A new ionoscopiform fsh (Holostei: Halecomorphi) from the Middle Triassic (Anisian) of Yunnan, China postprint

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Abstract

Ionoscopiformes, an extinct clade of halecomorphs, is considered the sister group to Amiiformes. Ionoscopiform fossils were previously found mainly in the late Middle Triassic (Ladinian) and Late Jurassic strata of Europe and the Early Cretaceous strata of the New World. In recent years, ionoscopiform fish fossils (Robustichthys and Panxianichthys) have been discovered from the early Middle Triassic (Anisian) strata of Yunnan and Guizhou, respectively, representing the first discovery of this order in China. Based on six well-preserved fish specimens from the early Middle Triassic (Pelsonian, Anisian, ~244 Ma) marine deposits in Luoping, Yunnan, a new genus and species of Ionoscopiformes, Subortichthys triassicus gen. et sp. nov., is named. Subortichthys triassicus is the second ionoscopiform fish discovered from the Luoping Biota and represents one of the oldest fossil records of Ionoscopiformes, providing important information for understanding the origin and early diversification of this order. Subortichthys can be unequivocally assigned to Halecomorphi because it possesses two synapomorphies of this clade: the symplectic articulating with the lower jaw and a notched posterior margin of the maxilla. Results of the phylogenetic analysis place Subortichthys at the base of Ionoscopiformes within the phylogenetic framework of Halecomorphi, because it bears the important diagnostic feature of this order—a sensory canal in the maxilla (an ionoscopiform synapomorphy)—but lacks the derived features of other ionoscopiform fishes. Notably, Subortichthys possesses some unique features, such as the presence of three or four pairs of extrascapulars and a much expanded third infraorbital posteriorly contacting the preopercle. The discovery of Subortichthys indicates that the early diversification of ionoscopiform fishes in South China (located in the eastern part of the Paleotethys Ocean during the Triassic) occurred at least by the early Middle Triassic (Anisian).

Full Text

Preamble

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A New Ionoscopiform Fish (Holostei: Halecomorphi) from the Middle Triassic (Anisian) of Yunnan, China

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Abstract
Ionoscopiformes, sister to Amiiformes, are an extinct group of halecomorph fishes previously known mainly from the late Middle Triassic (Ladinian) and Late Jurassic of Europe and the Early Cretaceous of the New World. They have not been known in China until recently when two ionoscopiforms (*Robustichthys* and *Panxianichthys*) were discovered from the early Middle Triassic (Anisian) of Yunnan and Guizhou, respectively. Here, we describe a new ionoscopiform, *Subortichthys triassicus* gen. et sp. nov., based on six well-preserved specimens from the early Middle Triassic (Pelsonian, Anisian, ~244 Ma) marine deposits exposed in Luoping, eastern Yunnan, China. This discovery documents the second ionoscopiform from the Luoping fossil beds and represents one of the oldest ionoscopiforms in the world, providing important information for understanding the origin and early diversification of this group. *Subortichthys* is an unambiguous halecomorph as it possesses two synapomorphies of this clade: a symplectic articulating with the lower jaw and a notched posterior margin of the maxilla. Within the phylogenetic framework of Halecomorphi, our phylogenetic analysis places *Subortichthys* at the base of Ionoscopiformes because it bears a sensory canal in the maxilla (an ionoscopiform synapomorphy) but lacks derived features of other ionoscopiforms. Notably, *Subortichthys* is distinguished from other members of this order by a unique combination of features, such as the presence of three or four pairs of extrascapulars and a much-expanded third infraorbital that contacts the preopercle posteriorly. The new material reveals that the earliest diversification of ionoscopiforms was well underway in South China (then part of the eastern Paleotethys Ocean) by the early Middle Triassic (Anisian).

Key words: Luoping, Yunnan; Triassic; Ionoscopiformes, Halecomorphi; osteology; phylogeny

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Halecomorphi represent one of three major subdivisions of crown-group Neopterygii and have long attracted the attention of paleoichthyologists interested in phylogenetic and comparative studies of neopterygian fishes (Patterson, 1973; Grande and Bemis, 1998). Although extant halecomorphs are represented by only a single species, *Amia calva* (the bowfin, renowned as a 'living fossil') from freshwater environments in central and eastern North America, this clade possesses a rich fossil record. The earliest halecomorphs, assigned to Parasemionotiformes, are confined to Early Triassic marine deposits; the placement of the Permian *Brachydegma* within Parasemionotiformes (Hurley et al., 2007) has been rejected by subsequent studies (Near et al., 2012; Xu et al., 2014a). Most parasemionotiforms (except *Watsonulus*) still require detailed comparative description and taxonomic revision (Olsen, 1984; Grande and Bemis, 1998).

Ionoscopiformes represent another fascinating group of marine halecomorphs generally considered the sister group to Amiiformes. For decades, ionoscopiforms were known primarily from the Late Jurassic of Europe and the Early Cretaceous of the New World (Schaeffer, 1960, 1971; Bartram, 1975; Maisey, 1991; Grande and Bemis, 1998; Brito, 2000; Alvarado-Ortega and Espinosa-Arrubarrena, 2008; Lane and Ebert, 2012; Machado et al., 2013). Potential ionoscopiforms were also reported from the late Middle Triassic (Ladinian) of Italy and Austria, but these are based on poorly preserved specimens (De Alessandri, 1910; Sieber, 1955; López-Arbarello et al., 2014). Recently, convincing ionoscopiforms based on well-preserved specimens have been discovered in the early Middle Triassic (Anisian) of South China (Xu et al., 2014b; Xu and Shen, 2015) and the Middle Jurassic of Africa (Taverne, 2015), providing new insights into the origin and early evolution of this group.

In China, two previously known ionoscopiforms are *Robustichthys luopingensis* and *Panxianichthys imparilis* from the Middle Triassic (Pelsonian, Anisian) of Luoping, Yunnan Province and Panxian, Guizhou Province, respectively. *Robustichthys* represents the earliest ionoscopiform, providing a minimum age estimate for the origin of this order (Xu et al., 2014b). *Panxianichthys*, probably slightly younger than *Robustichthys* (Benton et al., 2013), exhibits some features more primitive than *Robustichthys*, documenting the most basal ionoscopiform previously known (Xu and Shen, 2015). Here, we report the discovery of a new ionoscopiform based on six exceptionally well-preserved specimens from the same fossil beds that yielded *Robustichthys* (upper member of the Guanling Formation, ~244 Ma) in Luoping, eastern Yunnan (Zhang et al., 2009; Hu et al., 2011; Benton et al., 2013). This new discovery prompted a phylogenetic analysis to reassess interrelationships within Ionoscopiformes.

1. Material and Methods

Fossil specimens were prepared mechanically and are housed in the fossil collection of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences. Illustrations were drawn using an Olympus SZX7 microscope with a camera lucida attachment and further processed using Adobe Photoshop CS4. The relative positions of fins and scale counts were recorded following Westoll (1944). Although we accept that actinopterygian frontals and parietals are homologous to sarcopterygian parietals and postparietals, respectively (Schultze, 1993), we nevertheless utilize traditional actinopterygian nomenclature following Grande and Bemis (1998) to facilitate comparison with most existing literature. Tree searches were conducted using the heuristic search algorithm in PAUP* 4.0b10 (Swofford, 2003). All characters were unordered and equally weighted.

2. Systematic Paleontology

Neopterygii Regan, 1923
Holostei Müller, 1845
Halecomorphi Cope, 1972
Ionoscopiformes Grande & Bemis, 1998
Subortichthys triassicus gen. et sp. nov. (Figs. 1–4)

Etymology: The generic name *Subortichthys* derives from *subortus* (Latin, meaning revival) and *ichthys* (Greek, meaning fish). The specific epithet refers to the Triassic (the first period of the Mesozoic Era), alluding to both the age of the taxon and the common occurrence of three extrascapulars on each side of the skull.

Holotype: IVPP V 20051, a nearly complete, laterally compressed specimen lacking the right pectoral fin.

Referred specimens: IVPP V 19003, V 20052, V 20680, V 22950, and V 22951—five nearly complete specimens.

Locality and horizon: Luoping, Yunnan, China; second (upper) member of the Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Diagnosis: A basal ionoscopiform distinguished from other members of this order by the following combination of features: frontal trapezoidal, nearly four times as long as the square parietal; dermopterotic 1.5 times as long as parietal; supraorbital sensory canal contacting anterior pit-line in parietal; three pairs of extrascapulars typically present (four pairs occasionally); three supraorbitals; five infraorbitals; third infraorbital much expanded, contacting preopercle posteriorly; three or four suborbitals; quadratojugal splint-like; supramaxilla single, half the length of maxilla; maxilla elongate, extending posteriorly to level of middle portion of parietal; 12 pairs of branchiostegal rays; 10–13 rays in each pectoral fin; 10–11 principal dorsal rays; eight anal rays; 18 principal caudal rays; rhomboidal scales with serrated posterior margin; scale formula D18–19/P7–8, A15–16, C27–28/T30–32.

3. Description and Comparison

General Morphology and Size

Subortichthys is a small halecomorph with a blunt snout, fusiform body, and moderately forked caudal fin [FIGURE:1]. The dorsal fin inserts slightly posterior to the pelvic fin origins, while the anal fin is positioned in the posterior quarter of the body. The holotype [FIGURE:1A] has a standard length (SL) of 62 mm and a total length of ~80 mm. The smallest specimen [FIGURE:1B] has an SL of 43 mm, while the largest specimen (V 20680; see online supplementary material) reaches 72 mm SL. The head is relatively large, comprising about one-third of SL. Maximum body depth, slightly greater than head length, occurs midway between the opercular margin and the dorsal fin origin. Cranial bone surfaces are ornamented with ganoine ridges and tubercles.

Snout and Skull Roof

The canal-bearing bones of the snout consist of a median rostral, paired nasals, and antorbitals

. The median rostral is small and subtriangular, contacting the nasal posterodorsally, the antorbital laterally, and the premaxilla ventrally. The ethmoid commissural sensory canal runs transversely through the anterior portion of this bone. The paired nasals meet at the midline; each is small and plate-like with a curved lateral margin and straight medial margin. The posterior nostril lies between the nasal and antorbital, while the anterior nostril probably opens near the junction of the nasal, rostral, and antorbital as in other holosteans. The anterior portion of the supraorbital sensory canal is enclosed within the nasal, indicated by several pores on this bone. The antorbitals are elongate and slightly curved, with an expanded posterior portion and tapering anterior arm that extends medially to contact the rostral. The posterior margin of the antorbital forms the anterior orbital margin, and the ethmoid commissural canal contacts the infraorbital sensory canal at the middle portion of the antorbital.

The frontal is trapezoidal, four times as long as the square parietal [FIGURE:2, 3B]. It widens posteriorly, with the posterior portion twice as wide as the anterior. The frontal contacts the parietal and dermopterotic posteriorly in a sinuous suture. The supraorbital sensory canal enters the frontal from the nasal, runs

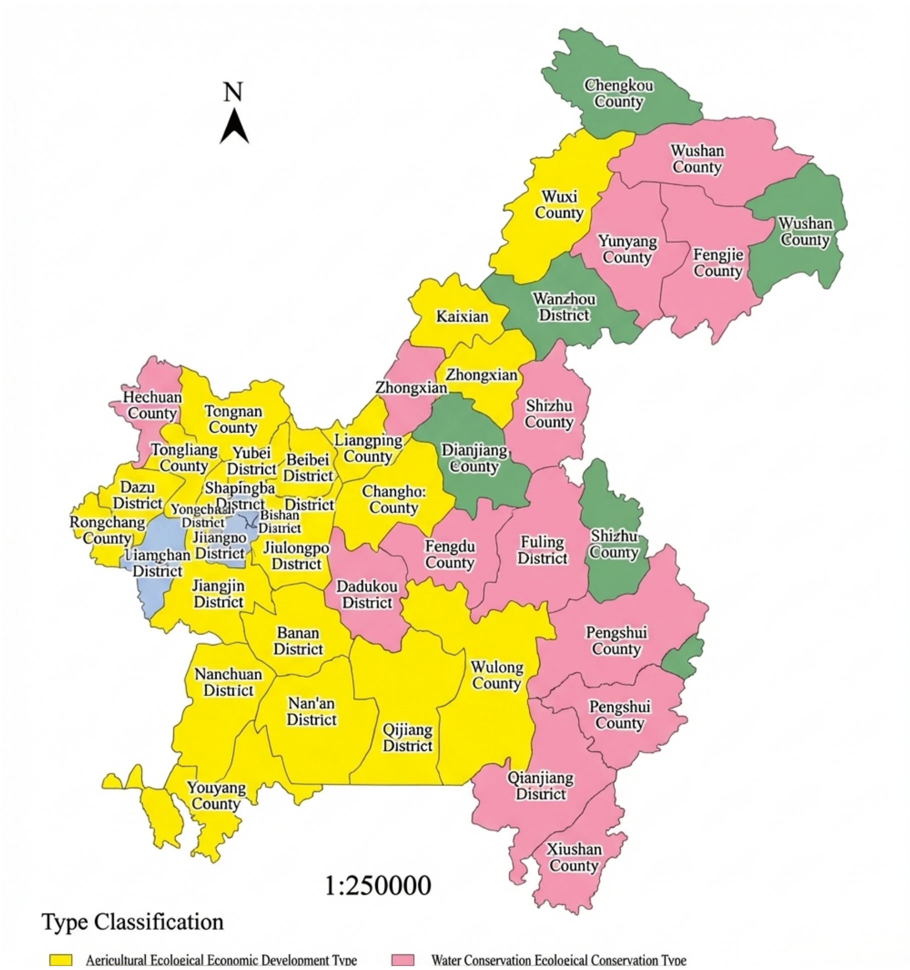

Figure 1: Figure 2

longitudinally through this bone, and posteriorly contacts the anterior pit-line in the parietal. The parietal is nearly square, half as wide as the posterior portion of the frontal. The posterior pit-line is relatively short, located at the posteromedial portion of the parietal. The middle pit-line is quite long, extending from the posterolateral portion of the parietal, running laterally into the dermopterotic, and terminating near the temporal sensory canal in this bone. The dermopterotic is trapezoidal, nearly 1.5 times as long as the parietal. The temporal sensory canal runs longitudinally through the dermopterotic, indicated by a line of approximately ten small pores near the lateral margin of this bone.

Three extrascapulars are present on each side of the skull in five type specimens, while V 20680 exhibits four extrascapulars on the left side. This likely represents intraspecific variation among individuals rather than interspecific variation, as these specimens are consistent in most other features (except for the number and shape of suborbitals, which may represent another intraspecific variation; see below). These extrascapulars are nearly trapezoidal and vary slightly in size among specimens. The supratemporal commissure runs transversely through the extrascapulars, indicated by several small pores at the middle portions of these bones.

Circumorbital Bones

Three supraorbitals are present; they are rectangular and approximately equal in length. In contrast, *Panxianichthys* and *Robustichthys* have only two supraorbitals, while other ionoscopiforms generally have four or more. Five infraorbitals are present

. The first is sub-trapezoidal with a triangular anterior portion inserting between the antorbital and maxilla; the second is elongate and low; the third is much expanded, contacting the preopercle posteriorly; the fourth is small and trapezoidal, 1.5 times deeper than long (V 22950); and the fifth is rectangular, nearly equal to the fourth in depth.

The dermosphenotic is trapezoidal, narrowing ventrally. The conjunction of the infraorbital and temporal canals occurs near the dorsal margin of this bone. The sphenotic has a small triangular dermal component that contacts the dermosphenotic anteriorly, the dermopterotic dorsally, and the upper suborbital ventrally.

Three suborbitals are present in four specimens: the upper is small and trapezoidal, the middle is large and pentagonal, and the lower is small and triangular. In V 22950, four suborbitals are present; the second is the largest, below which two smaller ones occupy the position of the triangular lower suborbital in other specimens. Three suborbitals are also present in most other ionoscopiforms (*Panxianichthys*, *Ophiopsis*, *Ionoscopus*, and *Quetzalichthys*). In contrast, *Macrepistius* has five suborbitals (Schaeffer, 1960), while *Robustichthys* (Xu et al., 2014b) and *Teoichthys* (Applegate, 1988; Machado et al., 2013) have eight or more.

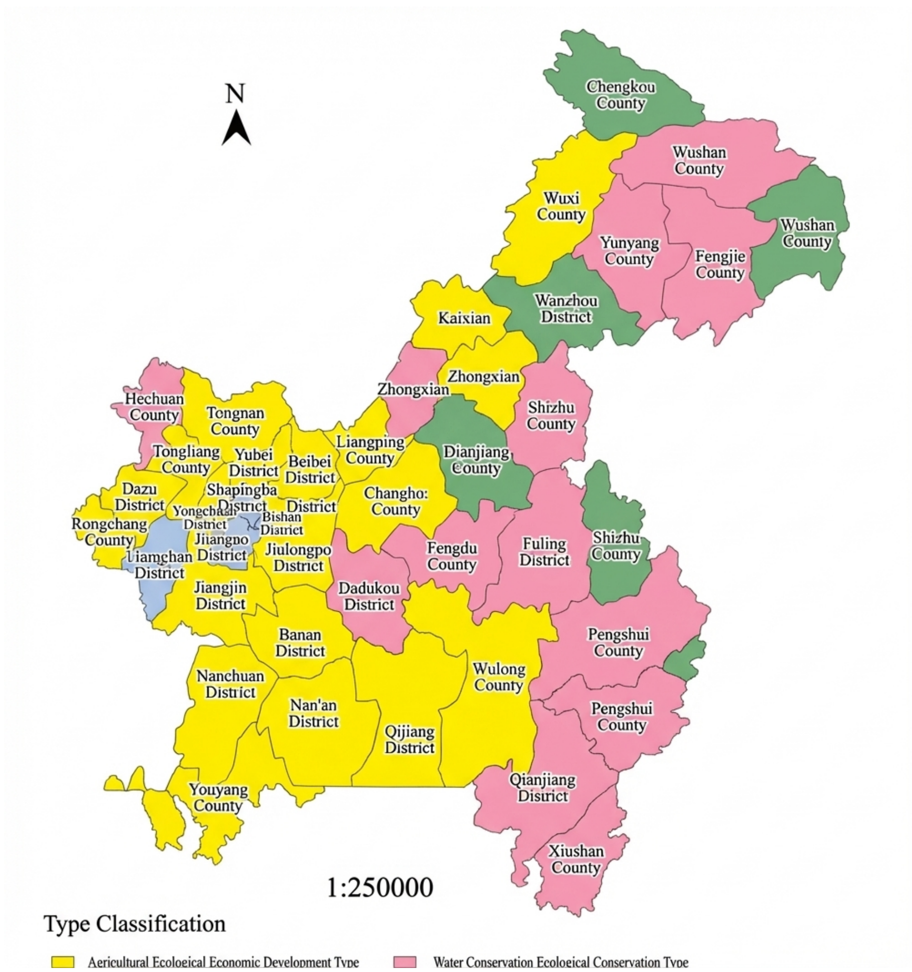

Figure 2: Figure 2

Sclerotic bones are partly preserved near the orbital rim. They are thin and curved, but their number cannot be determined.

Palatal Bones and Suspensorium

Because all specimens are laterally compressed, the palatal bones can only be observed through the orbit, including at least the parasphenoid, entopterygoid, ectopterygoid, and dermopalatine. The oral margins of these bones are covered by dense conical teeth [FIGURE:3]. Teeth on the parasphenoid and entopterygoid are very small, while those on the dermopalatine are notably larger.

The hyomandibular, laterally covered by the suborbitals and preopercle, cannot be directly observed in most specimens (except V 22951). X-ray computed tomography reveals this bone relatively well in the holotype [FIGURE:3F]. In V 22951, the suborbitals and preopercle are missing, leaving the hyomandibular almost fully exposed (see online supplementary material). It is hatchet-shaped and vertically positioned, with a single broad facet articulating with the ventral side of the braincase dorsally. A foramen at the middle portion of the hyomandibula may have transmitted the hyomandibular branch of the facial nerve.

The quadrate is partly exposed below the third infraorbital and posterior to the maxilla [FIGURE:2B, 3C–E]. It is small and nearly fan-shaped, articulating ventrally with the lower jaw.

The quadratojugal is splint-like, tapering dorsally [FIGURE:2A, 3A, D]. It rests on the anterior edge of the ventral portion of the preopercle. The ventral portion of the quadratojugal contacts the symplectic medially and does not contact the lower jaw [FIGURE:3D].

The symplectic is rod-like (V 22951), resembling that in *Robustichthys* (Xu et al., 2014b). It has a slightly expanded dorsal portion and a large ventral condyle that articulates with the lower jaw. Corresponding to this condyle, the lower jaw has a distinct notch in the dorsal margin of its posterior portion [FIGURE:3A].

Jaws

The upper jaw on each side of the skull includes a premaxilla, maxilla, and supramaxilla [FIGURE:2, 3]. The premaxilla is relatively large, bearing a robust nasal process. Because of nasal overlap, the fenestra for the olfactory nerve cannot be observed in this nasal process. Approximately ten conical teeth are present along the oral margin of the premaxilla, nearly equal in size to those on the anterior portion of the maxilla.

The maxilla is elongate and low, bearing a peg-like anterior process and a distinct notch at its posterior margin. Presence of this posterior maxillary notch has been considered a halecomorph synapomorphy (Grande and Bemis, 1998). The anterior dorsal margin of the maxilla is slightly excavated for the first infraorbital, while the posterior dorsal margin is more excavated for the supramaxilla. The supramaxilla is about half the length of the maxilla, tapering at both ends.

The lower jaw is elongate, bearing a well-expanded coronoid process at its posterior portion. Four elements are discernible in lateral view: the dentary, angular, supra-angular, and retroarticular. The dentary is wedge-shaped, contacting the angular posteriorly in a sinuous suture. The angular is trapezoidal, about one-third the length of the lower jaw. The supra-angular is only partly exposed in V 20680 [FIGURE:3C], and its complete shape remains unknown. The retroarticular is very small [FIGURE:2A], contacting the posteroventral portion of the angular anteriorly. A few coronoid bones are exposed in the medial view of the lower jaw [FIGURE:2A, 3A]. They are small plate-like bones covered by dense conical teeth that are slightly smaller than those along the oral margin of the dentary.

Operculo-gular Series

The opercle is large and trapezoidal, 1.5 times deeper than long. The subopercle is sickle-shaped, nearly half as deep as the opercle, bearing a small triangular anterodorsal process that inserts between the preopercle and opercle. The interopercle is relatively short and nearly square. The preopercle is narrow and crescent-shaped, carrying a sensory canal parallel to its anterior margin with a line of small pores near its posterior margin.

Twelve pairs of branchiostegal rays are present [FIGURE:2B]. They are elongated and gradually broaden posteriorly. The median gular is oval, slightly over half the length of the lower jaw, with a short transverse pit-line present at its middle portion.

Girdles and Fins

Each pectoral girdle comprises a posttemporal, supracleithrum, cleithrum, and two postcleithra. The posttemporal is large and sub-trapezoidal with a rounded posterior margin. A sensory canal runs longitudinally through the anterolateral portion of the posttemporal and enters the supracleithrum. The supracleithrum is deep and trapezoidal, anteriorly inclined and partly overlapped by the opercle. The cleithrum is large and curved, bearing a conspicuous posteroventral notch for pectoral fin insertion. The two postcleithra are plate-like; the dorsal is twice as deep as the ventral.

The pectoral fins are large, inserting low on the body, each bearing 10–13 distally segmented and branched rays. One or two basal fulcra and a series of fringing fulcra are associated with the leading ray.

The pelvic girdles are not exposed. The pelvic fins are small, originating at the 7th or 8th vertical scale row, each bearing five distally segmented and branched rays preceded by two basal fulcra and a series of fringing fulcra.

The dorsal fin originates above the 18th or 19th vertical scale row. It is triangular, composed of 11 principal rays. The first principal ray is distally segmented and unbranched, preceded by a relatively long rudimentary ray, three basal fulcra, and a series of fringing fulcra; the remaining rays are branched distally. The anal fin originates below the 15th or 16th vertical scale row and has eight distally segmented rays. The first ray is unbranched, preceded by three or four basal fulcra and a series of fringing fulcra, while the remaining rays are branched distally.

The caudal fin is hemi-heterocercal with a moderately forked profile, bearing 18 principal rays with nine in each lobe [FIGURE:4]. The dorsal and ventral marginal principal rays are segmented and unbranched, while the middle rays are segmented and branched up to three times. Additionally, there are one rudimentary ray and eight basal fulcra in the dorsal lobe, and three rudimentary rays and two basal fulcra in the ventral lobe. Fringing fulcra are present in both lobes.

Scales

The body is fully covered with rhombic scales arranged in 30–32 vertical rows along the main lateral line [FIGURE:1; see also supplementary material]. Seven or eight additional rows of scales extend into the epaxial lobe of the caudal fin [FIGURE:4]. Scales in the anterior flank region are 1.5 times deeper than wide, gradually becoming lower and smaller dorsally, ventrally, and posteriorly. Besides the main lateral line, an additional lateral line is indicated by a line of approximately ten small pores on scales in the predorsal region. Most scales, except those covering the epaxial lobe of the caudal fin, have 2–8 acute projections at the posterior margin. Pegs and anterodorsal extensions are exposed on some scales in the anterior flank region.

4. Phylogenetic Relationships and Implications

To illuminate the phylogenetic position of *Subortichthys*, we performed a phylogenetic analysis based on a data matrix of 112 characters coded across 31 neopterygian taxa, with the stem-neopterygian '*Perleidus* madagascariensis' selected for outgroup comparison (see online supplementary material). The analysis yielded nine most parsimonious trees (tree length = 239; consistency index = 0.5523; retention index = 0.7221). *Subortichthys* was recovered at the base of Ionoscopiformes [FIGURE:5].

Subortichthys is an unambiguous halecomorph, possessing two synapomorphies of this clade: a symplectic articulating with the lower jaw and a notched posterior margin of the maxilla. Patterson (1973) first proposed symplectic involvement in the jaw hinge as a halecomorph synapomorphy, a hypothesis widely accepted by subsequent authors (Gardiner et al., 1996; Grande and Bemis, 1998; Alvarado-Ortega and Espinosa-Arrubarrena, 2008; Lane and Ebert, 2012; Brito and Alvarado-Ortega, 2013; Xu et al., 2014b; López-Arbarello et al., 2014; Xu and Shen, 2015; Taverne, 2015; Sun et al., 2017). Although Brito (1988) argued that the symplectic of the aspidorhynchid *Vinctifer* also articulated with the lower jaw, this was not confirmed by Maisey (1991), who described the symplectic of *Vinctifer* as not reaching the lower jaw. A symplectic articulating with the lower jaw has not been documented in other aspidorhynchid genera. Brito and Alvarado-Ortega (2013) suggested that *Vinctifer* might represent convergent evolution with halecomorphs in this feature.

Grande and Bemis (1998) proposed an excavated posterior margin of the maxilla as a halecomorph synapomorphy. However, Brito and Alvarado-Ortega (2013) argued that this feature is ambiguous in Parasemionotiformes and considered it a synapomorphy of the clade Ionoscopiformes + Amiiformes (= Halecomorphi minus Parasemionotiformes). Among parasemionotiforms, only *Watsonulus* has been well studied; previous studies (Olsen, 1984; Grande and Bemis, 1998) showed that a small notch was present at the posterior margin of the maxilla in well-preserved specimens of this taxon. We therefore agree with Grande and Bemis (1998) in considering an excavated posterior margin of the maxilla a halecomorph synapomorphy, although further studies are needed to determine if this structure is present in other parasemionotiforms. *Subortichthys*, similar to *Panxianichthys*, *Robustichthys*, and most other non-parasemionotiform halecomorphs, possesses an excavated posterior margin of the maxilla. This postmaxillary notch is secondarily lost in a few halecomorphs (e.g., *Amblysemius*, Grande and Bemis, 1998; and *Cipactlichthys*, Brito and Alvarado-Ortega, 2013).

Presence of a single supramaxilla was once considered a halecomorph synapomorphy (Grande and Bemis, 1998). *Subortichthys* does possess a single supramaxilla, as in other halecomorphs. However, a supramaxilla is also present in basal ginglymodians and some teleosts outside Halecomorphi. Results of our analysis, consistent with recent studies (Brito and Alvarado-Ortega, 2013; Xu et al., 2014b; Xu and Shen, 2015), support this feature as a synapomorphy of crown-group Neopterygii.

Compared with other halecomorphs, *Subortichthys* is more derived than Parasemionotiformes (represented by *Watsonulus*), sharing a derived feature with other ionoscopiforms and amiiforms: a dermosphenotic firmly sutured to and forming part of the skull roof. Furthermore, *Subortichthys* possesses a synapomorphy of Ionoscopiformes—presence of a sensory canal in the maxilla. However, it lacks three derived features of other ionoscopiforms that have been considered synapomorphies of this order (Grande and Bemis, 1998; Alvarado-Ortega and Espinosa-Arrubarrena, 2008): relatively long parietals, a posteriorly inclined lower border of the last infraorbital, and an infraorbital flange of the dermosphenotic bearing an infraorbital sensory canal. Therefore, *Subortichthys* is placed at the base of Ionoscopiformes.

Subortichthys is distinguished from other ionoscopiforms by having three or four pairs of extrascapulars, a large third infraorbital contacting the preopercle posteriorly, and a long maxilla extending to the level of the middle portion of the parietal. In comparison, *Panxianichthys* and other ionoscopiforms generally have a single pair of extrascapulars (Schaeffer, 1960; Bartram, 1975; Maisey, 1991; Brito, 2000; Lane and Ebert, 2012; Machado et al., 2013; López-Arbarello et al., 2014; Xu et al., 2014b; Xu and Shen, 2015; Sun et al., 2017). Three or more pairs of extrascapulars are otherwise present in two sinamiid amiiforms (*Sinamia* and *Ikechaoamia*) and some derived ginglymodians (*Obaicthys* and *Atractosteus*) (Grande and Bemis, 1998; Grande, 2010), but our analysis indicates these may have evolved independently. A large third infraorbital contacting the preopercle was previously known only in some teleosts (e.g., pholidophorids; Arratia, 2013) among crown-group Neopterygii. *Subortichthys* thus represents an interesting case of convergent evolution with early teleosts in this feature.

Moreover, *Subortichthys* has a long maxilla extending to the level of the middle portion of the parietal. A similar condition occurs in parasemionotiforms, several caturid amiiforms, and some teleosts among crown-group Neopterygii. In contrast, the maxilla is relatively short in other ionoscopiforms, with its posterior end commonly not exceeding the anterior margin of the parietal.

Subortichthys retains primitive ionoscopiform conditions in having a splint-like quadratojugal and a quite long antorbital. *Panxianichthys* also has a splint-like quadratojugal (personal observation). *Robustichthys* and more derived ionoscopiforms lack a splint-like quadratojugal (Xu et al., 2014b). Additionally, *Subortichthys* has a quite long antorbital with its posterior margin forming the anterior orbital margin, a condition similar to *Panxianichthys*, *Robustichthys*, *Oshunia*, and *Furo muensteri* but different from other ionoscopiforms, in which the antorbital is relatively short and does not contribute to the orbital margin.

Based on previously known geographical distribution, Ionoscopiformes were inferred to have originated in Europe and subsequently dispersed to the New World (Alvarado-Ortega and Espinosa-Arrubarrena, 2008). However, recent discoveries of two ionoscopiforms from South China indicated that this order had a wider distribution than previously appreciated (Xu et al., 2014b; Xu and Shen, 2015). Xu et al. (2014b) suggested that Ionoscopiformes probably originated in South China (then part of the eastern Paleotethys Ocean) and dispersed into Europe via the Paleotethys Ocean. The discovery of *Subortichthys* further supports this hypothesis. The new material reveals that the earliest diversification of ionoscopiforms was well underway in South China by the early Middle Triassic (Anisian).

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Supplementary material can be found at the Vertebrate PalAsiatica website

(http://english.ivpp.cas.cn/sp/PalAsiatica/vp_{list}/) in Vol. 55, Issue 2.

A New Genus and Species of Ionoscopiform (Holostei: Halecomorphi) from the Middle Triassic (Anisian) of Yunnan

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Abstract: Ionoscopiformes, an extinct clade of halecomorph fishes and sister group to Amiiformes, were previously known primarily from the late Middle Triassic (Ladinian) and Late Jurassic of Europe and the Early Cretaceous of the New World. The first Chinese records were two ionoscopiforms (*Robustichthys* and *Panxianichthys*) recently discovered in the early Middle Triassic (Anisian) of Yunnan and Guizhou, respectively. Based on six well-preserved fish fossils from the early Middle Triassic (Pelsonian, Anisian, ~244 Ma) marine strata of Luoping, eastern Yunnan, we name a new genus and species, *Subortichthys triassicus* gen. et sp. nov. *Subortichthys* represents the second ionoscopiform from the Luoping Biota and one of the oldest ionoscopiform records worldwide, providing crucial information for understanding the origin and early diversification of this group. *Subortichthys* is unambiguously a halecomorph, possessing two synapomorphies of the clade: symplectic articulation with the lower jaw and a notched posterior maxillary margin. Phylogenetic analysis places *Subortichthys* at the base of Ionoscopiformes because it possesses the ionoscopiform synapomorphy of a sensory canal in the maxilla but lacks derived features of other ionoscopiforms. Notably, *Subortichthys* is distinguished by a unique combination of characters, including three or four pairs of extrascapulars and a greatly expanded third infraorbital that contacts the preopercle posteriorly. This discovery demonstrates that the early diversification of ionoscopiforms in South China (located in the eastern Paleotethys Ocean during the Triassic) had already occurred by the early Middle Triassic (Anisian).

Keywords: Luoping, Yunnan; Triassic; Ionoscopiformes; Halecomorphi; osteology; phylogeny

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