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Panxianichthys imparilis gen. et sp. nov., a new ionoscopiform (Halecomorphi) from the Middle Triassic of Guizhou, China

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Abstract　The Ionoscopiformes are a fossil lineage of halecomorphs known only from the Mesozoic marine deposits. Because of their close relationships with the Amiiformes, the Ionoscopiformes are phylogenetically important in investigating the early evolution and biogeography of the Halecomorphi. However, fossil evidence of early ionoscopiforms was scarce; until recently, *Robustichthys* from the Middle Triassic Luoping Biota, eastern Yunnan, China, represents the oldest and only known ionoscopiform in the Triassic. Here we report the discovery of a new ionoscopiform, *Panxianichthys imparilis* gen. et sp. nov., on the basis of two well preserved specimens from the Middle Triassic Panxian Biota, western Guizhou, China. The discovery documents the second ionoscopiform in the Middle Triassic; although *Panxianichthys* is slightly younger than *Robustichthys*, it is significantly older than other members of this group from the Late Jurassic of Europe, and Early Cretaceous of North and South America. *Panxianichthys* possesses an important synapomorphy of the Ionoscopiformes: a sensory canal in the maxilla, but retains some primitive characters unknown in other ionoscopiforms. Results of our phylogenetic analysis recover *Panxianichthys* as the most primitive ionoscopiform, and provide new insight on the early evolution of this clade. The interrelationships of the Ionoscopidae have been reassessed; *Quetzalichthys* is regarded more closely related to *Ionoscopus* than to *Oshunia*. In addition, our analysis supports the reassessment of *Furo muensteri* as an ophiopsid ionoscopiform. The successive discoveries of *Robustichthys* and *Panxianichthys* from China indicate that the early diversification of the Ionoscopiformes is more rapid than previously thought.

Key words　Guizhou, China; Middle Triassic; Panxian Biota, Holostei, Halecomorphi

The Halecomorphi are one of four major actinopterygian subdivisions outside of teleosts (the largest group of the vertebrates), together with cladistians (e.g., bichirs), chondrosteans (e.g., sturgeons and paddlefishes), and ginglymodians (e.g., gars) (Grande and Bemis, 1998; Nelson, 2006; Near et al., 2012; Sallan, 2014). Traditionally, the Halecomorphi have been regarded as the sister group of Teleostei (Patterson, 1973; Grande and Bemis, 1998), but recent

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studies have suggested that the Halecomorphi may be more closely related to the Ginglymodi than to the Teleostei, with the Halecomorphi and the Ginglymodi grouped in a clade Holostei (Hurley et al., 2007; Grande, 2010; Xu and Wu, 2012; Near et al., 2012; Xu et al., 2014a). Thus, phylogenetic studies of halecomorphs bear important significances on the early divergence of the Holostei and the origin of the Teleostei.

Although the Halecomorphi are represented by a single extant species, *Amia calva* (bownfin) from the freshwater environments in central and eastern North America, this clade has a rich fossil record. The Halecomorphi other than the Amiiformes have been divided into two orders, the Paraseminotiformes and the Ionoscopiformes (Grande and Bemis, 1998). The Paraseminotiformes, generally regarded as the most basal halecomorph lineage, have a geological range confined in the Early Triassic (there are still debates on the affinities of potential Permian paraseminotiforms, Hurley et al., 2007; Near et al., 2012; Xu et al., 2014a). The Ionoscopiformes, closely related to the Amiiformes, were known from the Middle Triassic of South China, Late Jurassic of Europe, and Early Cretaceous of the New World (Schaeffer, 1960, 1971; Bartram, 1975; Applegate, 1988; Grande and Bemis, 1998; Alvarado-Ortega and Espinosa-Arrubarrena, 2008; Machado et al., 2013; Xu et al., 2014b). Until recently, *Robustichthys* from the Middle Triassic (Anisian, 242–247 Ma) Luoping Biota, eastern Yunnan, China, represents the oldest known ionoscopiform (Xu et al., 2014b). Additionally, potential ionoscopiforms (questionably assigned to *Ophiopsis*) have been reported from the Middle Triassic (Ladinian) of Lombardy in Italy (Alessandri, 1910) or Carinthia in Austria (Sieber, 1955) and the Lower Cretaceous of Brazil (Brito, 2000), but they are based on poorly preserved specimens. Other possible ionoscopiforms include the Early Jurassic (Sinemurian) *Heterolepidotus* and Late Jurassic (Kimmeridgian) *Brachyichthys*, but both need further studies (Schaeffer, 1960; Gardiner et al., 1996). Consequently, there is a conspicuous stratigraphic gap (~90 Ma) between the earliest known ionoscopiform from China and those much younger members (e.g., *Ionoscopus* and *Ophiopsis*) from the Kimmeridgian (152–157 Ma) of Europe. The limited fossil evidence of early ionoscopiforms hampers understanding of the evolutionary origin and geographical distribution of this clade. The interrelationships within the Ionoscopiformes remain unstable (Fig. 1).

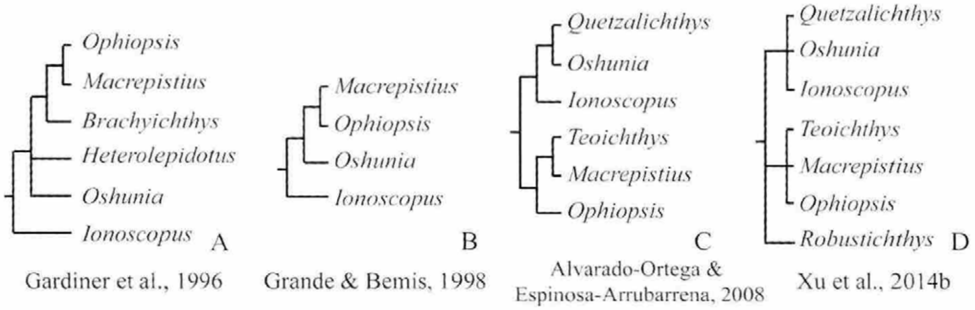

Fig. 1 Previous hypotheses on the interrelationships of the Ionoscopiformes

Here, we report the discovery of a new ionoscopiform based on two specimens from the upper part of the Member II of the Guanling Formation exposed in Xinmin of Panxian County, western Guizhou. The new taxon represents the most basal ionoscopiform, and highlights the evolutionary origin of this clade. The fossil locality is about 80 km northeast to the type locality of the recently reported ionoscopiform *Robustichthys*. A detailed geological survey showed that specimens of *Robustichthys* were collected from the middle part of the Member II of the Guanling Formation exposed in Luoping, Yunnan Province; thus, the new taxon is slightly younger than *Robustichthys* although the fossil beds of both taxa were referred to the same stage (Anisian) of the Middle Triassic by the conodont analysis (Sun et al., 2006; Zhang et al., 2008; Jiang et al., 2009; Hu et al., 2011; Benton et al., 2013). Along with the new fish, other taxa from the same locality and horizon include taxonomically diverse invertebrates, marine reptiles, and several other kinds of fishes; the whole fossil assemblage has been referred to the Panxian Fauna or Biota (Motani et al., 2008; Sun et al., 2008; Wu et al., 2013; see review of Benton et al., 2013).

1 Material and methods

All specimens are deposited at the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP). Illustrations were drawn under an Olympus SZX7 microscope with a camera lucida attachment, and further prepared using Adobe Photoshop and Illustrator software packages (CS5). The relative position of fins and scale count were expressed in a scale formula following Westoll (1944). Cladistic analysis was conducted on the basis of a data matrix expanded from Xu et al. (2014b). It includes 96 characters coded across 30 neopterygian taxa (see electronic supplementary material). Two ionoscopiforms have been added, including *Panxianichthys* described herein and the recently re-described *Furo muensteri* from the Late Jurassic (Kimmeridgian) of Europe (Lane and Ebert, 2012). Character coding for *F. muensteri* was based on Lane and Ebert (2012). The species name *Teoichthys kallistos* that was misspelled as *Teoichthys brevipina* in Xu et al. (2014b) has been corrected in this study. The data matrix was subjected to the parsimony analysis in PAUP* (version 4.0b10) (Swofford, 2003). All characters were equally weighted and treated as unordered.

Anatomical abbreviations an, anterior nostril; ang, angular; ao, antorbital; bf, basal fulcra; br, branchiostegal rays; cha, anterior ceratohyal; cl, cleithrum; den, dentary; dpt, dermopterotic; dsp, dermosphenotic; es, extrascapular; ff, fringing fulcra; fr, frontal; gu, gular; io, infraorbital; iop, interopercle; mx, maxilla; mxc, sensory canal on maxilla; n, nasal; op, opercle; pa, parietal; pcl, postcleithrum; pf, principal fin ray; pm, premaxilla; pn, posterior nostril; pop, preopercle; pscl, presupracleithrum; pt, posttemporal; qu, quadrate; r, rostral; rr, rudimentary fin ray; san, supra-angular; scl, supracleithrum; scr, sclerotic ring; smx, supramaxilla; so, suborbital; sop, subopercle; sp, sphenotic; su, supraorbital.

2 Systematic paleontology

Neopterygii Regan, 1923

Holostei Müller, 1845

Halecomorphi Cope, 1972

Ionoscopiformes Grande & Bemis, 1998

***Panxianichthys imparilis* gen. et sp. nov.**

(Figs. 2–5)

Etymology Panxian refers to the type locality in Panxian County, Guizhou Province; -*ichthys*, fish. Species epithet *imparilis* (Latin) means peculiar and unusual.

Holotype IVPP V 19971, a nearly complete specimen.

Paratype IVPP V 19972, a nearly complete, topotypic specimen.

Locality and horizon Panxian, Guizhou Province, China. Anisian, Middle Triassic, Member II of the Guanling Formation.

Diagnosis A new ionoscopiform fish distinguished from other members of this order by a combination of features: presence of two supraorbitals; absence of innerorbital flange of dermosphenotic; presence of seven infraorbitals with upper two infraorbitals tube-like; at least three suborbitals; dermopterotic roughly equal to parietal in length; triangular supramaxillary process on maxilla; slightly notched posterior margin of maxilla; three postcleithra; 12−13 dorsal fin rays; moderately forked posterior margin of caudal fin; 23 principal caudal fin rays; and scale formula of D23/P10–11, A20, C34–35/T39–40.

3 Description and comparison

General morphology and size The fish has a blunt snout, an elongate fusiform body with a moderately forked caudal fin. The great body depth lies slightly anterior to the origin of the dorsal fin. The holotype (Fig. 2) has a standard length (SL) of 159 mm, and a head length of 50 mm (accounting 31.4% of SL) from the tip of the snout to the end of the opercle. The paratype (Fig. 5A) is slightly smaller than the holotype, having a SL of 150 mm, a total length of about 200 mm, and a body depth of 67 mm. The general body form can be reconstructed on the basis of both specimens (Fig. 5C).

Snout The paired nasals, contacting each other medially, are deep and irregular. The anterior portion of the nasal is turned downwards and has a notch at its lateral margin. This notch, together with the tube-like anterior arm of the antorbital, forms the posterior nostril (Fig. 3). The anterior nostril probably opens near the junction of the nasal, rostral and antorbital (Fig. 4), deduced from other holosteans (Olsen, 1984; Grande and Bemis, 1998; Grande, 2010). The rostral is roughly tube-like with slightly expanded lateral horns. The antorbital has an elongate posterior portion that extends back to the orbit and contributes to the orbital margin; at the anterior portion of this bone, it has a curved, tube-like anterior arm that extends anteriorly beneath the nostrils to meet the small median rostral. Among the Ionoscopiformes, *Robustichthys* (Xu et al., 2014b), *Oshunia* (Maisey, 1991) and *Furo muensteri* (Lane and Ebert, 2012), similar to *Panxianichthys*, have an antorbital that extends back to the orbit, whereas other ionoscopiforms have a shorter and lower antorbital that is located anterior to the lachrymal and consequently does not contribute to the orbital margin.

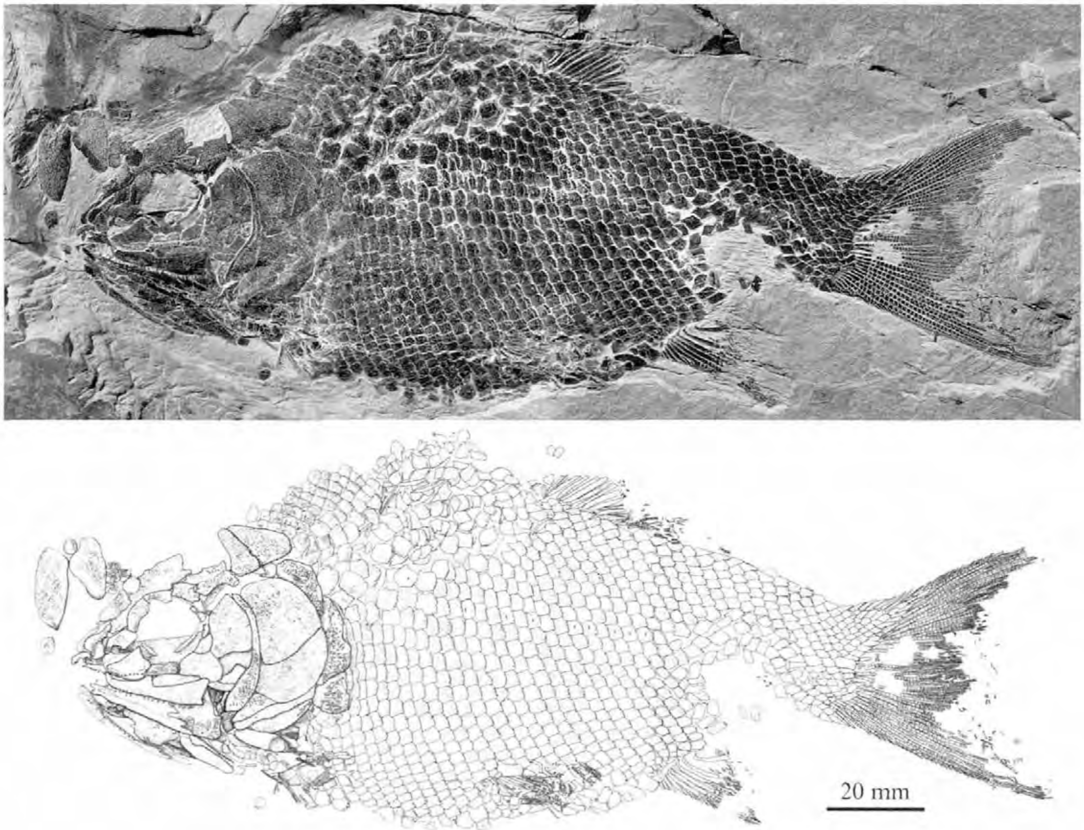

Fig. 2 *Panxianichthys imparilis* gen. et sp. nov., holotype (IVPP V 19971)

Skull roof The frontal is the largest bone of the skull roof, 2.5 times as long as the rectangular parietal. This bone is slightly constricted above the orbit, where it laterally contacts two supraorbitals (Fig. 3). Both supraorbitals are elongate and rectangular, with the posterior being two-thirds of the length of the anterior. Two supraorbitals are also present in *Robustichthys* (Xu et al., 2014b) and *Quetzalichthys* (Alvarado-Ortega and Espinosa-Arrubarrena, 2008), whereas they are absent in *Oshunia* (Maisey, 1991); three or more supraorbtials are commonly present in other ionoscopiforms (Schaeffer, 1960; Bartram, 1975; Applegate, 1988; Grande and Bemis, 1998; Lane and Ebert, 2012; Machado et al., 2013). The dermosphenotic is trapezoidal and firmly sutured into the skull roof, showing a derived condition of non-paraseminotiform halecomorphs; in contrast, the dermosphenotic is loosely hinged to side of the skull roof in paraseminotiforms and other neopterygians. As in other holosteans, the sphenotic has a small dermal component exposed on the skull roof. The dermopterotic is elongate and trapezoidal, nearly equal to the parietal in length. This

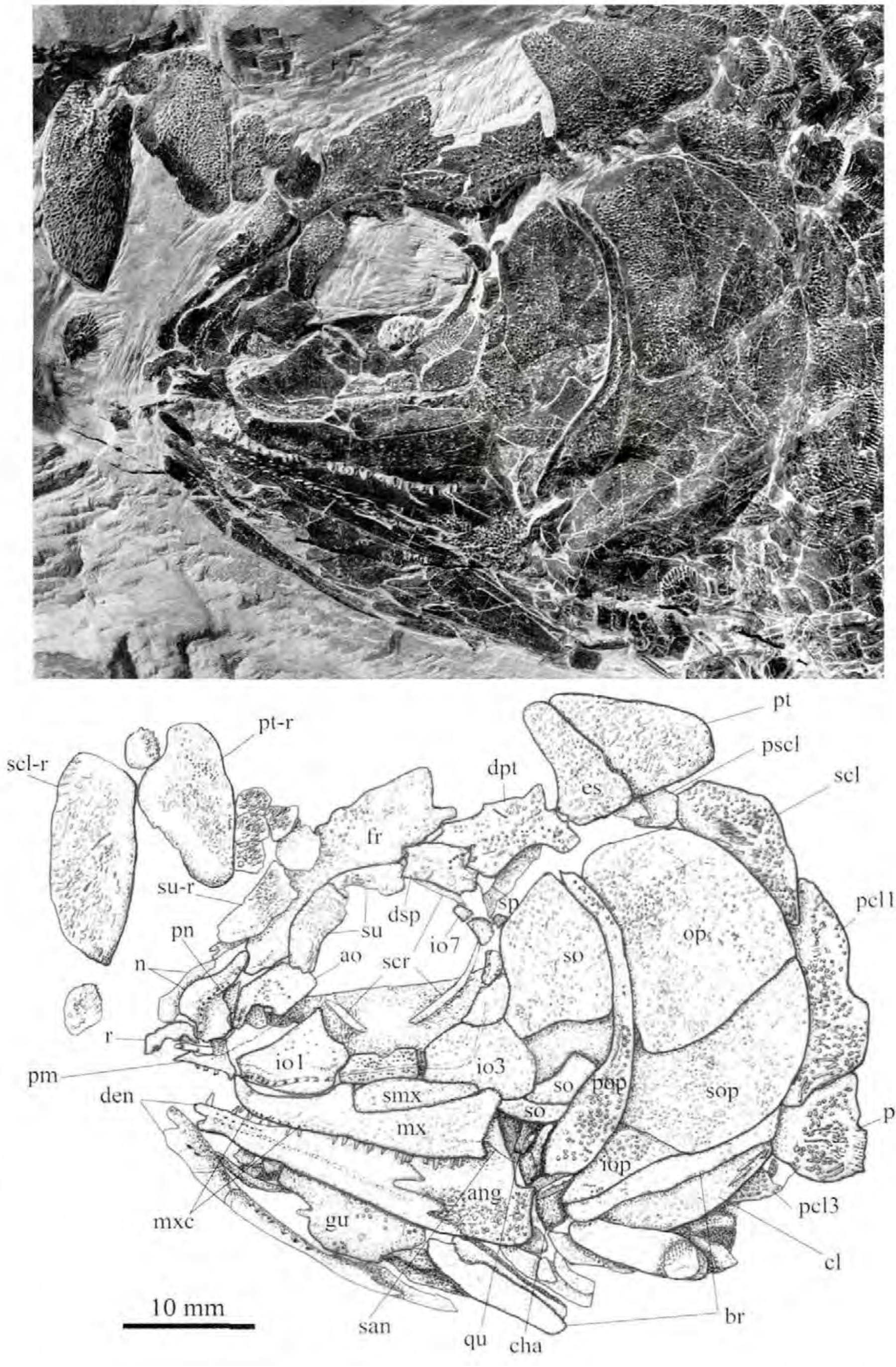

Fig. 3 Skull and pectoral girdle of *Panxianichthys imparilis* gen. et sp. nov., holotype (IVPP V 19971)

condition is similar to ophiopsids but different from non-ophiopsid halecomorphs, in which the dermopterotic is well longer than the parietal. At the back of the skull roof, there is a triangular extrascapular on each side, similar to the condition in non-sinamiid halecomorphs; sinamiids are distinguished in possession of at least three pairs of extrascapulars (Stensiö, 1935; Zhang, 2012).

Infraorbitals and suborbitals Seven infraorbitals are present between the dermosphenotic and antorbital (Fig. 3), showing the largest number of infraorbitals within this order. *Robustichthys* (Xu et al., 2014b) and *Ionoscopus* (Grande and Bemis, 1998) have five infraorbitals, whereas other ionoscopiforms commonly have four infraorbitals. The first (anterior-most) infraorbital (= lachrymal) and second infraorbital are longer than deep, similar to the condition in ionoscopids (Maisey, 1991; Grande and Bemis, 1998; Alvarado-Ortega and Espinosa-Arrubarrena, 2008) and the basal ophiopsid *Furo muensteri* (Lane and Ebert, 2012), but different from those of other ophiopsids (e.g., *Macrepistius*, *Teoichthys* and *Ophiopsis*) in which the anterior two infraorbitals are deeper than long. The third infraorbital is much expanded and roughly hexagonal. The fourth and fifth are small and quadrangular. The sixth and seventh are tube-like. The first to fifth infraorbitals are ornamented with ganoine tubercles, whereas the remaining two are smooth.

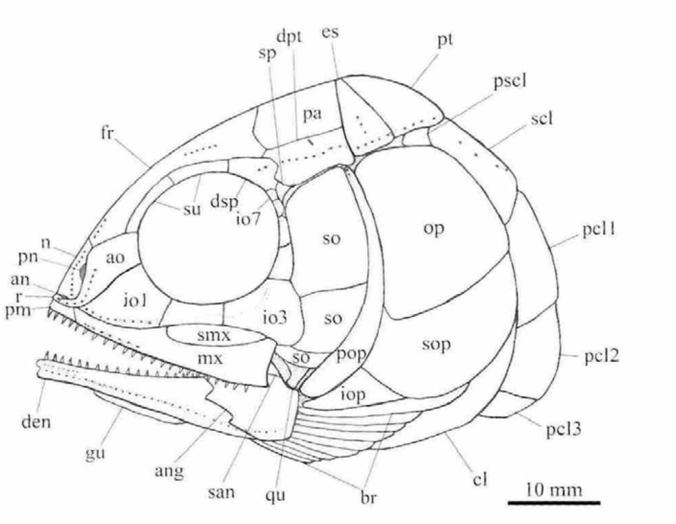

Fig. 4 Reconstruction of skull and pectoral girdle of *Panxianichthys imparilis* gen. et sp. nov.

At least three suborbitals are present between the preopercle and posterior infraorbitals. Among them, the upper is largest, being trapezoidal in shape, the middle is relatively small and probably trapezoidal, and the lower is smallest and elongate.

Palate and hyoid arch Because of taphonomic compression, the parasphenoid and some pterygoid bones can only be observed through the orbit. The partly exposed quadrate articulates with the lower jaw with a condyle. Neither the hyomandibular nor the symplectic is exposed. An elongate and plate-like bone preserved near the branchiostegal rays and interopercle is tentatively interpreted as the anterior ceratohyal according to its shape and position (Fig. 3).

Jaws The premaxilla shows a characteristic feature of the Holostei in having a deep nasal process that contacts the frontal dorsally. The maxilla is elongate and low. It bears a sensory canal, indicated by a linear series of sensory pores adjacent to the anteroventeral margin of the maxilla (Fig. 3). A large supramaxillary process is present at the middle part of the maxilla, similar to *Robustichthys* (Xu et al., 2014b). A less prominent but similarly positioned process was also known in some other halecomorphs (e.g., *Parasemionotus* and *Amia*; Lehman, 1952; Grande and Bemis, 1998). This process accommodates the rounded anterior end of an elongate supramaxilla that occupies about the half length of the maxilla. Posterior to the supramaxillary process, the maxilla slightly expands posteriorly, having a concave dorsal margin and a discrete posterior notch. Presence of this notch has been generally regarded as a synapomorphy of the Halecomorphi (Grande and Bemis, 1998; but see discussions of Arratia, 2013). About twenty conical teeth are present along the oral margin of the maxilla.

The lower jaw is elongate and strong. It becomes deeper posteriorly, bearing a coronoid process as commonly seen in crown-group neopterygians. The quadrate-mandibular articulation lies slightly posterior to the level of the posterior margin of the orbit. The elongate dentary contacts the angular posteriorly with a strongly interdigitated suture. The supra-angular is partly exposed, and contributes to the coronoid process. Teeth on the dentray are conical with a distally tapered point. The mandibular sensory canal is clearly visible in the holotype as a horizontally arranged series of 26 small pores on the dentary, parallel to the ventral margin of the bone. In addition, there is a series of eight smaller pores near the oral margin of the dentary.

Operculo-gular series The opercle is large and sub-trapezoidal. The subopercle is relatively small and low, having a pronounced anterodorsal process that inserts between the opercle and the preopercle. The interopercle is small and triangular, tapering anteroventrally. The preopercle is deep and crescent-shaped. The median gular is large and plate-like, being half the length of the dentary. The branchiostegal rays are elongate bones; their precise number cannot be ascertained due to taphonomic compression.

Pectoral girdle and paired fins The posttemporal is large and sub-triangular with a rounded posterior margin. The presupracleithrum is small and sub-circular, contacting the posttemporal medially, the opercle laterally, and the supracleithrum posteriorly. The supracleithrum is deep, anteriorly inclined and partly overlapped by the opercle. The lateral line runs through the dorsal position of the supracleithrum, marked by a linear series of sensory pores on these bones. There are three postcleithrae. Among them, the upper and the middle are trapezoidal; the upper is the largest, twice as deep as the middle, and the lower is the smallest, being triangular in shape. The cleithrum is large and sticker-shaped, partly overlapped anteriorly by the subopercle and branchiostegal series.

Each pectoral fin has at least twelve distally segmented and branched fin rays, preceded by a row of fringing fulcra. The pelvic fins originate below the 10th or 11th vertical scale row, and are much shorter than the pectoral fins. Each has six distally segmented and branched fin rays.

Median fins The dorsal fin originates above the 23rd vertical scale row. It has 12 distally segmented principal fin rays, showing the least number of principal dorsal fin rays in this order. The same number of principal fin rays are also present in *Furo muensteri* (Lane and Ebert, 2012), whereas more principal fin rays are present in other ionoscopiforms: 14–17 in *Teoichthys kallistos* (Machado et al., 2013), 16–18 in *Ionoscopus*, 21 in *Queztalichthys* (Alvarado-Ortega and Espinosa-Arrubarrena, 2008), 21–23 in *Robustichthys* (Xu et al., 2014b), 23–25 in *Ophiopsis procera* (Bartram, 1975), 25–30 in *Oshunia* (Maisey, 1991), 32 in *Macrepistius* (Schaeffer, 1960), and 65 in *Teoichthys kallistos* (Applegate, 1988). The first

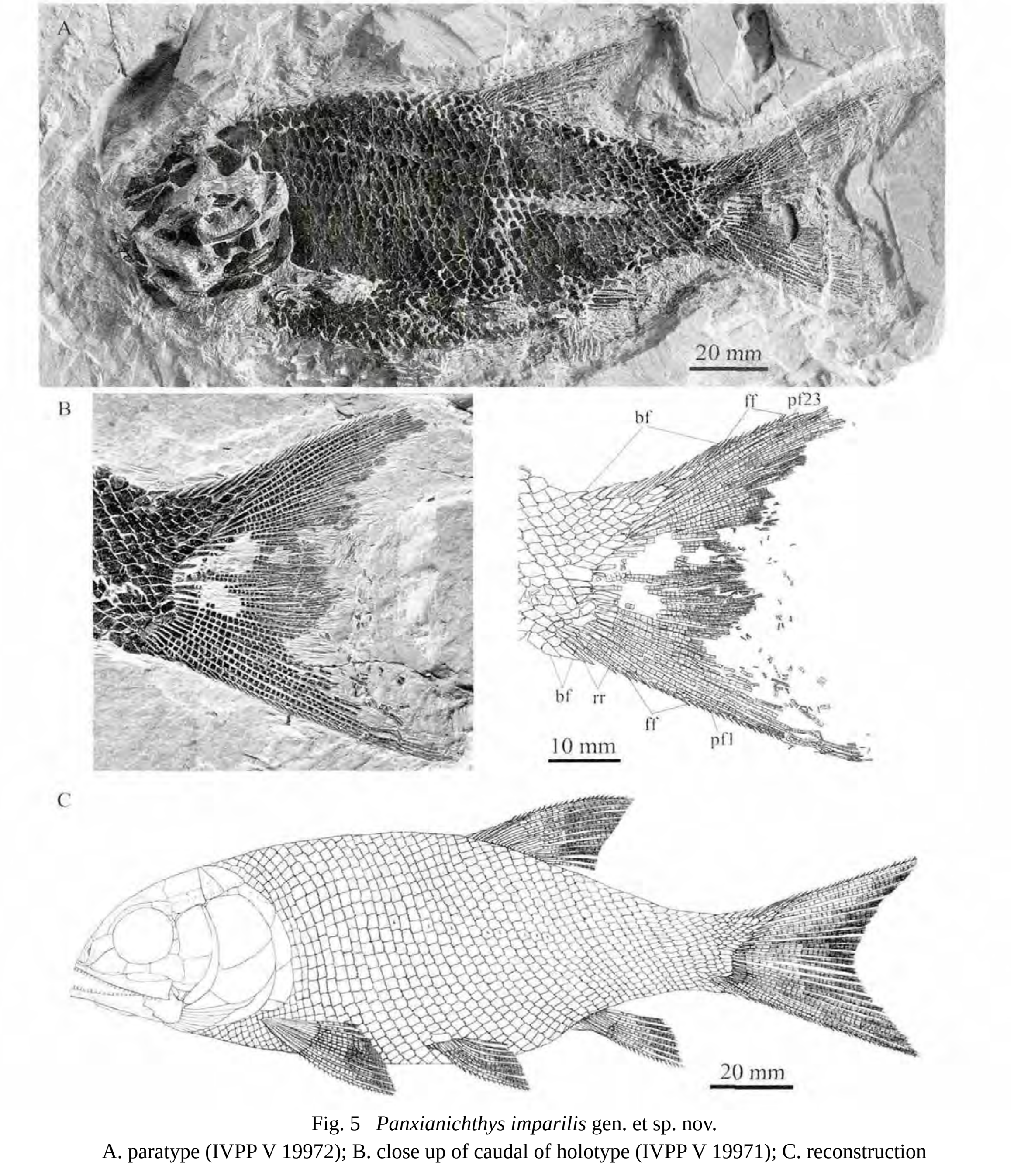

Fig. 5 *Panxianichthys imparilis* gen. et sp. nov.
A. paratype (IVPP V 19972); B. close up of caudal of holotype (IVPP V 19971); C. reconstruction

fin ray is unbranched, and is preceded by four basal fulcra and a row of fringing fulcra. The remaining fin rays branch distally.

The anal fin originates below the 20th vertical scale row. It is smaller than the dorsal fin, having seven distally segmented fin rays. The first fin ray is unbranched, and the remaining fin rays branch distally. Four basal fulcra and a row of fringing fulcra are present.

The caudal fin is hemi-heterocercal, with a scaly lobe extending one third length of the dorsal lobe. The caudal fin has 23 principal fin rays with a moderately forked posterior margin (Fig. 5B). In addition, four rudimentary fin rays are present in the ventral caudal lobe. Eleven basal fulcra are present in the dorsal lobe and two in the ventral lobe. Fringing fulcra are present in both lobes.

Scales The body is covered by rhomboidal and ganoid scales. The scales are arranged in 34–35 vertical rows from the end of the pectoral girdle to the origin of the caudal fin. There are a total of 39–40 vertical rows of scales along the lateral line (Figs. 2, 5A). The scales on the anterior middle flank are slightly deeper than wide, and they gradually become lower dorsally, ventrally and posteriorly. An articular peg and an anterodorsal extension are exposed in several scales on the anterior flank region. The scales are ornamented by dense ridges with a serrated posterior margin.

4 Phylogenetic relationships and implications

The new taxon *Panxianichthys* shows diagnostic features of the Holostei (Grande, 2010; Xu and Wu, 2012; Xu et al., 2014b), including presence of a tube-like rostral, a tube-like canal bearing anterior arm of the antorbital, a deep nasal process of the premaxilla that is sutured to the frontal, and a dermal component on the sphenotic. To facilitate a comprehensive discussion of phylogenetic relationships of *Panxianichthys* with other holosteans, we have incorporated this taxon and *Furo muensteri* (Lane and Ebert, 2012) into a data matrix assembled by Xu et al. (2014b).

Results of our analysis recover *Panxianichthys* as a basal ionoscopiform within the Halecomorphi (Fig. 6). *Panxianichthys* shares a derived character with other halecomorphs, presence of a notched posterior margin of the maxilla; it is more derived than the Parasemionotiformes, possessing two synapomorphies of the ‘Ionoscopiformes-Amiiformes’ clade, a deep and narrow, crescent-shaped preopercle and a dermosphenotic firmly sutured to, and forming part of the skull roof (Grande and Bemis, 1998). *Panxianichthys* is further referred to the Ionoscopiformes because it possesses a synapomorphy of this clade, presence of a sensory canal in the maxilla (Alvarado-Ortega and Espinosa-Arrubarrena, 2008; Xu et al., 2014b). However, it lacks two synapomorphies of other ionoscopiforms, presence of a posteriorly inclined lower border of the last infraorbital, and an innerorbital flange of the dermosphenotic bearing an infraorbital sensory canal.

Results of our analysis provide new insights on the interrelationships of the Ionoscopidae. Grande and Bemis (1998) placed *Ionoscopus* at a basal position of the Ionoscopiformes, and recovered *Oshunia* as a sister taxon of the Ophiopsidae (sampled by *Ophiopsis* and *Macrepistius*). Alvarado-Ortega and Espinosa-Arrubarrena (2008) recovered *Ionoscopus* as a basal member of the Ionoscopidae, and *Oshunia* as a sister taxon of *Quetzalichthys*. However, the interrelationships of the Ionoscopidae were not well resolved in Xu et al. (2014b); three ionoscopid taxa formed a polytomy. Here, our analysis indicates that *Quetzalichthys* is more closely related to *Ionoscopus* than to *Oshunia*; *Oshunia* retains an elongate antorbital extending back to the orbital margin as in *Panxianichthys*, *Robustichthys* and *Furo muensteri*, whereas *Quetzalichthys* shares a derived feature with *Ionoscopus* in possession of a shorter antorbital that is located anterior to the lachrymal. In that context, the monophyly of the Ionoscopidae is supported by presence of amioid-type scales (convergently derived in most amiiforms) and a posterior notch of second infraorbital for supramaxilla (unknown in *Oshunia*).

Results of our analysis support the taxonomic reassessment of *Furo muensteri* as an ophiopsid (Lane and Ebert, 2012). *F. muensteri* possesses two synapomorphies of the Ophiopsidae, presence of a dermopterotic nearly as long as the parietal (convergently derived in *Panxianichthys*), and absence of lateral fossae on vertebral centra. Another possible ophiopsid synapomorphy, presence of solid, perichordally ossified, diplospondylous centra in adult-sized individuals, is still unknown in *F. muensteri* because of preservation. Additionally, *F. muensteri* lacks several derived features shared by other ophiopsids, including presence of a deep and large first infraorbital (= lachrymal), a relatively deep second infraorbital (deeper than long), a relatively short antorbital (not contributing to orbital margin), and lateral line ossicles extending onto caudal fin. Thus, *F. muensteri* is placed at a basal position of the Ophiopsidae.

Panxianichthys offers a new insight on the evolution of key ionoscopiform apomorphy. As well recognized by previous studies (Gardiner et al., 1996; Garnde and Bemis, 1998; Xu et al., 2014b), ionoscopiforms have a dermal component on the sphenotic that separates the last infraorbital from the dermosphenotic; consequently, the dermosphenotic has an innerorbital flange that bears an infraorbital sensory canal to meet the last infraorbital. This unusual feature was previously regarded as a synapomorphy of the Ionoscopiformes. However, *Panxianichthys* retains a primitive condition in lacking an innerorbital descending flange on the dermosphenotic. Instead, it bears two additional tube-like infraorbitals (seven infraorbitals in *Panxianichthys* vs. five in *Robustichthys* and *Ionoscopus*, and four in other ionoscopiforms). Both tube-like infraorbitals are smooth, distinctly different from other infraorbitals that are ornamented with ganoine tubercles. We speculate that the upper tube-like infraorbitals in *Panxianichthys* are homologous to the innerorbital flange of the dermosphenotic in other ionoscopiforms.

Panxianichthys documents the second ionoscopiform in the Middle Triassic and the first record of this group in the Panxian Biota. The new finding extends the geographical distribution of early ionoscopiforms from eastern Yunnan into western Guizhou, demonstrating a wider distribution than previously appreciated for this group. Although *Panxianichthys* is slightly younger than *Robustichthys* from the Luoping Biota, this taxon is significantly older than other members of this group from the Late Jurassic of Europe, and Early Cretaceous of the New World. In the Middle Triassic, South China was a part of the Palaeotethys Ocean. This Ocean would have provided an east-west corridor for dispersal and biological exchanges of ionoscopiforms between Europe and South China, as indicated by studies of other aquatic vertebrates (Xu et al., 2012; Benton et al., 2013). The successive discoveries of the oldest ionoscopiforms (*Panxianichthys* and *Robustichthys*) from South China do not fully prove that this area is the origin centre of the Ionoscopiformes, but these evidences provide a minimum estimate for the age of the origin of this group; the early diversification of the Ionoscopiformes is more rapid than previously thought.

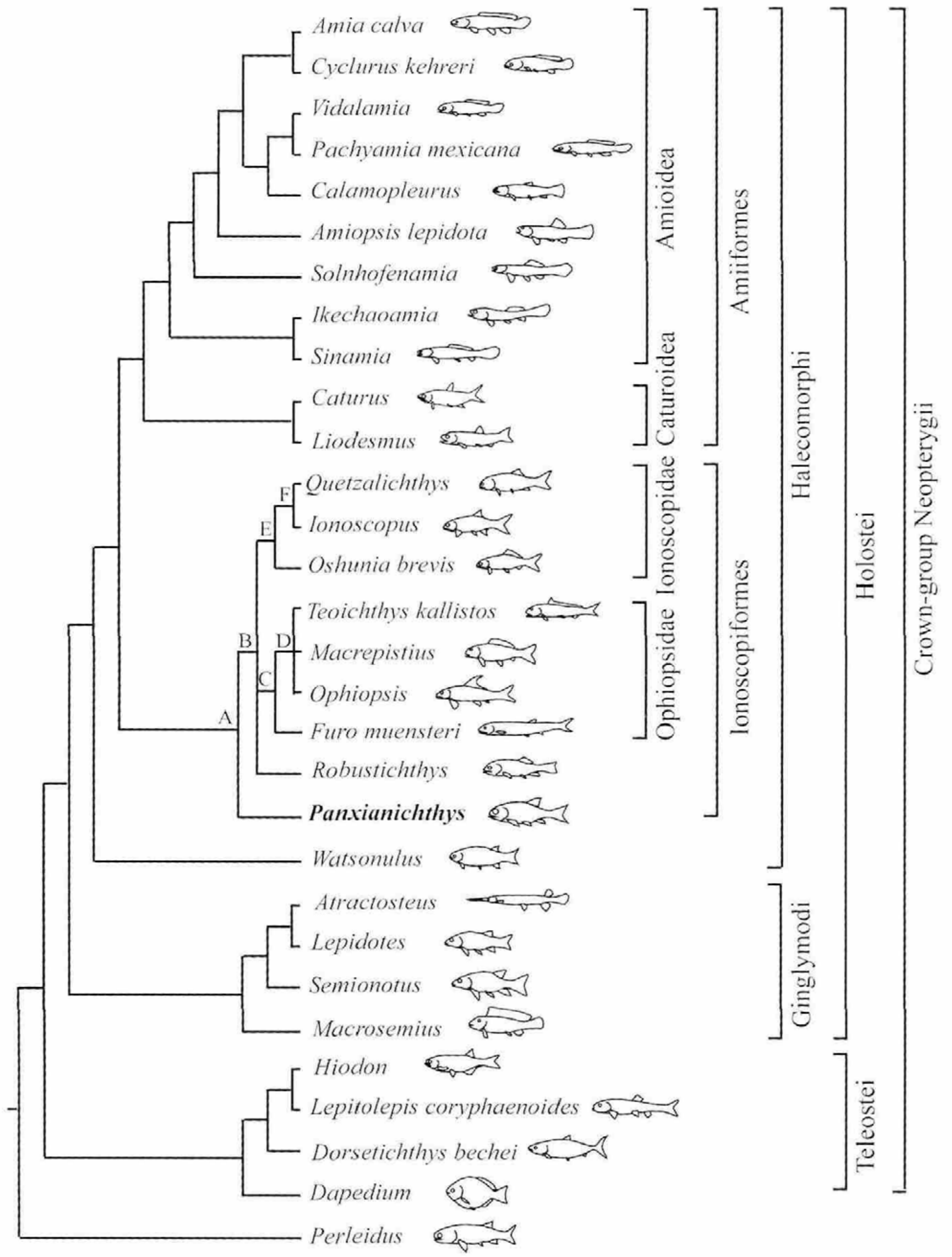

Fig. 6 Strict consensus of nine most parsimonious trees (TL = 212 steps; CI = 0.5425; RI = 0.7197), showing phylogenetic relationships of Ionoscopiformes with the Neopterygii

Character states supporting the clade Ionoscopiformes and its subclades include A, 18(1), 60(1), 77(1); B, 63(1)*, 81(1)*; C, 1(1), 4(3), 50(1); D, 43(1), 58(1), 78(1), 95(1); E, 4(1), 74(1)*, 96(1); F, 2(1), 26(1), 78(1)

Character states marked with an asterisk have a CI of 1.0

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贵州中三叠世预言鱼目(近鲱形类)一新属种：奇异盘县鱼 (*Panxianichthys imparilis* gen. et sp. nov.)

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摘要：预言鱼目是中生代海生近鲱形类的一个绝灭的支系。由于与弓鳍鱼目密切的亲缘关系，预言鱼目在研究近鲱形类的早期演化和生物地理学中具有重要意义。然而，早期预言鱼目的化石证据非常匮乏；直到最近，产于云南中三叠世罗平生物群的强壮鱼是该目中最古老的也是三叠纪唯一的成员。本文根据产于贵州西部中三叠世盘县动物群的两块保存良好的标本命名了预言鱼目一个新的属种，奇异盘县鱼(*Panxianichthys imparilis* gen. et sp. nov.)。盘县鱼的生存时代略晚于强壮鱼，但它比产于欧洲晚侏罗世和美洲早白垩世的预言鱼目其他成员要早很多。盘县鱼具有预言鱼目的共近裔性状，上颌骨上具有感觉管，但它保留了一些其他预言鱼目鱼类所不具有的原始特征。分支分析的研究结果表明盘县鱼是最原始的预言鱼目鱼类，为揭示预言鱼目的演化提供了新的信息。强壮鱼和盘县鱼的相继发现表明，预言鱼目的早期分异比我们之前想象的要快得多。

关键词：贵州，中三叠世，盘县生物群，全骨鱼类，近鲱形类
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