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Palaeontology

The oldest ionoscopiform from China sheds new light on the early evolution of halecomorph fishes

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The Halecomorphi are a major subdivision of the ray-finned fishes. Although living halecomorphs are represented solely by the freshwater bowfin, *Amia calva*, this clade has a rich fossil history, and the resolution of interrelationships among extinct members is central to the problem of understanding the origin of the Teleostei, the largest clade of extant vertebrates. The Ionoscopiformes are extinct marine halecomorphs that were inferred to have originated in the Late Jurassic of Europe, and subsequently dispersed to the Early Cretaceous of the New World. Here, we report the discovery of a new ionoscopiform, *Robustichthys luopingensis* gen. et sp. nov., based on eight well-preserved specimens from the Anisian (242–247 Ma), Middle Triassic marine deposits of Luoping, eastern Yunnan Province, China. The new species documents the oldest known ionoscopiform, extending the stratigraphic range of this group by approximately 90 Ma, and the geographical distribution of this group into the Middle Triassic of South China, a part of eastern Palaeotethys Ocean. These new data provide a minimum estimate for the split of Ionoscopiformes from its sister clade Amiiformes and shed new light on the origin of ionoscopiform fishes.

1. Introduction

The Amiiformes and closely related fossil lineages, including Ionoscopiformes and Parasemionotiformes, comprise the clade Halecomorphi [1]. Today, halecomorphs are represented solely by the freshwater bowfin (*Amia calva*) from central and eastern North America. Previously, there was a conspicuous stratigraphic gap between definitive fossils attributable to the Parasemionotiformes in the Early Triassic (and there is still debate on the affinities of potential Permian parasemionotiforms [2,3]) and those attributable to the 'Ionoscopiformes–Amiiformes' clade in the Jurassic. Ionoscopiforms have been known only from the Late Jurassic of Europe and the Early Cretaceous of the New World [4–10], although potential ionoscopiforms, questionably assigned in the genus *Ophiopsis*, have been reported from the Middle Triassic (Ladinian) of Italy and Austria [11,12]. These, however, are based on poorly preserved specimens. Here, we report the discovery of a new ionoscopiform from the Middle Triassic Luoping Biota [13–16], Yunnan, China. This represents the first record of this clade in Asia. The age of the fossil beds (Anisian, 242–247 Ma) is well constrained by the conodont analysis [13], and therefore this taxon documents the earliest known ionoscopiform, predating the previously oldest record (e.g. *Ophiopsis* [10]) from the Kimmeridgian (152–157 Ma) of Europe by approximately 90 Ma. The fossil beds at this locality, composed of thinly laminated micritic limestone alternating with silty limestone, indicate a semi-enclosed intraplatform deposit environment [14,15].

2. Systematic palaeontology

Neopterygii Regan, 1923
Holostei Müller, 1845
Halecomorphi Cope, 1972
Ionoscopiformes Grande and Bemis, 1998
Robustichthys luopingensis gen. et sp. nov.

Etymology. The generic name is from the Latin *robustus*, meaning strong, and *ichthys*, meaning fish. The specific epithet refers to the fossil locality.

Holotype. IVPP V18568, a nearly complete skeleton with a head length 45 mm, a body depth 48 mm and a standard length 140 mm (figure 1*a*).

Referred material. IVPP V18569-18573; ZMNH M1690-1691.

Type locality and horizon. Luoping, Yunnan, China; Guanling Formation, Middle Triassic (Anisian).

Diagnosis. An ionoscopiform distinguished from other members of this order by a combination of features: presence of two rectangular supraorbitals; slightly concave posterior margin of caudal fin; second infraorbital with triangular, anteroventral portion articulating with lachrymal; large, triangular supramaxillary process on maxilla; nearly straight posterior margin of maxilla; nine to 10 branchiostegal rays; four postcleithra; 21–23 dorsal fin rays; about 10 anal fin rays; 26–29 principal caudal fin rays (electronic supplementary material, figure S1) and scale formula of D26/P13, A23, C39/T48.

3. Morphology and phylogeny

Robustichthys evidently shows diagnostic features of crown-neopterygians, e.g. a mobile maxilla with an internally directed articular head, a vertical suspensorium, a supramaxilla and an interopercle, but its phylogenetic position within this clade was obscure. To resolve this problem, we conducted a phylogenetic analysis based on a data matrix of 96 characters coded across 28 neopterygian taxa (see the electronic supplementary material). The results of our analysis resolve *Robustichthys* as an ionoscopiform, although the interrelationships within this order are not well resolved (figure 2; electronic supplementary material, figure S4).

Traditionally, the Halecomorphi have been regarded as the sister group of Teleostei, but recent studies have suggested that the Halecomorphi may be more closely related to Ginglymodi than to Teleostei, with Halecomorphi and Ginglymodi grouped in a clade Holostei [2,3,16,17]. Our analysis supports the later hypothesis. *Robustichthys* is referred to the Holostei because it possesses three derived features of this clade: (i) a tube-like canal bearing anterior arm of the antorbital, (ii) a deep nasal process of the premaxilla that is sutured to the frontal and (iii) a dermal component on the sphenotic. The first feature is well known in our specimens of *Robustichthys*, in which a hook-shaped antorbital is exceptionally well preserved (figure 1*b*; electronic supplementary material, figure S3). The anterior portion of this bone has a curved, tube-like anterior arm that extends anteriorly beneath the nostrils to meet a small median rostral. Second, *Robustichthys* has a deep nasal process of the premaxilla (figure 2*c*), as commonly seen in other holosteans [16,17]. This process was clearly illustrated in the renowned ionoscopiform *Ophiopsis* [10], although it was not described for other ionoscopiforms probably because of preservation. Finally, the sphenotic and dermosphenotic are not fused to each other in holosteans, and their sphenotic has a small dermal component exposed on the skull roof. This exposed component is usually tiny in other holosteans, but it is large in almost all well-known ionoscopiforms (see comments in [18]). As in other ionoscopiforms, the sphenotic of *Robustichthys* has a large exposed portion that separates the dermosphenotic from the last infraorbital bone (figure 1*b*). This bone differs from infraorbitals and the dermosphenotic in lacking sensory canals.

Compared within the Holostei, *Robustichthys* lacks diagnostic features of ginglymods (e.g. presence of two or more lachrymals) [17], but shares certain derived features with other halecomorphs. Three synapomorphies were previously proposed to support the monophyly of the Halecomorphi [1]: (i) a double articulation of the lower jaw, (ii) a supramaxilla and (iii) a notched posterior margin of the maxilla. Results of our analysis suggest that only the first is convincing. In *Robustichthys*, both symplectic and quadrate are well exposed (figure 1*b*,*d*; electronic supplementary material, figure S2). The symplectic lies behind the quadrate, and both bones articulate with the lower jaw, evidently showing an *Amia*-like jaw joint. Brito [19] (but see [20]) and Arratia [21], respectively, suggested that the symplectic was also articulated with the lower jaw in an aspidorhynchid teleosteomorph *Vinctifer* and some pholidophorids, but this likely represents convergent evolution. Second, *Robustichthys* do have a supramaxilla, but this feature has been reinterpreted as a synapomorphy of the crown-group Neopterygii because it is widely known in halecomorphs, seminotids and some basal teleosts ([16,17], see more comments in [21]). Third, *Robustichthys* has a nearly straight posterior margin of the maxilla, similar to a few halecomorphs (e.g. *Amblysemius* [1]), but different from other halecomorphs, in which a conspicuously notched posterior margin is present. Recently, Arratia [21] noted that some basal teleosts (e.g. *Pholidoctenus*) also have a conspicuously notched posterior margin of the maxilla, indicating that this feature is homoplastic when some basal teleosts are added to the phylogenetic analysis. Additionally, it is noteworthy that *Robustichthys*, similar to other halecomorphs, has a large median gular (figure 1*c*); by contrast, basal teleosts have a smaller and narrower median gular [21] and ginglymods lack a gular [17].

Within the Halecomorphi, *Robustichthys* possesses two derived characters of the 'Ionoscopiformes–Amiiformes' clade: (i) a deep and narrow, crescent-shaped preopercle and (ii) a dermosphenotic firmly sutured to, and forming part of the skull roof. Additionally, *Robustichthys* shares three derived features with other ionoscopiforms: (i) a sensory canal in the maxilla, (ii) a posteriorly inclined lower border of the last infraorbital and (iii) an innerorbital flange of the dermosphenotic bearing an infraorbital sensory canal. Our analysis supports that the above three features are synapomorphies of the Ionoscopiformes, consistent with [8]. The first feature was well known from ionoscopiforms [4–10]. Although a maxillary pit-line was also known from the semionotiform *Lepidotes* [22] and the basal actinopterygian *Cheirolepis* [23], these most likely represent convergent evolution. In *Robustichthys*, a linear series of small pores adjacent to the ventral margin of this bone is present in all our specimens with a maxilla (figure 1*f*; electronic supplementary material, figure S3). These pores are clearly not ornaments of the bone but represent a branch of infraorbital sensory canal branched from the

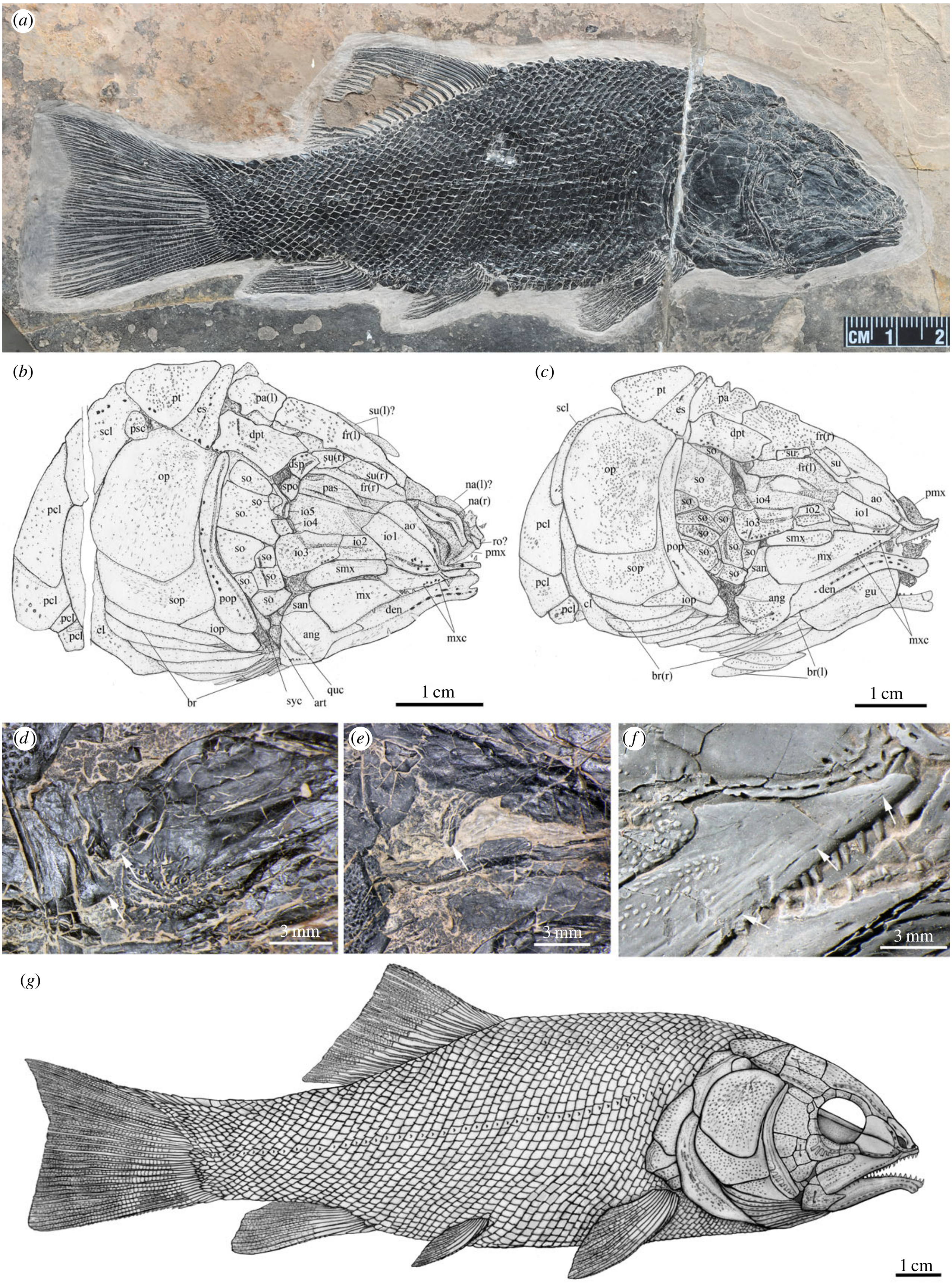

Figure 1. (*a*) *Robustichthys luopingensis* gen. et sp. nov. IVPP V18568 (holotype), complete skeleton; (*b*) skull and pectoral girdle in holotype and (*c*) ZMNH M1691; (*d*) IVPP V18571, close-up of symplectic and quadrate, and (*e*) anteroventral flange of dermosphenotic bearing infraorbital sensory canal; (*f*) ZMNH M1690 coated with ammonium chloride, close-up of maxillary sensory canal; (*g*) reconstruction of phenotype. *ao*, antorbital; *ang*, angular; art, articular; *br*, branchiostegal ray; *cl*, cleithrum; *den*, dentary; *dpt*, dermopterotic; *dsp*, dermosphenotic; *es*, extrascapula; *fr*, frontal; *gu*, gular; io, infraorbital; *iop*, interopercle; mx, maxilla; mxc, maxillary canal; na, nasal; op, opercle; pa, parietal; pas, parasphenoid; pcl, postcleithrum; pmx, premaxilla; pop, preopercle; psc, presupracleithrum, pt, posttemporal; quc, condyle of quadrate; ro, rostral; san, supra-angular; scl, supracleithrum; smx, supramaxilla; so, suborbital; sop, subopercle; su, supraorbital; syc, condyle of symplectic. (Online version in colour.)

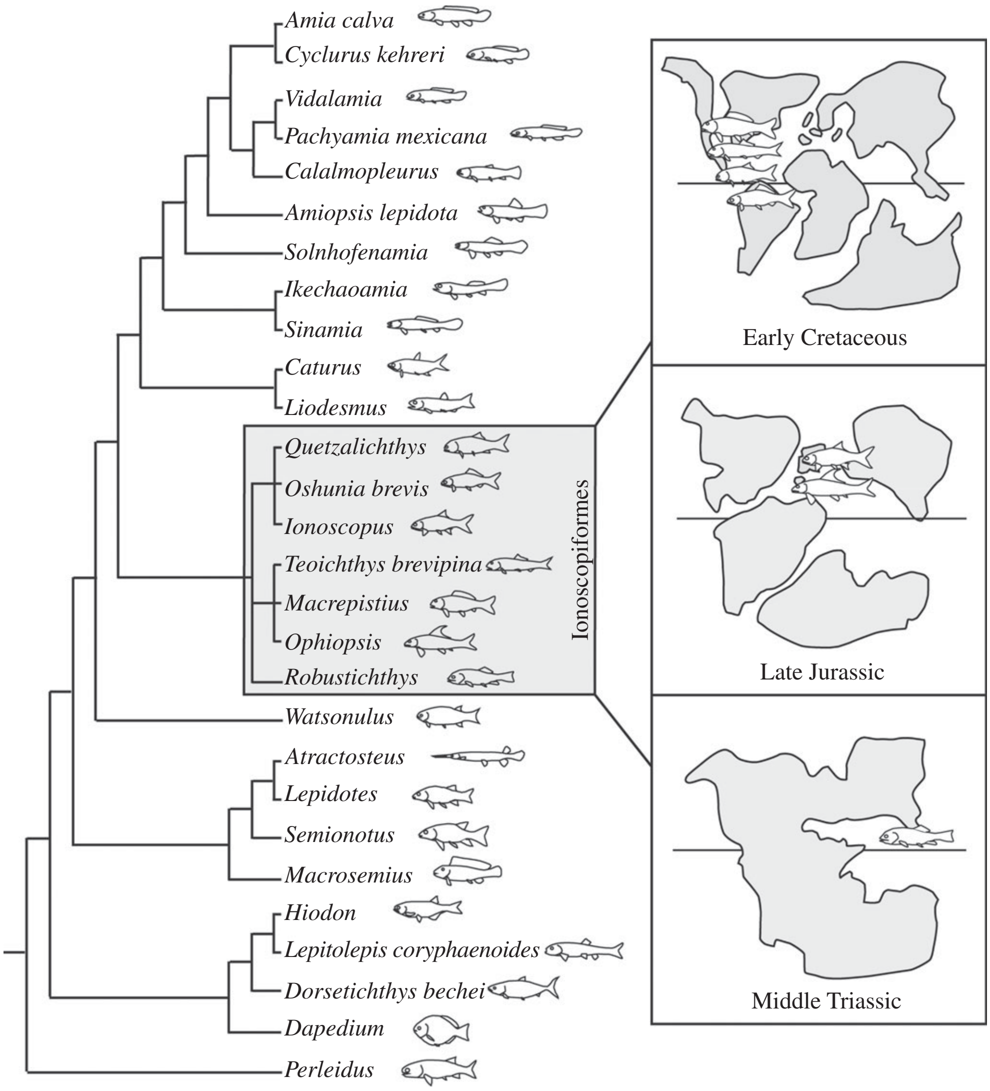

Figure 2. Strict consensus of 15 most parsimonius trees illustrating phylogenetic relationships of *R. luopingensis* gen. et sp. nov. within Neopterygii, and maps illustrating geographical distribution of Ionoscopiformes in three different geological epochs. Cladogram section and distribution maps of Ionoscopiformes have been highlighted with a rectangles. See the electronic supplementary material for data matrix and character changes at nodes.

lachrymal as in other ionoscopiforms [4–10]. Second, a posteriorly inclined lower border of the last infraorbital is evidently present in *Robustichthys* (figure 1*b*), and this feature appears phylogenetically related to the third feature, an innerorbital descending flange of the dermosphenotic. As mentioned above, the exposed part of the sphenotic of ionoscopiforms is large and separates the last infraorbital from the dermosphenotic; this causes that the infraorbital sensory canal must turn medially to meet an innerorbital descending flange of the dermosphenotic. The descending flange of the dermosphenotic of *Robustichthys*, well preserved in IVPP V18571 (figure 1*e*), bears a sensory canal near its orbital margin as in other ionoscopiforms (e.g. *Ophiopsis* [10]).

4. Ecological implications

The discovery of *Robustichthys* sheds new light on the origin of the Ionoscopiformes. Based on the previously known geographical distribution, the Ionoscopiformes were inferred to have originated in the Late Jurassic of Europe and subsequently dispersed to the Early Cretaceous of the New World [8]. However, the discovery of *Robustichthys* extends the geographical distribution of this group into the Middle Triassic of South China (figure 2), demonstrating a much older origin and a wider distribution than previously appreciated for this group. In the Middle Triassic, a vast supercontinent of Pangaea existed, and South China was a part of Palaeotethys Ocean [13–15]. The Palaeotethys 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 [15]. *Robustichthys* documents the oldest known ionoscopiform, extending the stratigraphic range of this group by approximately 90 Ma. It provides a minimum estimate for the split of Ionoscopiformes from its sister clade Amiiformes: no later than the early stage of the Middle Triassic (Anisian, 242–247 Ma), which is close to the first record of the Halecomorphi in the late stage of the Early Triassic (Olenekian, 247–251 Ma). The origin and early evolution of ionoscopiforms should be reconsidered in light of these new data.

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