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First revision

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A new perleidid neopterygian fish from the Early Triassic (Dienerian, Induan) of South China, with a reassessment of the relationships of Perleidiformes

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Neopterygii is the largest clade of ray-finned fishes, including Teleostei, Holostei, and their closely related fossil taxa. This clade was first documented in Early Carboniferous and underwent rapid evolutionary radiation during the Early to Middle Triassic. This paper describes a perleidid neopterygian, *Teffichthys elegans* sp. nov., based on 13 well-preserved specimens from the lower Daye Formation (Dienerian, Induan) in Guizhou, China. The new species documents one of the oldest perleidids, and its studies provide insights into the early diversification of this family. The results of a phylogenetic analysis recover *Teffichthys elegans* sp. nov. as a sister taxon to *Teffichthys madagascariensis* within the Perleididae. *T. elegans* sp. nov. shares three derived features of Perleididae: the length of the anteroventral margin of the dermohyal nearly half the length of the anterodorsal margin of the preopercle; the anteroventral margin of the preopercle nearly equal to the anterior margin of the subopercle in length; and the anteroventral margin of the preopercle 1-2 times as long as the anterodorsal margin of the preopercle. It possesses diagnostic features of *Teffichthys* but differs from *T. madagascariensis* by the following features: presence of three supraorbitals; six pairs of branchiostegals rays; relative deep anterodorsal process of subopercle; absence of spine on the posterior margin of jugal; and pterygial formula of D26/P14, A22, C36/T39-41. The Perleidiformes are restricted to include only the Perleididae, and other previously alleged ‘perleidiform’ families (e.g., Hydropessidae and Gabanellidae) are excluded to maintain the monophyly of this order. Similar to many other perleidids, *T. elegans* sp. nov. is likely a durophagous predator with dentition combining grasping and crushing morphologies. The new finding also provides an important addition to our understanding of the trophic structure of the Early Triassic marine ecosystem in South China.

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Abstract

Neopterygii is the largest clade of ray-finned fishes, including Teleostei, Holostei, and their closely related fossil taxa. This clade was first documented in Early Carboniferous and underwent rapid evolutionary radiation during the Early to Middle Triassic. This paper describes a perleidid neopterygian, *Teffichthys elegans* sp. nov., based on 13 well-preserved specimens from the lower Daye Formation (Dienerian, Induan) in Guizhou, China. The new species documents one of the oldest perleidids, and its studies provide insights into the early diversification of this family. The results of a phylogenetic analysis recover *Teffichthys elegans* sp. nov. as a sister taxon to *Teffichthys madagascariensis* within the Perleididae. *T. elegans* sp. nov. shares three derived features of Perleididae: the length of the anteroventral margin of the dermohyal nearly half the length of the anterodorsal margin of the preopercle; the anteroventral margin of the preopercle nearly equal to the anterior margin of the subopercle in length; and the anteroventral margin of the preopercle 1-2 times as long as the anterodorsal margin of the preopercle. It possesses diagnostic features of *Teffichthys* but differs from *T. madagascariensis* by the following features: presence of three supraorbitals; six pairs of branchiostegals rays; relative deep anterodorsal process of subopercle; absence of spine on the posterior margin of jugal; and pterygial formula of D26/P14, A22, C36/T39-41. The Perleidiformes are restricted to include only the Perleididae, and other previously alleged ‘perleidiform’ families (e.g.,

Hydropessidae and Gabanellidae) are excluded to maintain the monophyly of this order. Similar to many other perleidids, *T. elegans* sp. nov. is likely a durophagous predator with dentition combining grasping and crushing morphologies. The new finding also provides an important addition to our understanding of the trophic structure of the Early Triassic marine ecosystem in South China.

1. Introduction

The Permian-Triassic mass extinction was the biggest biotic extinction in the Phanerozoic, wiping out more than 80-90% of marine species (Erwin 2006; Song et al. 2013; Fan et al. 2020). Benthic animals, especially reef-building taxa, were severely decimated during the Permian-Triassic crisis (Kiessling 2010). However, the diversity of nekton (cephalopods and fishes) was less impacted, probably because of their high motility (Song et al. 2018). As an important component of the Modern Evolutionary Fauna, Neopterygii underwent an essential early evolution stage during the Early Triassic (Sepkoski 1981; Tintori et al. 2014; López-Arbarello & Sferco 2018; Romano 2021).

Consisting of Teleostei, Holostei, and closely related taxa, Neopterygii occupies a predominant position in the composition of living ray-finned fishes, which has not always been the case throughout Earth's history (Arratia 1999; Friedman 2015; Nelson et al. 2016; López-Arbarello & Sferco 2018; Xu 2020b). Since the earliest fossil recorded from the Mississippian (Early Carboniferous), Neopterygii maintained a very low diversity until the end-Permian (Near et al. 2012; Xu et al. 2014(Near et al. 2012). Neopterygii was less affected by the Permian-Triassic mass extinction (Scheyer et al. 2014; Vázquez & Clapham 2017; Smithwick & Stubbs 2018) and experienced rapid evolutionary radiation during the Early Triassic (Xu & Gao 2011; Tintori et al. 2014; Friedman 2015; Romano et al. 2016a).

To date, Early Triassic neopterygians have been identified on all continents except South America and Antarctica. Africa, particularly South Africa, Kenya, Tanzania, and Angola, is the main locality of Early Triassic freshwater neopterygians. They have also been recovered in Australia, China, Russia, France and Germany (Fig. 1A). Over the last century, Early Triassic marine neopterygian localities have been uncovered in East Greenland, Madagascar, West Canada, and Spitsbergen. Recently, some marine neopterygians during this period have been reported from South China, India, and the Western USA (Fig. 1A).

During the Early Triassic, members of Neopterygii were mainly represented by stem-neopterygian taxa (Romano et al. 2016b), with only a few holosteans reported, namely *Angolaichthys* (Teixeira 1948), *Paracentrophorus* (Gardiner 1960), and *Tungusichthys* (Berg 1941). The unambiguous representative genera of the Early Triassic Neopterygii include

Australosomus, *Watsonulus*, *Helmolepis*, *Plesioperleidus*, and *Teffichthys*, all of which have been confirmed in cladistic analyses (Stensiö 1932; Lehman 1952; Jin et al. 2003; Mutter 2005; Tong et al. 2006; Marramà et al. 2017). In addition, *Albertonia* and *Parasemionotus*, which are supposed to be Neopterygii but still need formal cladistic analyses, were also widespread during the Early Triassic (Lehman, 1952; Davies et al., 1997).

Perleidiformes are a group of stem-neopterygian taxa that lived in both marine and freshwater environments in the Triassic. The paraphyly of the traditional Perleidiformes has been noticed in many previous phylogenetic studies (Supplementary Table T1; Xu et al. 2015; Xu et al. 2018; Wen et al. 2019). Since being erected by Berg (1937), 13 families have been assigned to this order (Berg 1940; Gardiner 1967; Hutchinson 1973; Bürgin 1992; Tintori & Lombardo 1996; Lombardo & Tintori 2004; López-Arbarello & Zavattieri 2008; Sun et al. 2012; Tintori et al. 2016). Among them, nine families were moved to other orders or abandoned: Luganoiidae and Fuyuanperleididae were moved to Luganoiiformes, Cleithrolepidae and Polzbergiidae were moved to Polzbergiiformes, Platysiagidae was placed in its own order Platysiagiformes, Pseudobeaconiidae was included in Louwoichthyiformes, and Teleopterinidae was moved to Amphicentriformes. Aetheodontidae was abandoned by the type and only known genus of this family assigned to Perleididae. Habroichthyidae and Colobodontidae were excluded from this order (Griffith 1977; Bürgin 1992; López-Arbarello & Zavattieri 2008; Van Der Laan 2018; Xu 2020b). Consequently, Perleidiformes includes three families: Perleididae, Hydropessidae, and Gabanellidae. The latter two families only include a single genus each: *Hydropessum* Broom 1913 from Hydropessidae Hutchinson 1973 and *Gabanellia* Tintori & Lombardo 1996 from Gabanellidae Tintori & Lombardo 1996 (Hutchinson 1973; Tintori & Lombardo 1996).

Perleididae is known from many Triassic fish localities and has a complicated taxonomic history. More than 30 genera have been grouped in this family. Nevertheless, many of them were revised later. At present, 16 genera are currently remained in Perleididae: *Meidiichthys*, *Perleidus*, *Manlietta*, *Procheirichthys*, *Plesioperleidus*, *Aetheodontus*, *Meridensia*, *Alvinia*, *Eoperleidus*, *Megaperleidus*, *Endennia*, *Paraperleidus*, *Diandongperleidus*, *Luopingperleidus*, *Chaohuperleidus*, and *Moradebrichthys* (Brough 1931; Wade 1935; Su & Li 1983; Bürgin 1992; Sytchevskaya 1999; Lombardo & Brambillasca 2005; Zhao & Lu 2007; Geng et al. 2012; Sun et al. 2013; Cartanyà et al. 2019). It should be noted that the relationships of most of these genera still require further strict phylogenetic analysis.

The taxonomy of Perleididae in the Early Triassic is controversial. Except for *Chaohuperleidus*, all perleidids in the Early Triassic have historically been placed in the genus *Perleidus* (Stensiö, 1921; Stensiö, 1932; Piveteau, 1934; Lehman, 1952; Su, 1981). Lombardo (2001) proposed that all current Early Triassic *Perleidus*-like fishes should be excluded from *Perleidus* due to the absence of epaxial rays. Later, Marramà et al. (2017) erected a new genus

Teffichthys, and proposed that, except *Plesioperleidus*, all other Early Triassic *Perleidus*-like fishes should be included in *Teffichthys*.

Abundant Early Triassic Neopterygii have been found in South China over the last 40 years, providing essential material to study the early evolution of Neopterygii and the origin of the modern evolution of fish fauna. Hitherto, 11 Neopterygii genera have been described from the Early Triassic in China (Su 1981; Su & Li 1983; Qian et al. 1997; Liu et al. 2002; Jin et al. 2003; Tong et al. 2006; Li 2009; Sun et al. 2013; Qiu et al. 2019). They were mainly identified from Jurong, Jiangsu Province and Chaohu, Anhui Province, including seven and five genera, respectively (Fig. 1B). Interestingly, except for *Paraperleidus* from the Griensbachian (Early Induan), all the Early Triassic Neopterygii in China came from the Olenekian.

Here we describe a new perleidid based on 13 specimens from the Lower Triassic Daye Formation at two sections (Gujiao and Lianhuacun) near Guiyang, Guizhou Province (Fig. 1B). A calcareous concretion and 12 flat specimens from black shales are described in this paper. The fossil beds are deposited in a basin or basin-margin environment (Dai et al., 2019). During the Early Triassic, Guiyang was located on the southern edge of the Yangtze Platform. In addition to the new perleidid, other fossils from the localities include several other types of bony fishes (e.g., coelacanths, parasemionotids) and invertebrates (e.g., bivalves, ammonoids). The age of the fossil beds is dated as Dienerian (Induan, Early Triassic), based on ammonoid and conodont biostratigraphy (Qin et al. 1993; Mu et al. 2007; Bruehwiler et al. 2008; Dai et al. 2019).

2. Materials & Methods

All materials were stored at the YiFu Museum of China University of Geoscience, Wuhan (CUGM). The specimens were prepared using air chisels under a microscope. A three-dimensionally preserved skull of the holotype (CUGM K2-E2601) was prepared from both sides. A CT scan was performed while useless information was obtained due to the internal mineralization. The specimens were photographed using a Canon 70D camera with a Micro EF lens with a focal length of 100 mm and f/2.8 aperture. Microscopic images were taken under a Leica S8 APO stereomicroscope. Illustrations were drawn using Adobe Photoshop CS6 and Coreldraw X7 software. The relative position of the fins and scale counts were expressed following Westoll (1944). The traditional actinopterygian terminology (e.g., Bürgin, 1992; Grande & Bemis, 1998) is followed.

To explore the phylogeny of Perleididae, a cladistic analysis was conducted based on materials of *Teffichthys elegans* sp. nov., and direct observations on materials of *Paraperleidus* (ZMNHM M1401) and *Plesioperleidus* (ZMNHM M8499, 8500; CUGM J2203a; IVPP V5343). In addition, we added *Moradebrichthys* and *Chaohuperleidus*, both of which are well preserved and were placed in Perleididae (Sun et al. 2013; Cartanyà et al. 2019; Dai et al. 2021). In order to explore the positions of Hydropessidae, and Gabanellidae, we also added *Hydropessum* and *Gabanellia* based on paper materials (Hutchinson 1973; Tintori & Lombardo 1996). The phylogenetic analysis was based on an updated dataset revised from the data matrix of Xu (2021), containing 142 characters coded for 66 taxa. All characters were unordered and unweighted, and the basal actinopterygian *Moythomasia durgaringa* was selected as the outgroup taxon. Phylogenetic analyses were performed using the heuristic search algorithm (gaps treated as missing data, 500 random addition sequence replicates, tree bisection-reconnection [TBR] branch-swapping, with five trees held at each step and multiple trees saved) in PAUP* 4.0a169 (Swofford 2003).

Anatomical abbreviations: ang, angular bone; ao, antorbital bone; bf, basal fulcrum; br, branchiostegal rays; cl, cleithrum; cla, clavicle; den, dentary; dh, dermohyal; dsp, dermosphenotic; exs, extrascapular; ff, fringing fulcrum; fr, frontal bone; ju, jugal; hm, hyomandibular; la, lacrimal bone; lg, lateral gular; mgu, medial gular; mx, maxilla; na, nasal; op, opercle; pa, parietal; pas, parasphenoid; pcl, postcleithrum; pop, preopercle; prr, procurrent ray; pr, principal ray; psp, postspiracular bone; pt, posttemporal; ro, rostral; sc, scale; scl, supracleithrum; so, suborbital; sop, subopercle; sr, sclerotic bone; su, supraorbital bone; s-ju, spiny process along the dorsal margin of the jugal.

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3. Results

3.1 Systematic paleontology

Infraclass Actinopteri Cope, 1871
Superdivision Neopterygii Regan, 1923
Order Perleidiformes Berg, 1937

Family Perleididae Brough, 1931

Genus *Teffichthys* Marramà et al., 2017

Species *Teffichthys elegans* sp. nov.

LSID urn:lsid:zoobank.org:act:7AD93E0E-25F6-415E-8BBD-43872084F3D8

(Figs. 2–9).

Etymology. The specific epithet 'elegans' means elegant.

Holotype. CUGM K2-E2601. A specimen was preserved in a calcareous concretion, with the snout region and upper lobe of the caudal fin missing.

Paratype. CUGM K2-E2602-2604.

Referred specimens. CUGM K2-E2605-2613.

Type Locality and Horizon. Lianhuacun Village, Guiding County and Gujiao Village, Longli County of Guizhou Province, China; Daye Formation; Dienerian, Early Triassic.

Diagnosis. A new species of *Teffichthys* distinguished from the type species of this genus by the following features (autapomorphies identified with an asterisk): presence of three supraorbitals; six pairs of branchiostegals rays; relative deep anterodorsal process of subopercle; absence of spine on the posterior margin of jugal; and pterygial formula of D26/P14, A22, C36/T39-41 (*).

3.2 Description

General Morphology and Size. *Teffichthys elegans* sp. nov. has a blunt snout, an elongate and fusiform body, and a forked, nearly equilobated caudal fin (Figs. 2, 3). The dorsal fin is larger than the anal fin and inserts slightly posterior to the origins of the pelvic fins. It has a standard length (SL; the length from the tip of the snout to the posterior extremity of the caudal peduncle) of 125–148 mm. The orbital region is relatively large, and its length accounts for 7.7-9.5% of the SL. The maximum depth of the body, located at the midway between the pectoral and dorsal fins, ranges from 37 mm to 51 mm. Head length and body depth accounted for 21.6–24.2% and 27.8–34.5% of the SL, respectively. The general body form is reconstructed based on the holotype and CUGM K2-E2602-2609 (Figs. 2-8).

Snout. A median rostral and a pair of nasals and antorbitals are discernable from the snout region, and the premaxillae are poorly known because of incomplete preservation.

The rostral is the largest element of the snout region, being half of the length of the frontal (Figs. 5B-D). It is broad and shield-like, reaching its maximum width lower to the boundary between nasal and antorbital, and then it becomes narrower up and down. There are no teeth on the rostral, excluding the possibility that it contributes to the oral margin. A distinct notch for the anterior nostril is present at the middle level of the lateral margin of the rostral (Fig. 5B). The surface of this bone is ornamented with tubercules (Figs. 5B-D), and the ethmoid sensory canal is hard to identify.

The nasals are dorsoventrally elongated, shorter than the rostral in length. It tapers dorsally and contacts the frontal and supraorbital dorsally, the antorbital ventrally, and the rostral medially. Similar to the rostral, the nasal is also ornamented with small tubercles on its external surface. A short anterior portion of the supraorbital sensory canal is present in the dorsal half of the nasal (Fig. 5B).

The antorbital is rectangular, twice as long as it is wide. It contacts the nasal dorsally, the rostral anteriorly, the maxilla ventrally, and the lacrimal posteriorly (Figs. 5B-D). The posterior edge of the antorbital forms a part of the anterior margin of the orbit. It also bears dense small round tubercles on the surface. The infraorbital canal and ethmoid sensory canal meet on the upper portion of the antorbital (Fig. 5B).

The premaxilla is small, bearing more than two conical teeth (Fig. 6B). It contacts the rostral and antorbital dorsally and the maxilla posteriorly.

Skull Roof. The skull roof is composed of a pair of frontals, parietals, dermopterotics, and extrascapulars (Figs. 4E, F; 5C, D). The frontals are broad and trapezoidal in shape, slightly tapering anteriorly. Each frontal contacts its counterpart medially along a zigzag suture, and the parietal posteriorly with a wavy posterior suture. The short anterior part of the frontals is missing in the holotype, while from specimen CUGM K2-E2604, it is unambiguous that the anterior region of the frontal contacts its counterpart medially. The length of the frontal is approximately twice the length of the parietal. The frontal reaches its greatest width at the level of the posterior border of the orbit and slightly narrows towards the parietals.

The parietals are relatively small, rectangular in shape, and slightly broader than long (Figs. 4E, F). The median suture between the parietals is slightly curved. Each parietal contacts the dermopterotic laterally and the extrascapular posteriorly.

The supraorbital sensory canal runs longitudinally through the frontals along a sigmoid line, enters the parietal, and extends backwards for a short distance in this bone (Figs. 4 and 5C, D). A middle pit-line can be recognized on the left parietal; the posterior pit-line on the right parietal is also discernable (Figs. 5C, D).

The dermopterotics are anteroposteriorly elongated, nearly twice the length of the parietal (Figs. 4A-F). They contact the posterior portion of the frontal and the full length of the parietal medially. The supratemporal sensory canal runs through the dermopterotic longitudinally and posteriorly enters the extrascapular through a notch at its anterior margin.

The extrascapulars are subtriangular in shape (Figs. 4A-F). Each extrascapular tapers medially and contacts its counterpart medially, the parietal and the dermopterotic anteriorly, and the posttemporal posteriorly. The supratemporal commissure runs through the anterior portions of both extrascapulars as is indicated by a series of small tubercles.

All these skull roof bones are ornamented with dense tubercles, well preserved on specimen CUGM K2-E2604. Some ridges can be detected on the surface of extrascapulars, which are usually parallel to the bone margin.

Circumorbital Bones. There is a series of three rectangular to trapezoidal supraorbitals, contacting the frontal medially, the nasal anteriorly, and the dermosphenotic posteriorly (Figs. 4A, B; 5C, D). Among them, the first (anteriormost) supraorbital is the largest of the series, ornamented with strong ridges and tubercles. The second supraorbital is shorter and ornamented with weak tubercles. The third (posteriormost) supraorbital is nearly the same length as the second one, with weak ornamentation on the surface. It was split into two parts in the holotype (Fig. 5A).

Two infraorbitals, the lacrimal and the jugal, are present (Figs. 4A-D; 5C, D). The lacrimal is elongate, dorsoventrally short, and slightly concave dorsally. It is not fused with the maxilla. The jugal is roughly crescent and more expanded dorsally. It bears a prominent spiny process along its dorsal margin, which might be the channel of the infraorbital sensory canal. In addition, a tubercle occurs in the anterior portion of the jugal on both sides (Figs. 4A-D).

The dermosphenotic is key-stone shaped and dorsally expanded, slightly deeper than wide. The bone contacts the frontal and dermopterotic dorsally and the jugal ventrally. The infraorbital sensory canal extends through the entire length of the infraorbital and dermosphenotic, and then enters the dermopterotic posteriorly, and connects with the supratemporal sensory canal.

Cheek. There are two suborbitals (Figs. 4C, D). The anterior suborbital is located posterior to the dermosphenotic. It is quadrangular in shape, slightly shorter than the dermosphenotic, and has a smooth posterior margin. The posterior suborbital is smaller and subtriangular, contacting the anterior suborbital anteriorly, the preopercle ventrally, and the dermopterotic dorsally.

The dermohyal bone is quadrangular, contacting the dermopterotic dorsally, and the preopercle ventrally (Figs. 4A-D). It has a relatively large size compared with other Perleididae.

The postspiracular bone (Figs. 4C, D) is small, elongate, and nearly smooth, contacting the extrascapular dorsally, the dermohyal anteriorly, the opercle ventrally, and the posttemporal posteriorly. Notably, it is only exposed on the left side of the holotype.

The maxilla is anteriorly elongated and posteriorly expanded in shape, contacting the preopercle with a gently curved posterodorsal suture. It bears a row of approximately 25 conical teeth along the slightly curved oral margin, and the size of the teeth decreases posteriorly (Figs. 4, 5). The lateral surface of the maxilla is ornamented with dense tubercles and ridges, although some of them were lost during specimen preparation.

Palatal bones and suspensorium. The hyomandibula is not exposed. The rounded molariform teeth of the palatal bones are present, exposed next to the posterior-dorsal portion of the maxilla (Fig. 6D).

Lower jaw. The dentary is exposed on both sides of the holotype. It is slender and elongated with a nearly straight oral margin and a convex ventral margin, posteriorly bounded by a small angular (Figs. 4A, B). The dentition along the oral margin of the dentary consists of more than 24 peg-like teeth, and their length also decreases posteriorly. The supra-angular and coronoid process are not discernible. The angular is small and irregular in lateral view, tapering anteroventrally. The dentary is ornamented with small tubercles and transverse running, interrupted ridges, and the latter are mainly distributed near the oral margin. The mandibular sensory canal crosses ventrally the entire length of the dentary and the angular.

Operculogular Series. The opercle is subtriangular in shape, having a nearly straight margin with the dermohyal anterodorsally. The subopercle is trapezoidal in shape with a concave dorsal margin. It is larger than the opercle, possessing a moderately developed anterodorsal process (Figs. 4, 5).

The preopercle is large and broad, contacting the second infraorbital (jugal) and suborbital anteriorly, the dermopterotic dorsally, and the dermohyal and opercle posteriorly. The ventral part of the preopercle is wedged between the maxilla and the subopercle. The dorsal part of the preopercle is also pointed, in contact with the dermopterotic by the suborbital and dermohyal. The preopercular sensory canal extends along the posterior margin of this bone, indicated by a series of small pores (Figs. 4, 5).

Six pairs of branchiostegal rays are present below the dentary and angular. Four pairs are mediolaterally elongated and nearly equal in size in the anterior region (Figs. 4A, B). The latter two pairs broaden posteriorly, having the same width as the anterior branchiostegal rays. A large and nearly oval bone, anterior to branchiostegals, is interpreted as the median gular (Fig. 6A). It shows a tapered anterior margin and convex posterior margin. The median gular is approximately one-third the length of the dentary. Only the right lateral gular is preserved. It is trapezoidal in shape and is overlapped by the first branchiostegal ray in the posterior portion (Figs. 5A, B).

Pectoral Girdle and Paired fins. The posttemporals are subrectangular in shape and widely separated from each other by the mid-dorsal scales (Figs. 4E, F). The posttemporal contacts the dermopterotic anteriorly, the opercle laterally, and the supracleithrum posteriorly. The supracleithrum is a large bone, deep and quadrangular, inclined forward, ornamented with dense tubercles and ridges mainly on the middle and anterior portion of this bone. There are two vertically arranged postcleithrums below the supracleithrum, showing dense tubercles on the surface. The dorsal postcleithrum is rectangular in shape, with its dorsal process overlapped by the supracleithrum. The ventral postcleithrum is irregular in shape, with a concave dorsal margin, smaller than the dorsal postcleithrum. The cleithrum is elongated, curved, and inclined backwards. It is partly overlapped anteriorly by the subopercle, mainly ornamented with ridges on the surface.

The pectoral fins insert low on the body. The exoskeletal part of the pectoral fin is large, nearly the same size as the anal fin, and each consists of 16 distally segmented and twice branched rays (Fig. 9A). The first ray is preceded by more than 10 fringing fulcra and two basal fulcra (Figs. 4A, B). There are at least five short, rod-like radials between the cleithrum and the exoskeletal portion of the pectoral fin (Figs. 4A, B). The endoskeletal part of the pectoral fin is not exposed.

The pelvic fin originates at the 14th vertical scale row. It is smaller than the pectoral fin, and contains six distally segmented fin rays, preceded by two basal fulcra and at least 13 fringing fulcra (Fig. 8C). The first pelvic ray is unbranched, and the remaining five rays are twice branched distally.

Median fins. The dorsal fin originates above the 26th vertical scale row (Fig. 8B). It is composed of three procurrent rays and 12 principal rays, preceded by three basal fulcra and at least 16 fringing fulcra. All rays are segmented distally. The procurrent rays become longer posteriorly, and the third procurrent ray is the longest one, being approximately three times the length of the first principal ray. The first principal ray, slightly shorter than the second, is unbranched, and the other rays are distally twice branched. The second principal ray is the longest ray of the dorsal fin and other principal rays become shorter posteriorly. There are seven exposed thick, rod-like pterygiophores supporting the dorsal fin. Each of them nearly corresponds to a single fin ray, indicating that rays and pterygiophores are nearly equal in number (Fig. 8B).

The anal fin originates below the origin of the 22th vertical scale row. It contains two procurrent rays and 9 principal rays. The fin contains two unbranched rays, preceded by two basal fulcra (Fig. 8A). All rays are segmented distally and only the first three rays are unbranched. Both of the procurrent rays are associated with fringing fulcra in their anterior margin. Notably, the first procurrent ray is very short, nearly one-third of the second one. The endoskeleton of the anal fin is not exposed.

The caudal fin, well preserved in specimens CUGM K2-E2607-2608 (Figs. 3A, B; 9B-D), is abbreviated heterocercal (backbone only extending slightly into upper lobe of the caudal fin, (Thomas et al. 2007) with a forked posterior profile. The caudal fin consists of 20-23 principal rays. There are three procurrent rays and seven epaxial basal fulcra in the dorsal lobe (Fig. 4B), and six procurrent rays and two basal fulcra in the ventral lobe (Figs. 9C, D). The surfaces of rays are ornamented with slender tubercles, parallel to the direction of fin rays, generally one to two in number (Figs. 9C, D).

Squamation. The body is entirely covered by ganoid scales. The scales are arranged in 39-41 vertical rows along the lateral line (Figs. 2, 3). The lateral line scales are the deepest in each vertical row. Each of them has a small notch at its posterior margin and two small pores that are present anteriorly in some of them. The lateral line scales are deep in the anterior region. They decrease gradually in size toward the posterior region and become rhomboidal on the caudal peduncle. In the anterior region of the trunk, the scales are deep and narrow, with numerous well-developed denticles at the posterior margin, and tubercles and ridges are well developed on the free field. In contrast, in the posterior flank region, the scales are rhomboidal and smooth, and the denticles at the posterior margin gradually decrease in number posteriorly.

3.3 Character comparisons

The major difference between *Teffichthys elegans* sp. nov. and *Perleidus* are the suborbital and the teeth on the jaws (Fig. 10). *T. elegans* sp. nov. has two suborbitals, leading to a thin connection between the preopercle and dermopterotic. In addition, *Perleidus* possesses a posteriorly serrated suborbital, leading to a broad contact region between the preopercle and dermopterotic. Moreover, the teeth of *Perleidus* are stronger than those of *T. elegans* sp. nov. Unlike *Plesiofuro* and *Meidiichthys*, *Teffichthys elegans* sp. nov. has two infraorbitals (three in *Plesiofuro*, one in *Meidiichthys*), two suborbitals (one in *Plesiofuro* and *Meidiichthys*), six branchiostegals (five in *Plesiofuro*, four in *Meidiichthys*), and presence of epaxial procurrent rays in the caudal fin (absence of epaxial procurrent rays in *Plesiofuro* and *Meidiichthys*; Fig. 10; Table 1).

Teffichthys elegans sp. nov. can be distinguished from *Paraperleidus* by the following features: presence of two suborbitals, the width of the posttemporal being half of the width of the extrascapular, and anterior portions of nasals separated by rostral (Supplementary figures S1, S2; Table 1). In addition, the standard length of *T. elegans* sp. nov. is approximately 148 mm, much smaller than *Paraperleidus*, which reaches 265 mm in standard length (Zhao & Lu 2007). Notably, *Paraperleidus* differs from other perleidids based on several features. First, the nasal bones are joined in the midline and located posterior to the rostral. In stem-neopterygians, this feature is otherwise present in Platysiagiformes and *Thoracopterus* in Peltopleuriformes. Second, the width of posttemporal is nearly the same as the width of extrascapular. Only *Meidiichthys*, *Plesiofuro*, and *Plesioperleidus* contain the same feature in Perleididae. Third, it has less than three epaxial procurrent rays in the caudal fin, which are different from *Perleidus*, *Plesiofuro*, and *Meidiichthys* (Supplementary figure S2D).

Teffichthys elegans sp. nov. differs from *Plesioperleidus* based on the following features: width of posttemporal being only half of the width of extrascapular, absence of fused lacrimomaxilla, absence of an anteriorly extended portion of preopercle, and presence of two suborbitals (Supplementary figures S1, S2; Table 1). In addition, *Plesioperleidus* differs from other perleidids based on the following features: width of posttemporal being nearly the same as the width of extrascapular, similar to *Paraperleidus*; fusion of the lacrimal with the maxilla occurred in some specimen (e.g., IVPP V5343, CUGM J2203a; Supplementary figure S2E), similar to the conditions in *Feroxichthys* and Luganoiiformes; and presence of an anteriorly extended ventral portion of preopercle, which is absent in other Perleididae.

Teffichthys elegans sp. nov. differs from *Teffichthys madagascariensis* in several features (Fig. 10; Table 1). First, six pairs of branchiostegal rays appear in *T. elegans* sp. nov., while *T. madagascariensis* has four to five. Second, the posterior margin of the jugal in *T. madagascariensis* bears developed spines, which are not present in *T. elegans* sp. nov. Third, four supraorbitals are present in *T. madagascariensis*, while three supraorbitals occur in *T. elegans* sp. nov. Fourth, presence of a relative deep anterodorsal process of subopercle in *T. elegans* sp. nov. vs. absence in *T. madagascariensis*.

3.4 Phylogenetic affinities

The phylogenetic analysis results in 54 most parsimonious trees (tree length = 484 steps, consistency index = 0.401, retention index = 0.752), the strict consensus of which is presented in Fig. 11. In the cladogram, Perleididae is recovered as a stem lineage of neopterygians, nest between Colobodontidae and Louwoichthyiformes.

The Perleididae shares the following derived features of Colobodontidae and more derived neopterygians: presence of molariform teeth on the oral bones (absent in *Plesiofuro*, Louwoichthyidae, *Altisolepis*, *Venusichthys*, and more derived neopterygians), width of posttemporals being about half width of extrascapular series (reversal in *Plesiofuro*, *Meidiichthys*, *Paraperleidus*, *Plesioperleidus*, and some crown-neopterygians), quadratojugal much reduced or lost (splint-like in *Lepisosteus*, *Semionotus*, and *Kyphosichthys*), equal number of dorsal and anal fin rays relative to pterygiophores, and dorsal and anal fin rays only being segmented distally. Perleididae and more derived neopterygians are placed above Colobodontidae based on the following features: presence of no more than six pairs of branchiostegals (reversal in *Thoracopterus* and some crown-neopterygians), and 24 or fewer principal rays in both lobes of the caudal fin (reversal in *Ctenognathichthys*, *Luopingichthys*, *Fuyuanperleidus*, and *Caturus*). Perleididae lacks the derived features of Louwoichthyiformes and more derived neopterygians: the ratio of dermopterotic length to parietal length was less than two (reversal in *Dipteronotus*, *Moradebrichthys*, and some crown-neopterygians) and the anteroventral corner of the preopercle is lower than the ventral end of the opercle (absent in Peltopleuriformes, *Habroichthys*, and crown-neopterygians).

In Perleididae, *Meidiichthys* and *Plesiofuro* form a sister group by sharing the absence of the epaxial procurrent rays. *Paraperleidus*, *Plesioperleidus*, and *Meidiichthys*-*Plesiofuro* clade form a polytomy clade, supported by the following feature: width of the posttemporal is nearly as wide as the extrascapular. Further up, *Teffichthys elegans* sp. nov. and *Teffichthys madagascariensis* form a sister group by the presence of two suborbitals. The sister relationship between the *Teffichthys* clade and the polytomy clade is supported by less than three epaxial procurrent rays and absence of epaxial principal rays. The former is more derived than the latter due to the width of the posttemporal nearly half of the width of the extrascapular. *Perleidus* is recovered at the top of the Perleididae by the following feature: presence of more than three epaxial procurrent rays and presence of epaxial principal rays.

Notably, two genera, previously referred to the Perleididae, are herein reallocated to other families. *Chaohuperleidus* is recovered as a member of Colobodontidae due to possessing two synapomorphies of this family: presence of a prominent anterodorsal process of the subopercle and presence of rounded ganoid tubercles on the principal caudal fin rays (Sun et al. 2013, Fig. 5). *Moradebrichthys* is herein recovered at the base of Thoracopteridae and forms a sister group to *Wushaichthys* and more derived taxa of this family. It possesses several synapomorphies of Thoracopteridae: laterally expanded frontals, parietal fused with the dermopterotic, and posttemporal contacting extrascapular posterolaterally and separating this bone from contact with its counterpart.

Two families, Gabanellidae and Hydropessidae, are excluded from the Perleidiformes. In the result of our phylogenetic analysis, *Gabanellia*, included in Gabanellidae before, is recovered in Colobodontidae by the following features: presence of prominent anteroventral extension of subopercle, the length of anteroventral margin of preopercle (when the preopercle contact with the maxilla) nearly same as the length of anterodorsal margin of the preopercle. *Hydropessum*, included in Hydropessidae before, is recovered in Polzbergiiformes by the absence of teeth on the maxilla and the posterior end of the maxilla ending below the posterior orbital margin.

In addition, results of our analysis provide new insights into the phylogenetic relationships of some stem-neopterygian taxa. *Redfieldius* and *Helichthys* are recovered as a sister group due to the absence of dermopterotic/preopercle contact. *Peltopleurus tyrannos* form a sister taxon to *Peltopleurus nitidus* by the presence of following features: anal fin being larger than dorsal fin, presence of a single suborbital, presence of a broad suborbital posterior to the dermosphenotic, with the same depth with each other, absence of epaxial principal rays in caudal fin, and the length of the anteroventral margin of the preopercle (when the preopercle contact with the maxilla) nearly the same as the length of the anterior margin of the subopercle

4. Discussion

4.1 The monophyly of Perleididae and Perleidiformes

The monophyly of Perleididae can be supported by three synapomorphies: the length of the anteroventral margin of the dermohyal (Supplementary figure S3) nearly half of the length of the anterodorsal margin of the preopercle (unknown in *Paraperleidus* due to poor preservation; present in *Australosomus* and *Platysiagum*); the anteroventral margin of the preopercle (when the preopercle contact with the maxilla) is nearly equal to the anterior margin of the subopercle in length (independently evolved in Platysiagiformes, Luganoiiformes, and *Peltopleurus*); and the anteroventral margin of the preopercle (when the preopercle contact with the maxilla) is 1-2 times as long as anterodorsal margin of the preopercle (also present in *Australosomus* and *Colobodus*). We remove *Procheirichthys*, *Aetheodontus*, *Meridensia*, *Alvinia*, *Megaperleidus*, *Endennia*, *Chaohuperleidus*, and *Moradebrichthys* out of the Perleididae as they lack above three synapomorphies (Wade 1935; Bürgin 1992; Sytchevskaya 1999; Lombardo & Brambillasca 2005; Sun et al. 2013; Cartanyà et al. 2019). Additionally, the taxonomic positions of *Diandongperleidus* and *Luopingperleidus* are ambiguous due to the poor preservation and require further studies. At present, the monophyly of Perleididae is still weakly supported, pending more works in the future.

We propose that the Perleididae as the only valid family of the Perleidiformes. Hydropessidae and Gabanellidae were once referred to the Perleidiformes. However, *Hydropessum* shows many features resembling Polzbergiiformes other than Perleididae, such as the absence of teeth on the maxilla and posterior end of the maxilla ending below the posterior orbital margin (Broom 1909; Hutchinson 1973). Additionally, *Gabanellia* possesses several features unlike Perleididae either: presence of a modified anal fin, presence of more than ten branchiostegal rays, and presence of powerful teeth of different sizes in the dentition (Tintori & Lombardo 1996). As such, we remove them from the Perleidiformes to keep the monophyly of this order.

4.2 Biogeographical and ecological implications

Perleididae (as redefined herein) reached a cosmopolitan distribution in the late Induan and early Olenekian. Similar cosmopolitanism has also been documented in ammonoids and terrestrial tetrapods during the Early Triassic (Brayard et al. 2006; Button et al. 2017; Dai & Song 2020). Following this, Perleididae was restricted to the eastern rim of the Paleotethys Ocean in the Anisian and appeared at the western rim of this ocean in the Ladinian (Fig. 12). In the Induan, Perleididae was discovered in South China, East Greenland, and Madagascar

(Stensiö 1932; Lehman 1952; Zhao & Lu 2007; Marramà et al. 2017). At the beginning of the Olenekian, Perleididae underwent rapid radiation. It was present in Spitsbergen, South China, and Madagascar during the Smithian, demonstrating a global distribution pattern (Woodward 1912; Stensiö 1921; Lehman 1952; Jin et al. 2003; Marramà et al. 2017). There is no record of Perleididae in the Spathian when fishes were rarely reported (Romano 2021). In addition, there are some taxa of Perleididae from North China and Angola that lack specific ages at the stage/substage level and require further examination (Antunes et al. 1990; Xu et al. 2015). In the Middle Triassic, Perleididae was discovered in South China in the Anisian, showing its latest record from southern Europe in the Ladinian (Brough 1931; Hutchinson 1973; Lombardo 2001; Lombardo et al. 2011).

The discovery of *Teffichthys elegans* sp. nov. in Guizhou documents the first record of neopterygians in the Upper Yangtze region of South China. Previously, Early Triassic fish fossil localities in China mainly focused on the Middle and Lower Yangtze region, namely Jurong, Jiangsu (Qian et al. 1997; Liu et al. 2002; Jin et al. 2003), Chaohu, Anhui (Tong et al. 2006), and Huangshi, Hubei (Su & Li 1983). However, the new species described here comes from eastern Guizhou in the Upper Yangtze region.

The combination of conical teeth on the dentition and molariform teeth of the oral margin bones of *Teffichthys elegans* sp. nov. provide excellent grasping and crushing abilities, enabling it to hunt various prey. As a predator, *Teffichthys elegans* sp. nov. possessed a streamlined body and a large orbital region, providing sustained swimming ability and good visual acuity. In addition, it had a long maxilla with a triangular postorbital portion and a relatively stout dentary with conical teeth occupying most of the oral margin of the jaws. The molariform teeth found in *Teffichthys elegans* sp. nov. demonstrate their ability to feed on hard-shelled organisms, such as crustaceans, bivalves, and ammonoids, which also yielded from the same horizon at Gujiao section (Dai et al. 2018). In Perleididae, *Teffichthys* and *Perleidus* possess a similar feeding apparatus (Lombardo 2001; Marramà et al. 2017). However, *Teffichthys elegans* sp. nov. is the largest durophagous predator of Perleididae known to date. Compared with Colobodontidae, which is a large durophagous predatory fish (Bürgin et al. 1996; Mutter 2004; Xu 2020a), the peg-like and molariform teeth of *Teffichthys elegans* sp. nov. were less developed, indicating that it may has been a secondary consumer resembling parasemionotids and platysiagids (normally below 200 mm) in the Early Triassic (Scheyer et al. 2014).

5. Conclusions

The discovery of *Teffichthys elegans* sp. nov. from the Induan (Dienerian), Early Triassic of Guizhou, South China shed light on the stem-neopterygians of China after the Permian/Triassic mass extinction. The results of this phylogenetic analysis recovered Perleididae as a monophyletic group. *Teffichthys elegans* sp. nov. is recovered as a member of Perleididae, forming a sister group of *Teffichthys madagascariensis*. *Paraperleidus* and *Plesioperleidus* were placed above *Plesiofuro* and *Meidiichthys* in Perleididae. *Chaohuperleidus* and *Moradebrichthys* were moved to Colobodontidae and Thoracopteridae, respectively. Hydropessidae and Gabanellidae were removed from Perleidiformes to maintain the monophyly of this order. As the largest durophagous predator in Perleididae, the combination of molariform and conical teeth of *Teffichthys elegans* sp. nov. were well adapted for grasping and crushing, helping it succeed in the Early Triassic.

Acknowledgements

We thank Toni Bürgin, Carlo Romano, Kenneth De Baets and an anonymous reviewer for helpful comments on an early version of the manuscript. We thank Lijun Zhao for the specimen observation of *Paraperleidus* and *Plesioperleidus* in Zhejiang Museum of Natural History, Hangzhou, China. We thank the National infrastructure of Mineral Rock and Fossil Resources for Science and Technology of Yifu Museum of China University of Geoscience for the management of the specimens. We thank Yiran Cao, Xin Yang, Shuxun Yuan, and Yi Wang for their assistance in the fieldwork.

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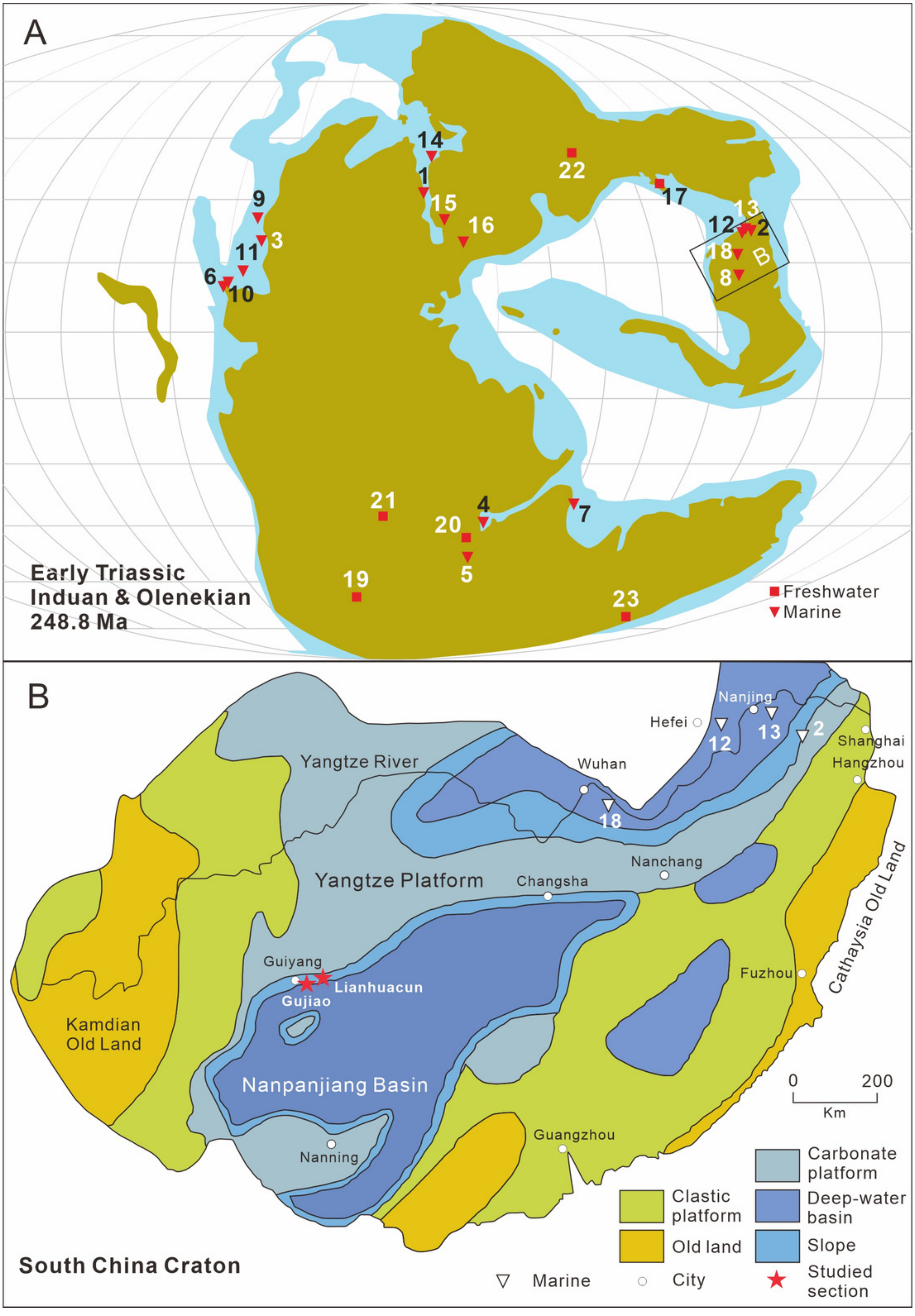
Figure 1

Distribution of Early Triassic Actinopterygii and Studied location

A. Early Triassic Actinopterygii localities shown on the Paleogeographic Maps , modified from Scotese, 2014. 1, East Greenland (e.g. Stensiö 1932; Nielsen 1942, 1949); 2, Zhejiang, China (Zhao & Lu 2007); 3, Alberta, Canada (e.g. Lambe 1916; Neuman 2015); 4, Northwestern Madagascar (e.g. Lehman 1952; Marramà et al. 2017); 5, Southwest Madagascar (e.g. Lehman et al. 1959); 6, Elko County, Nevada, USA (Romano et al. 2017); 7, India, Spiti (Romano et al. 2016b) ; 8, Guizhou, China (this paper); 9, British Columbia, Canada (e.g. Schaeffer et al. 1976; Mutter 2005); 10, Esmeralda County, Nevada, USA (Romano et al. 2019); 11, Idaho, USA (Romano et al. 2012); 12, Jiangsu, China (e.g. Qian et al. 1997; Qiu et al. 2019); 13, Anhui, China (e.g. Tong et al. 2006, Sun et al. 2013); 14, Spitsbergen (e.g. Woodward 1912; Stensiö 1921); 15, Poland (Frech 1903–1908); 16, Germany and France boundary (Gall 1974); 17, Gansu, China (Xu et al. 2015); 18, Hubei, China (Su & Li 1983); 19, South Africa (e.g. Brough 1931; Hutchinson 1973); 20, Tanzania (Haughton 1936); 21, Angola (e.g. Antunes et al. 1990; Murray 2000); 22, Siberia, Russia (Sytchevskaya 1999); 23, Tasmania, Australia (Dziewa 1980). Griensbachian: 1-2; Dienerian: 1, 3-8; Smithian: 9-14; Spathian: 11, 13-16; Early Triassic (stage indet.): 17-23. Neopterygii localities: 1-9, 12-19, 21-23. B. Map showing the fossil locality of *Teffichthys elegans* sp. nov. and Actinopterygii from South China, modified from Feng et al. 1997. 11 Actinopterygii from South China: 2, *Paraperleidus* from Zhejiang, China (Zhao & Lu 2007); 13, *Plesioperleidus*, *Lepidotes*, *Stensionotus*, *Jurongia*, *Qingshania*, *Suius*, *Peia* from Jiangsu, China (Qian et al. 1997; Liu et al. 2002; Jin et al. 2003; Li,2009; Qiu et al. 2019); 12, *Plesioperleidus*, *Chaohuperleidus*, *Jurongia*, *Qingshania*, *Suius* from Anhui, China (Su 1981; Tong et al. 2006; Sun et al. 2013); 18, *Plesioperleidus* from Hubei, China (Su & Li 1983).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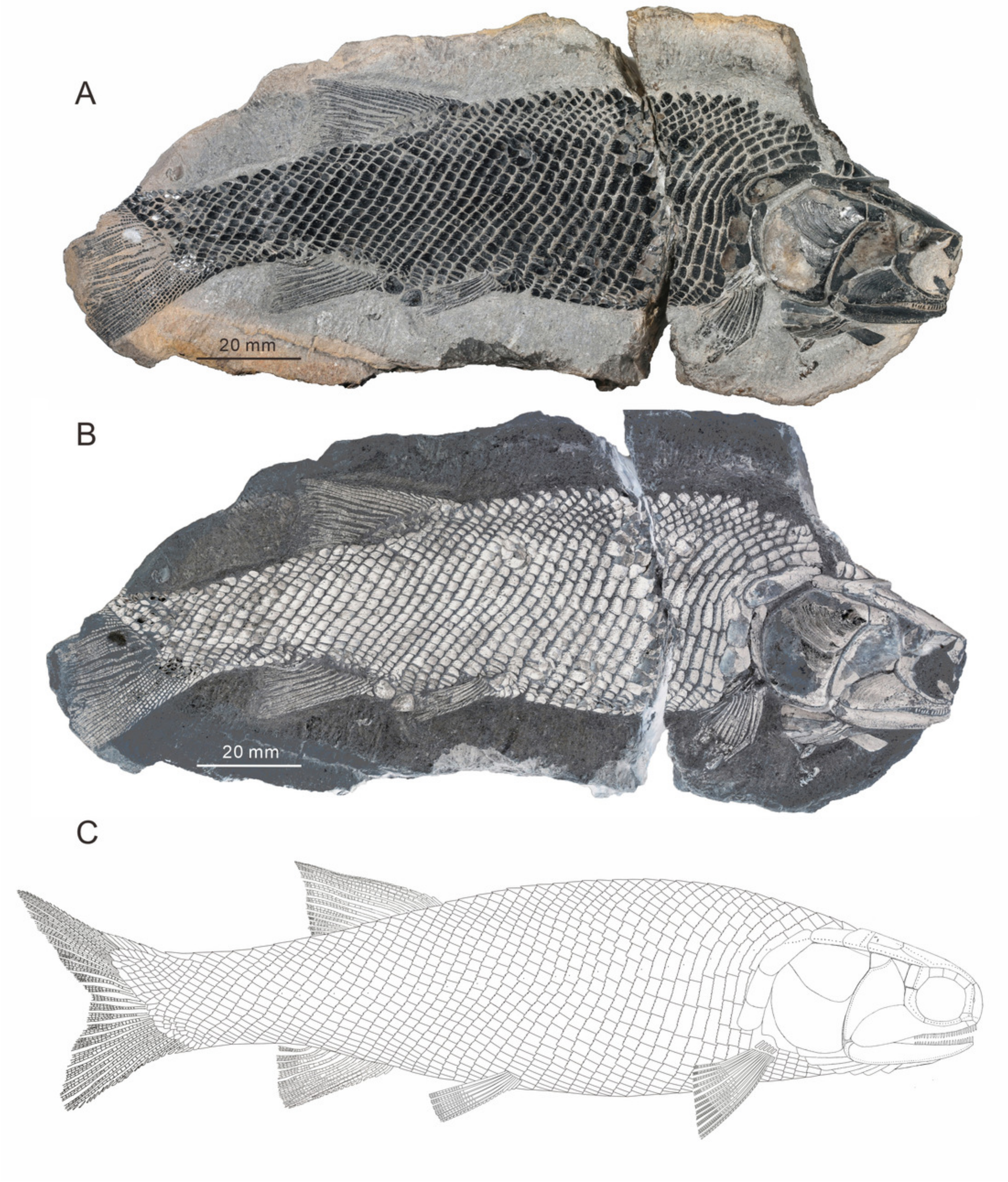
B
Freshwater
Marine
B
Yangtze River
Yangtze Platform
Nanjing
Hefei
Wuhan
Shanghai
Hangzhou
Nanchang
Changsha
Guiyang
Lianhuacun
Gujiao
Fuzhou
Cathaysia Old Land
Kamdian Old Land
Nanpanjiang Basin
Nanning
Guangzhou
0
200
Km
Carbonate platform
Clastic platform
Deep-water basin
Old land
Slope
Marine
City
Studied section
South China Craton

Figure 2

Holotype and the reconstruction of *Teffichthys elegans* sp. nov.

(A-B) CUGM K2-E2601, holotype from the upper part of Daye Formation at Lianhuacun section. (A) photo of the specimen (B) invert counterpart of the specimen. (C) reconstruction.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C

Figure 3

Two paratypes of *Teffichthys elegans* sp. nov.

(A) CUGM K2-E2602. (B) CUGM K2-E2603. Both of them from the late Dienerian at Gujiao section.

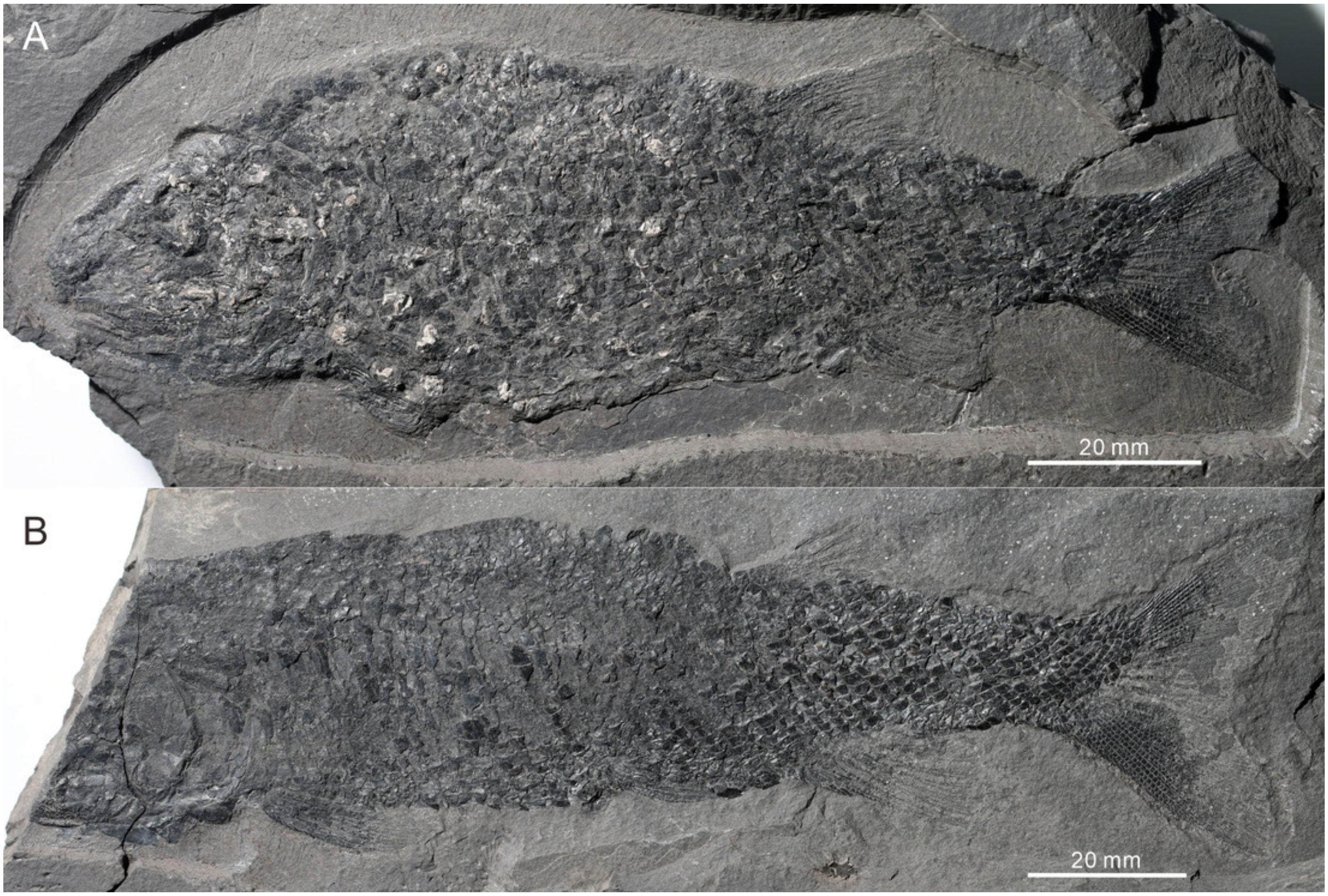

Figure 4

Skull and pectoral girdle of CUGM K2-E2601, holotype from the upper part of Daye Formation at Lianhuacun section.

(A) right view photograph. (B) right view line-drawing. (C) left side photograph. (D) left side line-drawing. (E) skull roof photograph. (F) skull roof line-drawing.

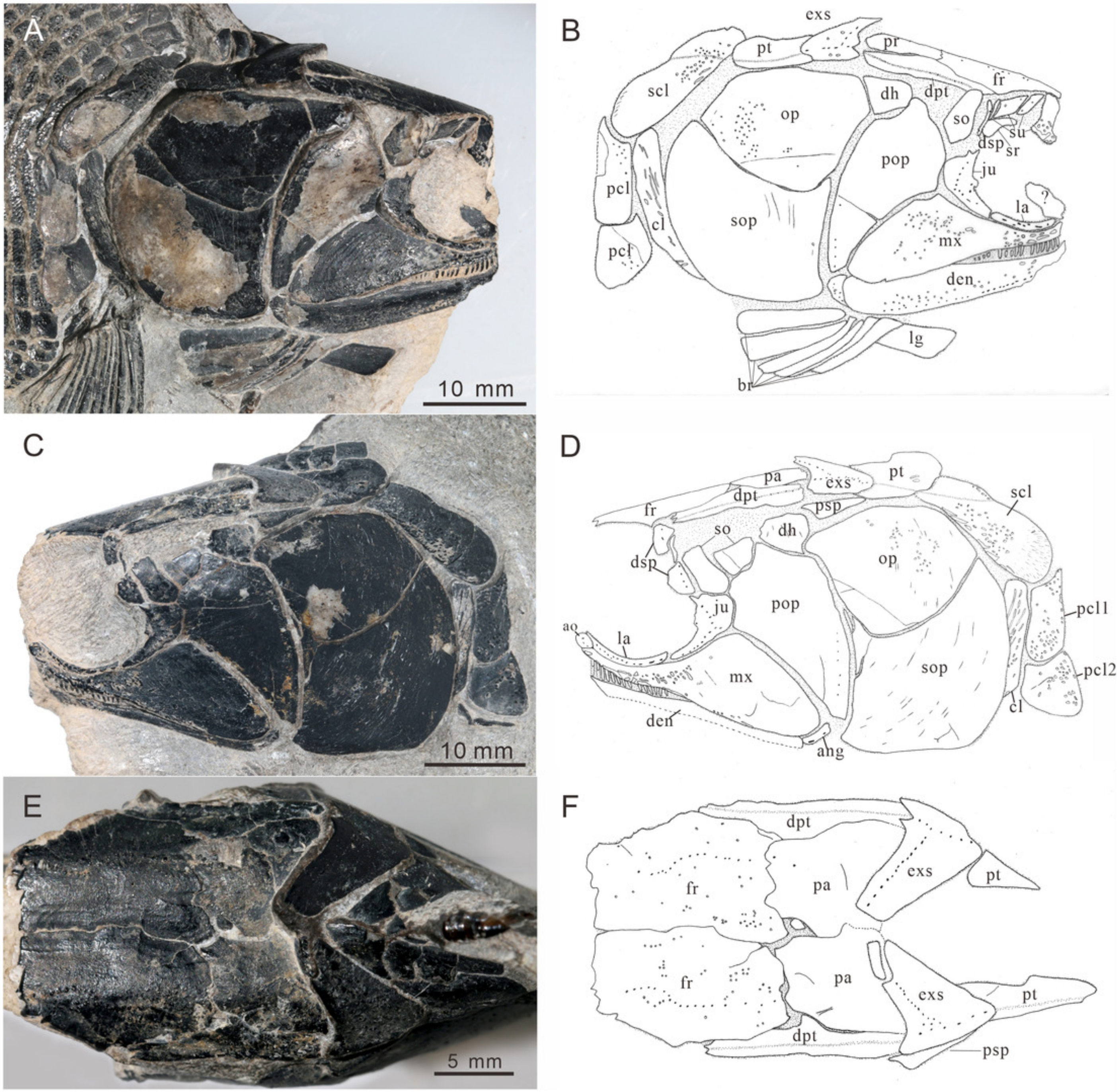
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Figure 5

Skull and pectoral girdle of *Teffichthys elegans* sp. nov.

(A) CUGM K2-E2601, orbital region. (B) CUGM K2-E2605, snout region. (C-D) CUGM K2-E2604; (C) skull and pectoral girdle, (D) line-drawing. All of them from the late Dienerian at Gujiao section.

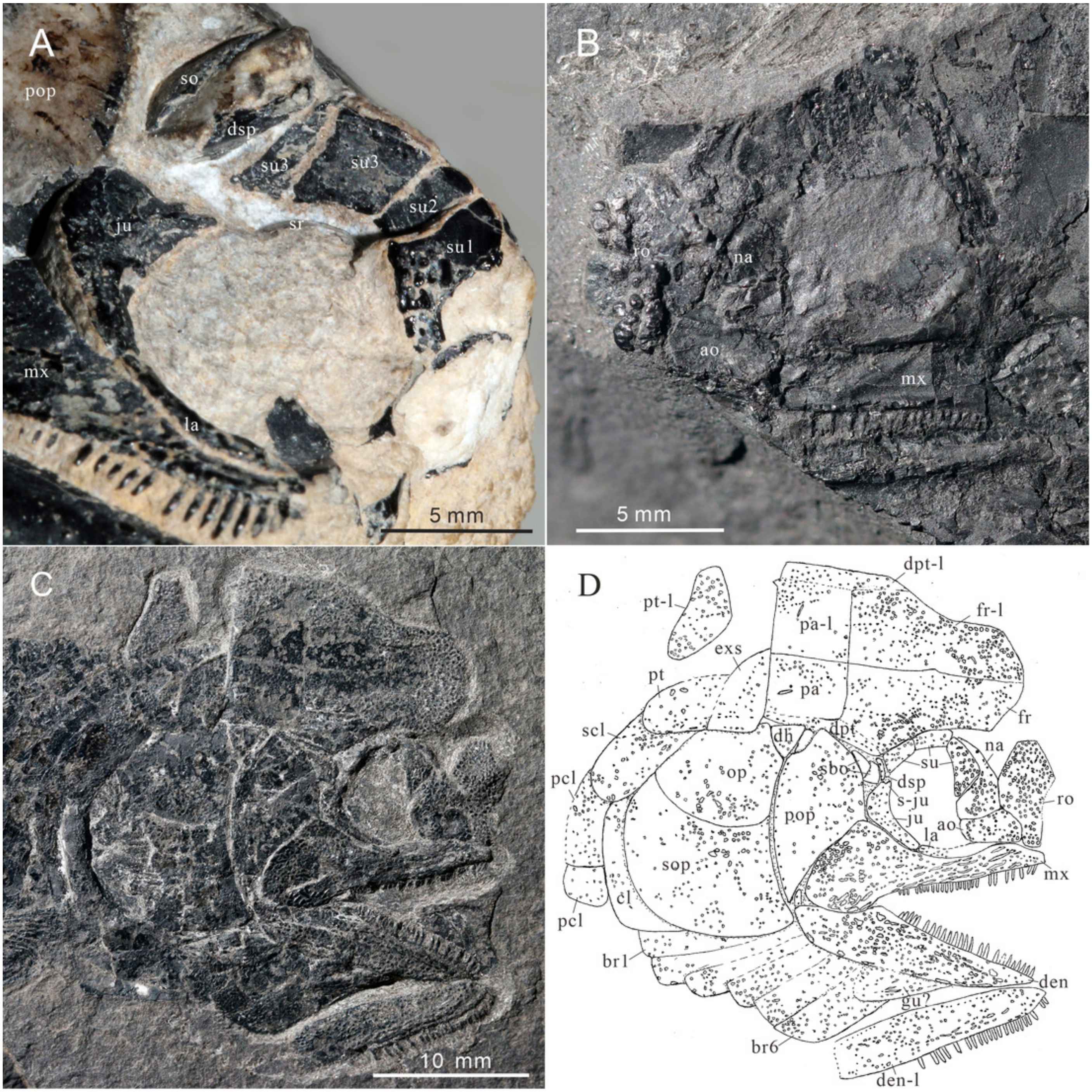
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Figure 6

Gular, premaxilla and molariform teeth of *Teffichthys elegans* sp. nov.

(A-C) CUGM K2-E2607; (A) head, (B) premaxilla, (C) middle gular. (D) CUGM K2-E2602, molariform teeth, indicated by arrows.

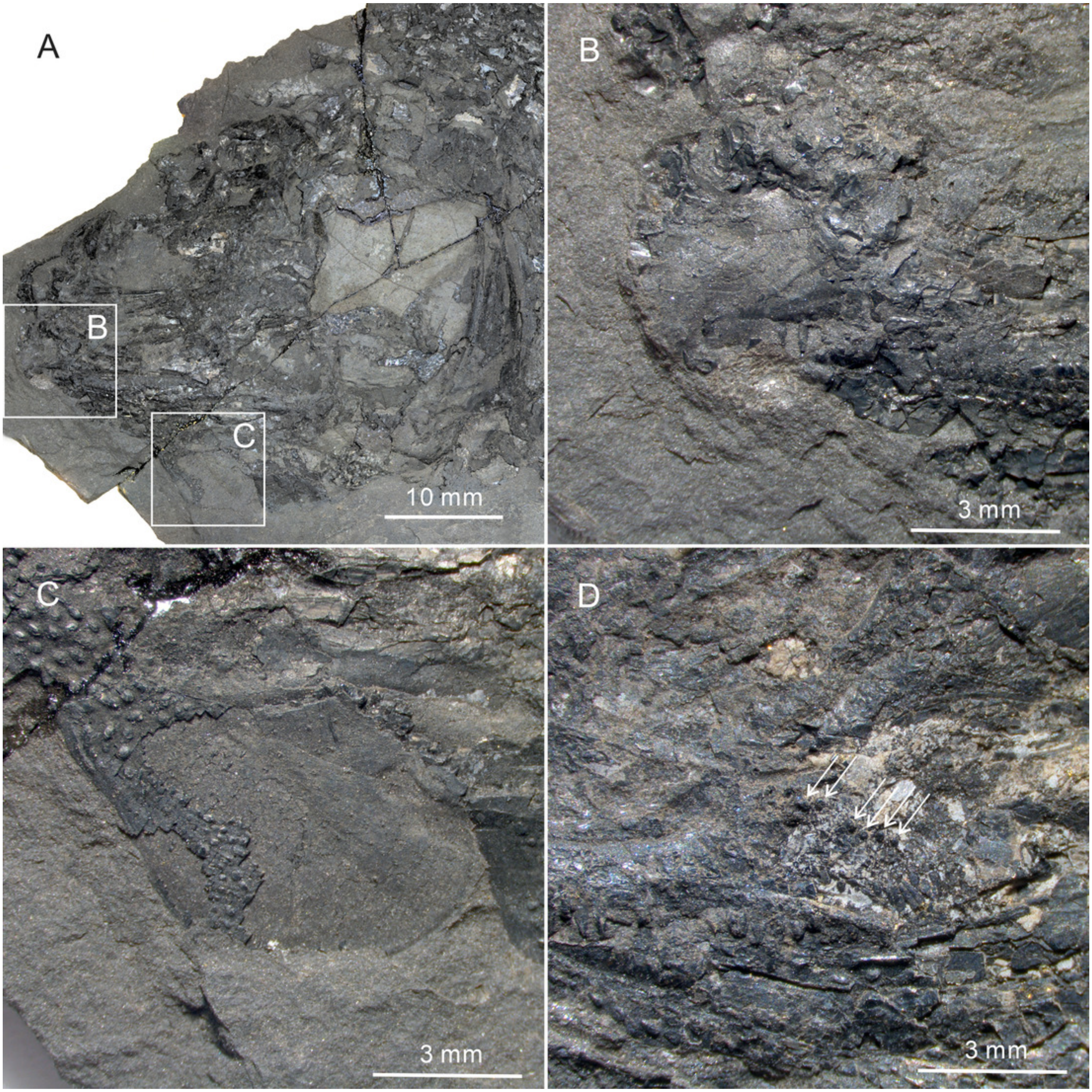
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Figure 7

Reconstruction of skull and pectoral girdle (without fin) of *Teffichthys elegans* sp. nov. from the late Dienerian (Induan, Early Triassic) at Gujiao and Lianhuacun section.

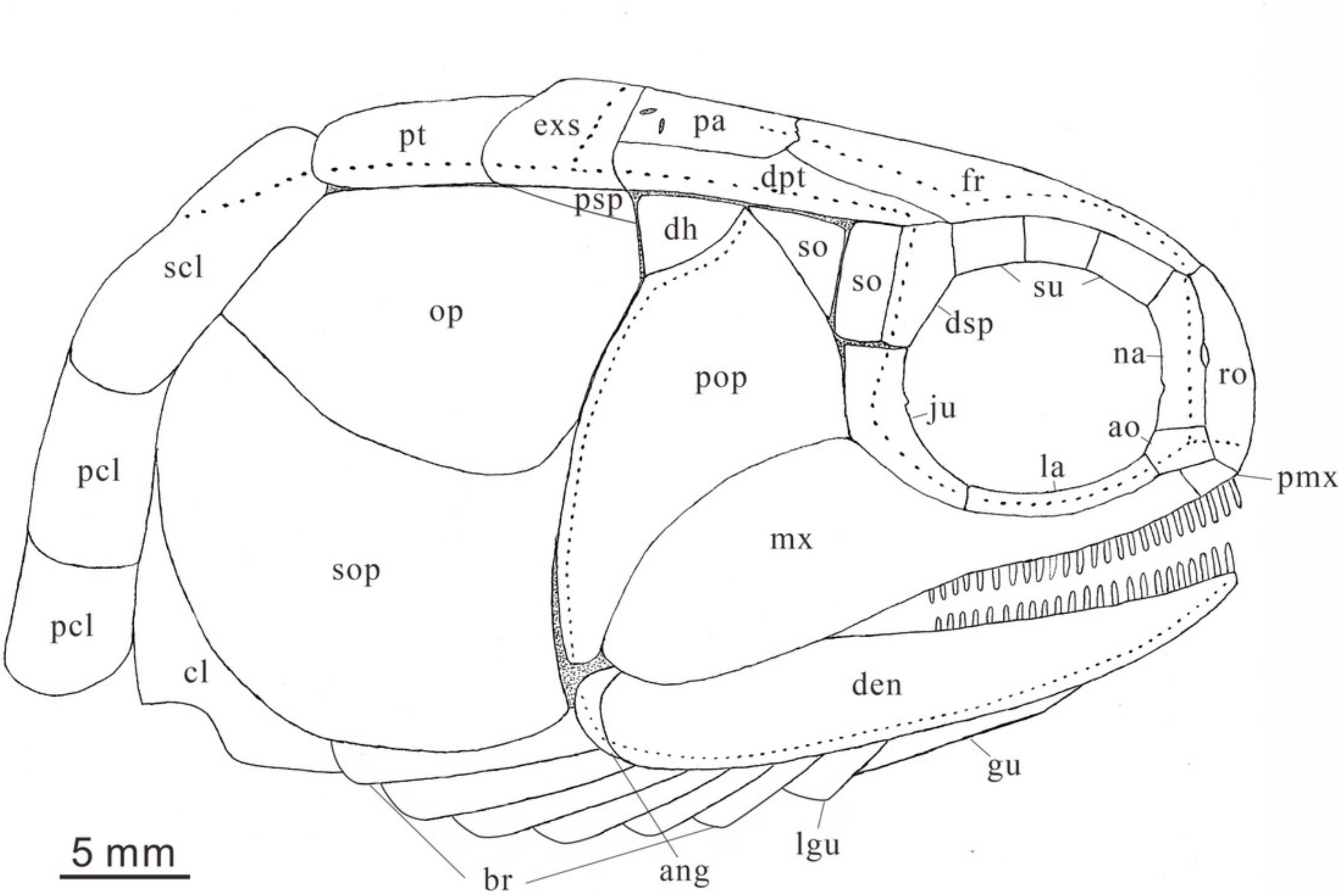

Figure 8

Fins of *Teffichthys elegans* sp. nov. of CUGM K2-E2601, holotype from the upper part of Daye Formation at Lianhuacun section.

(A) anal fin. (B) dorsal fin. (C) right pelvic fin; (D) right pectoral fin.

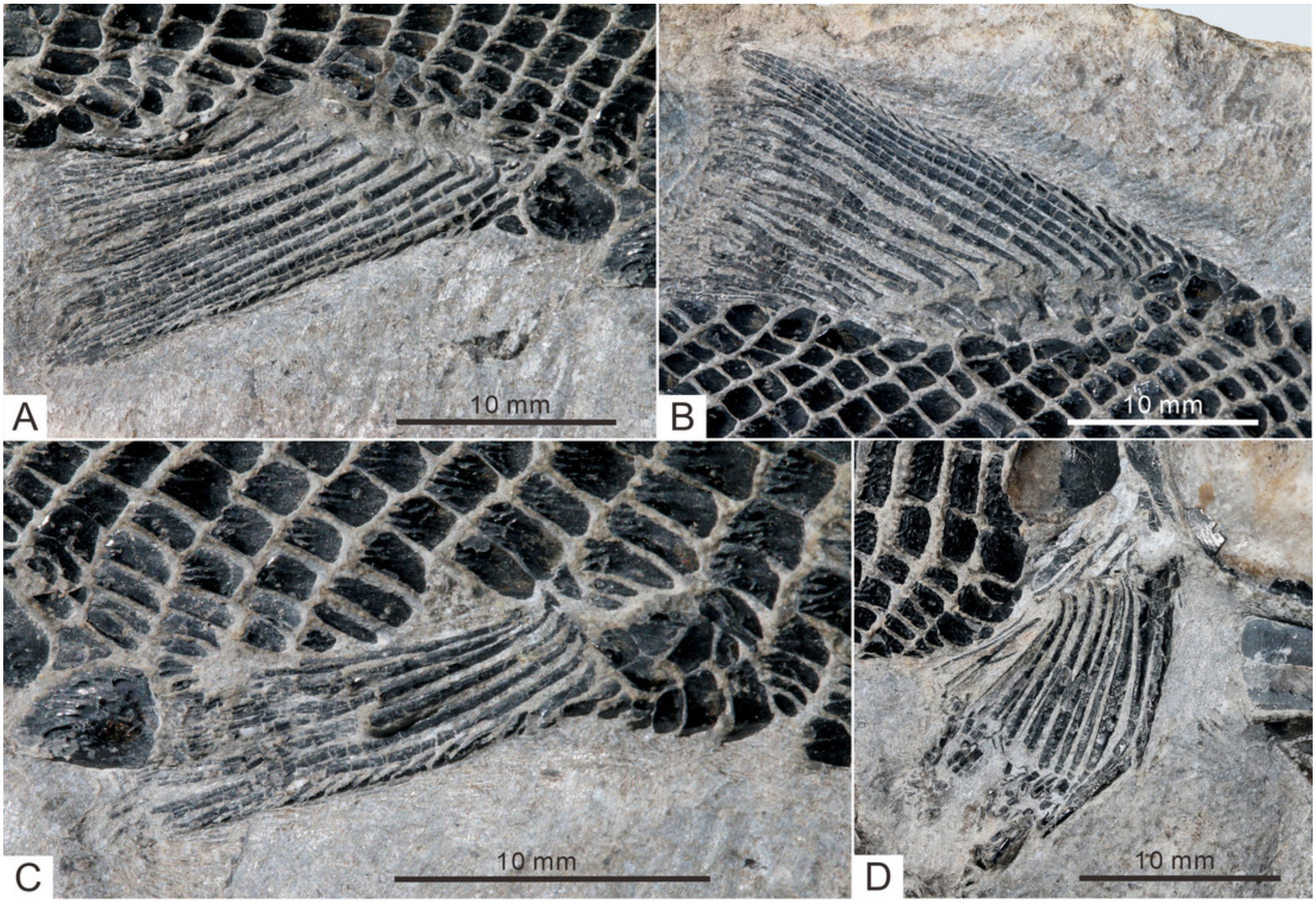

Figure 9

Pectoral fin and Caudal fin of *Teffichthys elegans* sp. nov.

(A) CUGM K2-E2606, pectoral fin. (B) CUGM K2-E2602, caudal fin. (C-D) CUGM K2-E2609; (C) caudal fin, (D) line-drawing of the caudal fin. All of them from the late Dienerian at Gujiao section.

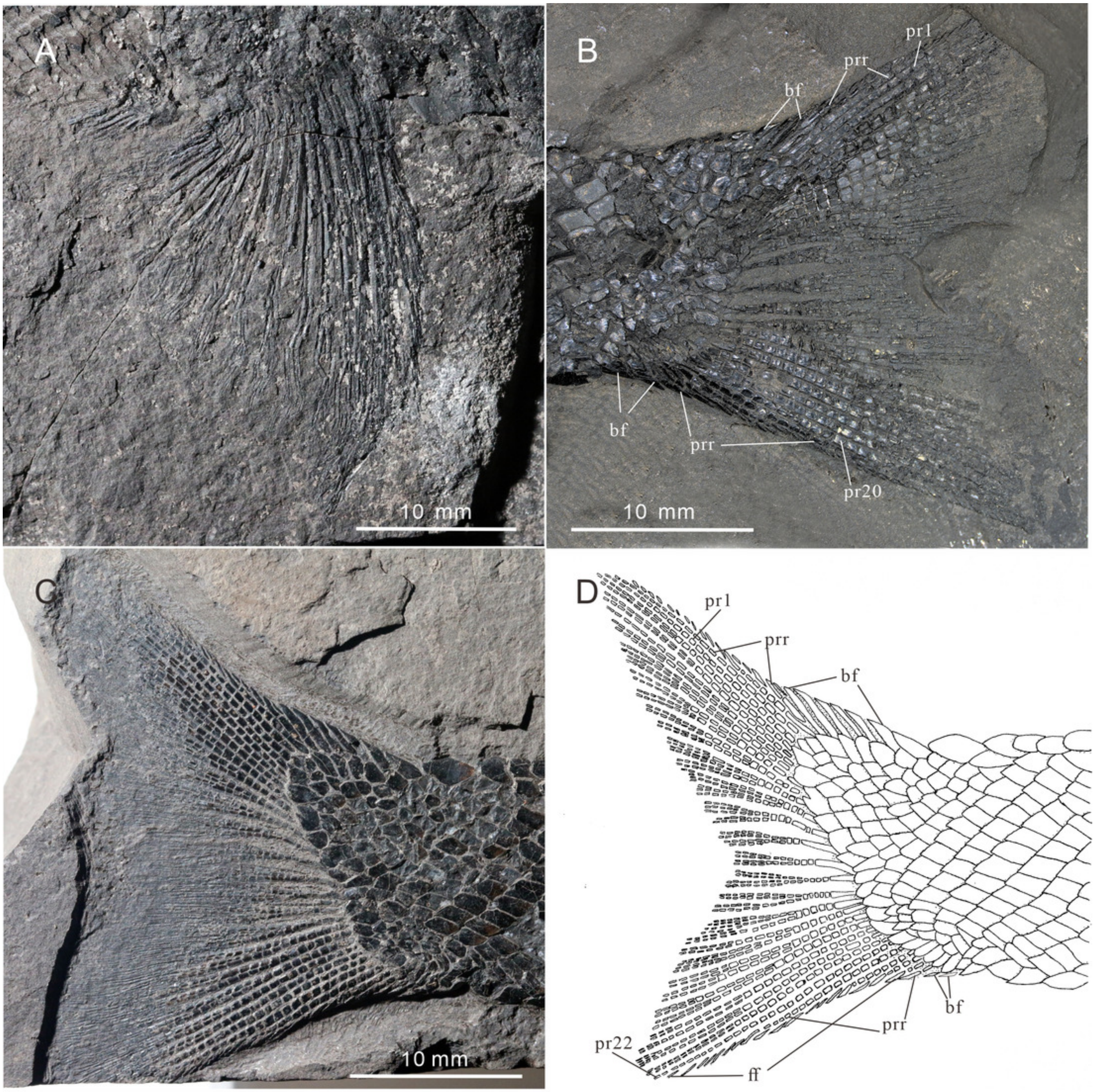
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Figure 10

Comparison of skull and pectoral girdle in Perleididae.

A. *Meidiichthys browni* (adapted from Hutchinson 1973); B. *Perleidus altolepis* (adopted from Lombardo 2001); C. *Teffichthys madagascariensis* (adapted from Marrama et al. 2017); D. *Plesiofuro mingshuica* (adapted from Xu, 2015).

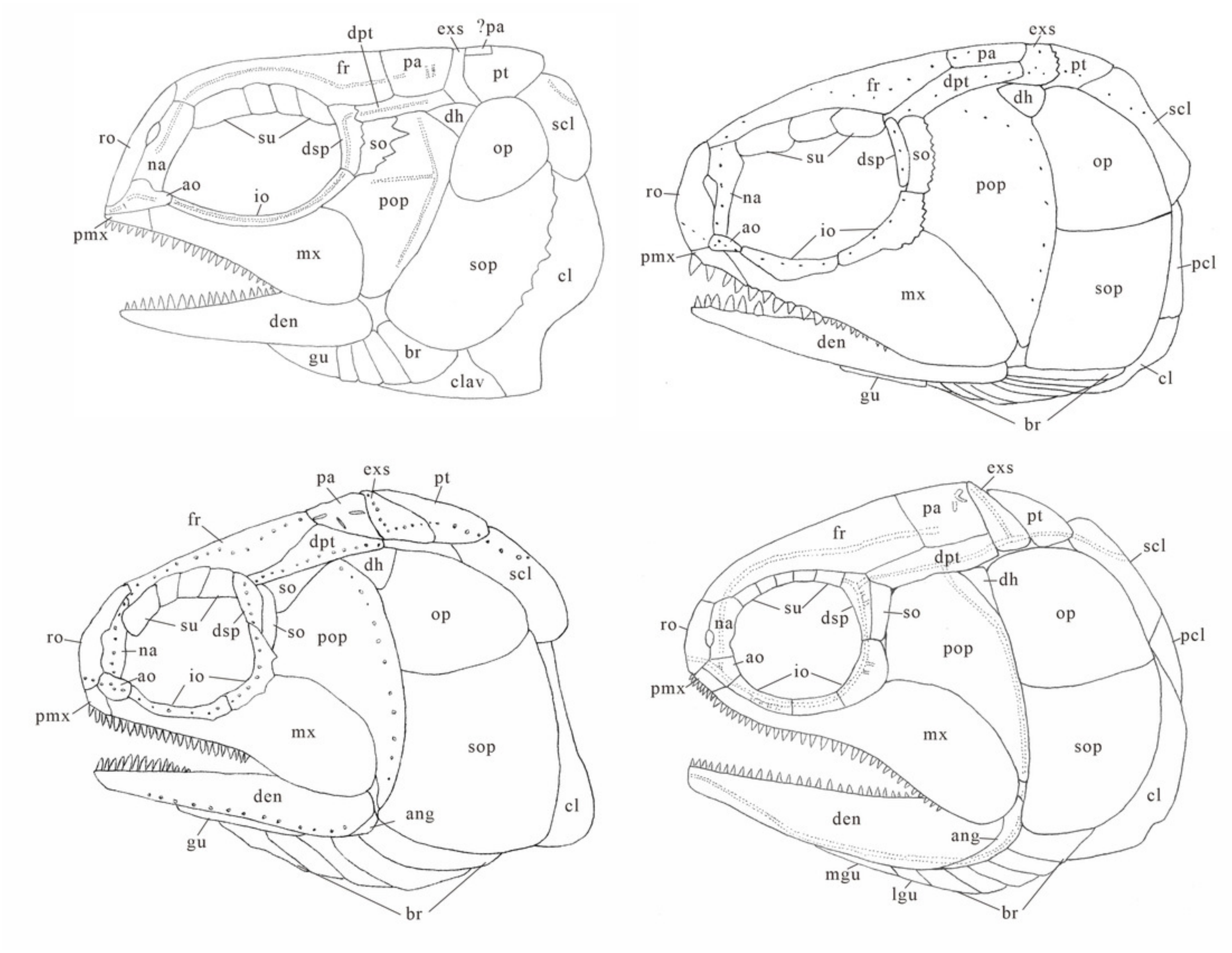

Figure 11

Strict consensus of phylogenetic analysis of Perleididae and relative Actinopterygii.

Strict consensus of 54 most parsimonious trees (tree length = 484 steps, consistency index = 0.401, retention index = 0.752), illustrating the phylogenetic position of *Teffichthys elegans* sp. nov. within the Actinopterygii. Numbers above nodes indicate Bremer decay indices.

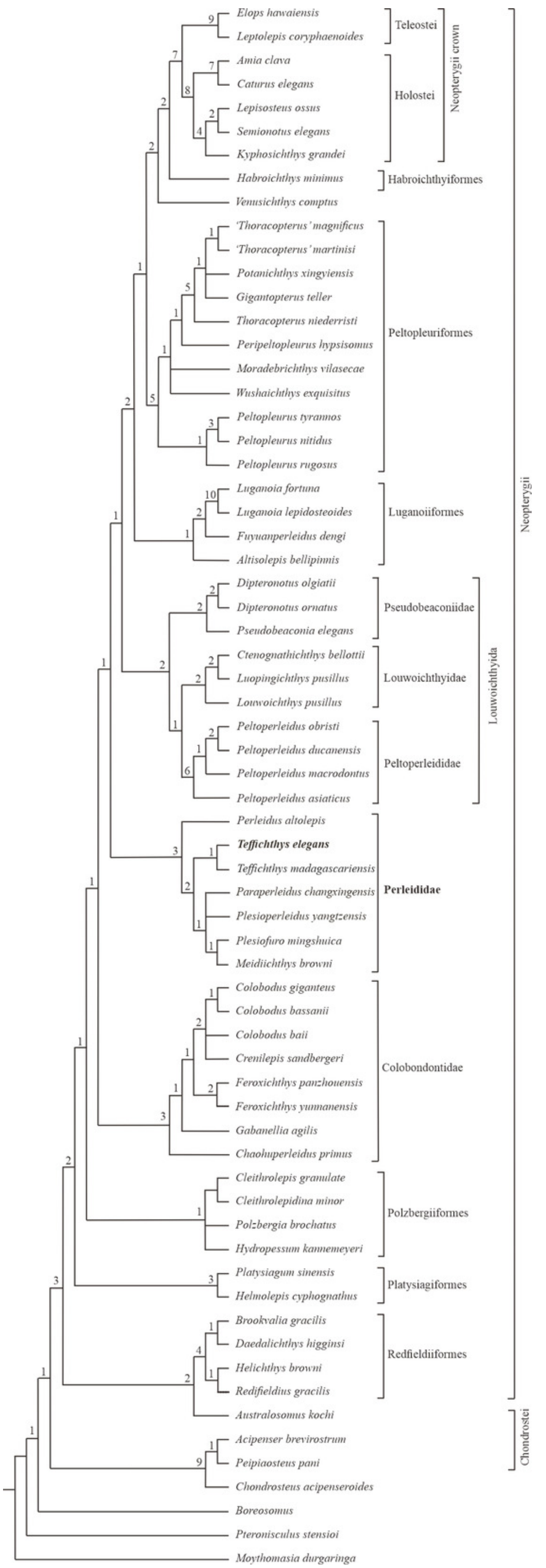
Elops hawaiensis
Leptolepis coryphaenoides
Teleostei
Amia clava
Caturus elegans
Lepisosteus ossus
Semionotus elegans
Kyphosichthys grandei
Holostei
Neopterygii crown
Habroichthys minimus
Habroichthyiformes
Venusichthys comptus
'Thoracopterus' magnificus
'Thoracopterus' martinisi
Potanichthys xingyiensis
Gigantopterus teller
Thoracopterus niederristi
Peripeltopleurus hypsisomus
Moradebrichthys vilasecae
Wushaichthys exquisitus
Peltopleurus tyrannos
Peltopleurus nitidus
Peltopleurus rugosus
Peltopleuriformes
Luganoia fortuna
Luganoia lepidosteoides
Fuyuanperleidus dengi
Altisolepis bellipinnis
Luganoiiformes
Neopterygii
Dipteronotus olgiatii
Dipteronotus ornatus
Pseudobeaconia elegans
Pseudobeaconiidae
Ctenognathichthys bellottii
Luopingichthys pusillus
Louwoichthys pusillus
Louwoichthyidae
Louwoichthyida
Peltoperleidus obristi
Peltoperleidus ducanensis
Peltoperleidus macrodontus
Peltoperleidus asiaticus
Peltoperleididae
Perleidus altolepis
Teffichthys elegans
Teffichthys madagascariensis
Paraperleidus changxingensis
Plesioperleidus yangtzensis
Plesiofuro mingshuica
Meidiichthys browni
Perleididae
Colobodus giganteus
Colobodus bassanii
Colobodus baii
Crenilepis sandbergeri
Feroxichthys panzhouensis
Feroxichthys yunnanensis
Gabanellia agilis
Chaohuperleidus primus
Colobondontidae
Cleithrolepis granulate
Cleithrolepidina minor
Polzbergia brochatus
Hydropessum kannemeyeri
Polzbergiiformes
Platysiagum sinensis
Helmolepis cyphognathus
Platysiagiformes
Brookvalia gracilis
Daedalichthys higginsi
Helichthys browni
Redfieldius gracilis
Redfieldiiformes
Australosomus kochi
Acipenser brevirostrum
Peipiaosteus pani
Chondrosteus acipenseroides
Chondrostei
Boreosomus
Pteronisculus stensioi
Moythomasia durgaringa

Figure 12

The paleogeographic distribution of Perleididae in Early and Middle Triassic, modified from (Scotese 2014).

Abbreviated stratigraphic intervals: Gr, Griesbachian; Di, Dienerian; Sm, Smithian; Sp, Spathian; Ae, Aegean; Bi, Bithynian; Pe, Pelsonian; Illy, Illyrian; Fass, Fassanian; Long, Longobardian.

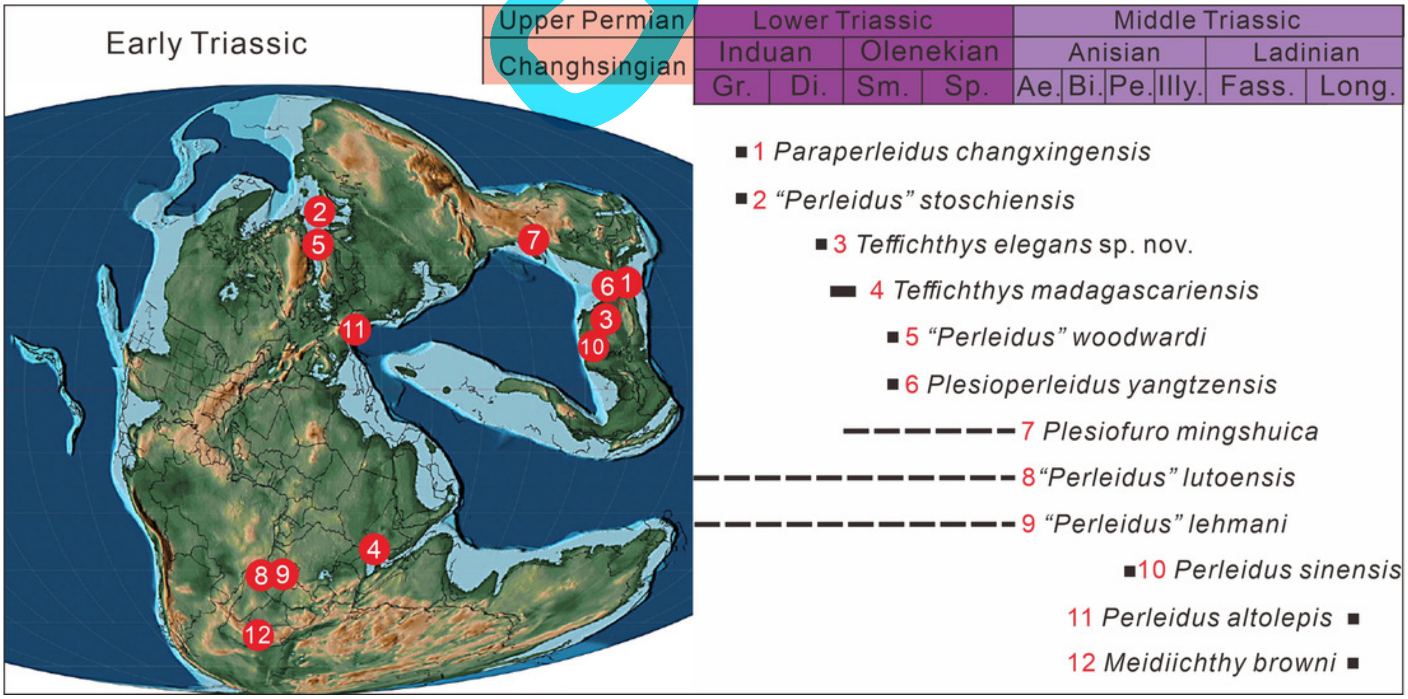

Table 1(on next page)

Summary of characters used to differ members of Perleididae.

Data from Lombardo 2001; Marramà et al. 2017; Zhao and Lu 2007; Jin 2003; Xu 2015; Brough 1931. *Paraperleidus* and *Plesioperleidus* are based on personal observation (GH Xu and ZW Yuan). TL, total length; PH, based on reconstruction picture.

Species	Br	Su	Io	So	Pt/exs	Psp	Ppr	Na contact	La fused with mx	Formula	SL/mm
Perleidus altolepis	6	3	2	1	1/2	absent	present	absent	absent	D19/P12A19C35/T37 (PH)	＜120
***Teffichthys elegans* sp. nov.**	6	3	2	2	1/2	present	present	absent	absent	D26/P14A22C36/T39	>148
Teffichthys madagascariensis	4-5	4	2	2	1/2	absent	present	absent	absent	D25/P13A21C37/T40	51-129
Paraperleidus changxingensis	?	3	2	1	1	absent	present	present	absent	?	265(TL)
Plesioperleidus yangtzensis	6	3	1	1	1	absent	present	absent	present	D30/P15A25C46/T51	200(TL)
Plesiofuro mingshuica	5	5	3	1	1	absent	absent	absent	absent	D28/P14A25C39/T44	90-120
Meidiichthys browni	4	4	1	1	1	absent	absent	absent	absent	D21/P13A21C35/T38 (PH)	65-100(TL)