Taxonomic revision of Sinoeugnathus kueichowensis(Halecomorphi, Holostei) from the Middle Triassic ofGuizhou and Yunnan, China postprint

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Abstract

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Full Text

Preamble

Taxonomic Revision of *Sinoeugnathus kueichowensis* (Halecomorphi, Holostei) from the Middle Triassic of Guizhou and Yunnan, China

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Abstract

The previously alleged 'eugnathid amiiform' *Sinoeugnathus kueichowensis* is a small-sized halecomorph from the Middle Triassic (Ladinian) marine deposits of Guizhou and Yunnan, China. We provide a morphological redescription and taxonomic revision of this taxon based on detailed examination of 15 new specimens. Among them, IVPP V24315 (standard length = 64 mm) is designated as the neotype, given that the holotype is missing. Study of these specimens revealed several morphological details previously undescribed or misidentified for this taxon, including a hatchet-shaped antorbital, two broad suborbitals, a sensory canal in the maxilla, and three pairs of extrascapulars. For the first time, *Sinoeugnathus* was incorporated into an analysis of halecomorph phylogeny, and the results recover it as the sister taxon of the Anisian *Subortichthys* from Luoping, Yunnan. Both are grouped with two Ladinian genera—*Allolepidotus* and *Eoeugnathus* from the Monte San Giorgio area—into a monophyletic group (herein named Subortichthyidae fam. nov.) at the base of Ionoscopiformes. This taxonomic reassessment provides new insights into the phylogeny and paleogeographic evolution of Ionoscopiformes.

Key words: Guizhou and Yunnan, Middle Triassic, Ionoscopiformes, Halecomorphi, osteology, phylogeny

1. Introduction

Holostei comprises two divisions: Halecomorphi (e.g., bowfin) and Ginglymodi (e.g., gars) (Cavin, 2010; Grande, 2010; Xu, 2019). Recent morphological and molecular studies consistently recover Holostei as a monophyletic group sister to Teleostei (e.g., carps and salmons), but the origin and early evolution of this clade remain obscure due to insufficient study of fossil records (Hurley et al., 2007; Near et al., 2012; López-Arbarello and Sferco, 2018). Paleozoic holosteans are scarce and taxonomically ambiguous. The Late Permian (Wuchiapingian) *Acentrophorus* is likely the earliest holostean but still requires restudy and formal analysis (Gill, 1923; Friedman, 2015). The earliest unambiguous holosteans are represented by Early Triassic parasemionotiform halecomorphs (Olsen, 1984; Grande and Bemis, 1998). During the Middle Triassic, holosteans underwent rapid radiation, represented mainly by ionoscopiform halecomorphs (Xu et al., 2014; Xu and Shen, 2015; Xu and Ma, 2018) and some ginglymodians (Bürgin, 2004; Tintori and Lombardo, 2007; López-Arbarello et al., 2011; Xu and Wu, 2012; Xu et al., 2018). To date, 14 holostean species (in 13 genera) have been reported from the Middle Triassic marine rock succession in Yunnan and

Guizhou provinces, Southwest China (Xu, 2019). These fossils are important for understanding early holostean evolution, but some taxa are poorly known morphologically and controversial taxonomically, urgently requiring detailed description and revision.

Sinoeugnathus kueichowensis Su, 1959 is one such taxonomically controversial holostean that was incompletely described based on a single specimen (IVPP V2443) from Middle Triassic (Ladinian) marine deposits exposed at Dingxiao, Xingyi, Guizhou Province. Su (1959) regarded *Sinoeugnathus* as a close relative of *Eoeugnathus* from the Middle Triassic of Italy and Switzerland (Brough, 1939; Herzog, 2003) and classified it within the halecomorph family Eugnathidae Nicholson & Lydekker, 1889, a junior synonym of Caturidae Owen, 1860 (Patterson, 1973). Unfortunately, the holotype of *S. kueichowensis* was later lost for unknown reasons, and our understanding of this taxon has long relied solely on Su's (1959) original description and illustration. In the last decade, 15 well-preserved specimens referable to this species were collected by the second author from the same fossil horizon at Xingyi in Guizhou and at Fuyuan and Shizong in Yunnan. Study of these specimens revealed that some morphological details were previously undescribed or misidentified for *Sinoeugnathus*, casting doubt on its attribution to Caturidae. This paper presents a taxonomic revision of this taxon.

Sinoeugnathus kueichowensis was recovered from dark grey thin- to medium-bedded marlites and argillaceous limestones in the lower part of the Zhuganpo Member of the Falang Formation in western Guizhou and eastern Yunnan. Besides *Sinoeugnathus*, coexisting vertebrates include several other ray-finned fishes (Su, 1959; Jin, 2001; Liu et al., 2002, 2003; Xu et al., 2012, 2015, 2018; Xu and Ma, 2018; Tintori et al., 2014, 2015; Xu, 2020), a coelacanth (Geng et al., 2009), and diverse marine reptiles (Young, 1958; Li, 2006; Li C et al., 2016; Jiang et al., 2020; Shang et al., 2020). This entire fossil assemblage has been named the Xingyi Fauna or Biota (Li, 2006; Benton et al., 2013). Biostratigraphical studies of ammonoids (Zou et al., 2015) suggest a late Middle Triassic (Ladinian) age for this fauna, supported by zircon U-Pb dating (240.8$±$1.8 Ma) of the fossil beds (Li et al., 2016).

2. Material and Methods

All specimens are curated in the fossil collections of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences. They were mechanically prepared with sharp steel needles. For better contrast, some specimens were dusted with ammonium chloride (NH_4Cl) before photography. The relative position of fins and scale counts were recorded following Westoll (1944). To illuminate the phylogenetic position of *Sinoeugnathus* within Holostei, we incorporated it into a data matrix slightly expanded from Xu (2019). A new character was proposed (Char. 225 in the electronic supplementary material), and the current data matrix includes 225 morphological characters coded across 62 extant and fossil terminal taxa. All characters were unordered and equally weighted. Besides *Sinoeugnathus*, two taxonomically controversial halecomorph taxa—*Eoeugnathus* and *Allolepidotus* from the Middle Triassic of Europe (Brough, 1939; Lombardo, 2001; Herzog, 2003)—were also added. *Pteronisculus stensiöi* was selected for outgroup comparison. Tree searches were conducted using the heuristic search algorithm in PAUP* (v. 4.0a169) with 1000 random addition sequence replicates, holding five trees at each step, with tree bisection and reconnection (TBR) strategy enabled and maxtrees set to automatically increase by 100 (Swofford, 2003).

Anatomical abbreviations: ang, angular; ao, antorbital; apl, anterior pit line; bf, basal fulcrum; br, branchiostegal ray; cl, cleithrum; den, dentary; dpt, dermopterotic; dsp, dermosphenotic; es, extrascapular; ff, fringing fulcrum; fr, frontal; gu, gular; hm, hyomandibula; hmf, foramen for the hyomandibular trunk of facial nerve (VII); io, infraorbital; iop, interopercle; le, lateral ethmoid; mpl, middle pit line; mx, maxilla; na, nasal; op, opercle; pa, parietal; pas, parasphenoid; pcl, postcleithrum; pf, principle fin ray; pmx, premaxilla; pop, preopercle; ppl, posterior pit line; prr, procurrent ray; pt, posttemporal; qj, quadratojugal; qu, quadrate; r, rostral; scl, supracleithrum; scr, sclerotic bones; smx, supramaxilla; so, suborbital; sop, subopercle; sp, sphenotic; su, supraorbital; sy, symplectic; vo, vomer.

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3. Systematic Paleontology

Actinopterygii Cope, 1887
Neopterygii Regan, 1923
Holostei Müller, 1845
Halecomorphi Cope, 1872
Ionoscopiformes Grande & Bemis, 1998
Subortichthyidae fam. nov.

Diagnosis: Small-sized ionoscopiforms distinguished from other members of this order by the following derived features (those unique among ionoscopiforms are marked with an asterisk): frontal about four times as long as parietal; two or three supraorbitals; one to three suborbitals; quadrate almost fully covered by posterior portion of maxilla (*); elongate maxilla extending posterior to coronoid process of lower jaw (*); supramaxillary process of maxilla relatively small; 12 pairs of branchiostegal rays; 30–35 lateral line scales (*); complete row of elongate scales between last lateral line scale and uppermost caudal fin ray (*).

Included genera: *Subortichthys*, *Sinoeugnathus*, *Eoeugnathus*, and *Allolepidotus.*

Type genus: *Subortichthys.*

Geographical distribution and age: Luoping, Fuyuan, and Shizong in Yunnan, and Xingyi in Guizhou, China; Lombardy, Italy; Grisons and Canton Ticino, Switzerland. Pelsonian (Anisian) to Ladinian, Middle Triassic.

***Sinoeugnathus kueichowensis* Su, 1959**

Neotype: IVPP V24315, a nearly complete, laterally compressed specimen with a standard length of 64.2 mm from Xiemi, Wusha, Xingyi.

Referred specimens: IVPP V19007, 30793, and 30794 from Xiemi Village, Wusha Town, Xingyi City, Guizhou Province; V24314, 24316, 24317, 24320, 30784–30787 from Jiyangshan Village, Fuyuan County, Yunnan Province; V30788–30790 from Shizong County, Qujing City, Yunnan Province.

Locality and horizon: Xiemi and Wusha, Guizhou; Jiyangshan, Fuyuan, and Shizong, Yunnan. Zhuganpo Member of the Falang Formation, Ladinian, Middle Triassic.

Emended diagnosis: A subortichthyid distinguished from other members of this family by the following features (those unique among subortichthyids are marked with an asterisk): parietal rectangular, with width/length ratio of ~0.7; dermopterotic nearly twice as long as parietal; antorbital hatchet-shaped, with single large sensory pore at its posterior portion (*); three pairs of extrascapulars; third infraorbital relatively large but free from contact with preopercle; two large suborbitals extending posteriorly and partly covering preopercle; opercle fan-shaped, with length nearly equal to depth; 15 rays in each pectoral fin; seven principal dorsal rays; nine principal anal rays; 15 principal caudal fin rays; and scale formula of D16/P6–7, A14, C28–29/T33–34.

4. Comparative Description

General morphology and size: *Sinoeugnathus kueichowensis* is a small-sized ionoscopiform with a blunt snout, fusiform body, and moderately forked caudal fin. The dorsal fin originates slightly behind the pelvic fins, and the anal fin inserts at the posterior one-quarter of the body. Among ten nearly completely preserved specimens, standard lengths range from 52.2 to 69.6 mm (Table 1). Maximum body depth lies midway between the posterior margin of the opercle and the origin of the dorsal fin. In the neotype (Fig. 1A [Figure 1: see original paper]), head length and body depth account for 33% and 42% of standard length, respectively. The outer surfaces of cranial bones are ornamented with ganoine tubercles and ridges (Figs. 2–4). The general body form (Fig. 1C) can be reconstructed based on V24315 (Fig. 1A) and V30784 (Fig. 1B).

Snout: The canal-bearing bones in the snout region consist of a median rostral and paired nasals and antorbitals (Figs. 2–4). The rostral is small and curved, with a concave anterior margin and convex posterior margin. It contacts the nasal dorsally, the antorbital laterally, and the premaxilla ventrally.

The anterior commissure of the lateral line system is enclosed in this bone (Figs. 2–4). The nasals are elongate with a tapering posterodorsal tip inserting into the anterior portion of the frontal. The lateral margin of the nasal is concave for the posterior nostril. Analogous to the living bowfin, the anterior nostril is probably located between the nasal, rostral, and antorbital. The antorbitals are hatchet-shaped, having an elongate anteroventral extension and expanded posterior portion. Each antorbital contacts the rostral and premaxilla anteriorly and forms part of the anterior orbital margin posteriorly. A large sensory pore is discernible at the posterior portion of this bone (Figs. 2–4).

Skull roof: The skull table consists of paired frontals and parietals, dermopterotics, and three pairs of extrascapulars. The frontal, the largest component of the skull roof, is slightly more than four times as long as the parietal. It is roughly trapezoid, slightly constricted above the orbital region. The median suture between frontals is nearly straight. The anterior margin is concave, receiving the posterior portion of the nasal (Figs. 2–4). The supraorbital sensory canal enters this bone from the nasal, runs longitudinally through the bone, and enters the parietal posteriorly. The parietal is small and nearly rectangular, with a width/length ratio of about 0.7. It has a straight lateral margin bordering the dermopterotic and a convex anterior margin bordering the frontal. Three pit-lines originate in this bone (Fig. 3). The anterior pit-line is situated at the anterolateral portion of the parietal. The middle pit-line originates at the posterolateral portion of the bone and extends laterally into the dermopterotic. The posterior pit-line is located at the posterior portion of the parietal, extending medially for a short length in this bone.

The dermopterotic is trapezoidal, about twice as long as the parietal. It has a tapered anterior process that fits into a posterior notch of the frontal (Figs. 2–4). The temporal sensory canal extends longitudinally through this bone and enters the extrascapular posteriorly, indicated by a series of pores parallel to the lateral margin (Figs. 2, 3). The three extrascapulars are nearly trapezoidal or rectangular, with sizes varying slightly among specimens. The supratemporal commissure runs transversely through the extrascapulars, indicated by several pores at the middle portions of these bones.

Circumorbital bones: There are at least one supraorbital and five infraorbitals. A slightly detached posterior supraorbital is discernible in V24315 (Fig. 2). It is elongate and trapezoidal, being about one-third of orbital length. The first (anteriormost) infraorbital is long and cleaver-shaped, slightly expanded anteriorly. The second infraorbital is short and rectangular. The third infraorbital is large and pentagonal, tapering anteriorly. The fourth and fifth infraorbitals are small and slightly deeper than long, contacting the suborbitals posteriorly, the dermosphenotic dorsally, and the third infraorbital ventrally. The infraorbital sensory canal extends through the infraorbitals, indicated by some pits and canals near the orbital margins of these bones (Fig. 2).

The dermosphenotic is trapezoidal, similar in size to the last infraorbital (Figs. 2–4). It narrows ventrally and receives the infraorbital sensory canal from the latter bone. The sphenotic, unfused with the dermosphenotic, has an exposed dermal component on the skull roof as is common in other holosteans.

Two suborbitals are present. Both are broad and trapezoidal; the dorsal is larger, deeper than wide, and the ventral is relatively small, tapering ventrally (Figs. 2–4).

Two sclerotic bones are partly discernible near the orbit rim in V24315 (Fig. 2). They are thin and slightly curved.

Parasphenoid, palatoquadrate, and suspensorium: The parasphenoid and palatoquadrate can only be discerned through the orbit laterally; the former is elongate, contacting the latter laterally (Fig. 2). The quadrate is only partly exposed, with its anterodorsal portion laterally covered by the maxilla. It bears a strong condyle that articulates with the lower jaw.

The quadratojugal is narrow and splint-like (Figs. 2–4). It articulates with the posterolateral surface of the ventral portion of the quadrate and rests on the anterior edge of the preopercle.

The hyomandibula is laterally covered by two suborbitals and the preopercle and is not exposed in the specimens. X-ray scanning of V30785 reveals a hatchet-shaped, vertically positioned hyomandibula, with a foramen for the hyomandibular branch of the facial nerve in the middle. It has a single dorsal facet articulating with the posteroventral side of the braincase (Fig. 5 [Figure 5: see original paper]).

Most of the symplectic is laterally covered by the preopercle except for the ventral condyle of this bone. This condyle, together with the quadrate condyle, forms a double jaw joint with the lower jaw (Figs. 2, 3, 5D).

Jaws: The premaxilla is relatively large, having a horizontally expanded oral region and a posterodorsally directed nasal process (Figs. 2–4). It is uncertain whether the foramen for the olfactory nerve is present in the nasal process of this bone because of overlapping nasals. The maxilla is elongate, ending at the level of the jaw articulation. The middle portion of this bone slightly protrudes dorsally and forms a rudimentary supramaxillary process. Posterior to this process, the dorsal margin of the maxilla is distinctly concave for accommodating a supramaxilla (Figs. 2–4). The posterior margin of the maxilla is slightly concave, resembling the condition in *Subortichthys.* As in other ionoscopiforms, the maxilla encloses a branch of the infraorbital sensory canal, indicated by a longitudinal row of pores at the anterior half of the maxilla. The supramaxilla is about half the maxillary length. It is elongate, tapering at both ends. The oral margin of the maxilla is fully equipped with small conical teeth, numbering over forty (Fig. 2). Additionally, a row of 12 conical teeth is discernible along the oral margin of the premaxilla, slightly larger than those on the anterior portion of the maxilla (Fig. 3).

The lower jaw is elongate and not robust, with a height/length ratio of 0.18. The dentary is wedge-shaped, being the largest element of the lower jaw. It contacts the relatively small, trapezoidal angular posteriorly in a sinuous suture. The mandibular sensory canal extends longitudinally through the dentary and angular, indicated by eight or nine pores in the former and three pores in the latter (Figs. 2, 4). Three coronoid bones are exposed medial to the dentary (V30791). They are covered with small conical teeth.

Opercular series: The preopercle is narrow and crescent-shaped, with part of its dorsal portion anteriorly covered by two suborbitals. The dorsal tip of the preopercle contacts the posterolateral process of the dermopterotic, and its anteroventral tip nearly reaches the ventral end of the quadratojugal. The preopercular sensory canal runs dorsoventrally through the preopercle. Additionally, a series of pores near the posterior margin of this bone likely represents openings for branches of the preopercular sensory canal (Figs. 2–4). The opercle is large and fan-shaped, with depth nearly equal to its length. The posterior and dorsal margins are rounded, and the anterior and ventral margins are straight (Figs. 2–4). The subopercle is relatively small and nearly sickle-shaped, bearing a short triangular anterodorsal process. The interopercle is small and triangular. It tapers anteroventrally, with its anterodorsal portion laterally covered by the preopercle (Figs. 2–4).

Gular and branchiostegal rays: The median gular is elongate and subcircular, with a pointed anterior tip and relatively broad posterior end (Figs. 2, 3). Its length is slightly over half that of the lower jaw. Twelve pairs of branchiostegal rays are present in V24315 and V30784 (Figs. 2, 3), representing the maximum number in this taxon. They are elongate and plate-like, increasing in length posteriorly. The median gular and branchiostegal rays are ornamented with tubercles and ridges.

Girdles and fins: A posttemporal, supracleithrum, cleithrum, and three postcleithra are present on each side of the pectoral girdle. The posttemporal is subtriangular, with a rounded posterior margin. It tapers medially, with a narrow anterior portion overlapped by the extrascapulars. The lateral line extends longitudinally through the lateral portion of the posttemporal and enters the supracleithrum (Fig. 2). The supracleithrum is deep and anteriorly inclined, with its anterior portion slightly covered by the posttemporal and opercle. The complete shape of the cleithrum remains unknown because of overlapping of the opercular series in situ (Figs. 2–4). The exposed portion of the cleithrum is largely crescent-shaped, with its dorsal arm nearly equal to the horizontal arm (Figs. 2–4). Three postcleithra are associated with the cleithrum. The dorsal is the largest, as deep as the supracleithrum; the middle is trapezoidal, nearly half the size of the dorsal; and the ventral is smallest and triangular (Figs. 2–4).

The relatively large pectoral fins insert low on the body and each bears 15 distally segmented rays. The first leading ray is unbranched, preceded by a basal fulcrum and a series of fringing fulcra. The remaining rays are distally segmented (Fig. 6A [Figure 6: see original paper]).

The pelvic girdles are not exposed. The small pelvic fins insert at the 6th or

7th vertical scale row, each consisting of seven distally segmented rays. Several fringing fulcra are associated with the leading ray of the pelvic fin (Fig. 6B).

Median fins: The dorsal fin originates at the 16th vertical scale row, composed of seven distally segmented rays. The first ray is unbranched, preceded by two to three basal fulcra and several fringing fulcra; the remaining rays are branched distally (Fig. 6C).

The anal fin originates below the 14th vertical scale row, having nine distally segmented principal rays. The first principal ray is unbranched, preceded by a short rudimentary ray, a basal fulcrum, and a series of fringing fulcra, and the remaining rays are branched distally. The rudimentary ray is composed of two segments, less than one-fourth the length of the first principal ray (Fig. 6E).

The caudal fin is hemi-heterocercal, with a moderately forked profile. It has 15 principal rays, seven in the dorsal lobe. The dorsal and ventral marginal principal rays are segmented and unbranched, and the middle principal rays are segmented and branched up to three times. There are seven basal fulcra in the dorsal lobe and one or two basal fulcra and three rudimentary rays in the ventral lobe. Small leaf-like fringing fulcra are present in both lobes (Fig. 6D).

Squamation: The body is fully covered with rhomboid scales (Figs. 1, 6, 7). The scales are arranged in 33–34 vertical rows along the main lateral line. In addition, five rows of scales extend into the epaxial lobe of the caudal fin. Besides the ridge scales, there are 15–17 scales in the tenth vertical row on each side of the body, ten below the lateral line. The scales in the anterior flank region are about three times deeper than wide, and they gradually become shorter and smaller dorsally, ventrally, and posteriorly. Moreover, an enlarged lateral scute is discernible anterior to the anal fin. The lateral line scales bear a distinct notch in the middle of their posterior margin, likely for the opening of the lateral line. An additional lateral line is present, indicated by a series of small pores in the predorsal region. Most scales, except those covering the epaxial lobe of the caudal fin, have a serrated posterior margin with 1–4 acute projections. The external surfaces of scales are largely smooth except for small pores on some scales.

5.1. New Specimens and Neotype

The new specimens are referred to *Sinoeugnathus kueichowensis* based on their similarity to the missing holotype and the previously sole known specimen illustrated by Su (1959) in both morphology and size. Most strikingly, the maxillae in the new specimens are quite long, accounting for slightly over half of head length. Such a long maxilla, also present in the holotype of *S. kueichowensis*, is unknown in other holosteans from the same fossil beds (Liu et al., 2002, 2003; Xu and Ma, 2018; Xu et al., 2018). Additionally, the opercle in the new specimens is large and fan-shaped with rounded posterior and dorsal margins, consistent with the condition in the illustrated holotype (Su, 1959). Moreover, the new specimens and holotype show the same scale formula (D17/P6, A14, C27/T33). The proportions of head length and body depth to standard length in the new specimens (Table 1) are very similar to those of the holotype (SL = 53 mm; HL = 19 mm; BD = 22 mm). Among the new specimens, IVPP V24315 is best preserved and relatively large, and is therefore designated as the neotype of *S. kueichowensis*.

5.2. Phylogenetic Analysis

Phylogenetic analysis recovered 48 most parsimonious trees (tree length = 661 steps; consistency index = 0.4115; retention index = 0.7665). In the strict consensus tree (Fig. 8 [Figure 8: see original paper]), Parasemionotiformes (sampled by *Watsonulus*) is nested at the base of Halecomorphi, followed successively by Ionoscopiformes and Amiiformes, consistent with previous studies (Grande and Bemis, 1998; Xu and Ma, 2018; Xu, 2019). *Sinoeugnathus* possesses two synapomorphies of Halecomorphi: a symplectic articulating with the lower jaw and a notched posterior margin of the maxilla. Within this clade, it is resolved as an ionoscopiform, possessing a synapomorphy of this order—a sensory canal in the maxilla (Grande and Bemis, 1998; Xu, 2019). *Sinoeugnathus* is sister to the Anisian ionoscopiform *Subortichthys* from Luoping, Yunnan, and both, together with two European genera *Allolepidotus* and *Eoeugnathus*, form a monophyletic group (Subortichthyidae fam. nov.) at the base of Ionoscopiformes.

5.3. Taxonomic Revision and Comparison

Su (1959) noted the resemblances of *Sinoeugnathus* to *Eoeugnathus* in general body form, maxilla, and opercle, and referred the genus to the Eugnathidae (= Caturidae; Patterson, 1973). Besides these two genera, *Allolepidotus* and several other Triassic genera (e.g., *Heterolepidotus* and *Furo*) were previously also included in this family (Gardiner, 1960; Lombardo, 2001), but this taxonomic assignment was questioned by Patterson (1973), who placed three 'caturids' (*Allolepidotus*, *Eoeugnathus*, and *Sinoeugnathus*) in Parasemionotidae. However, parasemionotids are now confined to basal halecomorphs in the Early Triassic (Grande and Bemis, 1998). Later, Herzog (2003) revised *Eoeugnathus* and placed it in Section B (the clade Ionoscopiformes plus Amiiformes) of Halecomorphi without reference to a specific family or order. Ebert (2018) incorporated *Eoeugnathus* in a phylogenetic analysis and recovered it as sister to *Allolepidotus* within 'Panxianichthyformes' (Sun et al., 2016). However, the grade 'Panxianichthyformes' is likely paraphyletic, comprising basal members of Ionoscopiformes (Xu and Ma, 2018; Xu, 2019).

Our study confirms that *Sinoeugnathus* is not a caturid as previously suggested

(Su, 1959) because it lacks diagnostic features of this family, such as sharply carinate acrodin tooth caps on larger jaw teeth, an extremely slender rod-like maxilla, and 22 or more pairs of branchiostegal rays (López-Arbarello and Ebert, 2023). Instead, this genus is revised here as a subortichthyid, sharing four derived features with other members of this family (*Allolepidotus*, *Eoeugnathus*, and *Subortichthys*): a quadrate almost fully covered by the maxilla; a maxilla extending posterior to the coronoid process of the lower jaw; presence of 35 or fewer lateral line scales; and a complete row of elongate scales between the last lateral line scale and the uppermost caudal fin ray. Although these features have independently evolved in some other neopterygians, they are absent in other ionoscopiforms.

Sinoeugnathus is easily distinguished from other members of this family by the following features: (1) *Sinoeugnathus*, similar to *Subortichthys* (Ma and Xu, 2017), has three pairs of extrascapulars (Figs. 2–4), but *Eoeugnathus* (Herzog, 2003) and *Allolepidotus* (Lombardo, 2001) have only a single pair; outside Subortichthyidae, three pairs of extrascapulars have independently evolved in the ionoscopiform *Aisalepidotus* (Xu and Ma, 2018); (2) *Sinoeugnathus* has two suborbitals (Figs. 2–4), contrasting with counts in other subortichthyids (single in *Allolepidotus*; three in *Subortichthys* and *Eoeugnathus*); (3) the antorbital in *Sinoeugnathus* is relatively short and deep (Figs. 2–4), but in other subortichthyids the bone is relatively long and slender (Ma and Xu, 2017; Lombardo, 2001; Herzog, 2003); (4) *Sinoeugnathus* has a fan-shaped opercle with depth nearly equal to its length (Figs. 2–4); by contrast, the opercle in other subortichthyids is commonly trapezoidal, deeper than long; (5) *Sinoeugnathus* has only 15 principal caudal fin rays (Fig. 6D), fewer than in other subortichthyids (18 in *Subortichthys* and *Eoeugnathus*, and ~20 in *Allolepidotus*); and (6) the lateral line scales in the anterior flank region of *Sinoeugnathus* are notably deep (nearly 3 times deeper than wide), but those in other subortichthyids are relatively short (1.2–2 times deeper than wide).

5.4. Ecological Implications

Subortichthyids generally have a maximum standard length of no more than 100 mm. Among this family, *Sinoeugnathus* is the smallest, with a maximum standard length of 69.6 mm, while other subortichthyids are slightly larger (SL = 72 mm in *Subortichthys*, 85 mm in *Allolepidotus*, and 98 mm in *Eoeugnathus*). By contrast, other Triassic ionoscopiforms are significantly larger (SL = 159 mm in *Panxianichthys*, 273 mm in *Asialepidotus*, and 360 mm in *Robustichthys*; Table 2). Additionally, subortichthyids differ from other Triassic ionoscopiforms in dentition. The former have smaller and more numerous conical teeth in relatively slender and longer jaws than the latter. Moreover, subortichthyids have a shorter coronoid process of the lower jaw, with higher ratios of mandibular length to skull length and of maxillary length to mandibular length than non-subortichthyid ionoscopiforms (Table 2). Notably, teeth on the palatine are very weak in subortichthyids but stronger and blunt in other Triassic ionoscopiforms (e.g., *Asialepidotus*; Xu and Ma, 2018). Analogous to modern ray-finned fishes, the morphological divergence between small-sized subortichthyids and larger non-subortichthyid ionoscopiforms was probably driven by ecological specializations related to feeding and foraging, such as prey type, reaction distance, and swimming performance (Folkvord and Hunter, 1986; Scharf et al., 2000; Magnhagen and Heibo, 2001; Karpouzi and Stergiou, 2003). The absence of blunt palatine teeth indicates that subortichthyids probably fed on relatively soft prey mainly by biting (rather than crushing). As one of the small-sized holosteans in the Middle Triassic Xingyi Biota, *Sinoeugnathus* likely fed on small shrimps or other relatively soft invertebrates and was probably preyed upon by larger carnivorous fishes or marine reptiles in the same marine ecosystem (Benton et al., 2013).

Subortichthyids represent an early radiation of ionoscopiforms from the Middle Triassic of both Europe and South China, which at that time were located in the western and eastern realms of the Paleo-Tethys Ocean, respectively (Metcalfe, 2011). The recovery of European subortichthyids (*Allolepidotus* and *Eoeugnathus*) as successive sister taxa to Chinese subortichthyids suggests that this family might have originated in the western Tethys realm, with the Paleo-Tethys Ocean providing a west–east corridor for the long dispersal of subortichthyids into the eastern Tethys realm. This paleobiogeographic scenario contradicts current stratigraphic records of subortichthyids; the European subortichthyids are Ladinian, nearly coeval with *Sinoeugnathus* but slightly younger than the Anisian *Subortichthys* (the oldest record of this family from China). However, this contradiction may be caused by an incomplete fossil record of subortichthyids from Europe. If our current scenario of subortichthyid phylogeny is accepted, Anisian or even older records of subortichthyids are expected to be found in the western Tethys realm.

6. Conclusion

Detailed examination of 15 new specimens from the Middle Triassic (Ladinian) of Yunnan and Guizhou permitted thorough revision of the anatomy of *Sinoeugnathus kueichowensis*. This revision provides new insights into the anatomical diversity, phylogeny, and paleobiogeography of early ionoscopiforms. Phylogenetic analysis incorporating new anatomical data recovered *Sinoeugnathus* as sister to *Subortichthys* from the Middle Triassic (Anisian) of Yunnan, and both are grouped with two Ladinian genera—*Allolepidotus* and *Eoeugnathus* from the Monte San Giorgio area—into a monophyletic group (Subortichthyidae) at the base of Ionoscopiformes. The previous placement of *Sinoeugnathus* in Eugnathidae (= Caturidae) is firmly rejected. The proposed scenario of subortichthyid phylogeny combined with paleogeographic data suggests that the family may have originated in the western Tethys realm; early Middle Triassic (Anisian) subortichthyids are expected to be recovered in that realm. The morphological divergence between small-sized subortichthyids and larger non-subortichthyid ionoscopiforms is well recognized. With a maximum standard length of 69.6 mm, *S. kueichowensis* represents the smallest subortichthyid, which likely fed on small shrimps or other relatively soft invertebrates and was in turn preyed upon by larger carnivorous fishes or marine reptiles in the same marine ecosystem.

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References

Benton MJ, Zhang QY, Hu SX et al., 2013. Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo–Triassic mass extinction. *Earth Sci Rev*, 125: 199–243

Brough J, 1939. *The Triassic fishes of Besano, Lombardy.* London: British Museum (Natural History). 1–117

Bürgin T, 2004. *Eosemionotus ceresiensis* sp. nov., a new semionotiform fish (Actinopterygii, Halecostomi) from the Middle Triassic of Monte San Giorgio (Southern Switzerland). In: Arratia G, Tintori A eds. *Mesozoic Fishes 3–Systematics, Paleoenvironments and Biodiversity 3.* 239–251

Cavin L, 2010. Diversity of Mesozoic semionotiform fishes and the origin of gars (Lepisosteidae). *Naturwissenschaften*, 97:

Ebert M, 2018. *Cerinichthys koelblae*, gen. et sp. nov., from the Upper Jurassic of Cerin, France, and its phylogenetic setting, leading to a reassessment of the phylogenetic relationships of Halecomorphi (Actinopterygii). *J Vert Paleont*, 38: e1420071

Folkvord A, Hunter JR, 1986. Size-specific vulnerability of northern anchovy, *Engraulis mordax*, larvae to predation by fishes. *Fish Bull*, 84: 859–869

Friedman M, 2015. The early evolution of ray-finned fishes. *Paleontology*, 58: 213–228

Gardiner BG, 1960. A revision of certain actinopterygian and coelacanth fishes, chiefly from the Lower Lias. *Bull Br Mus Nat Hist Geol*, Geology, 4(7): 241–384

Geng BH, Zhu M, Jin F, 2009. A revision and phylogenetic analysis of *Guizhoucoelacanthus* (Sarcopterygii, Actinistia) from the Triassic of China. *Vert PalAsiat*, 47: 165–177

Gill EL, 1923. The Permian fishes of the genus *Acentrophorus*. *Proc Zool Soc Lond*, 93: 19–40

Grande L, 2010. An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of holostei. *Copeia*, 10(Suppl): 1–871

Grande L, Bemis WE, 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy: an empirical search for interconnected patterns of natural history. *Soc Vert Paleont Mem* (Suppl *J Vert Paleont*), 4: 1–690

Herzog A, 2003. Eine Neubeschreibung der Gattung *Eoeugnathus*, Brough, 1939 (Actinopterygii; Halecomorphi) aus der alpinen Mitteltrias Graubündens. *Paläönt Zeit*, 77(1): 223–240

Hurley IA, Mueller RL, Dunn KA et al., 2007. A new time-scale for ray-finned fish evolution. *Proc R Soc B*, 274: 489–

Jiang DY, Motani R, Tintori A et al., 2020. Evidence supporting predation of 4-m marine reptile by Triassic megapredator. *iScience*, 23: 101347

Jin F, 2001. Notes on the discovery of *Birgeria* in China. *Vert PalAsiat*, 39: 168–176

Karpouzi VS, Stergiou KI, 2003. The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *J Fish Biol*, 62: 1353–1365

Li C, Wu XC, Zhao LJ et al., 2016. A new armored archosauriform (Diapsida: Archosauromorpha) from the marine Middle Triassic of China, with implications for the diverse life styles of archosauriforms prior to the diversification of Archosauria. *Sci Nat*, 103: 95

Li JL, 2006. A brief summary of the Triassic marine reptiles of China. *Vert PalAsiat*, 44: 99–108

Li ZG, Sun ZY, Jiang DY et al., 2016. LA-ICP-MS Zircon U-Pb age of the fossil layer of Triassic Xingyi Fauna from Xingyi, Guizhou, and its significance. *Geol Rev*, 62: 779–790

Liu GB, Yin GZ, Wang XH, 2002. On the most primitive amiid fish from Upper Triassic of Xingyi, Guizhou. *Acta Palaeont Sin*, 41: 461–463

Liu GB, Yin GZ, Wang XH et al., 2003. New discovered fishes from *Keichousaurus* bearing horizon of Late Triassic in Xingyi of Guizhou. *Acta Palaeont Sin*, 42: 346–366

Lombardo C, 2001. Actinopterygians from the Middle Triassic of northern Italy and Canton Ticino (Switzerland): anatomical descriptions and nomenclatural problems. *Riv Ital Paleont Stratigr*, 107: 345–369

López-Arbarello A, Ebert M, 2023. Taxonomic status of the caturid genera (Halecomorphi, Caturidae) and their Late Jurassic species. *R Soc Open Sci*, 10: 221318

López-Arbarello A, Sferco E, 2018. Neopterygian phylogeny: the mergerassay. *R Soc Open Sci*, 5: 172337

López-Arbarello A, Sun ZY, Sferco E et al., 2011. New species of *Sangiorgioichthys* Tintori and Lombardo, 2007 (Neopterygii, Semionotiformes) from the Anisian of Luoping (Yunnan Province, South China). *Zootaxa*, 2749: 25–

Ma XY, Xu GH, 2017. A new ionoscopiform fish (Holostei: Halecomorphi, Ionoscopiformes) from the Middle Triassic (Anisian) of Yunnan, China. *Vert PalAsiat*, 55: 92–106

Magnhagen C, Heibo E, 2001. Gape size allometry in pike reflects variation between lakes in prey availability and relative body depth. *Funct Ecol*, 15: 754–762

Metcalfe I, 2011. Palaeozoic–Mesozoic history of SE Asia. In: Hall R, Cottam MA, Wilson MEJ eds. *The SE Asian Gateway: History and Tectonics of the Australia–Asia Collision*. Geol Soc, Spec Publ, London, 355: 7–35

Near TJ, Eytan RI, Dornburg A et al., 2012. Resolution of ray-finned fish phylogeny and timing of diversification. *Proc Nat Acad Sci*, 109: 13698–13703

Olsen PE, 1984. The skull and pectoral girdle of the parasemionotid fish *Watsonulus eugnathoides* from the Early Triassic Sakamena group of Madagascar, with comments on the relationships of the holostean fishes. *J Vert Paleont*, 4: 481–

Patterson C, 1973. Interrelationships of holosteans. In: Greenwood PH, Miles RS, Patterson C eds. *Interrelationships of Fishes*. *Zool J Linn Soc*, 53(Suppl): 233–305

Scharf SF, Juanes F, Rountree RA, 2000. Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar Ecol Prog Ser*, 208: 229–248

Shang QH, Wu XC, Li C, 2020. A new Ladinian nothosauroid (Sauropterygia) from Fuyuan, Yunnan Province, China. *J Vert Paleont*, 40: e1789651

Su DZ, 1959. Triassic fishes from Kueichow, Southwest China. *Vert PalAsiat*, 3: 205–210

Sun ZY, Tintori A, Xu YZ et al., 2016. A new non-parasemionotiform order of the Halecomorphi (Neopterygii, Actinopterygii) from the Middle Triassic of Tethys. *J Syst Palaeont*, 15: 223–240

Swofford DL, 2003. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods*). Version 4.0b10. Sunderland, Massachusetts: Sinauer Associates

Tintori A, Lombardo C, 2007. A new early Semionotidae (Semionotiformes, Actinopterygii) from the Upper Ladinian of the Monte San Giorgio area (southern Switzerland and northern Italy). *Riv Ital Paleont Stratigr*, 113: 369–381

Tintori A, Hitij T, Jiang DY et al., 2014. Triassic actinopterygian fishes: the recovery after the end-Permian crisis. *Integr Zool*, 9: 349–411

Tintori A, Sun ZY, Lombardo C et al., 2015. Oldest stem Teleostei from the late Ladinian (Middle Triassic) of southern China. *Riv Ital Paleont Stratigr*, 121: 285–296

Westoll TS, 1944. The Haplolepidae, a new family of Late Carboniferous bony fishes – a study in taxonomy and evolution. *Bull Am Mus Nat Hist*, 83: 1–121

Xu GH, 2019. Osteology and phylogeny of *Robustichthys luopingensis*, the largest holostean fish in the Middle Triassic. *PeerJ*, 7: e7184

Xu GH, 2020. A new species of *Luganoia* (Luganoiidae, Neopterygii) from the Middle Triassic Xingyi Biota, Guizhou, China. *Vert PalAsiat*, 58: 267–282

Xu GH, Ma XY, 2018. Redescription and phylogenetic reassessment of *Asialepidotus shinyiensis* (Holostei: Halecmorphi) from the Middle Triassic (Ladinian) of China. *Zool J Linn Soc*, 184(1): 95–114

Xu GH, Shen CC, 2015. *Panxianichthys imparilis* gen. et sp. nov., a new ionoscopiform (Halecomorphi) from the Middle Triassic of Guizhou, China. *Vert PalAsiat*, 53: 1–15

Xu GH, Wu FX, 2012. A deep-bodied ginglymodian fish from the Middle Triassic of eastern Yunnan Province, China, and the phylogeny of lower neopterygians. *Chinese Sci Bull*, 57: 111–118

Xu GH, Zhao LJ, Gao KQ et al., 2012. A new stem-neopterygian fish from the Middle Triassic of China shows the earliest over-water gliding strategy of the vertebrates. *Proc R Soc B*, 280: 20122261

Xu GH, Zhao LJ, Coates MI, 2014. The oldest ionoscopiform from China sheds new light on the early evolution of halecomorph fishes. *Biol Lett*, 10: 20140204

Xu GH, Gao KQ, Coates MI, 2015. Taxonomic revision of *Plesiofuro mingshuica* from the Lower Triassic of northern Gansu, China, and the relationships of early neopterygian clades. *J Vert Paleont*, 35(6): e1001515

Xu GH, Ma XY, Ren Y, 2018. *Fuyuanichthys wangi* gen. et sp. nov. from the Middle Triassic (Ladinian) of China highlights the early diversification of ginglymodian fishes. *PeerJ*, 6: e6054

Young CC, 1958. On the new pachypleurosauroidea from Keichow, South-West China. *Vert PalAsiat*, 2: 69–81

Zou XD, Balini M, Jiang DY et al., 2015. Ammonoids from the Zhuganpo Member of the Falang Formation at Nimaigu and their relevance for dating the Xingyi Fossil-Lagerstaette (late Ladinian, Guizhou, China). *Riv Ital Paleont Stratigr*, 121: 135–161

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