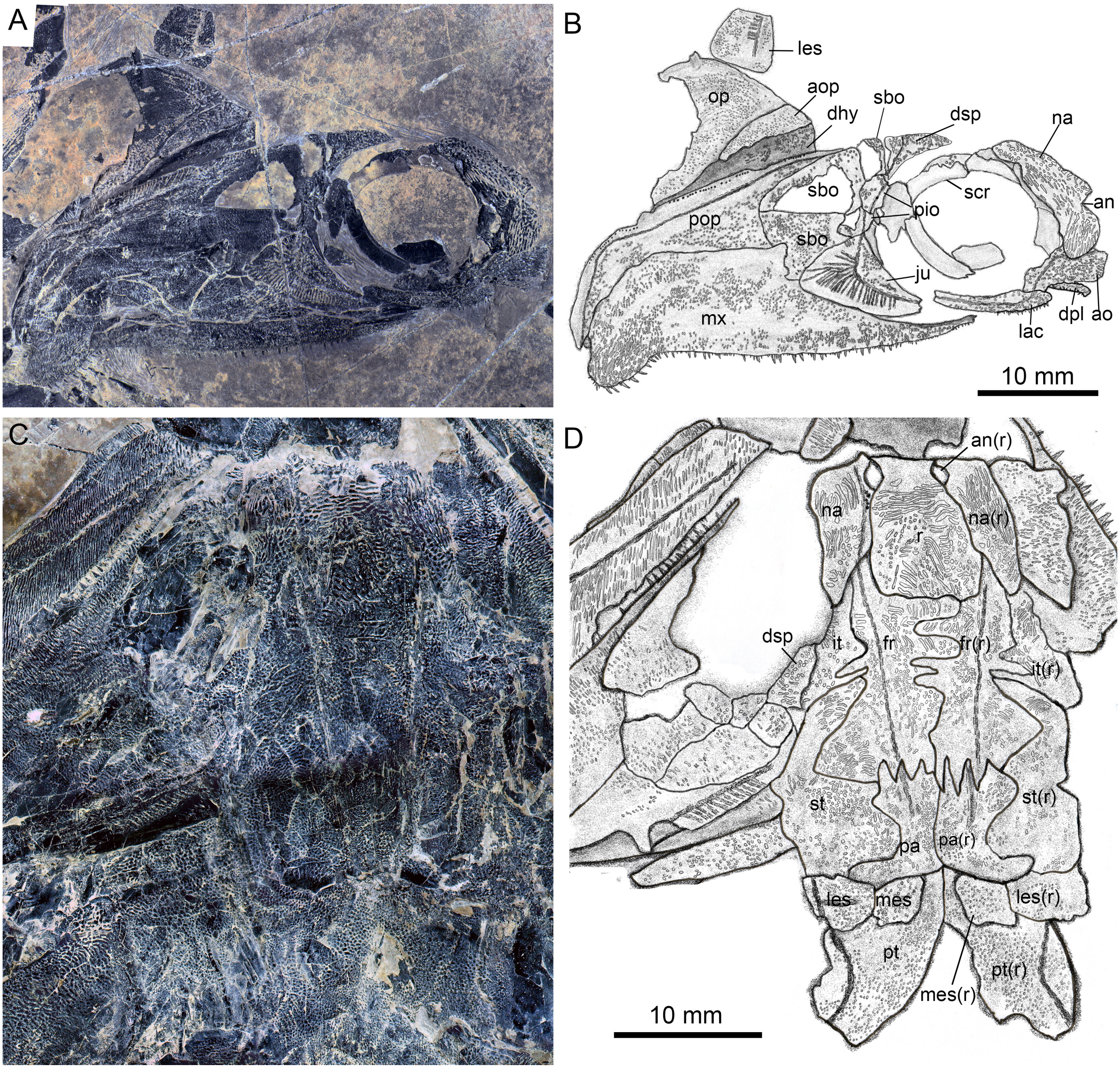

FIGURE 3. Skull of *Pteronisculus luopingensis* **sp. nov. A**, Photograph of the skull, IVPP V30888. **B**, Line drawing of the skull, IVPP V30888. **C**, Photograph of the skull, IVPP V25616. **D**, Line drawing of the skull, IVPP V25616.

Operculo–gular series. The opercle is large and parallelogram-shaped, three times as long as it is wide. The subopercle is nearly rhombic, one-third the size of the opercle. Nine elongate and lamellate branchiostegal rays are preserved posterior to the dentary in the holotype. The dorsalmost branchiostegal ray is notably deeper than the adjacent one. The complete series is still unknown in number because of incomplete preservation. Following the count in *Pteronisculus changae*, 15 branchiostegal rays were reconstructed for the new species described here (Fig. 6).

A median gular and a pair of lateral gulars are present. The median gular is relatively small and roughly elliptic, half as long as the lateral gular (Fig. 1C). Each lateral gular is relatively long and plate-like, a quarter of the lower jaw in length.

Parasphenoid and palatoquadrate. The parasphenoid is partly discernible through the orbit (Figs 1C, 2C, 4C). It has a slender anterior stem and a broad posterior plate. A short basipterygoid process and a deep ascending process are present on either side of the posterior portion of the parasphenoid (Fig. 4C). The ventral surface of the parasphenoid anterior to the ascending process is covered with dense small conical teeth. A notch anterior to the basipterygoid process would mark the passage for the efferent pseudobranchial artery (Gardiner, 1984).

The right palatoquadrate is well exposed in lateral view in IVPP V24337 (Fig. 2). The bone bears three

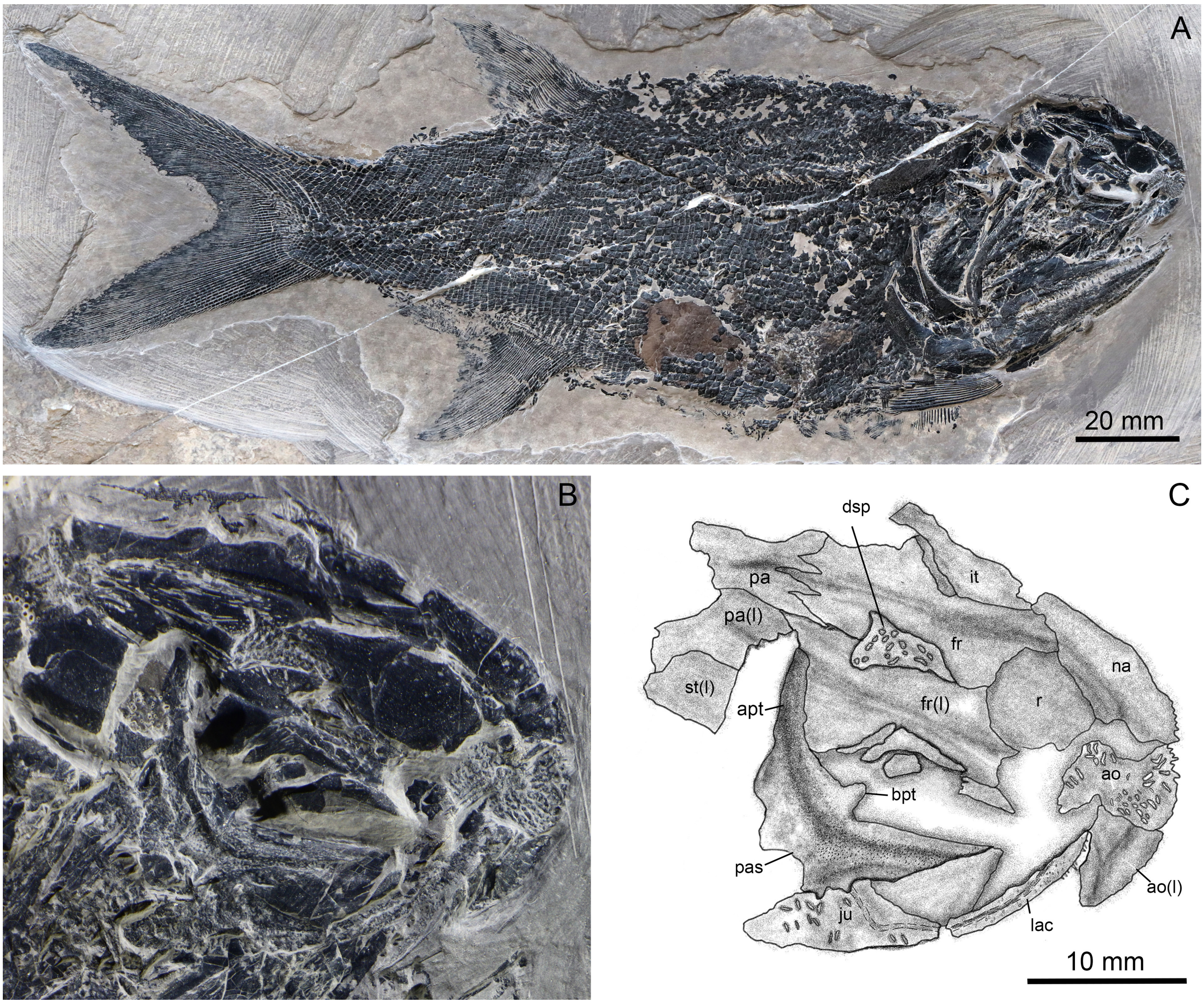

FIGURE 4. Specimen of *Pteronisculus luopingensis* **sp. nov.**, IVPP V20490. **A**, Complete specimen. **B**, Photograph of the skull. **C**, Line drawing of the skull.

distinct processes on its dorsal margin, *i.e.*, a posterior basal process and two anterior processes. A detached dermopalatine is exposed near the antorbital (Fig. 3B). It is elongate, bearing numerous small conical teeth on the medial surface of the bone.

Hyomandibular and interhyal. The hyomandibular is only partly exposed, as most of the bone is laterally covered by the dermohyal and preopercle. The interhyal is a small and cylindrical bone located ventral to the hyomandibular (Fig. 1C).

Lower jaw. The dentary is large and elongate, having a convex ventral margin, a curved posterior margin, and a slightly concave dorsal margin. The angular is slender and wedge-shaped, tapering anteroventrally. It contacts the dentary anteriorly and the small, elongate surangular dorsally (Fig. 2C). Additionally, a small, elongate coronoid is exposed near the anterior tip of the dentary. The dentition includes a row of sharp, large teeth interspersed with smaller denticles along the oral margin of the dentary and dense small teeth on the medial surface of the coronoid. The mandibular sensory canal is indicated by a groove and a series of small pores extending longitudinally through the lower jaw. As in other species of *Pteronisculus*, the canal is arched dorsally in the anterior half of the mandible (Figs 1C, 2C, 3C).

Pectoral girdle and paired fins. The fan-shaped posttemporal contacts the extrascapulars and parietals anteriorly (Fig. 1C). The supracleithrum is roughly elliptical, with its posterodorsal margin slightly concave. The cleithrum is large and curved. It has a deep dorsal arm contacting the supracleithrum dorsally, and a short anterior arm contacting the small and triangular clavicle anteriorly. Additionally, a small postcleithrum is present, inserting at the junction of the supracleithrum and the cleithrum. The external surfaces of these elements are ornamented by ridges and tubercles.

The large pectoral fins insert low on the body. Each pectoral fin is composed of 30 distally segmented rays,

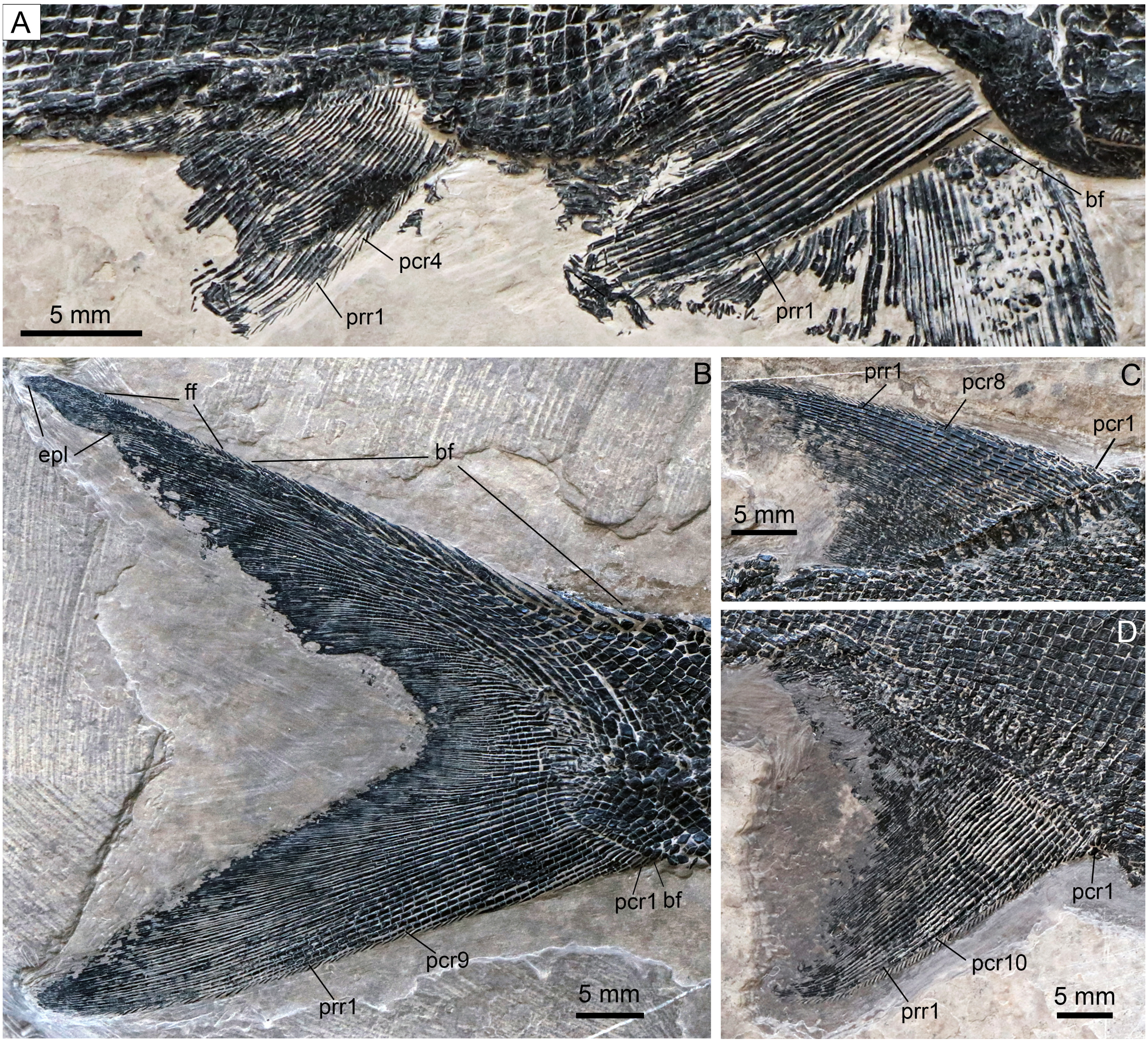

FIGURE 5. Fins of *Pteronisculus luopingensis* **sp. nov. A**, pectoral and pelvic fins, IVPP V24337. **B**, Caudal fin, IVPP V20490. **C**, Dorsal fin, IVPP V24388. **D**, Anal fin, IVPP V24388.

preceded by two basal fulcra (Fig. 5A). The rays are branched distally with the exception of the first ray. The pelvic fins originate at the 16th or 17th vertical scale row, and each is composed of four procurrent rays and ~40 principal rays. The rays are segmented throughout their length. Small fringing fulcra are present on the leading margins of both pectoral and pelvic fins.

Median fins. The triangular dorsal fin originates above the 54th vertical scale row, and the fin base occupies the length of 18 vertical scale rows. The fin is composed of eight procurrent rays and 30 principal rays, preceded by two small basal fulcra (Fig. 5C). All rays are segmented throughout their length. The procurrent rays and the first principal ray are unbranched; the second to fourth principal rays are branched once distally, and the remaining rays are branched twice. Seventeen proximal radials and 16 middle radials are distinguishable in the pterygiophores (IVPP V30888).

The anal fin originates below the 44th to 46th vertical scale row, and its base extends the length of 27 vertical scale rows. The fin is composed of 10 procurrent rays and 53 principal rays, preceded by a basal fulcrum (Fig. 5D). As in the dorsal fin, the rays are segmented throughout their length. The second to eighth principal rays branch once, and the remaining rays branch twice distally.

The caudal fin is deeply cleft, with the dorsal lobe slightly longer than the ventral lobe. A small epichordal lobe is present at the distal tip of the dorsal lobe (Fig. 5B). The caudal fin comprises approximately 80 principal fin rays and nine hypaxial procurrent rays. All procurrent rays and the first principal ray are unbranched; the second principal ray branches once distally, while the remaining

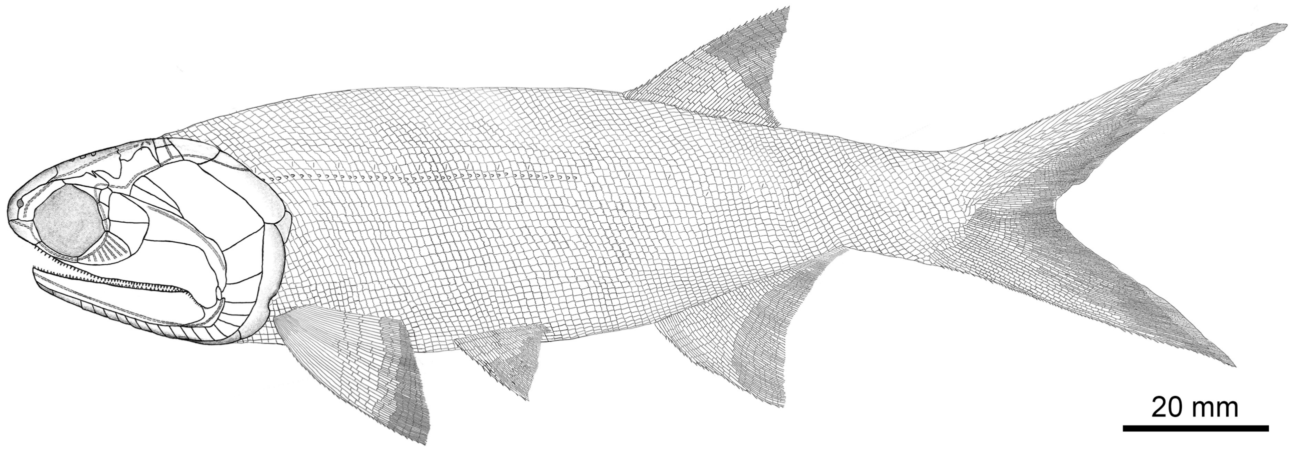

FIGURE 6. Reconstruction of *Pteronisculus luopingensis* **sp. nov.**

rays branch up to four times distally. There are 18 epaxial basal fulcra; they are elongate, leaf-like, and taper to a pointed tip posteriorly. The hypaxial basal fulcra are short, one or two in number. Additionally, small leaf-like fringing fulcra are present in both lobes of the caudal fin.

Squamation. The scales are arranged in 89–90 vertical scale rows between the posterior margin of the supracleithrum and the caudal inversion (Figs 1A, 2A, 4A). They are rhomboid with a serrated posterior margin, and their surfaces are ornamented with fine, diagonally directed ridges. The scales in the anterior flank region are slightly deeper than they are broad, and they gradually decrease in size and become broader than deep toward the dorsal and ventral regions. In the middle flank region on each side of the body in the holotype, 22 horizontal scale rows lie above the main lateral line and 23 below. The trajectory of the main lateral line is indicated by a series of small pores in the lateral-line scales. Every two to five lateral-line scales, or the scales immediately above the lateral line, have a dorsoventrally extended slit. Peg-and-socket articulations are exposed between some scales, as commonly seen in other early actinopterygians.

Discussion

Two recent phylogenetic analyses have incorporated multiple species of *Pteronisculus*, and their results consistently support the monophyly of the genus (Ren & Xu, 2021; Cavicchini *et al*., 2025). The new species is referred to *Pteronisculus* because it possesses several synapomorphies of the genus (Cavicchini *et al*., 2025), *i.e*., a toothed lacrimal contributing to the oral margin, the presence of more than two infraorbitals, a mandibular canal arched dorsally in the anterior half of the mandible, and the dorsalmost branchiostegal ray deeper than the adjacent one. Among them, only the first character is unambiguous for *Pteronisculus*, whereas the others are homoplastic (Cavicchini *et al*., 2025).

Pteronisculus luopingensis sp. nov. can be distinguished from other species of *Pteronisculus* by the following features: (1) *P. luopingensis* **sp. nov.** has three suborbitals. In comparison, other species of this genus (*P. stensioi*, *P. magnus*, *P. gunnari*, *P. changae*, and *P. nielseni*) generally have two suborbitals, whereas *P. cicatrosus* has five suborbitals (Lehman, 1952; Nielsen, 1942); (2) *P. luopingensis* **sp. nov.** has two postinfraorbitals between the jugal and the dermosphenotic, whereas other species of the genus have only one postinfraorbital; (3) *P. luopingensis* **sp. nov.** has a dermosphenotic shorter than the intertemporal (and lacks a dermosphenotic/nasal contact), whereas the dermosphenotic is longer than or nearly equal to the intertemporal in other species of the genus; (4) *P. luopingensis* **sp. nov.** has 89–90 lateral-line scales between the posterior margin of the supracleithrum and the caudal inversion, representing the largest number known in this genus. In comparison, *P. changae* has 83 lateral-line scales, and other species of the genus generally have 55–65 lateral-line scales (55–59 in *P. arcticus*, 63 in *P. stensioi*, ~65 in *P. aldingeri*, and 60–61 in *P. nielseni*; for comparisons of the pterygial formula in selected species of *Pteronisculus*, see Table 1); and (5) *P. luopingensis* **sp. nov.** has four procurrent rays and ~40 principal rays in each pelvic fin, also representing the largest number known in this genus; by contrast, other species of the genus generally have 14–24 rays in the pelvic fin.

The discovery of *P. luopingensis* **sp. nov.** documents the third species of *Pteronisculus* from the Luoping biota and provides an important addition to our understanding of the taxonomic diversity of Middle Triassic actinopterygians from the Yangtze Sea in South China, a part of the eastern Paleotethys Ocean. Outside China,

TABLE 1. Pterygial formula in selected species of *Pteroniscus*.

Species	D	P	A	C	T
Pteronisculus arcticus	33–35	14	30	?	55–59
P. stensioi	41–43	20	35	58	63
P. aldingeri	~40	16–18	37	~59	~65
P. nielseni	36–38	14	29–30	55–56	60–61
P. changae	53	15	44	71	83
P. luopingensis **sp. nov.**	54	16–17	44–46	80–81	89–90

Pteronisculus is known only from Early Triassic marine deposits in Europe, Madagascar, and North America (Stensiö, 1921, 1932; White, 1933; Nielsen, 1936, 1942; Lehman, 1952; Cavicchini *et al*., 2025). No convincing evidence of *Pteronisculus* is known from the western Paleotethyan realm in the Middle Triassic, leading to the previous preconception that this genus died out at the end of the Early Triassic. However, the successive discoveries of *P. nielseni* and *P. changae* from the Luoping biota indicate that *Pteronisculus* lived through the Early Triassic and survived at least into the early Middle Triassic (Xu *et al*., 2014b; Ren & Xu, 2021). The new finding of *P. luopingensis* **sp. nov.** further supports the Yangtze Sea as a refuge for the survival of this genus in the Middle Triassic.

Conclusion

The discovery of *Pteronisculus luopingensis* **sp. nov.** documents the third species of the genus from the Luoping biota. A comparison of the new species with other species of *Pteronisculus* is presented, and the validity of *P. luopingensis* **sp. nov.** is well supported by several autapomorphies on the skull (*e.g*., a relatively short dermosphenotic, three suborbitals, and two postinfraorbitals), the largest known number (~40) of pelvic fin rays, and the largest known number (~90) of lateral-line scales in the genus. The new finding enriches our understanding of the taxonomic diversity of actinopterygian fossils from the Yangtze Sea and further supports the area as a refuge for the survival of *Pteronisculus* in the Middle Triassic.

Acknowledgements

We thank M.-N. Lü for the specimen preparation. This research was funded by the National Natural Science Foundation of China (42172008), Science & Technology Fundamental Resources Investigation Program (Grant no. 2024FY100800), the Open Fund of the Observation and Research Station of Stratigraphy, Paleontology and Environmental Geology in Chaohu, MNR (Grant no. SPEG-2025-KF04), and Stable Supporting Fund of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences.

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