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 two ionoscopiforms (*Robustichthys* and *Panxianichthys*) were found from the early Middle Triassic (Anisian) of Yunnan and Guizhou, respectively. Here, a new ionoscopiform, *Subortichthys triassicus* gen. et sp. nov., is described on the basis of six well-preserved specimens from the early Middle Triassic (Pelsonian, Anisian, ~244 Ma) marine deposits exposed in Luoping, eastern Yunnan, China. The discovery documents the second ionoscopiform from the Luoping fossil beds and 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 the Halecomorphi, results of the phylogenetic analysis place *Subortichthys* at the base of the 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 with a unique combination of features, such as presence of three or four pairs of extrascapulars and a much expanded third infraorbital posteriorly contacting the preopercle. The new material reveals that the earliest diversification of ionoscopiforms was well undertaken in South China (a part of east Paleotethys Ocean then) by the early Middle Triassic (Anisian).

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

Halecomorphi are one of three main subdivisions of the crown-group Neopterygii. They have long attracted the attention of paleoichthyologists interested in phylogenetic and comparative studies of neopterygian fishes (Patterson, 1973; Grande and Bemis, 1998). Although

living halecomorphs are represented by a single species *Amia calva* (bowfin, renowned as 'living fossil') from the freshwater environments in central and eastern North America, this clade has a rich fossil history. The earliest halecomorphs, referred to the Parasemionotiformes, are confined in the Early Triassic marine deposits; the placement of the Permian *Brachydegma* in the Parasemionotiformes (Hurley et al., 2007) has been rejected by subsequent studies (Near et al., 2012; Xu et al., 2014a). Most parasemionotiforms (except *Watsonulus*) still need detailed comparative description and taxonomic revision (Olsen, 1984; Grande and Bemis, 1998). The Ionoscopiformes are another interesting group of marine halecomorphs that is generally considered as the sister group of the Amiiformes. In the past decades, ionoscopiforms were mainly known 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 they are based on poorly preserved specimens (De Alessandri, 1910; Sieber, 1955; López-Arbarello et al., 2014). Recently, convincing ionoscopiforms based on well-preserved specimens were found from the early Middle Triassic (Anisian) of South China (Xu et al., 2014b; Xu and Shen, 2015) and the Middle Jurassic of Africa (Taverne, 2015). These provide new insights on 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. Among them, *Robustichthys* represents the earliest ionoscopiform, providing a minimum estimate for the age of the origin of this order (Xu et al., 2014b). *Panxianichthys*, probably slightly younger than *Robustichthys* (Benton et al., 2013), shows 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 to those of *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). The new discovery stimulated a phylogenetic analysis to reassess the interrelationships of the Ionoscopiformes.

1   Material and methods

Fossil specimens were prepared mechanically, and stored at the fossil collection of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences. Illustrations were drawn under an Olympus SZX7 microscope with a camera lucida attachment, and further prepared using Adobe Photoshop CS4. The relative position of fins and scale counts were expressed following Westoll (1944). Although we accept that actinopterygian frontals and parietals are the homologues of sarcopterygian parietals and postparietals, respectively (Schultze, 1993), we nevertheless utilize the traditional actinopterygian

nomenclature following Grande and Bemis (1998) for ease of comparison with most existing literature. Tree searches were accomplished by 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   Genus epithet *Subort-* is derived from *subortus* (Latin), meaning revival; and *-ichthys*, fish. Species epithet is derived from Triassic (the first epoch of the Mesozoic), referring to the age of the taxon and also to the three extrascapulars commonly at each side of the skull.

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

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 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 square parietal; dermopterotic 1.5 times as long as parietal; supraorbital sensory canal contacting anterior pit-line in parietal; three pairs of extrascapulars in common condition (four pairs, occasionally); three supraorbitals; five infraorbitals; third infraorbital much expanded, contacting preopercle posteriorly; three or four suborbitals; quadratojugal splint-like; supramaxilla single, half of length of maxilla; maxilla much long, extending to level of middle portion of parietal posteriorly; 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; and scale formula of D18–19/P7–8, A15–16, C27–28/T30–32.

3   Description and comparison

General morphology and size   *Subortichthys* is a small-sized halecomorph with a blunt snout, a fusiform body and a moderately forked caudal fin (Fig. 1). The dorsal fin inserts slightly posterior to the origins of pelvic fins. The anal fin is located in the posterior quarter of the body. The holotype (Fig. 1A) has a standard length (SL) of 62 mm, and a total length of ~80 mm. The smallest specimen (Fig. 1B) has a SL of 43 mm, and the largest specimen (V
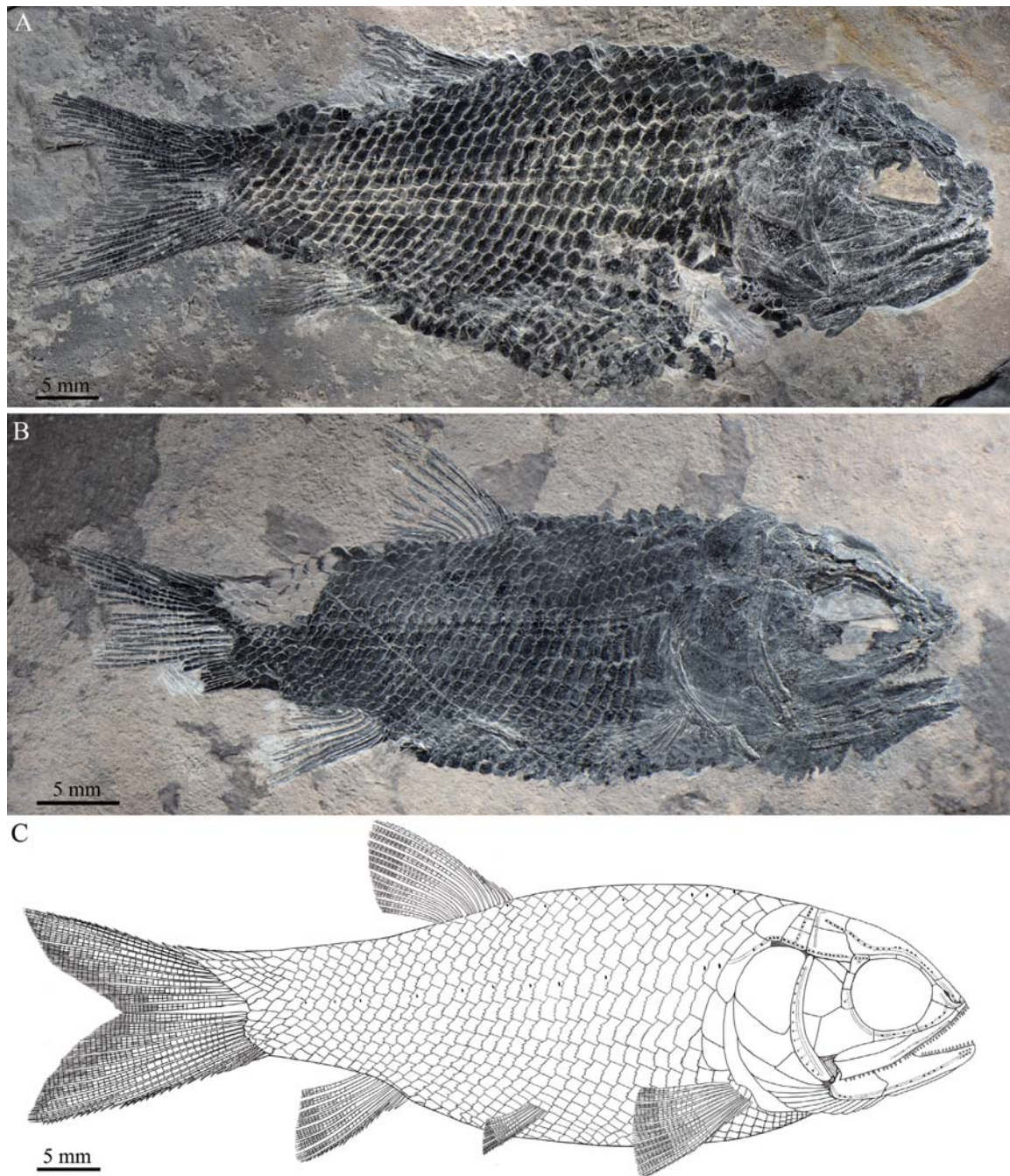
Fig. 1 *Subortichthys triassicus* gen. et sp. nov.
A. IVPP V 20051 (holotype); B. V 20052; C. reconstruction

20680, see the online supplementary material) reaches a SL of 72 mm. The head is relatively large; its length is about one-third of SL. The maximal body depth, slightly larger than the head length, lies midway between the end of the opercle and the origin of the dorsal fin. The outer surfaces of the cranial bones 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 (Fig. 2). 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 each other in the middle line. Each nasal is small and plate-like, having a curved lateral margin and a straight medial margin. The posterior nostril lies between the nasal and the antorbital; the anterior nostril probably opens near the junction of the nasal, rostral and antorbital, as in other holosteans. An anterior portion of the supraorbital sensory canal is enclosed in the nasal, indicated by several pores on this bone. The antorbitals are elongate and slightly curved, having an expanded posterior portion and a tapering anterior arm. The antorbital extends anteriorly and contacts the rostral medially. The posterior margin of the antorbital forms the anterior orbital margin. The ethmoid commissural canal contacts the infraorbital sensory canal at the middle portion of the antorbital.
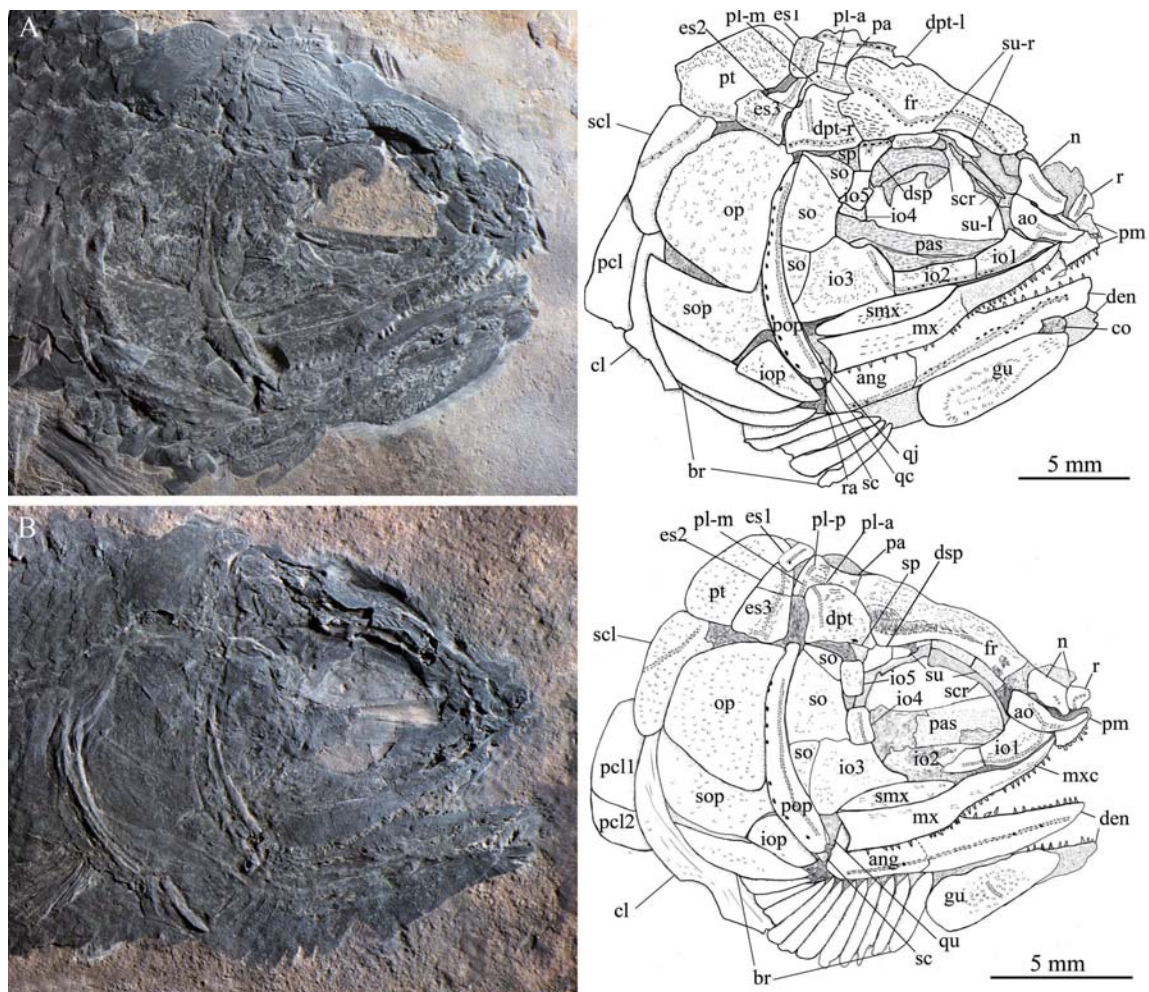

Fig. 2　Skull and pectoral girdle of *Subortichthys triassicus* gen. et sp. nov., coated with ammonium chloride
A. IVPP V 20051 (holotype); B. V 20052

Abbreviations: ang. angular; ao. antorbital; br. branchiostegal rays; cl. cleithrum; co. coronoid; den. dentary; dpt–l. left dermopterotic; dpt–r. right dermopterotic; dsp. dermosphenotic; es. extrascapular; fr. frontal; gu. gular; io. infraorbital; iop. interopercle; mx. maxilla; mxc. sensory canal on maxilla; n. nasal; op. opercle; pa. parietal; pas. parasphenoid; pcl. postcleithrum; pl–a. anterior pit line; pl–m. middle pit line; pl–p. posterior pit line; pm. premaxilla; pop. preopercle; pt. posttemporal; qc. quadrate condyle; qj. quadratojugal; qu. quadrate; r. rostral; ra. retroarticular; sc. sympletic condyle; scl. supracleithrum; scr. sclerotic ring; smx. supramaxilla; so. suborbital; sop. subopercle; sp. sphenotic; su. supraorbital

The frontal is trapezoidal, four times as long as the parietal (Figs. 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 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; it extends from the posterolateral portion of the parietal, runs laterally into the dermopterotic, and ends 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 about ten small pores near the lateral margin of this bone. Three extrascapulars are present at each side of the skull in five type specimens. Additionally, there are four extrascapulars at the left side of the skull in V 20680. This probably represents an intraspecific variation among different individuals (rather than an interspecific variation) because these specimens are consistent in most of other features (except the number and shape of suborbitals that might represent another intraspecific variation, see below). These extrascapulars are nearly trapezoidal, and their sizes slightly vary in different specimens. The supratemporal commissure runs transversely through the extrascapulars, indicated by several small pores at the middle portions of these bones.

Circumorbital bones   There are three supraorbitals. They are rectangular and largely equal in length. In comparison, *Panxianichthys* and *Robustichthys* have only two supraorbitals, and other ionoscopiforms generally have four or more supraorbitals. Five infraorbitals are present (Fig. 2). Among them, 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 is 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.

In four specimens, there are three suborbitals; 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 fit the place of the triangular lower suborbital in other specimens. Three suborbitals are also present in most of other ionoscopiforms (*Panxianichthys*, *Ophiopsis*, *Ionoscopus* and *Quetzalichthys*). By contrast, five suborbitals are present in *Macrepistius* (Schaeffer, 1960), and eight or more in *Robustichthys* (Xu et al., 2014b) and *Teoichthys* (Applegate, 1988; Machado et al., 2013).

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 palate 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 (Fig. 3A). The teeth on the parasphenoid and entopterygoid are very small, and 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). Via the X-ray computed tomography, this bone is relatively well revealed in the holotype (Fig. 3F). In V 22951, the suborbitals and preopercle are missing, and the hyomandibular is almost fully exposed (see the online supplementary material). It is hatchet-shaped and vertically positioned, with a single broad facet articulating with the ventral side of the braincase dorsally. There is a foramen at the middle portion of the hyomandibula, through which the hyomandibular branch of the facial nerve may pass.

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

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

Jaws   The upper jaw at each side of the skull includes a premaxilla, a maxilla and a supramaxilla (Figs. 2, 3). The premaxilla is relatively large, bearing a robust nasal process. Because of the overlap of the nasal, the fenestra for the olfactory nerve cannot be observed in this nasal process. About ten conical teeth are present along the oral margin of the premaxilla. The teeth are 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 as a halecomorph synapomorphy (Grande and Bemis, 1998). The anterior dorsal margin of the maxilla is slightly excavated for the first infraorbtial, and the posterior dorsal margin of this bone is more excavated for a 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, the dentary, angular, supra-angular and retroarticular are discernable in the lateral view. The dentary is wedge-shaped, posteriorly contacting the angular in a sinuous suture. The angular is trapezoidal, about one third of the length of the low jaw. The supra-angular, only partly exposed in V 20680 (Fig. 3C), is still unknown in its complete shape. The retroarticular is very small (Fig. 2A), contacting the posteroventral portion of the angular anteriorly. A few coronoid bones are exposed in the medial view of the low jaw (Figs. 2A, 3A). They are small plate-like bones, covered by dense conical teeth. These teeth 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. It bears a small triangular anterodorsal process that inserts between the preopercle and opercle. The interopercle is
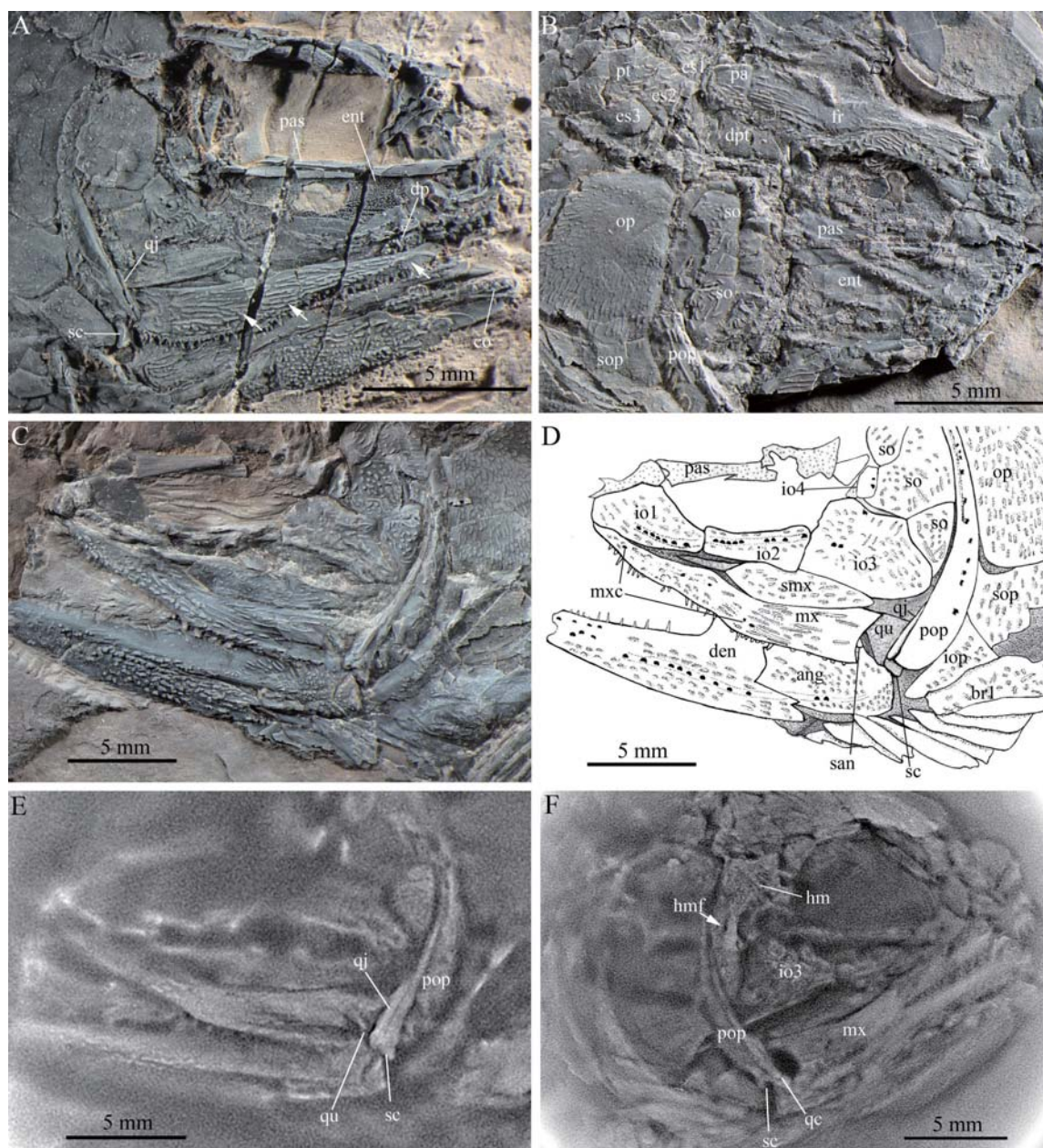

Fig. 3 *Subortichthys triassicus* gen. et sp. nov.
A. IVPP V 22950, arrows indicating the sensory pores on the maxilla; B. V 19003, parietal relatively short and nearly square in shape; C–E. V 20680: C. photo, D. line drawing; E. X-ray computed tomography, showing mainly the splint-like quadratojugal and the symplectic involvement in the jaw hinge; F. X-ray computed tomography of the skull of V 20051 (holotype), showing the hyomandibular
Abbreviations: dp. dermopalatine; ent. entopterygoid; hm. hyomandibular; hmf. foramen for the hyomandibular trunk of facial nerve (VII); san. supra-angular. For other abbreviations see Fig. 2. For complete specimens and sensory pores on the maxilla, see the online supplementary material

small and triangular, tapering anteroventrally. 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 (Fig. 2B). They are elongated, gradually broadened posteriorly. The median gular is oval, slightly over half the length of the lower jaw. A short traverse pit-line is present at the middle portion of this bone.

Girdles and fins　A posttemporal, a supracleithrum, a cleithrum, and two postcleithra can be identified in each pectoral girdle. 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. It is anteriorly inclined and partly overlapped by the opercle. The cleithrum is large and curved, bearing a conspicuous posteroventral notch for the pectoral fin insertion. Two postcleithra are plate-like; the dorsal is twice as deep as the ventral.

The pectoral fins are large, inserting low in the body. Each bears 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 bears 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, and the remaining rays are branched distally.

The caudal fin is hemi-heterocercal with a moderately forked profile. It has 18 principal rays, half in each lobe (Fig. 4). The dorsal and ventral marginal principal rays are segmented and unbranched, and the middle rays are segmented and branched up to three times. In addition, 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. The scales are arranged in 30–32 vertical rows along the main lateral line (Fig. 1; see also supplementary material). In addition, seven or eight rows of scales extend into the epaxial lobe of the caudal fin (Fig. 4). The scales in the anterior flank region are 1.5 times deeper than wide, and they gradually become lower and smaller dorsally, ventrally and posteriorly. Besides the main lateral line, there is an additional lateral line, indicated by a line of about ten small pores on the 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.
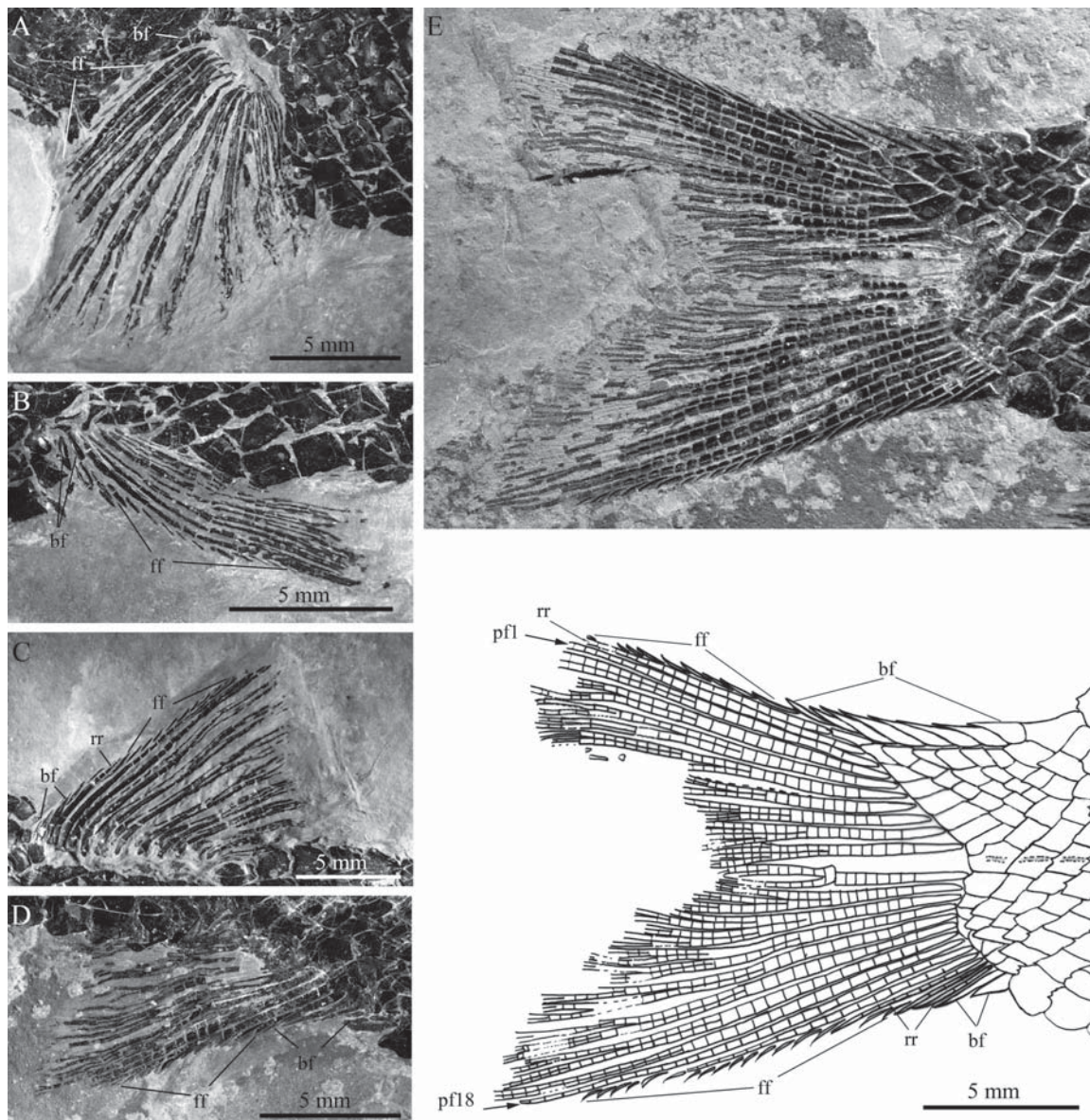
Fig. 4   Fins of *Subortichthys triassicus* gen. et sp. nov.
A–C. IVPP V 20680: A. pectoral fin, B. pelvic fin, C. dorsal fin;
D–E. V 20051 (holotype): D. anal fin, E. caudal fin
Abbreviations: bf. basal fulcra; ff. fringing fulcra; pf. principal fin rays; rr. rudimentary rays

4   Phylogenetic relationships and implications

In order 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 out-group comparison (see the online supplementary material). The phylogenetic analysis yielded nine most parsimonious trees (Tree length = 239; consistency index = 0.5523; retention index = 0.7221). *Subortichthys* was recovered at the base of the Ionoscopiformes (Fig. 5).

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. Patterson (1973) first proposed the symplectic involvement in the jaw hinge as a halecomorph synapomorphy, and this has been widely accepted by later 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 that the symplectic of *Vinctifer* did not reach the lower jaw. A symplectic articulating with the lower jaw has not been known in other aspidorhynchid genera. Brito and Alvarado-Ortega (2013) suggested that *Vinctifer* might represent a convergent evolution to halecomorphs in this feature.

Grande and Bemis (1998) proposed presence of an excavated posterior margin of the maxilla as a halecomorph synapomorphy. However, Brito and Alvarado-Ortega (2013) argued that an excavated posterior margin of the maxilla is ambiguous in the Parasemionotiformes and considered this feature as a synapomorphy of the clade Ionoscopiformes plus 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 thus agree with Grande and Bemis (1998) and consider an excavated posterior margin of the maxilla as a halecomorph synapomorphy, although further studies are needed to determine if this anatomical structure is present in other parasemionotiforms. *Subortichthys*, similar to *Panxianichthys*, *Robustichthys* and most other non-parasemionotiform halecomorphs, has 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 as a halecomorph synapomorphy (Grande and Bemis, 1998). *Subortichthys* does have a single supramaxilla, as in other halecomorphs. However, a supramaxilla is also present in basal ginglymodians and some teleosts outside of the Halecomorphi. Results of our analysis, consistent with recent others (Brito and Alvarado-Ortega, 2013; Xu et al., 2014b; Xu and Shen, 2015), support that this feature is a synapomorphy of the crown-group Neopterygii.

Compared with other halecomorphs, *Subortichthys* is more derived than the 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 the Ionoscopiformes, presence of a sensory canal in the maxilla. However, it lacks three derived features of other ionoscopiforms that were considered as synapomorphies of this order (Grande and Bemis, 1998; Alvarado-Ortega and Espinosa-Arrubarrena, 2008), i.e., presence of relatively long

parietals, a posteriorly inclined lower border of the last infraorbital, and an innerorbital flange of the dermosphenotic bearing an infraorbital sensory canal. Therefore, *Subortichthys* is placed at the base of the Ionoscopiformes.

Subortichthys is unique among ionoscopiforms in having three or four pairs of extrascapulars, a large third infraorbital posteriorly contacting the preopercle, and a long maxilla extending to the level of 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 results of our analysis indicate that they might be independently evolved. A large third infraorbital posteriorly contacting the preopercle was only known in some teleosts (e.g., pholidophorids; Arratia, 2013) among the crown-group Neopterygii. *Subortichthys* represents an interesting convergent evolution to early teleosts in this feature. Moreover, *Subortichthys* has a long maxilla extending to the level of middle portion
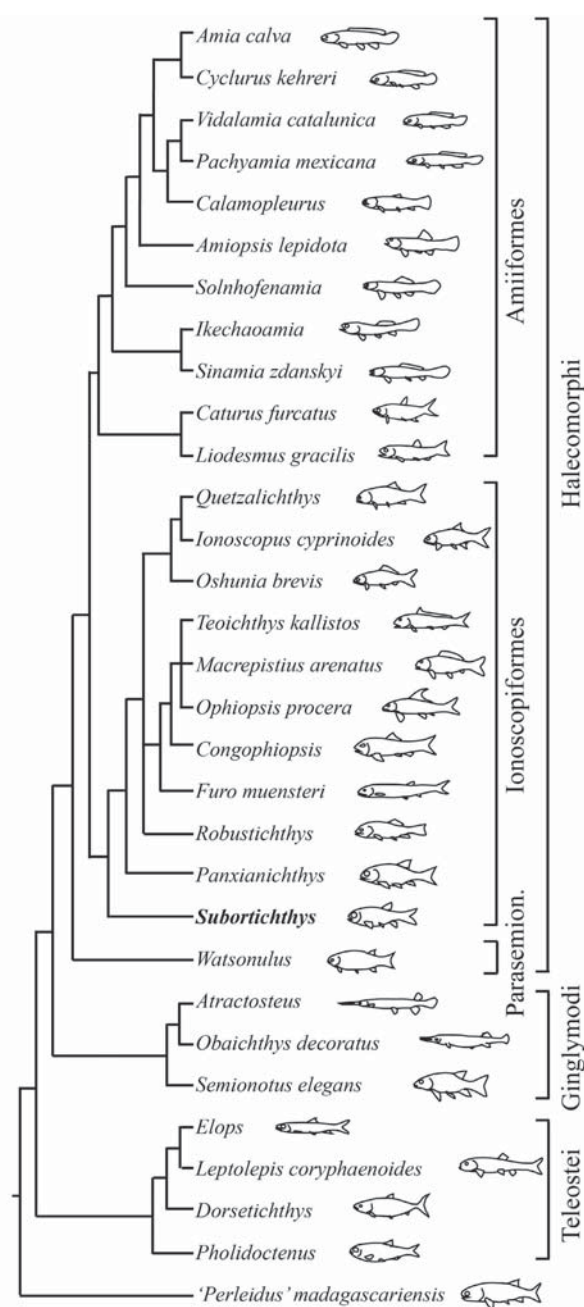

Fig. 5   Strict consensus of nine most parsimonious trees, illustrating the phylogenetic position of *Subortichthys triassicus* gen. et sp. nov. Parasemion. = Parasemionotiformes. For character descriptions and codings for the sampled taxa, see the online supplementary material

of the parietal. Similar condition is otherwise present in parasemionotiforms, several caturid amiiforms and some teleosts among the crown-group Neopterygii. By contrast, the maxilla is relatively short and its posterior end commonly does not exceed the anterior margin of the parietal in other ionoscopiforms.

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, showing 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 composition of the orbital margin.

Based on the previously known geographical distribution, the Ionoscopiformes were inferred to have originated in Europe and subsequently dispersed to the New World (Alvarado-Ortega and Espinosa-Arrubarrena, 2008). However, the recent discovery 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 the Ionoscopiformes probably originated in South China (a part of eastern Paleotethys Ocean); via the Paleotethys Ocean, this group dispersed into Europe. The discovery of *Subortichthys* further supports this hypothesis. The new material reveals that the earliest diversification of ionoscopiforms was well undertaken in South China by the early Middle Triassic (Anisian).

Supplementary material can be found at the website of Vertebrate PalAsiatica (http://english.ivpp.cas.cn/sp/PalAsiatica/vp_list/) in Vol. 55, Issue 2

云南中三叠世(安尼期)预言鱼目(全骨鱼类：近鲱形类)一新属种

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摘要：预言鱼目是近鲱形类的一个绝灭支系，被认为是弓鳍鱼目的姐妹群。预言鱼目化石过去主要发现于欧洲的中三叠世拉丁期和晚侏罗世地层以及新大陆的早白垩世地层。近年来，在云南和贵州的中三叠世安尼期地层中分别发现了一种预言鱼目鱼类化石(强壮鱼和盘县鱼)，代表了该目在中国的首次发现。根据产于云南罗平中三叠世安尼期(~244 Ma)海相地层中的6块保存良好的鱼化石，命名了预言鱼目一个新的属种，三叠复兴鱼(*Subortichthys*