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A new species of *Ptycholepis* (Ptycholepiformes, Actinopterygii) from the Middle Triassic (Anisian) of Luxi, Yunnan Province, China

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Abstract

The fossil taxon *Ptycholepis* is an extinct ray-finned fish genus ranging from the Middle Triassic to Jurassic, represented by the type species *P. bollensis* from the Early Jurassic of Germany, England and France and *P. barboi* near the Ladinian/Anisian boundary (~242 Ma) in the Monte San Giorgio area (southern Alps). Here, we report the discovery of a new species of this genus, *P. huoae* **sp. nov.** based on a well-preserved specimen from the Middle Triassic (Anisian, ~244 Ma) marine deposits in Luxi, Yunnan, China. The discovery documents the first record of *Ptycholepis* in China and fills the previous deficiency of marine ptycholepids in Asia. As the oldest species of *Ptycholepis*, the new finding predates the previously known oldest record from Europe by approximately two million years, demonstrating a longer geological range and wider biogeographical distribution than previously appreciated for the genus. A comparison of the new species with other species of *Ptycholepis* adds to our knowledge of the morphological diversity of the genus.

Keywords: Osteology, taxonomy, Ptycholepidae, Actinopterygii, Yunnan, Triassic

Introduction

The fossil taxon *Ptycholepis* is an extinct ray-finned fish genus that lived in the Middle Triassic to Jurassic. Until recently, at least 13 species have been referred to the genus (Mutter, 2011); besides the type species *P. bollensis* from the Early Jurassic of Germany, England and France (Agassiz, 1832; Aldinger, 1937; Gardiner, 1960; Wenz, 1967), other relatively well studied species include *P. barboi* and *P. priscus* found near the Ladinian/Anisian boundary (~242 Ma) in the Monte San Giorgio area (southern Alps) and *P. marshi* from the Late Triassic of North America (Schaeffer *et al*., 1975; Bürgin, 1992). *Ptycholepis* has a complex taxonomic history. The genus was originally misidentified as a furid in the Holostei (Agassiz, 1832). Aldinger (1937) suggested that *Ptycholepis* might be related to the basal actinopterygian *Boreosomus*, and referred it to the family Acrolepidae named by himself within the Palaeonisciformes. Brough (1939) disagreed on this taxonomic assignment, named the family Ptycholepidae for the genus and placed the family in the grade Subholostei. Andrews *et al*. (1967) further named the order Ptycholepiformes for the Ptycholepidae, which was later adopted by many other authors (*e.g*., Schaeffer *et al*., 1975; Mutter, 2011; Tintori *et al*., 2016; but see Bürgin, 1992).

Here, we report the discovery of a new species of *Ptycholepis* based on a nearly complete specimen collected from the Suomeiluo village in Luxi County, Yunnan Province, China. The fossil locality is about 50 km northwest of the type locality of the renowned

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Luoping Lagerstätte or Biota (Hu *et al*., 2011). The fossil was well preserved in laminated micritic limestone from the Second (Upper) Member of the Guanling Formation (for the geological context, see Huang *et al*., 2013; Wen *et al*., 2020; and Li *et al*., 2026). The age of the fossil beds (Pelsonian, Anisian, ~244 Ma) is well constrained by conodont biostratigraphy (Wen *et al*., 2020). As such, the discovery documents the oldest record of *Ptycholepis*. Along with the new species of *Ptycholepis* is a taxonomically rich fossil assemblage found in the last 12 years, including arthropods, echinoderms, molluscs, marine reptiles, coelacanths, chondrichthyans, and plants (*e.g*., Huang *et al*., 2013; Wen *et al*., 2020; Xu *et al*., 2022). In terms of age and biodiversity, the whole fossil assemblage (namely Luxi Biota) is comparable to the Luoping Biota (Zhang *et al*., 2009; Wu *et al*., 2009; Sun *et al*., 2009; Tintori *et al*., 2010; Xu & Wu, 2012; Wen *et al*., 2012; Benton *et al*., 2013; Xu *et al*., 2014, 2023; Ma & Xu, 2017). However, several marine reptiles (Xu *et al*., 2022; Li *et al*., 2026) and the new species of *Ptycholepis* described here are unknown from the Luoping Biota. The new finding represents the first record of *Ptycholepis* in China and enriches our understanding of the taxonomic diversity of ray-finned fishes from the eastern Paleo-Tethyan realm in the aftermath of the end-Permian mass extinction (Benton *et al*., 2013).

Material and methods

The studied specimen is curated at the fossil collections of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences in Beijing, China. It was mechanically prepared with air-chisels, accompanied by sharp steel needles. The relative position of fins and scale counts were expressed following Westoll (1944), in which the letters D, P, A and C are followed by a particular numerical value to denote 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.

Systematic palaeontology

Actinopterygii Cope, 1887
Ptycholepiformes Andrews, Gardiner, Miles & Patterson, 1967
Ptycholepidae Brough, 1939

***Ptycholepis* Agassiz, 1832**

Type species. *Ptycholepis bollensis* Agassiz, 1832.

Emended diagnosis. Body elegantly to deeply fusiform; paired antorbital-premaxillae in subrostral position; suborbitals numerous (8–20), elongate and overlapping anterior border of preopercle; preopercle nearly vertical, broadest at contact with maxilla; four to six pairs of branchiostegal rays; marginal teeth on the maxilla and dentary small, uniform and acuminate; origin of dorsal fin about midway between snout and caudal peduncle; caudal fin hemiheterocercal, equilobate and deeply cleft; all fins with fringing fulcra; scales rhomboidal behind pectoral girdle, elsewhere much longer than deep, with ganoine arranged in low, longitudinal ridges, frequently anastomosing; and posterior borders of scales denticulated.

Locality and horizon. Middle Triassic of southern Switzerland (Monte San Giorgio, Tessin) and southwestern China (Yunnan), Middle and Late Triassic of northern Italy (Raibl, Carinthia and Besano, Lombardy), Late Triassic of the United States (Virginia, New Jersey, Connecticut), Early Jurassic of England (Dorset, Leicestershire), Germany (Würtemberg) and France.

***Ptycholepis huoae* sp. nov.**

Holotype. IVPP V33715, a nearly complete, laterally compressed specimen with part of the skull roof and dorsal fin unexposed or missing.

Etymology. The specific epithet honours Jin-Mei Huo for her contribution to the fossil collection.

Diagnosis. A medium-sized species of *Ptycholepis* distinguishable from other species of the genus by the following combination of features: weak ornamentation on skull and lower jaw with small tubercles and short striae; nine elongate suborbitals; depth of postorbital blade of maxilla 28.2% of maxillary length; subopercle elongate, one-third of opercular length; six pairs of branchiostegal rays, uppermost not enlarged; lateral gular two-thirds of mandibular length; ~30 rays in each pectoral fin, most (except anterior three rays) of them segmented throughout their lengths; ~20 principal rays in anal fin; and scale formula of D?/P13, A25, C40/T45.

Locality and horizon. Luxi, Yunnan, China; Second (Upper) Member of Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Description. *General morphology and size*. Similar to other species of *Ptycholepis*, *P. huoae* **sp. nov.** has a blunt snout, a fusiform body and a hemiheteroceral caudal fin. The holotype (Figs 1, 2) has a head length of 70 mm, a standard length (the length from the tip of the snout to the posterior extremity of the caudal peduncle) of 235 mm, and a total length of ~275 mm. The body is fully

covered with rhomboidal scales. The vertebral column and dorsal and anal pterygiophores are not visible due to the squamation in situ.

Snout. In the snout region, a median rostral, a right nasal and a right antorbital-premaxilla are discernible in the holotype (Fig. 1B, C). The rostral is exposed medially in its posterior part. It is relatively large and roughly shield-like. The nasal is trapezoidal, longer than deep. The medial margin has a notch for the anterior nostril, and the lateral margin is slightly notched for the posterior nostril and defines the anterodorsal margin of the orbit. A short anterior portion of the supraorbital sensory canal extends into the nasal from the frontal, indicated by a line of five small pores on the posterior half of this bone.

The antorbital-premaxilla (= rostral-premaxilla of Schaeffer *et al*., 1975 or premaxilla of Bürgin, 1992) is trapezoidal, contacting the maxilla and lachrymal posteriorly. The junction of the infraorbital canal and the ethmoid commissure is enclosed in this bone. The ventral margin of the bone forms a short anterior length of the oral margin. There is no evidence that it bears any teeth, as in other species of *Ptycholepis* from the Triassic of Europe and North America (Schaeffer *et al*., 1975; Bürgin, 1992).

Skull roof. Only the anterior part of the skull roof is discernible, including part of right frontal and intertemporal; the suture between them is hard to identify because of taphonomic compression (Fig. 1C).

Palate. The palatal elements (*e.g*., pterygoid bones) can only be discernible through the orbit, and the poor state of preservation prevents any accurate descriptions of them.

Circumorbital series and cheek region. The circumorbital series includes a lachrymal, a jugal, a postinfraorbital, and a dermosphenotic (Fig. 1C). The partly preserved lachrymal has an elongate anterior portion that contacts the orbital rim of the maxilla ventrally. The jugal is a relatively large and triangular bone that expands posteriorly and contacts the maxilla ventrally and the ventral-most suborbital dorsally. The postinfraorbital

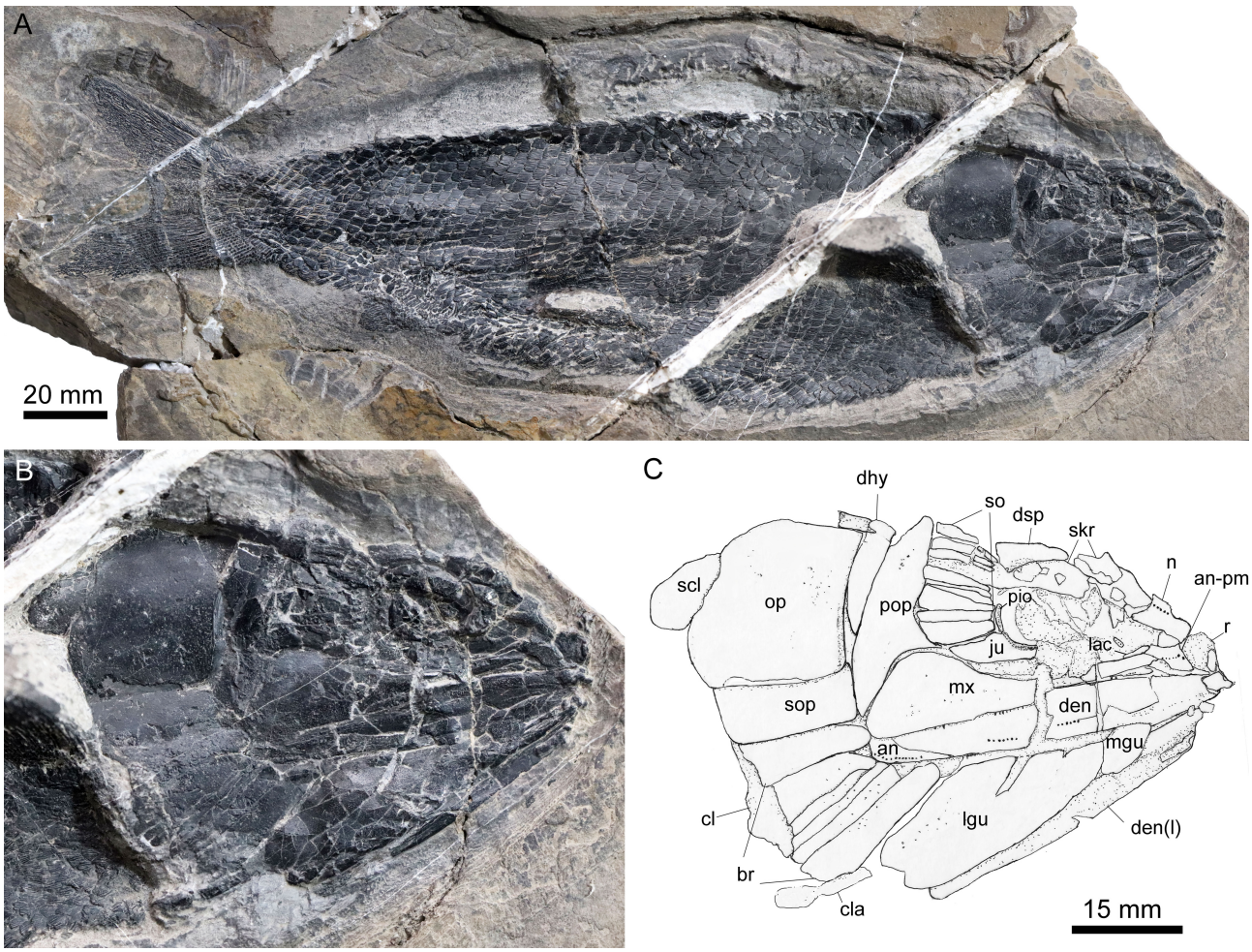

FIGURE 1. Holotype of *Ptycholepis huoae* **sp. nov.**, IVPP V 33715. **A**, Complete specimen. **B**, Photograph of the skull and pectoral girdle. **C**, Line drawing of the skull and pectoral girdle. Abbreviations: an, angular; an-pr, antorbital-premaxilla; br, branchiostegal rays; cl, cleithrum; cla, clavicle; den, dentary; dhy, dermohyal; dsp, dermosphenotic; ju, jugal; lac, lachrymal; lgu, lateral gular; mgu, medial gular; mx, maxilla; n, nasal; op, opercle; pio, postinfraorbital; pop, preopercle; r, rostral; scl, supracleithrum; skr, skull roofing bones; so, suborbital; sop, subopercle.

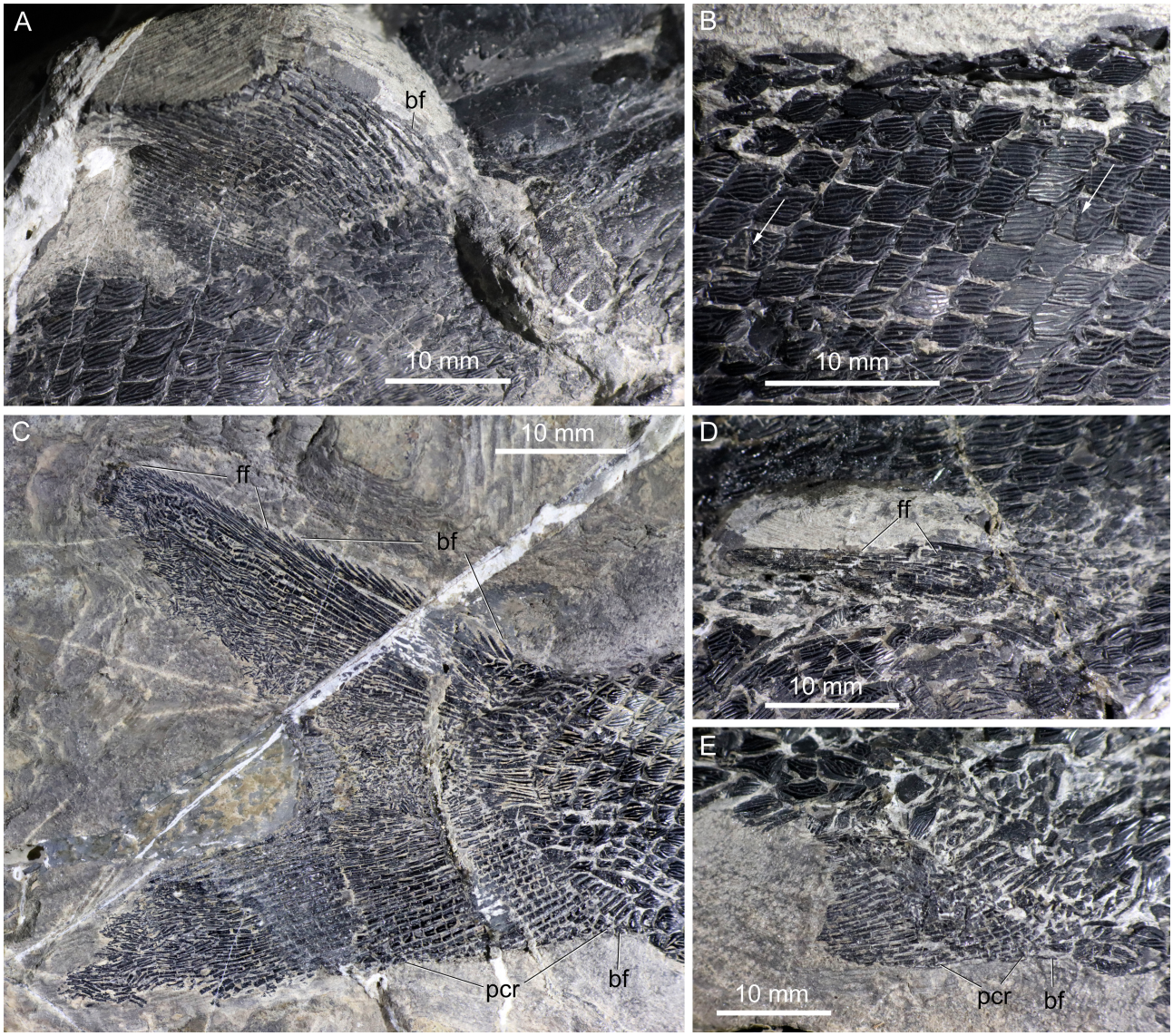

FIGURE 2. Fins and scales of *Ptycholepis huoae* **sp. nov.**, IVPP V 33715. **A**, Right pectoral fin. **B**, Scales above the anal fin with arrows indicating the dorsoventrally extended slit on the lateral-line scale. **C**, Caudal fin. **D**, Right pelvic fin. **E**, Anal fin. Abbreviations: bf, basal fulcrum; ff, fringing fulcra; pcr, procurrent ray.

is narrow and tube-like, contacting the suborbitals posteriorly. The slightly detached dermosphenotic is a triangular bone that tapers anteriorly.

There are nine suborbitals between the infraorbitals and the preopercle. They are elongate, trapezoidal or rectangular in shape. The preopercle is triradiate, having a deep bar and an anteriorly extending process. The anterior margin is overlapped by the suborbitals, and the posterior margin is convex and nearly vertical, contacting the anterior margin of the dermohyal, a short ventral portion of the anterior margin of the opercle and the anterior margin of the subopercle. The preopercular sensory canal is hard to trace in this bone. The dermohyal is deep and wedge-shaped, tapering ventrally. The maxilla has an elongate infraorbital ramus and a trapezoidal postorbital blade; the depth of this blade is 28.2% of the length of the whole maxilla. The ventral margin of the maxilla is nearly straight and bears numerous tiny teeth with a conical tip. The tooth tips were easily broken off during the fossil preparation.

Mandible. The lower jaw is two-thirds of the head length with two elements (dentary and angular) discernible in lateral view (Fig. 1C). The dentary is large and long, having a nearly straight dorsal (oral) margin and a convex ventral margin. The oral margin of the dentary bears tiny teeth similar to those of the maxilla. The angular is small and trapezoidal, contacting the dentary posteroventrally. The supra-angular is not exposed because of occlusion of jaws. The mandibular sensory canal extends the whole length of the mandible, with a series of small openings nearly parallel to the ventral margins of the dentary and angular.

Opercular-gular series. The opercle is large and trapezoidal, slightly deeper than long. It has a slightly concave anterior margin, a rounded posterior margin, and nearly straight dorsal and ventral margins. The subopercle is small and elongate, one-third of the opercular depth. Below the subopercle, six branchiostegal rays are present on the right side of the skull (Fig. 1C); they are elongate, lamellate bones.

The gular series is partly exposed below the mandible; the lateral gular is notably larger than the median gular, as is common in other early actinopterygians. The lateral gular is shield-like, slightly more than half of the mandibular length. The median gular is small and oval-shaped.

Paired girdles and fins. Of the pectoral girdle, the supracleithrum, cleithrum and clavicle are partly discernible, and the posttemporal is not exposed. The supracleithrum is a deep, plate-like bone that contacts the opercle anteriorly. The curved cleithrum and lamellate clavicle are overlapped by the branchiostegal rays, and their complete outlines are unknown. The pectoral fins insert low on the body, and each is composed of about 30 segmented rays, preceded by a long basal fulcrum (Fig. 2A). The anterior three rays are unbranched and distally segmented. The remaining rays are segmented throughout their lengths. The middle rays are missing in their distal portions, and posterior rays are complete and branched distally.

The pelvic girdle is not exposed. The pelvic fins insert at the 13th vertical scale row, and each is composed of about 12 segmented rays. The anterior two or three rays are distally segmented, and the others throughout their lengths. A series of small fringing fulcra is associated with the leading ray (Fig. 2D).

Median fins. The dorsal fin is missing or unexposed. The anal fin originates below the 25th vertical scale row. It has about 20 principal rays, preceded by four procurrent rays and a short basal fulcrum (Fig. 2E). The rays are segmented throughout their lengths.

The caudal fin is hemiheterocercal, composed of at least 35 segmented and distally branched rays (Fig. 2C). The fin has a deeply forked profile, and both lobes are nearly symmetrical in size. There are eight procurrent rays preceding the ventral-most principal ray; they are segmented and unbranched. In the dorsal and ventral margins of the fin, there are about 20 epaxial basal fulcra and a single short hypaxial basal fulcrum, respectively. The epaxial basal fulcra are elongate and taper posteriorly. Small leaf-like fringing fulcra are present in both lobes.

Scales. The scales are arranged in 45 vertical rows along the lateral line. The terminal axial scale lobe is narrow and pointed, extending along half length of the caudal lobe (Fig. 2C). The scales are generally rhomboidal or elongate with a slightly serrated posterior margin. The external surface is highly ornamented with four to nine longitudinal ridges and some small tubercles. The ornamentation and depth/length ratio of scales vary greatly, depending on their positions on the body (Fig. 2B). The scales in the anterior flank region are slightly deeper than long, and those in the posterior part of the body, near the ventral border of the body are very shallow and elongate. A dorsoventrally extended slit is present on some lateral line scales, similar to the condition in *Ptycholepis barboi*, *P. priscus* and *P. schaefferi* (Bürgin, 1992).

Discussion

Besides *Ptycholepis huoae* **sp. nov.** described here, at least 13 species have been referred to the genus *Ptycholepis* but many remain poorly known because of incomplete preservation (see the list in Mutter, 2011). Gardiner (1960), Schaeffer *et al*. (1975) and Bürgin (1992) redescribed *P. bollensis*, *P. marshi*, and *P. barboi*, respectively, and these provide the basis for our understanding of the morphology of the genus. *P. huoae* **sp. nov.** is referred to *Ptycholepis* as it possesses the following diagnostic features for the genus (emended by Shaeffer *et al*., 1975 and Bürgin, 1992): (1) presence of numerous (8–20), elongate suborbitals (= postorbitals of Bürgin, 1992) overlapping the anterior border of the preopercle; (2) a preopercle nearly vertical, broadest at contact with the maxilla; (3) four to six pairs of branchiostegal rays; (4) small, uniform and acuminate marginal teeth on the maxilla and dentary; (5) a hemiheterocercal, equilobate caudal fin; (6) scales rhomboidal behind the shoulder girdle, elsewhere much longer than deep, with ganoine arranged in low, longitudinal ridges, frequently anastomosing; and (7) posterior borders of scales denticulated.

Ptycholepis huoae **sp. nov.** represents the first record of this genus in China and the oldest species of the genus worldwide, demonstrating a wider biogeographical distribution than previously appreciated for the genus (Fig. 3). The previously oldest species of *Ptycholepis* were known from the western Paleo-Tethyan realm, including *P. barboi*, *P. magnus*, *P. priscus* and *P. schaefferi* near the Ladinian/Anisian boundary (~242 Ma) in the Monte San Giorgio area (southern Switzerland and northern Italy; Bürgin, 1992). The new species documents the first record of *Ptycholepis* in the eastern Paleo-Tethyan realm, and predates the European relatives by approximately two million years. It differs from other species of *Ptycholepis* by the following features: (1) most rays of the paired fins (except the anteriormost two or three rays) segmented throughout their lengths *vs.* all rays of paired fins distally segmented in other species of *Ptycholepis*; (2) lateral

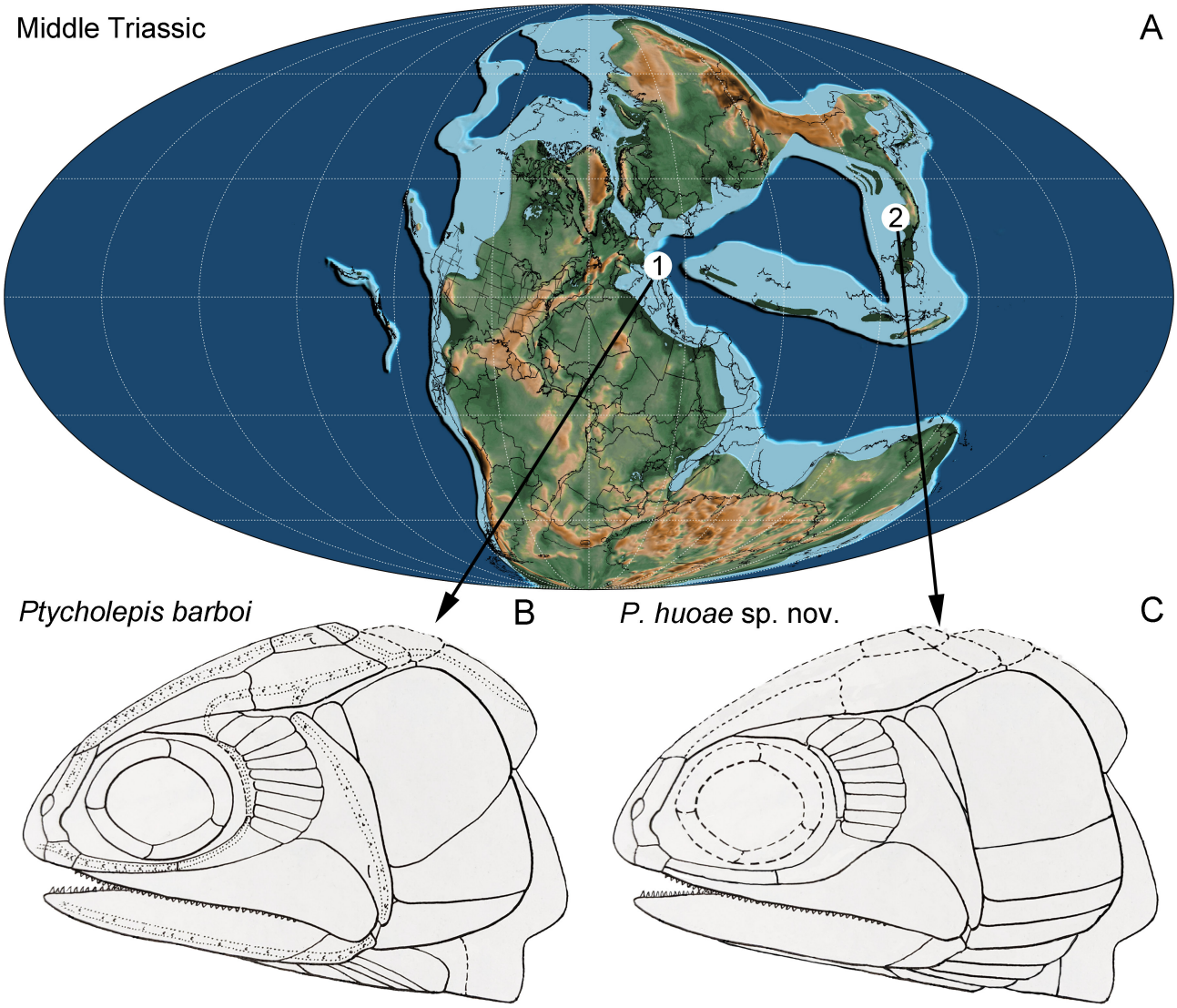

FIGURE 3. Palaeogeographical distribution of *Ptycholepis* in the Middle Triassic and reconstructions of head and pectoral girdle in two selected species. **A**, (1), *Ptycholepis* from the western Paleo-Tethyan realm, including *P. barboi*, *P. magnus*, *P. priscus*, and *P. schaefferi* from the Monte San Giorgio area; (2) *P. huoae* **sp. nov.** from Southwest China, eastern Paleo-Tethyan realm. -941394749 **B**, Reconstruction of head and pectoral girdle of *P. barboi* (modified from Bürgin, 1992). -941394749 **C**, Tentative reconstruction of head and pectoral girdle of *P. huoae* **sp. nov.** The Middle Triassic palaeogeographical map was adopted from Scotese *et al*. (2024).

gular two-thirds of the mandibular length *vs.* half or less of the mandibular length in other species of *Ptycholepis*; (3) weak ornamentation on the skull and lower jaw *vs.* strong ornamentation in other species of *Ptycholepis*; and (4) the uppermost branchiostegal ray not enlarged *vs.* notably enlarged in other species of *Ptycholepis.*

The discovery of *Ptycholepis huoae* **sp. nov.** fills the previous deficiency of marine ptycholepids in Asia. In China, ptycholepids were previously known only in continental (most likely freshwater) deposits, including *Boreosomus gansuensis* from the Early Triassic of Mingshui County, Gansu Province (Su, 1993; Li, 2008; Mutter, 2011), *Yuchoulepis szechuanensis* from the Middle Jurassic of Chongqing City and Luzhou City, Sichuan Province, *Chungkingichthys tachuensis* from the Middle Jurassic of Dazhu County, Sichuan Province (Su, 1974), and unnamed species from the Early Jurassic of Chongqing (Ren *et al*., 2024). Outside China, possible remains of *Ptycholepis* were collected from the Late Jurassic continental deposits (Phu Kradung Formation) of Thailand in Southeast Asia (Cavin *et al*., 2009). *P. marshi* from the Late Triassic of North America was likely freshwater or euryhaline (Schaeffer *et al*., 1975). By contrast, marine ptycholepids were previously known only from Europe (Brough, 1939; Bürgin, 1992). The discovery of *P. huoae* **sp. nov.** represents the first ptycholepid known from the marine ecosystems in Asia.

Conclusion

The recovery of *Ptycholepis huoae* **sp. nov.** from the Middle Triassic Luxi Biota documents the first species of the genus in China. A comparison of the new species with other species of *Ptycholepis* is presented, and the diagnostic features for the genus are emended. As the oldest species of *Ptycholepis*, the new finding predates the previously known oldest record from Europe by approximately two million years, and fills the previous deficiency of marine ptycholepids in Asia. As such, the new finding provides an important addition to our knowledge of the taxonomic diversity and biogeographical distribution of ptycholepids.

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