

A large peltopleurid fish (Actinopterygii: Peltopleuriformes) from the Middle Triassic of Yunnan and Guizhou, China

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Abstract Peltopleuriformes are a stem group of neopterygian fishes from the Middle–Late Triassic marine ecosystems in Europe and South China, including the Peltopleuridae and Thoracopteridae. Among them, peltopleurids are commonly small-sized fishes with a standard length (SL) rarely exceeding 55 mm. Here, a new peltopleurid, *Peltopleurus tyrannos* sp. nov., is described based on three well-preserved specimens from the Middle Triassic (Ladinian) of Fuyuan, Yunnan and Xingyi, Guizhou, China. The discovery documents the largest species (SL = 72 mm) of this genus in the Middle Triassic and provides new insights into the morphologic and trophic diversifications of peltopleurids. In addition to large conical teeth on the oral margins of the jaws, the new peltopleurid bears many blunt teeth of various sizes on the oral margin of the palatopterygoid, which may be used for crushing some hard-shelled invertebrates (e.g., crustaceans) or small armored fishes. By contrast, the more commonly founded relative, *P. orientalis*, from the same ecosystem (Xingyi Biota) is toothless and has a much smaller body size (SL = 26 mm), and probably represents a schooling fish that fed on small planktonic invertebrates. The new finding shows that *Peltopleurus* from the late Middle Triassic Xingyi Biota of South China had evolved into two different ecomorphotypes.

Key words Xingyi Biota, Middle Triassic, Peltopleuridae, Peltopleuriformes, trophic diversification

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Peltopleuriformes are an order of stem-neopterygian fishes from the Middle–Late Triassic marine ecosystems in Europe and South China (Kner, 1866, 1867; Woodward, 1895; Brough, 1939; Su, 1959; Beltan, 1972, 1975; Griffith, 1977; Lehman, 1979; B rigin, 1990, 1992; Tintori and Sassi, 1992; Lombardo, 1999; Liu et al., 2006; Xu et al., 2012, 2015a, b; Xu

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and Ma, 2016). The order (sensu Xu and Ma, 2016) includes two families, the Peltopleuridae and Thoracopteridae. Both show sexual dimorphism in the anal fin that is probably related to internal fertilization and viviparity (Bürgin, 1990; Lombardo, 1999; Xu et al., 2015b; Xu and Ma, 2016). In addition, the Thoracopteridae gradually evolved a series of features associated with overwater gliding, representing a remarkable case of convergent evolution with modern exocoetid flying fishes (Griffith, 1977; Lehman, 1979; Tintori and Sassi, 1992; Davenport, 1994; Xu et al., 2012, 2015b). As such, Peltopleuriformes have long attracted the attention of paleoichthyologists interested in the early diversification, reproduction and ecology of the Neopterygii, the largest group of living vertebrates (Nelson et al., 2016).

Peltopleurus is the type genus of the Peltopleuridae, including a dozen species from the Middle to Upper Triassic of Italy (Kner, 1866, 1867; Brough, 1939; Lombardo, 1999), Austria (Woodward, 1895; Griffith, 1977), Switzerland (Bürgin, 1990, 1992), Spain (Beltan, 1972, 1975) and South China (Su, 1959; Liu et al., 2006; Xu and Ma, 2016). Among them, *Peltopleurus orientalis* from the late Middle Triassic (Ladinian) of western Guizhou and eastern Yunnan was the first record of this genus in China (Su, 1959); although Lin et al. (2011) reassigned the species to the habroichthyid genus *Habroichthys*, this has been rejected by Xu and Ma (2016). The younger *P. brachycephalus* from the Late Triassic (Carnian) of Guanling, Guizhou was the second species of this genus in China (Liu et al., 2006), but it is based on a single poorly-preserved specimen and needs further study. Recently, Xu and Ma (2016) described the third species, *P. nitidus*, from the early Middle Triassic (Anisian) of Luoping, eastern Yunnan, which represents one of the oldest members in this genus. Here, we report the discovery of a new species of *Peltopleurus* based on three well-preserved specimens from the late Middle Triassic (Ladinian) of Shibilianshan, Fuyuan, eastern Yunnan and Wusha, Xingyi, western Guizhou, China. The discovery documents the largest known species of *Peltopleurus* in the Middle Triassic. The large size and superb preservation of the new species facilitate the description of much of its morphology that provides important information for understanding the early diversification of peltopleurids.

The new peltopleurid fossils are imbedded in the dark grey thin to medium bedded marlites and argillaceous limestones at the lower part of the Zhuganpo member of the Falang Formation. Also from the fossil beds are several other kinds of ray-finned fishes (Su, 1959; Jin, 2001; Liu et al., 2002, 2003; Xu et al., 2012, 2015b; Tintori et al., 2012, 2015; Xu and Ma, 2017), a coelacanth (Geng et al., 2009), and diverse marine reptiles (Young, 1958; Li and Jin, 2003, 2009; Li, 2006; Benton, 2013; Li C et al., 2016; Lu et al., 2017). The whole fossil assemblage was named the Xingyi Fauna, or Xingyi Biota (Benton, 2013; Lu et al., 2017). Biostratigraphical studies of invertebrates and marine reptiles (Young, 1958; Chen, 1985; Li and Jin, 2003, 2009; Zou et al., 2015; Li C et al., 2016) generally suggest a late Middle Triassic (Ladinian) age for this biota, as supported by the recent zircon U-Pb dating (240.8 ± 1.8 Ma; Li et al., 2016).

1 Material and method

All specimens are curated at the fossil collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, China (IVPP). The specimens were mechanically prepared with sharp steel needles. X-ray scanning was carried out using a micro computed laminography system at the Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences. For better contrast, two specimens (IVPP V 19986 and V 19988) were dusted with ammonium chloride (NH₄Cl) before being photographed. Tree searches were accomplished with the branch-and-bound algorithm in PAUP* 4.0b10 (Swofford, 2003). The relative position of fins and scale counts were expressed following Westoll (1944).

2 Systematic paleontology

Actinopterygii Cope, 1887

Neopterygii Regan, 1923

Peltopleuriformes Gardiner, 1967

Peltopleuridae Brough, 1939

Peltopleurus Kner, 1866

***Peltopleurus tyrannos* sp. nov.**

(Figs. 1–5)

Etymology The species name is from Latin *tyrannos*, meaning bully.

Holotype IVPP V 19986. A nearly complete specimen from Shibilianshan, Fuyuan, Yunnan Province (Fig. 1).

Paratype Two nearly complete specimens respectively from Wusha, Xingyi, Guizhou Province (V 19987, Fig. 2B), and Shibilianshan, Fuyuan, Yunnan Province (V 19988, Fig. 2A).

Locality and horizon Shibilianshan, Fuyuan, Yunnan, and Wusha, Xingyi, Guizhou, China; lower part of Zhuganpo member of the Falang Formation, Ladinian (~240±1.8 Ma, Li et al., 2016), Middle Triassic.

Diagnosis A large-sized species of *Peltopleurus* distinguished from other species of this genus by the following combination of features: two supraorbitals (as in *P. rugosus*, but three or four in other species); single suborbital (as in *P. nitidus*, but two or more in other species); two pairs of extrascapulars (as in *P. orientalis*, but three extrascapulars commonly in other species); linear ridges and tubercles on snout bones; large conical teeth on oral margins of both jaws; blunt teeth of various sizes on oral margin of palatopterygoid; preopercle vertical, with anteriorly expanded middle portion and tapered dorsal and ventral portions; opercle nearly twice as deep as subopercle; 16 principal caudal fin rays; fringing fulcra on all fins; posterior margins of anterior scales with many serrations (vs. one to three serrations in those of *P. nuptialis* and straight posterior margins of scales in other species); deepest lateral line scales eight times deeper than long; one and three horizontal rows of scales respectively above and

below lateral line scales on each side of anterior flank region; and squamation formula of D24/P11, A16–17, C29/T35.

3 Description

General morphology and size Similar to other *Peltopleurus* species, *P. tyrannos* has a blunt snout, an elongate fusiform body, and a moderately forked caudal fin (Figs. 1, 2). The holotype (Fig. 1) has a standard length (SL) of 71 mm and a total length (TL) of 82 mm. The

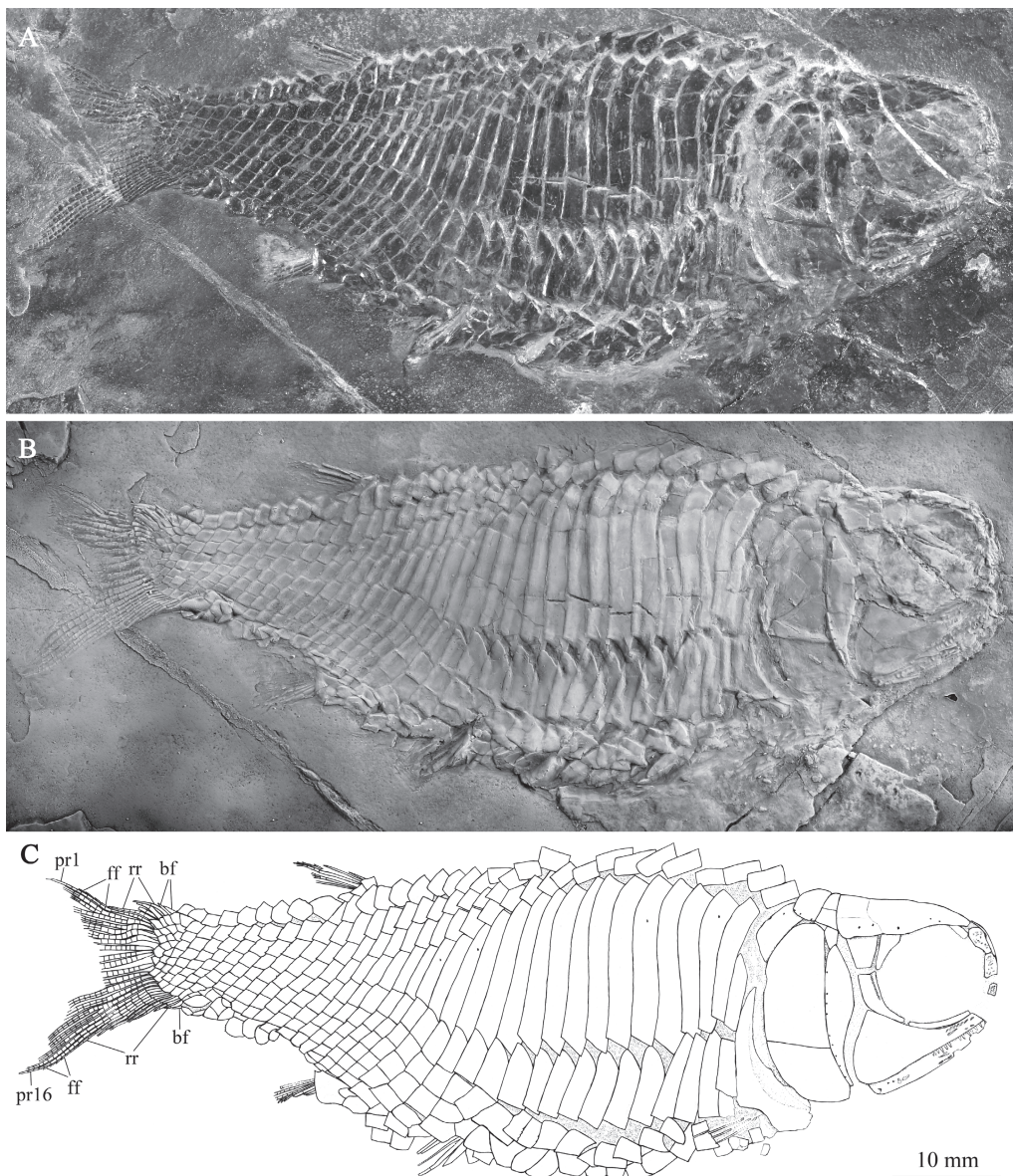


Fig. 1 Holotype of *Peltopleurus tyrannos* sp. nov., IVPP V 19986

A. original specimen; B. coated with ammonium chloride; C. line drawing

Abbreviations: bf. basal fulcrum; ff. fringing fulcrum; pr. principal ray; rr. rudimentary ray

largest specimen (Fig. 2B) has a SL of 72 mm and a TL of 83 mm. The head length, slightly shorter than the body depth, constitutes 29%–31% of SL.

Snout The median rostral consists of the majority of the blunt snout (Fig. 3). It is deep and slightly anteriorly convex, contacting the nasals and antorbitals laterally, the frontals dorsally, and the premaxillae ventrally. A notch for the anterior nostril is present at each lateral margin of this bone (Fig. 3A).

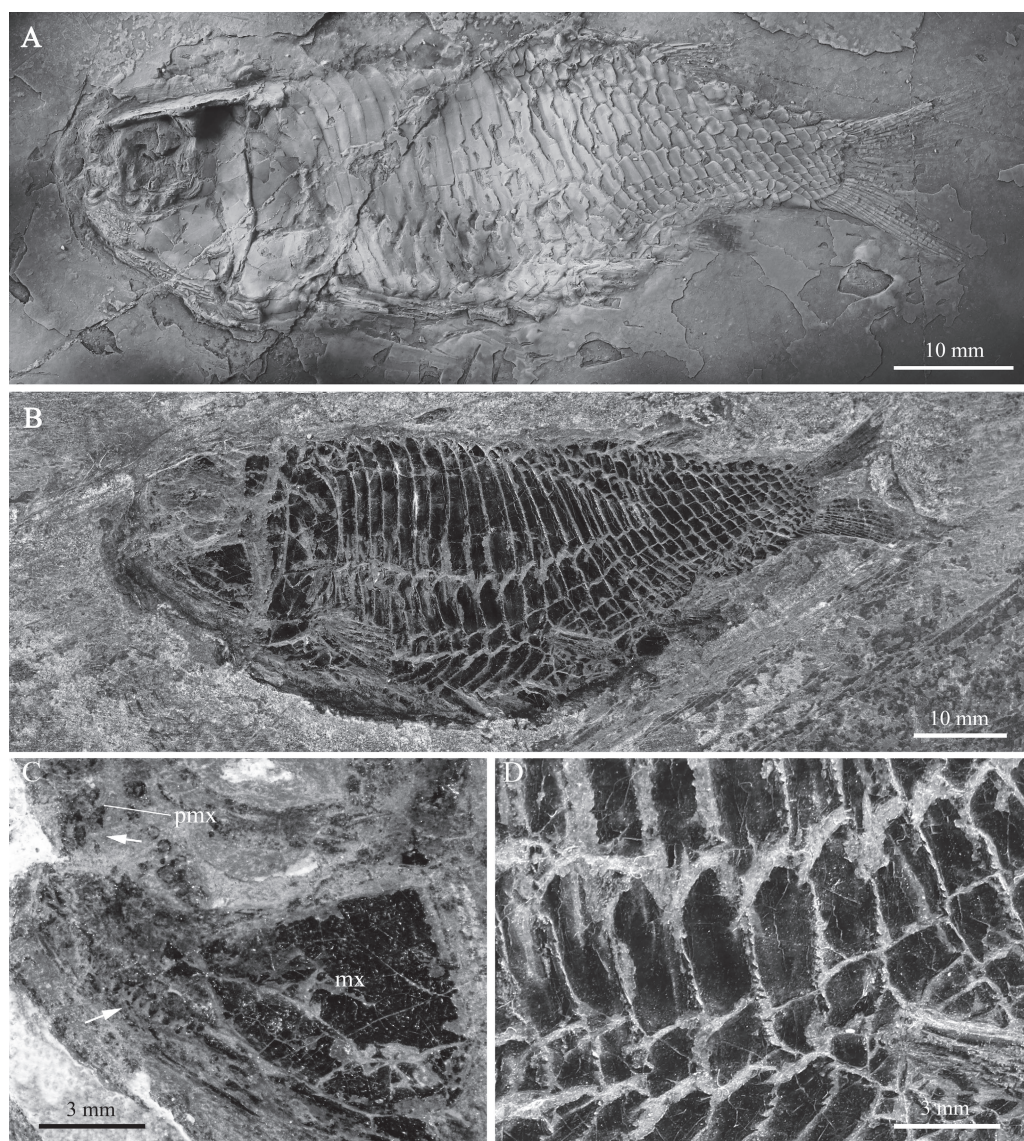


Fig. 2 *Peltopleurus tyrannos* sp. nov.

A. a nearly complete fish specimen (coated with ammonium chloride), IVPP V 19988; B. a nearly complete fish specimen, V 19987; C. upper jaw of B with arrows indicating teeth on its oral margin;

D. scales near the left pelvic fin of B

Abbreviations: pmx. premaxilla; mx. maxilla

As in other peltopleuriforms, both the nasal and antorbital form the anterior margin of the orbit (Fig. 3). The nasal is irregular, deeper than wide. The medial and lateral margins are notched for the anterior and posterior nostrils, respectively. The antorbital is rectangular and shorter than the nasal, forming the ventral portion of the anterior margin of the orbit. The nasals and antorbitals are strongly ornamented by linear ridges and tubercles, and for this reason, the sensory pores are hard to identify on these bones.

The premaxilla is small and nearly trapezoidal, bearing three or four large conical teeth on its oral margin (Fig. 2C).

Skull roof The frontals, parietals and dermopterotics tend to be fused into a broad plate with only faint sutures discernible between them, resembling the condition in *Cephaloxenus* (Brough, 1939; Bürgin, 1992) and *Peltopleurus nitidus* (Xu and Ma, 2016). The outer surfaces of the skull roof bones are smooth, similar to *P. nitidus*, *P. orientalis* and many other *Peltopleurus* species, but different to *Cephaloxenus* and *P. rugosus*, in which the skull is strongly ornamented by tubercles and ridges. The broad, elongate frontal is the largest element of the skull roof (3.5 times as long as the rectangular parietal). It first widens posteriorly, having its greatest width at the level of the posterior border of the orbit, and then slightly narrows posteriorly. The dermopterotic is trapezoidal and larger than the parietal, laterally contacting the posterior portion of the frontal and the whole length of the parietal.

There are two pairs of extrascapulars. They are trapezoidal bones; the lateral extrascapular is slightly larger than the medial one.

The supraorbital sensory canal enters the frontal from its anterolateral corner, runs longitudinally through the anterior two thirds of its length, and ends at the posterolateral portion of this bone. The pit lines on the parietals are not discernible due to the poor state of preservation. The supratemporal canal, indicated by two relatively large pores, runs longitudinally through the lateral portion of the dermopterotic and posteriorly enters the lateral extrascapular. The supratemporal commissural canal is enclosed in the middle portions of both extrascapulars.

Circumorbital series Similar to other peltopleuriforms, *P. tyrannos* has two infraorbitals between the antorbital and dermosphenotic. The first (anterior) is tube-like and convex ventrally, lying above the anterior half of the maxilla. The second is relatively large and deep with a rectangular dorsal portion that contacts the preopercle posteriorly and a tapered ventral portion that contacts the maxilla ventrally. The infraorbital sensory canal runs longitudinally through the first infraorbital, enters the second, and then runs dorsoventrally through this bone near its anterior margin. The dermosphenotic is narrow and keystone-shaped. It is inclined forward, contacting the supraorbital anteriorly and the suborbital posteriorly (Fig. 3A, B).

The supraorbitals are not fully exposed in all specimens. Through the X-ray scanning, the complete series of two right supraorbitals are discernible in V 19988 (Fig. 3C). Both supraorbitals are rectangular; the anterior is slightly longer than the posterior. In comparison,

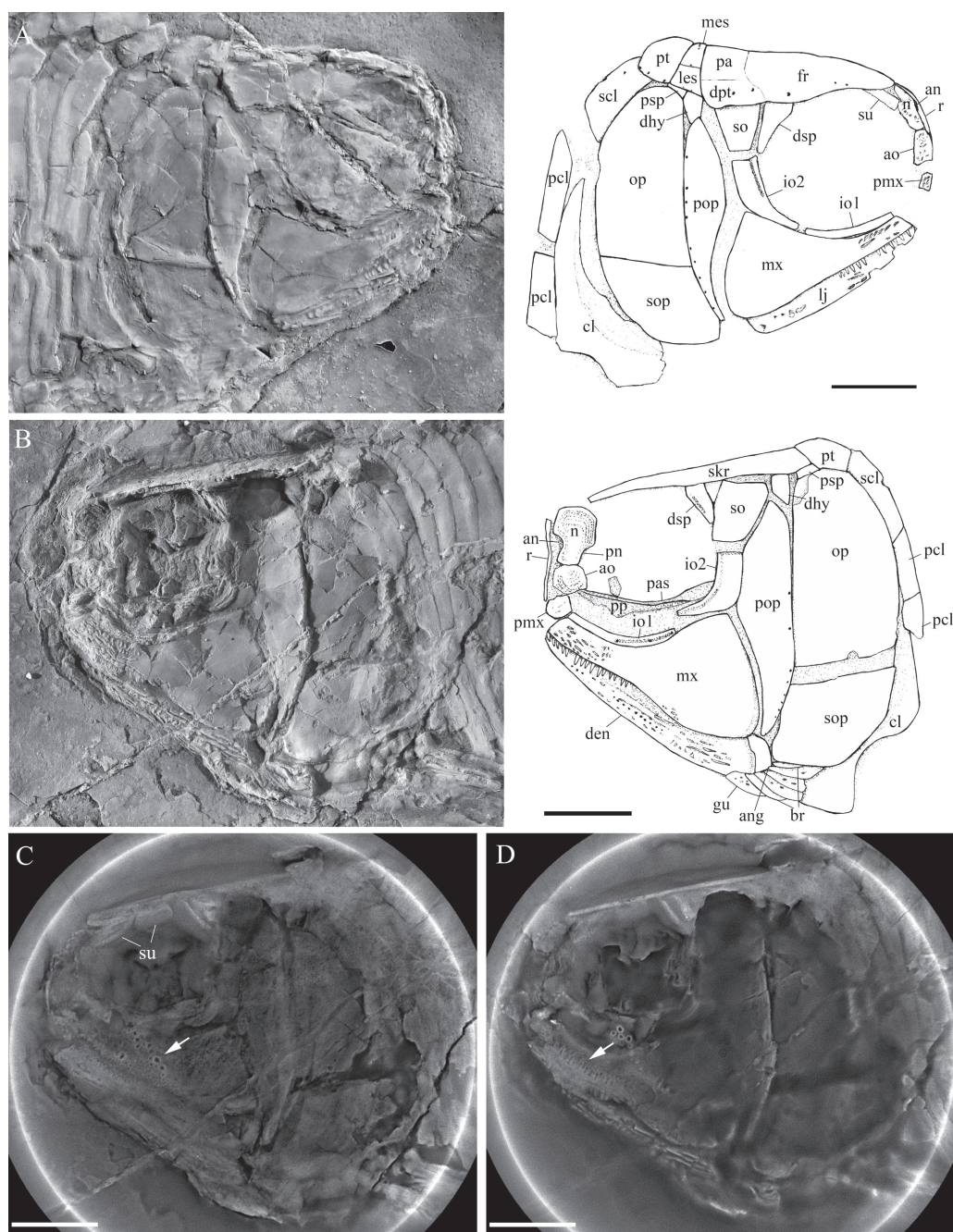


Fig. 3 Skull and pectoral girdle of *Peltopterus tyrannos* sp. nov., coated with ammonium chloride
A. IVPP V 19986; B. V 19988; C, D. micro-computed scanning slices of B, showing two supraorbitals (C),
with arrows pointing to large teeth on the oral margins of palatopterygoid (C) and dentary (D)

Abbreviations: an. anterior nostril; ang. angular; ao. antorbital; br. branchiostegal rays; cl. cleithrum;
den. dentary; dhy. dermohyal; dpt. dermopterotic; dsp. dermosphenotic; fr. frontal; gu. gular; io. infraorbital;
les. lateral extrascapular; lj. lower jaw; mes. medial extrascapular; mx. maxilla; n. nasal; op. opercle;
pa. parietal; pas. parasphenoid; pcl. postcleithrum; pmx. premaxilla; pn. posterior nostril; pop. preopercle;
pp. palatopterygoid; psp. postspiracle; pt. posttemporal; r. rostral; scl. supracleithrum; skr. skull roof;
so. suborbital; sop. subopercle; su. supraorbital. Scale bars=5 mm

P. rugosus also has two supraorbitals, but *P. nitidus* and other *Peltopleurus* species commonly have three or more supraorbitals (Brough, 1939; Bürgin, 1992; Xu and Ma, 2016).

Cheek bones There is a large suborbital that contacts the dermosphenoic anteriorly and the preopercle and dermohyal posteriorly (Fig. 3). It is trapezoidal and gradually becomes longer dorsally. A single suborbital is otherwise known in *P. nitidus*, and two or more suborbitals are generally present in other *Peltopleurus* species.

The preopercle is large and vertical, having an anteriorly expanded middle portion and tapering dorsal and ventral tips. The preopercular sensory canal runs dorsoventrally through this bone, indicated by a series of small pores near the posterior margin of this bone.

The dermohyal is a small trapezoidal bone that contacts the suborbital anteriorly, and the opercle and postspiracle posteriorly. Ventrally, it contacts the dorsal margin of the preopercle, and separates this bone from contact with the posterior portion of the skull roof.

The postspiracle is small and elongate, contacting the posttemporal posteriorly, the lateral extrascapular medially, and the opercle laterally.

The maxilla is robust, having a dorsoventrally short suborbital portion and a much dorsally expanded cheek portion. Most of the suborbital portion and a short ventral portion of the cheek expansion are ornamented with linear ridges and tubercles, and the rest of this bone is smooth (Fig. 3B). Fifteen large conical teeth are present along the oral margin of the anterior suborbital portion; among them, several anterior teeth are slightly posteriorly recurved.

Opercular-gular series Both the opercle and subopercle are trapezoidal with smooth outer surfaces; the former is twice as deep as the latter. The suture between the opercle and subopercle is slightly inclined posteriorly. The interopercle is absent, as in other stem-neopterygians and more primitive actinopterygians (Gardiner and Schaeffer, 1989; Xu et al., 2014, 2015a, b).

Six elongate and lamellate bones are preserved ventral to the posterior portion of the lower jaw and the anterior portion of the subopercle (Fig. 3B). According to their positions, the anterior one probably presents a median gular, and the rest five branchiostegal rays. Linear ridges and tubercles are present on these bones.

Lower jaw The lower jaw is wedge-shaped with two elements (dentary and angular) discernible in lateral view (Fig. 3B). The dentary is large and elongate, bearing large conical teeth similar to those on the oral margin of the maxilla (Fig. 3D). Linear ridges and tubercles are present on the ventral portion of the dentary. The angular is small and trapezoidal, contacting the dentary anteriorly. The supra-angular, known in several other peltopleuriforms, is not exposed because of the overlapping maxilla. The mandibular canal runs through the lower jaw, as indicated by a line of small pores adjacent to the ventral margin of the dentary.

Girdles and paired fins A posttemporal, a supracleithrum, two postcleithrae, and a cleithrum are discernible on each side of the pectoral girdle (Figs. 3A, B, 4).

The posttemporal is large and trapezoidal, contacting the extrascapulars anteriorly and the supracleithrum posteroventrally. The anteriorly inclined supracleithrum is rhomboid and nearly

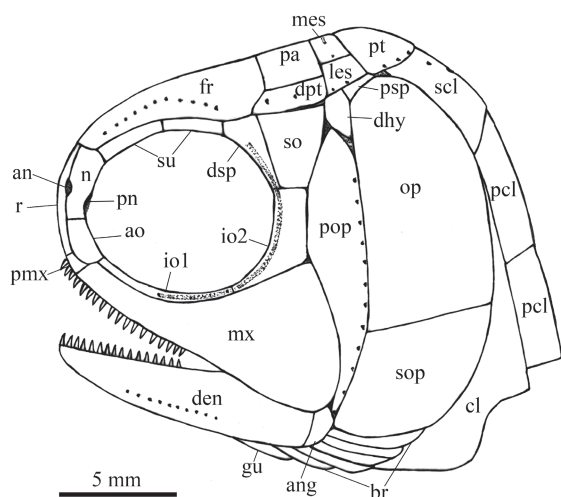


Fig. 4 Reconstruction of skull and pectoral girdle of *Peltopleurus tyrannos* sp. nov.

Abbreviations see Fig. 3

Among them, the first is strong and probably not branched, preceded by a basal fulcrum and a series of fringing fulcra, and the other rays are branched distally.

The pelvic girdle is not exposed. The pelvic fins are small and originate at the 11th vertical scale row; each consists of five or six distally segmented and branched fin rays, preceded by a basal fulcrum and a series of fringing fulcra.

Median fins The dorsal fin is small and originates above the 24th vertical scale row (Figs. 1, 2A, B, 5). It consists of seven distally segmented fin rays, preceded by two basal fulcra and a series of fringing fulcra. The first ray is unbranched and the others are branched distally.

The anal fin originates below the 16th or 17th vertical scale row. It consists of 11 fin rays, preceded by one or two basal fulcra and at least two fringing fulcra. There is a large lateral scute near the origin of the anal fin on each side of the body. Probably due to the small number of specimens, the sexual dimorphism of the anal fin in other peltopleuriforms (Bürgin, 1990, 1992; Lombardo, 1999; Tintori et al., 2012; Xu et al., 2015b; Xu and Ma, 2016) has not yet

half of the depth of the opercle. The lateral line enters the supracleithrum from the lateral portion of the posttemporal, runs obliquely through the dorsal portion of this bone, and enters the lateral line scale posteriorly.

There are two postcleithrae that contact the supracleithrum anterodorsally and the cleithrum anteriorly. Both are deep and rhomboid; the upper is slightly deeper than the ventral. The cleithrum is large and curved with a conspicuous postero-ventral notch for the pectoral fin insertion.

Each pectoral fin bears at least seven distally segmented fin rays (Fig. 2B).

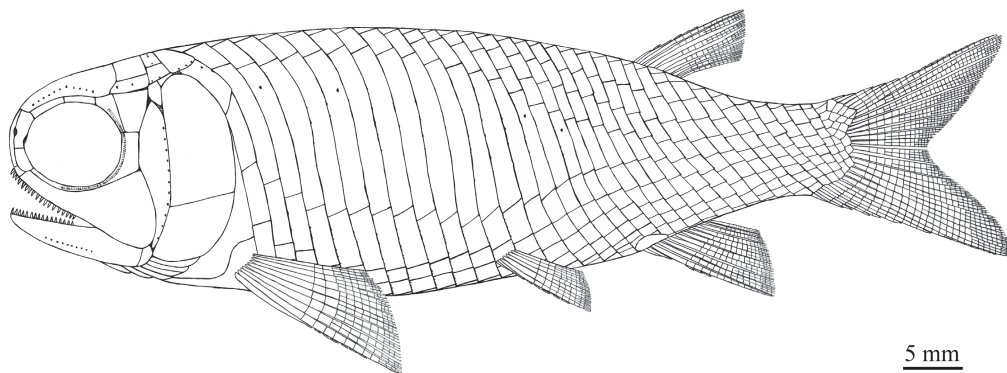


Fig. 5 Reconstruction of *Peltopleurus tyrannos* sp. nov.

been observed in that of *P. tyrannos*.

The caudal fin displays a greatly abbreviated heterocercal pattern with a moderately forked profile. The fin includes 16 principal rays. Among them, the dorsal and ventral marginal principal rays are segmented and unbranched, while the remaining rays are branched. In addition, there are two or three basal fulcra and four rudimentary fin rays in the dorsal lobe and a basal fulcrum and six or seven rudimentary fin rays in the ventral lobe. A series of small fringing fulcra is present in both lobes.

Squamation There are 35 vertical rows of scales along the lateral line of the body. Similar to other peltopleuriforms, the lateral line scales are greatly deepened in the anterior flank region. The deepest scales are eight times deeper than long. The sensory pores are present on four (the 2nd, 5th, 14th and 16th) lateral line scales in the holotype. In addition to the median scales, one and three horizontal rows of scales are present respectively above and below the lateral line scales at each side of the anterior flank region. In the caudal region, two and five horizontal rows of scales are present respectively above and below the lateral line scales. The outer surfaces of the scales are smooth. The posterior margins of scales in the anteroventral region of the body have many small serrations, and those in other regions are nearly straight (Fig. 2B, D). Peg-and-socket articulations are present as in other peltopleurids. A comparison of the squamation pattern of *Peltopleurus* species is presented in Table 1.

Table 1 Comparison of squamation pattern, size and age of *Peltopleurus* species

<i>Peltopleurus</i> species	Number of lateral line scales	Scale rows above and below lateral line in anterior trunk (above/below)		Maximum standard length (mm)	Age	Country
<i>P. humilis</i>	36–38	1	2 or 3	25	Norian	Austria
<i>P. splendens</i>	~38	2	0 or 1	~50	Carnian	Italy
<i>P. kneri</i>	48–49	1	0	~50	Carnian	Italy
<i>P. dirumptus</i>	~50	3	0	~80	Carnian	Austria
<i>P. brachycephalus</i>	37	1	1	68	Carnian	China
<i>P. lissocephalus</i>	37–40	2	3–4	55	Ladinian	Italy/Switzerland
<i>P. rugosus</i>	32–35	2	3	50	Ladinian	Italy/Switzerland
<i>P. nothocephalus</i>	32	1	0	36	Ladinian	Italy/Switzerland
<i>P. nuptialis</i>	32	2	1	25	Ladinian	Italy
<i>P. orientalis</i>	34–35	1	0	26	Ladinian	China
<i>P. tyrannos</i>	35	1	3	72	Ladinian	China
<i>P. nitidus</i>	33	2	2	30	Anisian	China

4 Phylogenetic analysis

To resolve the phylogenetic relationships of *Peltopleurus tyrannos*, a phylogenetic analysis was performed based on a data matrix expanded from Xu and Ma (2016). The present data matrix (see on-line supplementary material) includes 92 characters coded for 30 taxa. All characters were unordered and equally weighted. The stem-actinopteran *Pteronisculus* and living chondrosteian *Acipenser* were selected for out-group comparisons.

The phylogenetic analysis resulted in 18 most parsimonious trees (tree length=186

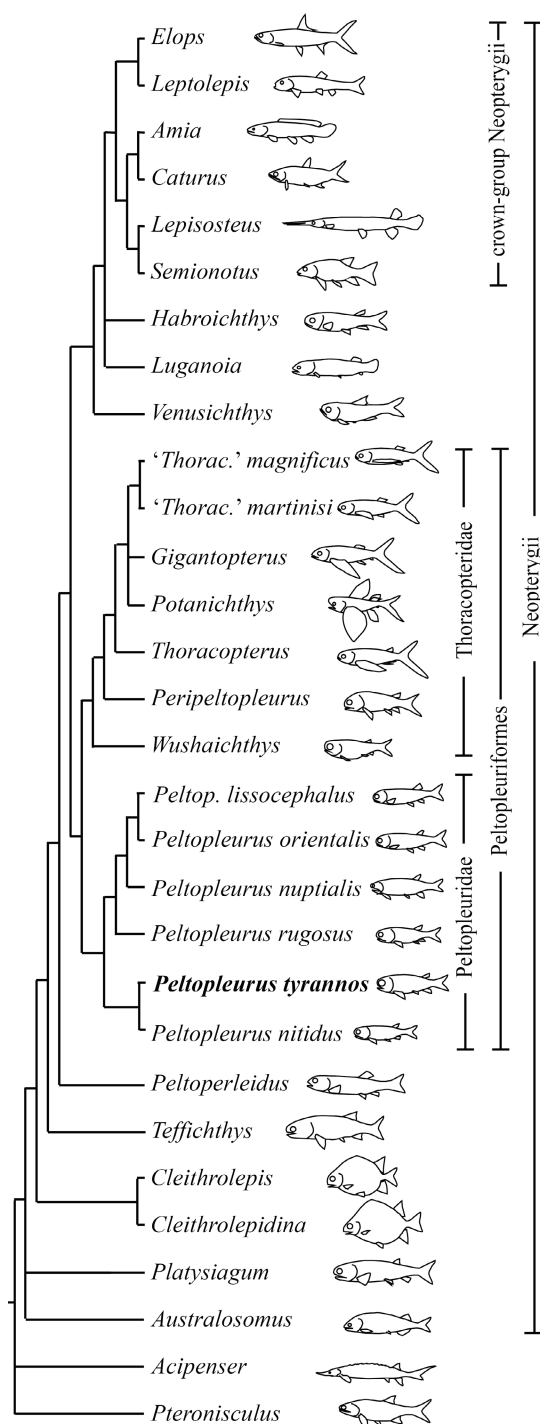


Fig. 6 Strict consensus of 18 most parsimonious trees, illustrating the phylogenetic position of *Peltopleurus tyrannos* sp. nov.

For character descriptions and codings for the sampled taxa, see the online supplementary material

steps, consistency index=0.586, retention index=0.779), the strict consensus of which is presented in Fig. 6. The results of our analysis support that the Peltopleuridae form the sister group of the Thoracopteriidae within the phylogenetic framework of Peltopleuriformes as found in the previous analysis (Xu and Ma, 2016). *P. tyrannos* is recovered as the sister taxon of *P. nitidus*; both species form a clade nested at the base of the Peltopleuridae.

P. tyrannos possesses four derived features of Peltopleuriformes: supraorbital sensory canal ending in the frontal; absence of a preopercle/dermopterotic contact; presence of a postspiracle; and presence of enlarged lateral scutes associated with the anal fin. It further possesses two derived features of the Peltopleuridae: presence of three or more extrascapulars and an opercle 1.5–2 times as large as the subopercle. The sister-taxon relationships between *P. tyrannos* and *P. nitidus* are supported by two derived features, presence of a single large suborbital, and presence of an anal fin larger than the dorsal fin.

5 Discussions

The superb preservation of *Peltopleurus tyrannos* provides important information for understanding the evolution of key features in Peltopleuriformes.

In the snout region, it shows a distinct premaxilla separated from the antorbital, which probably represents the general condition of this group. Previously, a ‘premaxilla’ resembling the fused premaxilla-antorbital in basal actinopterygians (Gardiner and Schaeffer, 1998; Gardiner et al., 2005;

Xu et al., 2014) was considered to be present in *P. lissocephalus* and *Peripeltopleurus* (Bürgin, 1992). This compound ‘premaxilla’ forms the anteroventral margin of the orbit and lacks any teeth, differing from that in most of other neopterygians. In *Peripeltopleurus*, the ‘premaxilla’ encloses the junction of the ethmoid and infraorbital canals, indicating that it may actually represent an antorbital.

In the cheek region, *P. tyrannos* shows a series of non-canal-bearing bones (e.g., suborbital, dermohyal and postspiracle) that flank the posterior portion of the skull roof and separate the opercular series from contact with the dermopterotic and extrascapular. This condition is also present in some other peltopleurids based on well-preserved specimens, including *P. nuptialis* (Xu and Ma, 2016) and *P. rugosus* (Brough, 1939; Bürgin, 1992; personal observation). Similarly positioned (probably homogenous) bones are present in basal thoracopterid *Wushaichthys*, although the postspiracle was labeled as the presupracleithrum and the dermohyal located anterior to it was not labeled (Xu et al., 2015b). Additionally, our examination shows that a well defined dermohyal (medially contacting the hyomandibular) and a postspiracle are present in the more derived thoracopterid *Potanichthys* (Xu et al., 2012); the dermohyal separates the preopercle from contact with the dermopterotic, resembling the condition in peltopleurids but differing from that of other stem-neopterygians. The results of our analysis support that the absence of the preopercle/dermopterotic contact and the presence of a postspiracle are synapomorphies of Peltopleuriformes (Xu and Ma, 2016).

In the posterior portion of the skull and the pectoral girdle, *P. tyrannos* has two pairs of extrascapulars. *P. orientalis* also has two pairs of extrascapulars (personal observation), but *P. nitidus* (Xu and Ma, 2016) and other *Peltopleurus* species (Brough, 1939; Bürgin, 1992) commonly have three extrascapulars (a pair of lateral extrascapulars and a single median one). These extrascapulars contact the posttemporals posteriorly, showing a primitive condition as seen in basal actinopterygians (Gardiner and Schaeffer, 1998; Xu et al., 2014). By contrast, thoracopterids have only a single pair of extrascapulars; as a derived feature of this family, each extrascapular contacts the posttemporal posteromedially and is separated from contact with its counterpart by the paired posttemporals (Xu et al., 2015b).

Peltopleurus tyrannos documents the largest species of this genus in the Middle Triassic. Having a standard length (SL) of up to 72 mm, the new species is significantly larger than *P. orientalis* (SL= 26 mm) and *P. nuptialis* (SL= 30 mm) in China, and all other Middle Triassic species of this genus from Europe, which have a SL no more than 55 mm (Table 1). Previously, large body-sized *Peltopleurus* were only known in the Late Triassic (Carnian), represented by *P. brachycephalus* (SL= 68 mm) in China and *P. dirumptus* (SL= ~80 mm) in Austria; the latter documents the largest species in this genus. As the age of *P. tyrannos* is well constrained (see Introduction, above), the new discovery indicates that the large-sized *Peltopleurus* occurred in nature earlier than previously thought.

Peltopleurus tyrannos is one of the rarely known ray-finned fishes in the Middle Triassic Xingyi Biota, in contrast to the numerically superior taxon *P. orientalis* from the

same biota. Represented by a dozen specimens in a relatively small ($\sim 0.01 \text{ m}^2$) slab, *P. orientalis* is probably a schooling fish feeding on small planktonic invertebrates; it resembles *P. lissocephalus* from the Middle Triassic of Monte San Giorgio (Bürgin, 1992) in lacking distinct teeth on the oral margins of the jaws. However, no schooling evidences of *P. tyrannos* were found in the multiple-year field collection at the localities. The large body size and robust pointed teeth on the anterior portions of the jaws indicate that *P. tyrannos* has a feeding mechanism and diet different from *P. orientalis* and *P. lissocephalus*. As revealed by the X-ray scanning, the oral margin of the palatopterygoid of *P. tyrannos* is covered with blunt teeth of various sizes, resembling those in *Peripelopleurus* (Bürgin, 1992) and *Potanichthys* (Xu et al., 2012). These teeth are probably used for crushing some hard-shelled invertebrates (e.g., crustaceans) or small armored fishes. We thus conclude that *Peltopleurus* from the late Middle Triassic Xingyi Biota in South China evolved into two different ecomorphotypes.

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Supplementary material can be found on the website of Vertebrate Palasiatica (http://english.ivpp.cas.cn/sp/Palasiatica/vp_list/) in Vol. 56.

云南、贵州中三叠世一种大型的肋鳞鱼(辐鳍鱼亚纲: 肋鳞鱼目)

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摘要: 肋鳞鱼目是新鳍鱼类的一个干群, 包括肋鳞鱼科和胸鳍鱼科, 生活于欧洲和华南中、晚三叠世海洋环境。其中肋鳞鱼科鱼类通常个体较小, 标准体长很少超过55 mm。根据最近发现于云南富源和贵州兴义中三叠世拉丁期($\sim 240 \text{ Ma}$)海相地层的3块保存良好的鱼化石, 命名了肋鳞鱼属一新种, 霸王肋鳞鱼(*Peltopleurus tyrannos* sp. nov.)。该发现代表了中三叠世个体最大的肋鳞鱼属物种(体长达72 mm), 为了解肋鳞鱼科的骨骼形态和摄食分异提供了新的信息。霸王肋鳞鱼不仅上、下颌口缘具有颇为粗壮的牙齿, 在口内的颞翼骨上还生长有许多不同大小的钝牙; 推测这些钝牙可能用于压碎一些带壳的无脊椎动物(如甲壳动物)和被硬鳞的小鱼, 这与此前在兴义生物群中发现的东方肋鳞鱼形成鲜明的对比: 东方

肋鳞鱼体型很小(标准体长为26 mm)、口缘无牙、个体数量丰富,可能代表了一种集群游动、捕食细小浮游无脊椎动物的肋鳞鱼物种。新的发现表明华南中三叠世兴义生物群中的肋鳞鱼属已进化出两种不同的生态类型。

关键词: 兴义生物群, 中三叠世, 肋鳞鱼科, 肋鳞鱼目, 摄食分异

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References

- Beltan L, 1972. La faune ichthyologique du Muschelkalk de la Catalogne. Mem Real Acad Cienc Artes, 41: 281–325
- Beltan L, 1975. A propos de l'ichthyofaune triassique de la catalogue espagnole. Colloques Int CNRS, 218: 273–280
- Benton M J, Zhang Q Y, Hu S X 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, 1990. Reproduction in Middle Triassic actinopterygians; complex fin structures and evidence of viviparity in fossil fishes. Zool J Linn Soc, 100: 379–391
- Bürgin T, 1992. Basal ray-finned fishes (Osteichthyes; Actinopterygii) from the Middle Triassic of Monte San Giorgio (Canton Tessin, Switzerland). Schweiz Paläont Abh, 114: 1–164
- Chen Z, 1985. Stratigraphical position of *Keichousaurus hui* from the Middle Triassic of southwestern Guizhou and its significance. Guizhou Geol, 5: 289–290
- Davenport J, 1994. How and why do flying fish fly? Rev Fish Biol Fish, 4: 184–214
- Gardiner B G, 1967. Further notes on palaeoniscoid fishes with a classification of the Chondrostei. Bull Br Mus Nat Hist (Geol), 14: 143–206
- Gardiner B G, Schaeffer B, 1989. Interrelationships of lower actinopterygian fishes. Zool J Linn Soc, 97: 135–187
- Gardiner B G, Schaeffer B, Masserie J A, 2005. A review of the lower actinopterygian phylogeny. Zool J Linn Soc, 144: 511–525
- Geng B H, Zhu M, Jin F, 2009. A revision and phylogenetic analysis of *Guizhoucoelacanthus* (Sarcopterygii, Actinistia) from the Triassic of China. Vert Palasiat, 47: 165–177
- Griffith J, 1977. The Upper Triassic fishes from Polzberg bei Lunz, Austria. Zool J Linn Soc, 60: 1–93
- Jin F, 2001. Notes on the discovery of *Birgeria* in China. Vert Palasiat, 39: 168–176
- Kner R, 1866. Die Fische der bituminösen Schiefer von Raibl in Kärnten. Sitz Akad Wiss Wien, 53: 152–197
- Kner R, 1867. Nachtrag zu der fossilen Fauna der Asphaltschiefer von Seefeld in Tirol. Sitz Akad Wiss Wien, 56: 898–913
- Lehman J P, 1979. Note sur les poissons du Trias de Lunz. I. *Thoracopterus* Bronn. Ann Naturhist Mus Wien, 82: 53–66
- Li C, Wu X C, Zhao L J 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 J L, 2006. A brief summary of the Triassic marine reptiles of China. Vert Palasiat, 44: 99–108
- Li J L, Jin F, 2003. New advances of the research on *Keichousaurus* reptile fauna. Prog Nat Sci, 13: 796–800
- Li J L, Jin F, 2009. Swimming in the Ocean Two Hundred Million Years Ago: Triassic Marine Reptile and Environment of South China. Beijing: Science Press. 1–145
- Li Z G, Sun Z Y, Jiang D Y 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

- Lin H Q, Sun Z Y, Tinori A et al., 2011. A new species of *Habroichthys* Brough, 1939 (Actinopterygii; Peltopleuriformes) from the Pelsonian (Anisian, Middle Triassic) of Yunnan Province, South China. *Neues Jahrb Geol Paläont Abh*, 262: 79–89
- Liu G B, Yin G Z, Wang X H, 2002. On the most primitive amiid fish from Upper Triassic of Xingyi, Guizhou. *Acta Palaeont Sin*, 41: 461–463
- Liu G B, Yin G Z, Wang X H et al., 2003. New discovered fishes from *Keichousaurus* bearing horizon of Late Triassic in Xingyi of Guizhou. *Acta Palaeont Sin*, 42: 346–366
- Liu G B, Yin G Z, Luo Y M et al., 2006. Preliminary examination of fish fossils from Upper Triassic Wayao Member of Falang Formation in Guanling of Guizhou. *Acta Palaeont Sin*, 45: 1–20
- Lombardo C, 1999. Sexual dimorphism in a new species of the actinopterygian *Peltopleurus* from the Triassic of northern Italy. *Palaeontology*, 412: 741–760
- Lu H, Jiang D Y, Motani R et al., 2017. Middle Triassic Xingyi Fauna: showing turnover of marine reptiles from coastal to oceanic environments. *Palaeoworld*, doi: 10.1016/j.palwor.2017.05.005
- Nelson J S, Grande T C, Wilson M V H, 2016. *Fishes of the World*. 5th ed. Hoboken, New Jersey: John Wiley & Sons, Inc. 1–707
- Su D Z, 1959. Triassic fishes from Kueichow, Southwest China. *Vert PalAsiat*, 3: 205–210
- Swofford D L, 2003. PAUP*. Phylogenetic Analysis Using Parsimony (* and other Methods), version 4. Sunderland, Massachusetts: Sinauer Associates
- Tintori A, Sassi D, 1992. *Thoracopterus* Bronn (Osteichthyes: Actinopterygii): a gliding fish from the Upper Triassic of Europe. *J Vert Paleont*, 12: 265–283
- Tintori A, Sun Z Y, Lombardo C et al., 2012. A new flying fish from the late Ladinian (Middle Triassic) of Wusha (Guizhou Province, southern China). *Gortania*, 33: 39–50
- Tintori A, Sun Z Y, Ni P G et al., 2015. Oldest stem Teleostei from the late Ladinian (Middle Triassic) of southern China. *Riv Ital Paleont Stratigr*, 121: 285–296
- Westoll T S, 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
- Woodward A S, 1895. Catalogue of the Fossil Fishes in the British Museum (Natural History), Part III. London: Trustees of the British Museum. 1–544
- Xu G H, Ma X Y, 2016. A Middle Triassic stem-neopterygian fish from China sheds new light on the peltopleuriform phylogeny and internal fertilization. *Chin Sci Bull*, 61: 1766–1774
- Xu G H, Ma X Y, 2017. Taxonomic revision of *Asialepidotus shingyiensis* Su, 1959 (Halecomorphi, Holostei) from the Middle Triassic (Ladinian) of Guizhou and Yunnan, China. *Res Know*, 3: 36–38
- Xu G H, Zhao L J, Gao K Q 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 G H, Gao K Q, Finarelli J A, 2014. A revision of the Middle Triassic scanilepiform fish *Fukangichthys longidorsalis* from Xinjiang, China, with comments on the phylogeny of the Actinopteri. *J Vert Paleont*, 34: 747–759
- Xu G H, Gao K Q, Coates M I, 2015a. Taxonomic revision of *Plesiofuro mingshuica* from the Lower Triassic of northern Gansu, China, and the relationships of early neopterygian clades. *J Vert Paleont*, 35: e1001515
- Xu G H, Zhao L J, Shen C C, 2015b. A Middle Triassic thoracopterid from China highlights the evolutionary origin of overwater gliding in early ray-finned fishes. *Biol Lett*, 11: 20140960
- Young C C, 1958. On the new pachypleurosauroida from Keichow, Southwest China. *Vert PalAsiat*, 2: 69–81
- Zou X D, Balini M, Jiang D Y 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