

Exceptional fossils from China highlight the origin and early diversification of ionoscopiform halecomorphs

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Abstract - Ionoscoformes, sister to Amiiiformes, are an extinct group of marine halecomorphs. In the past decades, ionoscoformes were known from the Late Jurassic of Europe and the Early Cretaceous of the New World. Here, we introduce the fourth ionoscoform known from China, *Subortichthys triassicus* Ma and Xu, 2017 from the early Middle Triassic (Pelsonian, Anisian) of Luoping, Yunnan Province. This paper summarizes information on the osteology of *Robustichthys*, *Subortichthys* and *Panxianichthys* based on well-preserved specimens. The new material reveals that the earliest diversification of ionoscoformes was well underway in South China by the early Middle Triassic (Anisian).

Keywords: Triassic, ionoscoformes, osteology, phylogeny, South China

1. Introduction

Ionoscoformes, sister to Amiiiformes, are an extinct group of marine halecomorphs (sensu Grande, 2010). In the past decades, ionoscoformes 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 ionoscoformes 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, 1995; López-Arbarello *et al.*, 2014). Recently, convincing ionoscoformes represented by well-preserved specimens were found from the early Middle Triassic (Anisian) of South China (Xu *et al.*, 2014; Xu and Shen, 2015; Ma and Xu, 2017) (Fig. 1) and the Middle Jurassic of Africa (Taverne, 2015). These provide new insights into the origin and early evolution of the Ionoscoformes.

In China, the first known ionoscoform is *Robustichthys luopingensis* Xu *et al.*, 2014 from the early Middle Triassic (Pelsonian, Anisian) of Luoping, Yunnan Province. Although Sun *et al.* (2017) argued that *Robustichthys* was a basal ginglymodian, this hypothesis is not supported by our analysis (Ma and Xu, 2017; see discussion below). *Panxianichthys imparilis* Xu and Shen, 2015 from the early Middle Triassic (Pelsonian, Anisian) of Panxian, Guizhou Province is the second ionoscoform known from China. It is probably slightly younger than *Robustichthys* (Benton *et al.*, 2013) but shows some features more primitive than the latter taxon. Additionally, *Asialepidotus shingyiensis* Su, 1959 from the late Middle Triassic (Ladinian) of western Guizhou and eastern Yunnan is recently reinterpreted as another ionoscoform (Xu and Ma, in press). Here, we introduce the fourth ionoscoform known from China, *Subortichthys triassicus* Ma and Xu, 2017 from the early Middle Triassic (Pelsonian, Anisian) of Luoping, Yunnan Province, and discuss its implications on the early diversification of this group.

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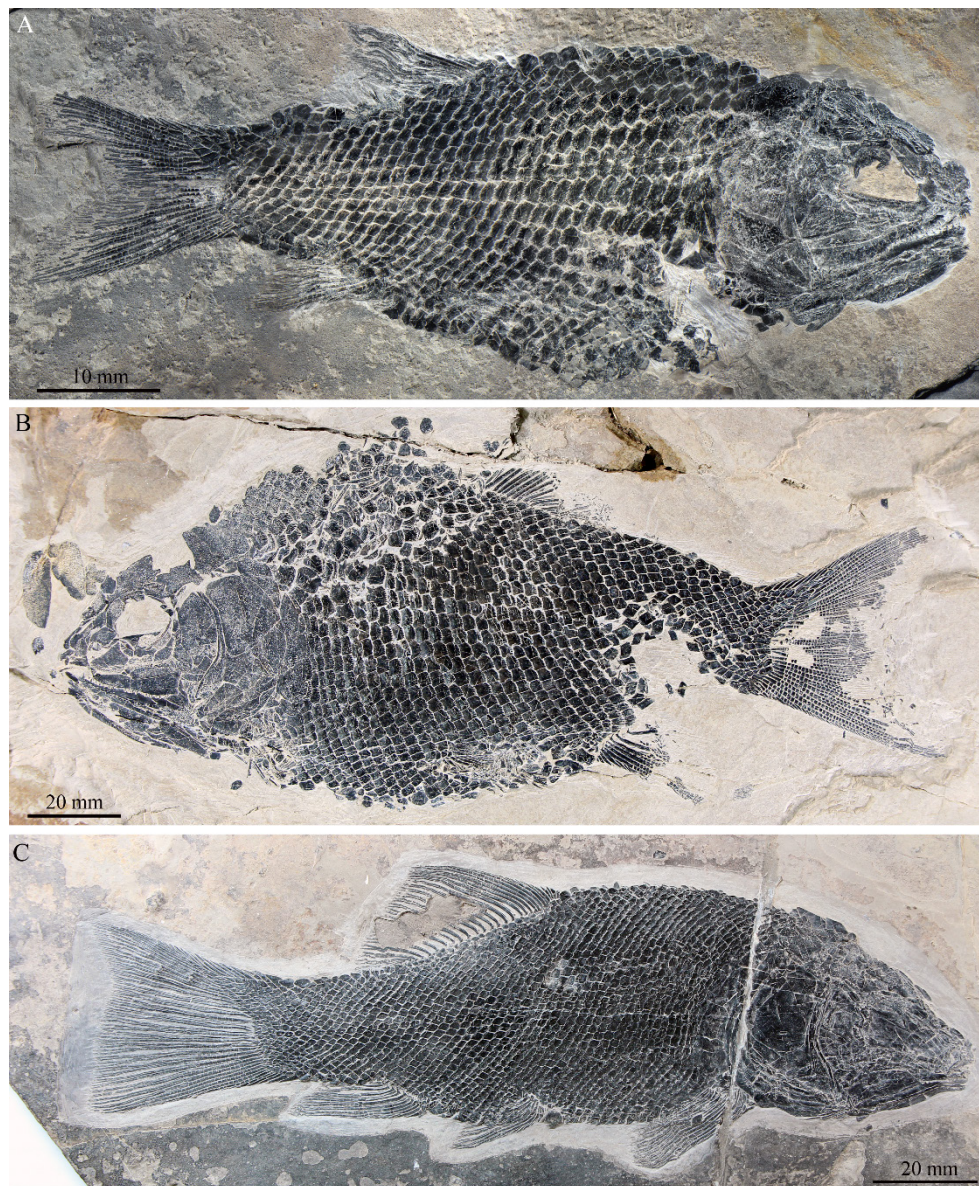


Figure 1. A. *Suborichthys triassicus* IVPP V 20051; B. *Panxianichthys imparilis* IVPP V 19971; C. *Robustichthys luopingensis* IVPP V 18568

2. Materials and methods

This paper summarizes information on the osteology of *Robustichthys*, *Subortichthys* and *Panxianichthys* based on well-preserved specimens stored at the fossil collection of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, and ten specimens of *Panxianichthys* in the collections of Geological Museum of Peking University, Paleontological Collection (GMPKU-P), including *Robustichthys luopingensis* IVPP V 18568-18573; ZMNH M 1690-1691. *Subortichthys triassicus* IVPP V 19003, 20051, 20052, 20680, 22950, 22951. *Panxianichthys imparilis* IVPP V 19971 and 19972, GMPKU-P 1194, 1195, 1344, 1345, 3316-3121. A phylogenetic analysis was performed based on a data matrix of 112 characters coded across 31 neopterygian taxa (Ma and Xu, 2017). Tree searches were

accomplished by the heuristic search algorithm in PAUP* 4.0b10 (Swofford, 2003). All characters were unordered and equally weighted.

3. Results

The phylogenetic analysis yielded nine most parsimonious trees (Tree length = 239; consistency index = 0.5523; retention index = 0.7221). The results of our analysis support that the Parasemionotiformes (represented by *Watsonulus*) are basal halecomorphs, and the Ionoscopiformes consist of the sister group of the Amiiformes (Fig. 2). *Subortichthys* is recovered at the base of the Ionoscopiformes. *Panxianichthys* is more derived than *Subortichthys*, and forms the sister taxon of *Robustichthys* and all other ionoscopiforms.

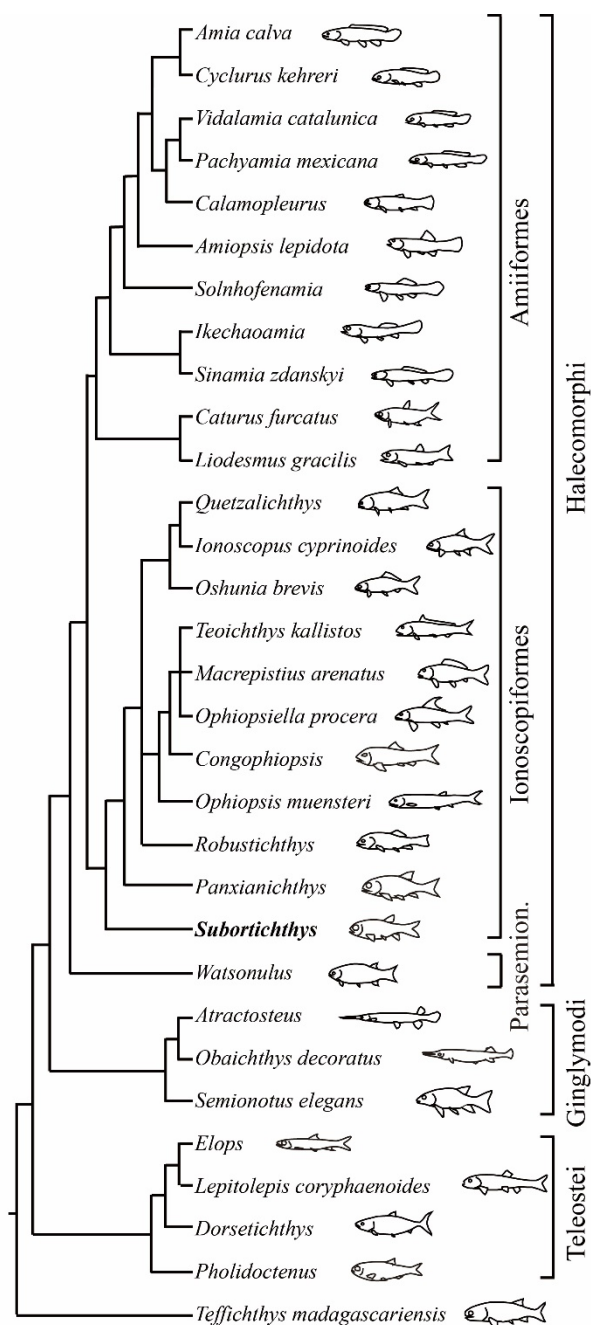


Figure 2. Strict consensus of nine most parsimonious trees, illustrating the phylogenetic interrelationships of the Ionoscopiforme. Parasemion. = Parasemionotiformes. For character descriptions and codings for the sampled taxa, see the online supplementary material associated with Ma and Xu (2017)

4. Discussions and conclusions

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. It is more derived than the Parasemionotiformes, 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), e.g., 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. *Panxianichthys* is more derived than *Subortichthys* in having relatively long parietals with a width-to length ratio range not exceeding 0.9. *Robustichthys*, more derived than *Panxianichthys*, shares three derived features with all other ionoscopiforms: presence of a posteriorly inclined posterior border of the last infraorbital, presence of an innerorbital descending flange on the dermosphenotic, and absence of a distinct quadratojugal.

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 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.*, 2014; 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 (*Obaichthys* and *Atractosteus*) (Grande and Bemis, 1998; Grande, 2010), but results of our analysis indicate that they were 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 the middle portion of the parietal. A 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 very long antorbital. *Panxianichthys* also has a splint-like quadratojugal (personal observation). *Robustichthys* and more derived ionoscopiforms lack a splint-like quadratojugal (Xu *et al.*, 2014). Additionally, *Subortichthys* has a very long antorbital with its posterior margin forming the anterior orbital margin, showing a condition similar to *Panxianichthys*, *Robustichthys*, *Oshunia* and *Ophiopsis muensteri* (Lane and Ebert, 2015) but different from that of 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 Ionoscopiforms 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.*, 2014; Xu and Shen, 2015). Xu *et al.* (2014) suggested that the Ionoscopiforms probably originated in South China (part of the 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 underway in South China by the early Middle Triassic (Anisian).

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