Guiyangichthys elegans gen. et sp. nov., a perleidid neopterygian fish from the Early Triassic (Dienerian, Induan) of South China (#68488)

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Zhiwei Yuan [1] , **Guang-Hui Xu** [Corresp., 2, 3] , **Xu Dai** [1] , **Fengyu Wang** [1] , **Xiaokang Liu** [1] , **Enhao Jia** [1] , **Luyi Miao** [1] , **Haijun Song** [Corresp. 1]

[1] State Key Laboratory of Biogeology and Environmental Geology, School of Earth Sciences, China University of Geosciences, Wuhan, China

[2] Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China

[3] CAS Center for Excellence in Life and Paleoenvironment, Beijing, China

Corresponding Authors: Guang-Hui Xu, Haijun Song
Email address: xuguanghui@ivpp.ac.cn, haijunsong@cug.edu.cn

Neopterygii is the largest clade of extant ray-finned fishes, including Teleostei, Holostei, and their closely related fossil taxa. This clade underwent rapid evolutionary radiation during the Early to Middle Triassic. This paper describes a perleidid neopterygian, *Guiyangichthys elegans* gen. et sp. nov., based on 13 well-preserved specimens from the lower Daye Formation (Dienerian, Induan) in Guizhou, China. *Guiyangichthys* documents one of the oldest perleidids, and its studies provide insights into the early diversification of this family. *Guiyangichthys* shares two derived features of Perleididae, the preopercle process length of dermohyal nearly being half the length of the anterodorsal process of the preopercle, and the anteroventral corner of the preopercle being nearly the same horizon as the ventral end of opercle. It differs from other members of this clade in the following features: presence of postspiracle, presence of three supraorbitals, two infraorbitals, six pairs of branchiostegal rays, and a relatively deep anterodorsal process of the subopercle. Results of a phylogenetic analysis recover *Guiyangichthys* as a sister taxon to *Teffichthys* within the Perleididae (Perleidiformes) and provide new insights into the interrelationships of early neopterygian clades. The Perleidiformes are constricted to include only the Perleididae, and other previously alleged 'perleidiform' families (e.g., Hydropessidae and Gabanellidae) are removed to maintain the monophyly of this order. Similar to many other perleidids, it is likely a durophagous predator with dentition combining grasping and crushing morphologies. The new finding provides an important addition for our understanding of the trophic structure of the Early Triassic marine ecosystem in South China.

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[1] State Key Laboratory of Biogeology and Environmental Geology, School of Earth Science, China University of Geosciences, 430074 Wuhan, China
[2] Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China
[3] CAS Center for Excellence in Life and Paleoenvironment, Beijing, China
*E-mail: haijunsong@cug.edu.cn; xuguanghui@ivpp.ac.cn

Abstract

Neopterygii is the largest clade of extant ray-finned fishes, including Teleostei, Holostei, and their closely related fossil taxa. This clade underwent rapid evolutionary radiation during the Early to Middle Triassic. This paper describes a perleidid neopterygian, *Guiyangichthys elegans* gen. et sp. nov., based on 13 well-preserved specimens from the lower Daye Formation (Dienerian, Induan) in Guizhou, China. *Guiyangichthys* documents one of the oldest perleidids, and its studies provide insights into the early diversification of this family. *Guiyangichthys* shares two derived features of Perleididae, the preopercle process length of dermohyal nearly being half the length of the anterodorsal process of the preopercle, and the anteroventral corner of the preopercle being nearly the same horizon as the ventral end of opercle. It differs from other members of this clade in the following features: presence of postspiracle, presence of three supraorbitals, two infraorbitals, six pairs of branchiostegal rays, and a relatively deep anterodorsal process of the subopercle. Results of a phylogenetic analysis recover *Guiyangichthys* as a sister taxon to *Teffichthys* within the Perleididae (Perleidiformes) and provide new insights into the interrelationships of early neopterygian clades. The Perleidiformes are constricted to include only the Perleididae, and other previously alleged 'perleidiform' families (e.g., Hydropessidae and Gabanellidae) are removed to maintain the monophyly of this

order. Similar to many other perleidids, it is likely a durophagous predator with dentition combining grasping and crushing morphologies. The new finding provides an important addition for our understanding of the trophic structure of the Early Triassic marine ecosystem in South China.

1. Introduction

The Permian-Triassic massive 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 extinct 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, fishes 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 fossil 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 (Hurley et al. 2007; Xu et al. 2014). 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, and France (Fig. 1A). Over the last century, Early Triassic marine neopterygian localities have been uncovered in East Greenland, Madagascar, West Canada, and Spitzbergen. Recently, some marine neopterygians during this period have been reported from South China, India, and America (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 *Tungusichthy* (Berg 1941). The representative genera of the Early Triassic Neopterygii include *Australosomus*, *Watsonulus*, *Albertonia*, *Helmolepis*, *Plesioperleidus*, *Parasemionotus*, and *Teffichthys* (Stensiö

1932; Lehman 1952; Jin et al. 2003; Mutter 2005; Tong et al. 2006; Marrama et al. 2017).

Perleidiformes are a group of stem-neopterygian taxa that lived in both marine and freshwater environments in the Triassic. The paraphyly of Perleidiformes has been detected in many previous phylogenetic studies (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 1973b; 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 replaced in Platysiagiformes, Pseudobeaconiidae was included in Louwoichthyiformes, Teleopterinidae was moved to Amphicentriformes. Aetheodontidae was abandoned by the unique 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, the Perleidiformes include three families: Perleididae, Hydropessidae, and Gabanellidae. The latter two families only include a single genus each: *Hydropessum* from Hydropessidae and *Gabanellia* from Gabanellidae (Hutchinson 1973b; Tintori & Lombardo 1996).

Perleididae is known from many Triassic fish localities and has a complicated taxonomic history. More than 30 genera have been identified in this family. Nevertheless, many of them were revised later. At present, 16 genera were valid: *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 most of these genera were based only on classic studies and require further strict phylogenetic analysis.

The taxonomy of Perleididae in the Early Triassic is controversial. Except for *Chaohuperleidus*, all Perleididae in the Early Triassic have been placed in the *Perleidus*. Lombardo (2001) insisted that all current Early Triassic *Perleidus*-like fishes should be excluded from *Perleidus* due to the absence of epaxial rays. Recently, Marrama et al. (2017) erected a new genus *Teffichthys* and proposed that, except *Plesioperleidus*, all of the Early Triassic *Perleidus*-like fishes should be included in the new genus. Recently, Ma et al. (2021) reported that observation of the specimens indicated that *Teffichthys* has three epaxial procurrent rays.

Abundant Early Triassic Neopterygii have been found in South China over the last 40 years, providing an 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 the *Paraperleidus* from the Griensbachian, 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. During the Early Triassic, Guiyang was located on the southern edge of the Yangtze Platform. Besides 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 ammonoids and conodonts biostratigraphy (Qin et al. 1993; Mu et al. 2007; Bruehwiler et al. 2008; Dai et al. 2019).

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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. The specimens were photographed using a Canon 70D camera with a Micro EF lens with a focal length 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).

To explore the phylogeny of Perleididae, a cladistic analysis was conducted based on materials of *Guiyangichthys* gen. nov. of this paper, and direct observations of *Paraperleidus* and *Plesioperleidus*. In addition, we added *Moradebrichthys* and *Chaohuperleidus*, both of which were well preserved and were placed in Perleididae (Sun et al. 2013; Cartanyà et al. 2019; Dai et al. 2021). The phylogenetic analysis was based on an updated dataset revised from the data matrix of Xu (2021), containing 138 characters coded for 64 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; den, dentary; dh, dermohyal; dsp, dermosphenotic; exsc, extrascapular; ff, fringing fulcrum; fr, frontal bone; ju, jugal; la, lacrimal bone; lg, lateral gular; mx, maxilla; op, opercle; pa, parietal; pcl, postcleithrum; pop, preopercle; ppr, procurrent ray; pr, principal ray; psp, postspiracle; pt, posttemporal; sc, scale; scl, supracleithrum; so, suborbital; sop, subopercle; sr, sclerotic bone; su, supraorbital bone.

3. Results

3.1 Systematic paleontology

Infraclass Actinopteri Cope, 1871
Superdivision Neopterygii Regan, 1923
Order Perleidiformes Berg, 1937
Family Perleididae Brough, 1931
Genus *Guiyangichthys* gen. nov.
LSID urn:lsid:zoobank.org:act:D516B686-825D-4990-9929-9996D6C971A6

Etymology. The generic epithet “Guiyang” means the city near the two sections, and the Greek suffix “-ichthys” means fish.

Type species. *Guiyangichthys elegans* sp. nov.

Diagnosis. Same as for the type and only known species.

Species *Guiyangichthys 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 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 Perleididae distinguished from other members of this family by the following features (autapomorphies identified with an asterisk): presence of postspiracle (*); presence of three supraorbitals; presence of two infraorbitals; six pairs of branchiostegals rays; relative deep anterodorsal process of subopercle; the lacrimal separated from maxilla; the nasals don't contact with each other; the width of posttemporal is half of the width of extrascapular; presence of epaxial procurrent rays; pterygial formula of D26/P14, A22, C36/T39-41 (*).

3.2 Description

General Morphology and Size. *Guiyangichthys elegans* has a blunt snout, an elongate and fusiform body, and a forked, nearly equilibrated 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. The head length and body depth account 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, 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 partial 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 frontals medially. The length of the frontal is about twice the length of the parietal. The frontal reaches its greatest width at the posterior border of the orbit and slightly narrows towards the parietals.

The parietals are relatively small, rectangular in shape, 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 backward 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, indicated by a series of small tubercles.

All these skull roof bones are ornamented with dense tubercles and some ridges.

Circumorbital Bones. There are three rectangular or 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 has been split into two parts of the holotype (Fig. 5A).

Two infraorbitals are present (Figs. 4A-D; 5C, D). The lacrimal is elongate, dorsoventrally short, and slightly concave dorsally. 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 the dermopterotic dorsally, and the jugal ventrally. The infraorbital sensory canal extends through the entire length of the infraorbital and dermosphenotic, then enters the dermopterotic posteriorly.

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 preopercle is large and broad, contacting with 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 preopercle sensory canal extends along the posterior margin of this bone, indicated by a series of small pores (Figs. 4, 5).

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 postspiracle (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 same element also appeared in the description of "*Perleidus*" *piveteaui* (Lehman 1952). But we think this element should be presupracleithrum, as it is next to supracleithrum and behind the back of the opercle. Thus, it is the first appearance of this bone in Perleididae. The postspiracle only appeared in Peltopleuriformes before.

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

Palatal bones and suspensorium. The hyomandibula is not exposed. The rounded molariform teeth of the pterygoid bones are present, exposed in 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 pig-like teeth, and their length also decreases posteriorly. The supra-angular is not discernible. The angular is small and irregular in lateral view, tapering anteroventrally. The dentary is ornamented with small tubercles and ridges, the latter is mainly distributed near the oral margin. The mandibular sensory canal crosses ventrally the entire length of the dentary and the angular.

Opercular Series. The opercle is subtriangular in shape, having a nearly straight margin with the dermohyal in the anterodorsally margin. The subopercle is trapezoidal in shape with a sunken dorsal margin, larger than the opercle, possessing a moderately developed anterodorsal process, which is absent in other Perleididae except for *Plesioperleidus* (Figs. 4, 5).

Six pairs of branchiostegal rays are present below the dentary and angular. Four pairs are elongated and nearly equal in size in the anterior region (Figs. 4A, B). The latter two pairs broaden posteriorly, having the same width with 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 round posterior margin, being about one-third the length of the dentary. The right lateral gular is trapezoidal in shape, and it 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). It 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. 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 is overlapped by the supracleithrum. The ventral postcleithrum is irregular in shape, with a sunk dorsal margin, smaller than the dorsal one. The cleithrum is elongate and curved, inclined backward, and partly overlapped anteriorly by the subopercle, mainly ornamented with ridges on the surface.

The pectoral fins insert low on the body. They are large and each consists of 16 distally segmented and branched rays (Fig. 9A). The first ray is preceded by a series of fringing fulcra and two basal fulcra (Figs. 4A, B). There are at least five short rod-like radials between the cleithrum and the proximal portion of the pectoral fin (Figs. 4A, B).

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

Median fins. The dorsal fin originates above the origin of the 26th vertical scale row (Fig. 8B). It is composed of three procurrent rays and 12 principal rays, preceded by three basal fulcra and a series of fringing fulcra. All rays are segmented distally. The procurrent rays become longer posteriorly, and the third procurrent ray is the longest one, being about one-third the length of the first principal ray. The first principal ray, slightly shorter than the second, is unbranched and other rays are distally branched. The second principal ray is the longest ray of the dorsal fin and other principal rays become shorter posteriorly. There are seven exposed radials in the pterygiophores supporting the dorsal fin. Each of them nearly corresponds to a single fin ray, indicating that rays and radials 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, two unbranched rays, preceded by two basal fulcra (Fig. 8A). All rays are segmented distally, the first three rays are unbranched. Both of the procurrent rays associated fringing fulcra in their anterior margin. Notably, the first procurrent ray is very short, nearly one-third of the second one.

The caudal fin, well preserved in specimens CUGM K2-E2607-2608 (Figs. 3A, B; 9B-D), is abbreviated heterocercal with a forked posterior profile. The 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 steak tubercles, paralleled with the direction of fin rays, generally one to two in number (Figs. 9C, D). Tubercles that appeared on the surface of caudal fins also occurred in Colobodontidae, but they are rounded or elongated in shape.

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 largest in each vertical row. Each of them has a small notch at its posterior margin and two small pores which are present anteriorly in some lateral scales. 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. At 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 surface. Whereas at the posterior flank region, the scales are rhomboidal and smooth, and the denticles at the posterior margin gradually decrease in number posteriorly.

3.3 Phylogenetic affinities

The phylogenetic analysis resulted in 90 most parsimonious trees (tree length = 463 steps, consistency index = 0.420, retention index = 0.755), the strict consensus of which is present in Fig. 11. In the cladogram, Perleididae was recovered as a stem lineage of neopterygians, nested between Colobodontidae and Louwoichthyiformes.

The Perleididae shared the following derived features of Colobodontidae and more derived neopterygians: presence of molariform teeth on the oral bones (absent in *Plesiofuro*, Louwoichthyidae, *Altolepis*, *Venusichthys*, and more derived neopterygians), much reduced or lost quadratojugal (become splint-like shape in *Lepisosteus*, *Semionotus*, and *Kyphosichthys*), equal number of dorsal and anal fin rays relative to radials, and dorsal and anal fin rays only being segmented distally. Perleididae and more derived neopterygians were placed above Colobodontidae based on the following features: the dermosphenotic were not in contact with the preopercle (reversal in *Pseudobeaconia* and *Habroichthys*), presence of fewer than six pairs of branchiostegals (reversal in *Thoracopterus* and some crown-neopterygians), and 24 or fewer principal rays in caudal fin (reversal in *Ctenognathichthys*, *Luopingichthys*, *Fuyuanperleidus*, and *Caturus*). Perleididae lacked the derived features of Louwoichthyiformes and more derived neopterygians: ratio of dermopterotic length to parietal length was less than two (reversal in *Dipteronotus*, *Moradebrichthys*, and some crown-neopterygians) and presence of five or fewer epaxial basal fulcra (reversal in *Peltoperleidus*, *Venusichthys*, and many crown-neopterygians).

In Perleididae, *Perleidus* was recovered at the base of the Perleididae because it lacks derived feature of other members of this family, less than three epaxial procurrent rays. Above *Perleidus*, *Meidiichthys* and *Plesiofuro* formed a sister group by the absence of the epaxial procurrent rays. *Paraperleidus*, *Plesioperleidus*, and *Meidiichthys*-*Plesiofuro* clade formed a polytomy clade, supported by the features that width of the posttemporal nearly as wide as the extrascapular. Further up, *Guiyangichthys* and *Teffichthys* formed a sister group by the presence of two suborbitals. The sister relationship between *Guiyangichthys*-*Teffichthys* clade and the polytomy clade was supported by less than three epaxial procurrent rays. The former was more derived than the latter due to the presence of width of the posttemporal nearly half of the width of the extrascapular.

Notably, two genera, previously referred to as Perleididae, were replaced in other families. *Chaohuperleidus* was recovered as a member of Colobodontidae due to three synapomorphies of this family: anterior portions of frontals partly separated by median rostral bone, presence of prominent anterodorsal process of the subopercle, and presence of rounded ganoid tubercles on the principal caudal fin rays. *Moradebrichthys* was replaced at the base of Thoracopteridae and formed a sister group with *Wushaichthys* and more derived taxa of this family. It possessed 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.

In addition, phylogenetic relationships of some stem-neopterygian taxa were changed in the results of the analysis. *Redfieldius* and *Helichthys* were recovered as a sister group due to the absence of dermopterotic/preopercle contact. *Peltopleurus nitidus* formed a sister group with *Peltopleurus nitidus* by the presence of three features: anal fin being larger than dorsal fin, presence of a single suborbital, and presence of a broad suborbital posterior to the dermosphenotic, with the same depth with each other.

4. Discussion

4.1 The monophyly of Perleididae and Perleidiformes

The monophyly of Perleididae can be supported by two synapomorphies: the preopercle process length of dermohyal nearly being half the length of the anterodorsal process of the preopercle (unknown in *Paraperleidus* due to poor preservation; present in *Australosomus* and *Platysiagum*), and the anteroventral corner of the preopercle being nearly the same horizon as the ventral end of opercle (independently evolved in Redfieldiiformes, Platysiagiformes, and some Peltopleuriformes). Therefore, *Procheirichthys*, *Aetheodontus*, *Meridensia*, *Alvinia*, *Megaperleidus*, *Endennia*, *Chaohuperleidus*, and *Moradebrichthys* should be removed from Perleididae by the absence of the two synapomorphies (Wade 1935; Bürgin 1992; Sytchevskaya 1999; Lombardo & Brambillasca 2005; Sun et al. 2013; Cartanyà et al. 2019). *Eoperleidus* and *Megaperleidus* were erected based on fragmentary materials. However, they can be removed from Perleididae by the presence of two dermohyals and accessory opercle in *Eoperleidus* and a very deep dermohyal in *Megaperleidus* (Sytchevskaya 1999). The taxonomic positions of *Diandongperleidus* and *Luopingperleidus* are ambiguous due to the poor preservation and require further materials. At present, the phylogeny of Perleididae is still weakly supported, the revision of previous species and the discovery of more materials should be focused on in future works.

We propose that Perleididae as the single valid family of Perleidiformes to ensure its monophyly. Hydropessidae and Gabanellidae, previously referred to this order, were erected based on poorly preserved materials, hindering a convincing phylogenetic analysis. *Hydropessum* in Hydropessidae 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 1973b). *Gabanellia* in Gabanellidae is a near-apex predator, possessing several features unlike Perleididae: presence of a modified anal fin, presence of more than ten branchiostegal rays, and presence of uneven teeth in the powerful dentition (Tintori & Lombardo 1996). The specific phylogenetic relationships between these two families require further research. We propose removing them from Perleidiformes to recover the monophyly of this group.

4.2 Character comparisons

The major difference between *Guiyangichthys* gen. nov. and *Perleidus* is the suborbital and the teeth on the jaws. *Guiyangichthys* gen. 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 *Guiyangichthys* gen. nov. Unlike *Plesiofuro* and *Meidiichthys*, *Guiyangichthys* gen. nov. has two infraorbitals (three in *Plesiofuro*, one in *Meidiichthys*), two suborbitals (one in both *Plesiofuro* and *Meidiichthys*), six branchiostegals (five in *Plesiofuro*, four in *Meidiichthys*), and epaxial procurrent rays in caudal fin (only occurred in *Guiyangichthys* gen. nov., Table 1).

Guiyangichthys gen. nov. can be distinguished from *Paraperleidus* by the following features: presence of two suborbitals, the width of posttemporal half of the width of extrascapular, and nasals being separated by rostral (Table 1). In addition, the standard length of *Guiyangichthys* gen. nov. is approximately 148 mm, much smaller than *Paraperleidus*, which reaches 265 mm in standard length (Zhao & Lu 2007). Notably, *Paraperleidus* differs from other Perleididae based on several features. First, the nasal bones are joined in the midline and located posterior to the rostrals. In stem-neopterygians, this feature only occurs in Platysiagiformes and *Thoracopterus* in Peltopleuriformes. Second, the width of posttemporal is nearly the same as the width of extrascapular. *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*.

Guiyangichthys gen. nov. differs from *Plesioperleidus* based on the following features: width of posttemporal being only half of the width of extrascapular, absence of fused lacrimo-maxilla, absence of an anteriorly extended portion of preopercle, and presence of two suborbitals (Table 1). In addition, *Plesioperleidus* differs from other Perleididae based on the following features: width of posttemporal being nearly the same as the width of extrascapular, similar to *Paraperleidus*; the lacrimal being fused with the maxilla, which also appears in *Feroxichthys* and Luganoiiformes; and presence of an anteriorly extended ventral portion of preopercle, which is absent in other Perleididae.

Guiyangichthys gen. nov. is more closely related to *Teffichthys* than other taxa of Perleididae. It differs from *Teffichthys* based on several features (Table 1). First, six pairs of branchiostegal rays appear in *Guiyangichthys* gen. nov., while *Teffichthys* has four to five. Second, the posterior margin of the jugal in *Teffichthys* bears developed spines, which are not present in *Guiyangichthys* gen. nov. Third, four supraorbitals appear in *Teffichthys*, while three supraorbitals occur in *Guiyangichthys* gen. nov. Fourth, the postspiracle is only present in *Guiyangichthys* gen. nov. Fifth, *Guiyangichthys* gen. nov. is larger than *Teffichthys*. At present, the largest specimen of *Teffichthys* is 129 mm in standard length, while *Guiyangichthys* gen. nov. is more than 148 mm in standard length. Moreover, the base of the dorsal and anal fins lacks one or two horizontal scale rows of *Guiyangichthys* gen. nov., indicating that it is still a juvenile.

4.3 Biogeographical and ecological implications

Perleididae reached a cosmopolitan distribution in the early Olenekian. Similar cosmopolitanisms have 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, it 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. 11). In the Induan, Perleididae was discovered in South China, East Greenland, and Madagascar (Stensiö 1932; Lehman 1952; Zhao & Lu 2007; Marrama et al. 2017). At the beginning of the Olenekian, Perleididae underwent rapid radiation. It was present in Spitsbergen, South China, Western Canada, and Madagascar during the Smithian, demonstrating a global distribution pattern (Woodward 1912; Stensiö 1921; Lehman 1952; Schaeffer et al. 1976; Jin et al. 2003; Marrama 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 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 1973b; Lombardo 2001; Lombardo et al. 2011).

The discovery of *Guiyangichthys elegans* 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), 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 *Guiyangichthys* provides excellent grasping and crushing abilities, enabling it to hunt various prey. As a predator, *Guiyangichthys* possessed a streamlined form body shape 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 *Guiyangichthys* 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 the Perleididae, *Teffichthys* and *Perleidus* possessed a similar feeding apparatus (Lombardo 2001; Marrama et al. 2017). However, *Guiyangichthys* is the largest durophagous predator of Perleididae known to date. Compared with the Colobodontidae, which was a large durophagous predatory fish (Bürgin et al. 1996; Mutter 2004; Xu 2020a), the peg-like and molariform teeth of *Guiyangichthys* were less developed, indicating that it may have 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 *Guiyangichthys elegans* gen. et 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. *Guiyangichthys* gen. is recovered as a member of Perleididae, forming a sister group with *Teffichthys*. *Paraperleidus* and *Plesioperleidus* were placed above *Plesiofuro* and *Meidiichthys* in Perleididae. *Chaohuperleidus* and *Moradebrichthys* were moved to Colobodontidae and Thoracopteridae, respectively. The Hydropessidae and Gabanellidae were removed from Perleidiformes to keep the monophyly of this order. As the largest durophagous predator in Perleididae, the combination of molariform and conical teeth of *Guiyangichthys* were well adapted for grasping and crushing, helping it succeed in the Early Triassic.

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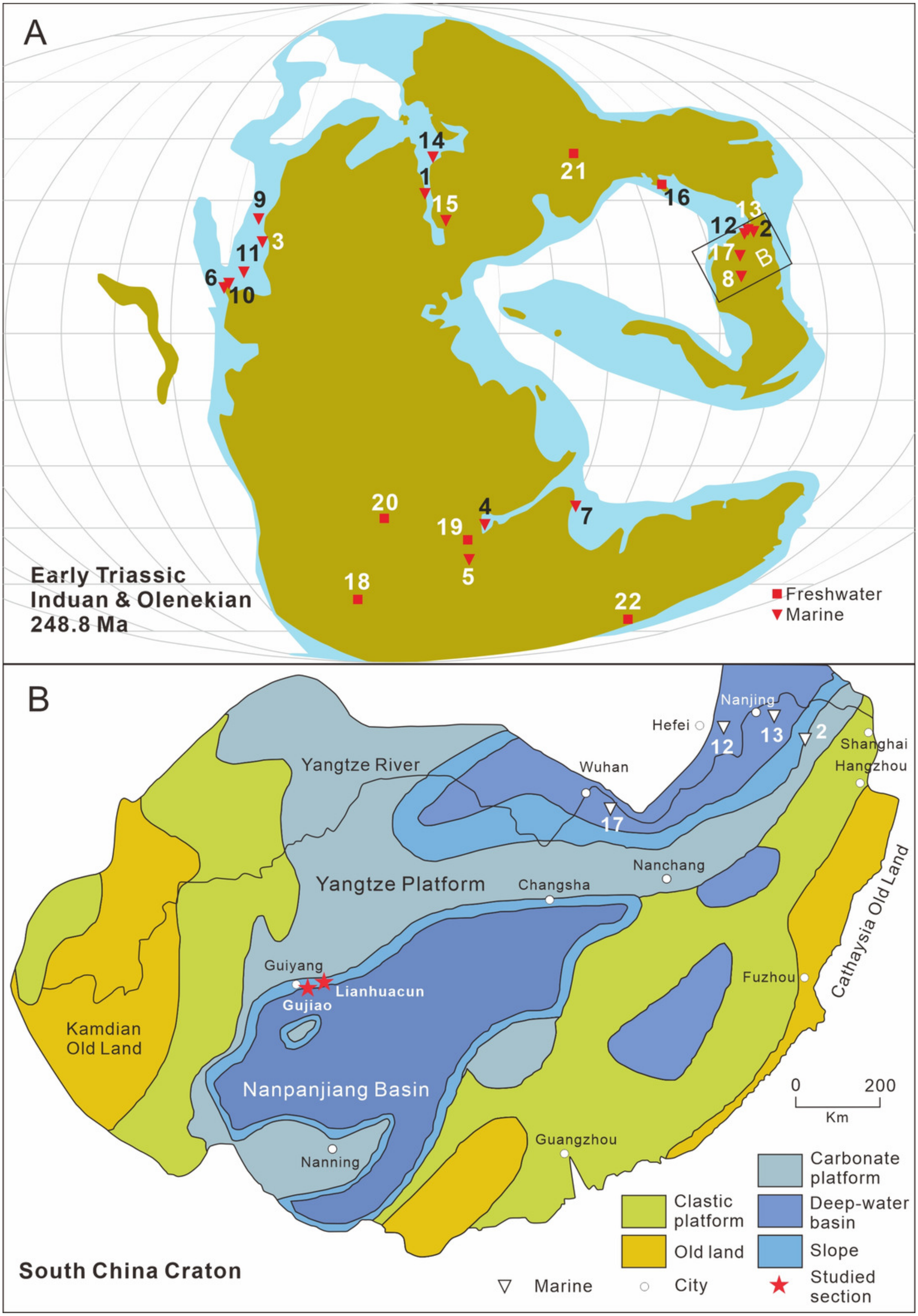
Figure 1

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, 1949); 2, Zhejiang, China (Zhao & Lu, 2007); 3, Alberta, Canada (e.g. Lambe, 1916; Neuman, 2015); 4, Northwestern Madagascar (e.g. Lehman, 1952; Marrama et al., 2017); 5, Southeast Madagascar (e.g. Lehman et al., 1959); 6, Elko County, Nevada, America (Romano et al., 2019); 7, India, Spiti (Romano et al. 2016) ; 8, Guizhou, China (this paper); 9, British Columbia, Canada (e.g. Schaeffer et al., 1976; Mutter, 2005); 10, Esmeralda County, Nevada, America (Romano et al., 2017); 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 (Romano et al., 2017); 16, Gansu, China (Xu et al., 2015); 17, Hubei, China (Su & Li, 1983); 18, South Africa (e.g. Brough, 1931; Hutchinson, 1973); 19, Tanzania (Haughton, 1936); 20, Angola (e.g. Antunes et al., 1990; Murray, 2000); 21, Siberia, Russia (Sytchevskaya, 1999); 22, Tasmania, Australia (Dziewa, 1980); Griensbachian: 1-2; Dienerian: 1, 3-8; Smithian: 9-14; Spathian: 11, 13-15; Early Triassic (stage indet.): 16-22. Neopterygii localities: 1-9, 12-18, 20-22. B. Map showing the fossil locality of *Guiyangichthys elegans* gen. et 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); 17, *Plesioperleidus* from Hubei, China (Su & Li, 1983);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Early Triassic
Induan & Olenekian
248.8 Ma
■ Freshwater
▼ Marine
B
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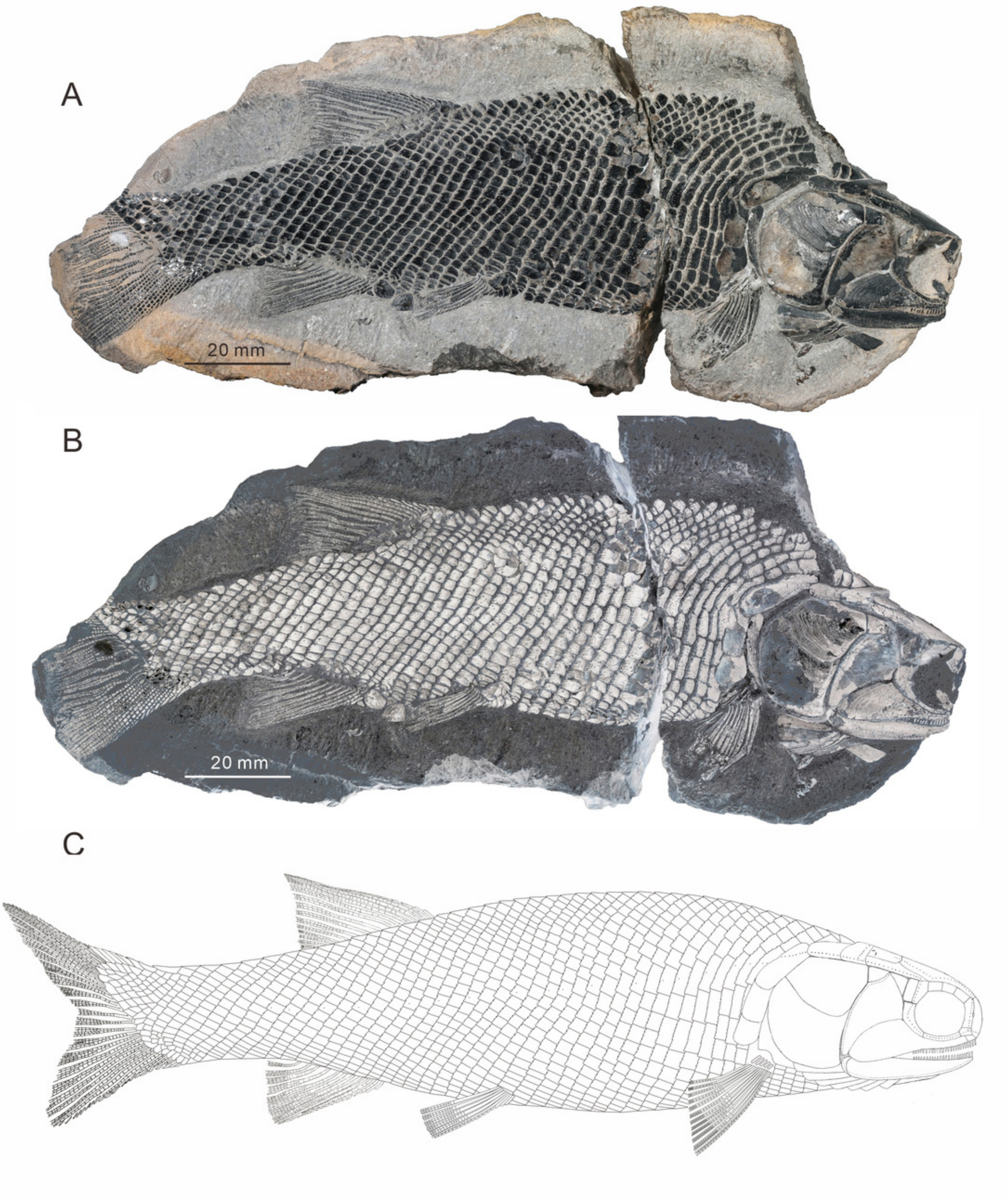
Hefei
12
13
2
Shanghai
Hangzhou
Yangtze River
Wuhan
17
Nanchang
Yangtze Platform
Changsha
Guiyang
Lianhuacun
Gujiao
Fuzhou
Cathaysia Old Land
Kamdian
Old Land
Nanpanjiang Basin
0
200
Km
Guangzhou
Nanning
Carbonate platform
Clastic platform
Deep-water basin
Old land
Slope
South China Craton
▽ Marine
○ City
★ Studied section

Figure 2

Holotype and the reconstruction of *Guiyangichthys elegans* gen. et sp. nov.

(A) CUGM K2-E2601, holotype. (B) Inverse state of the specimen. (C) Reconstruction.


A
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B
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C

Figure 3

Two paratypes of *Guiyangichthys elegans* gen. et sp. nov.

(A) CUGM K2-E2602. (B) CUGM K2-E2603.

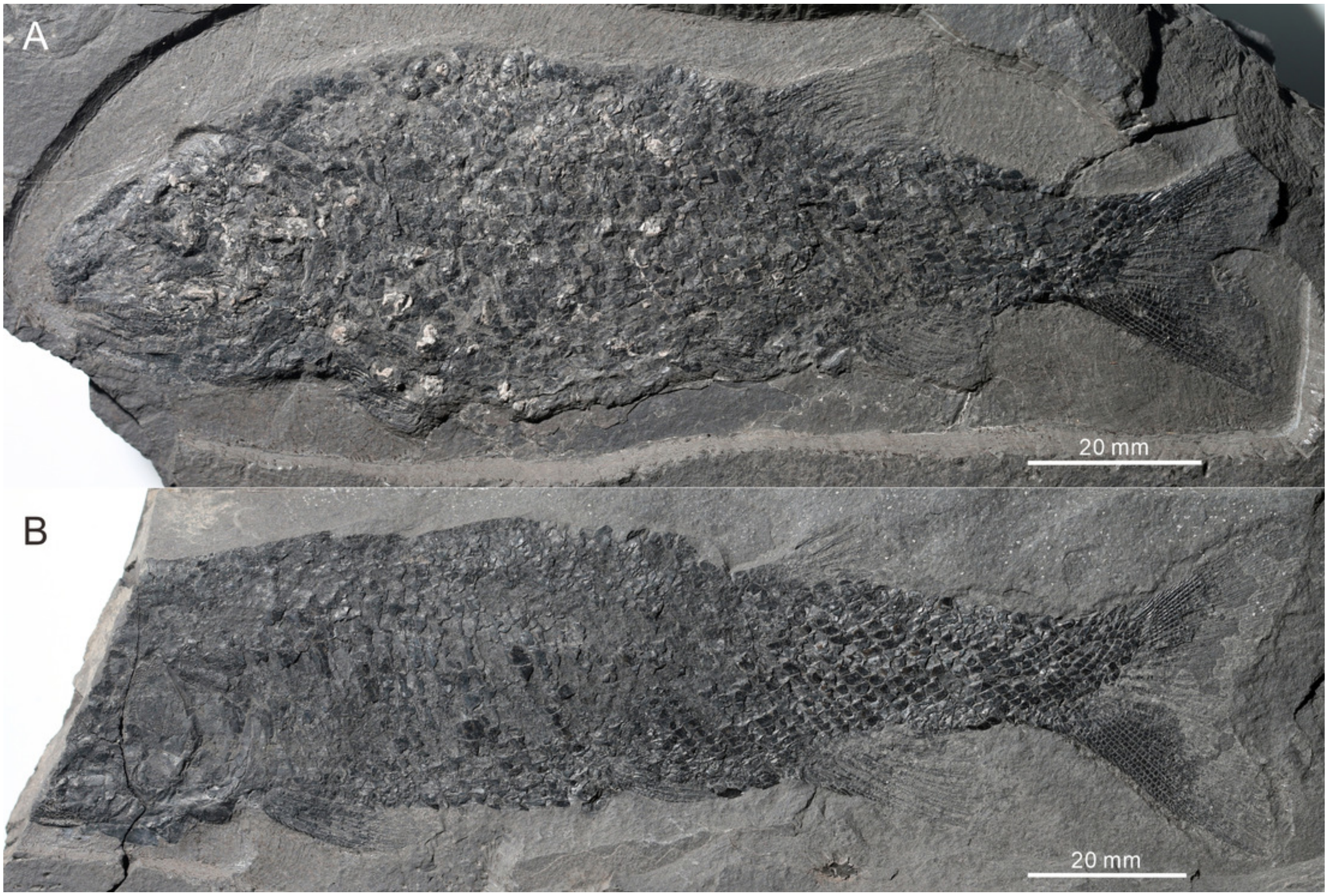
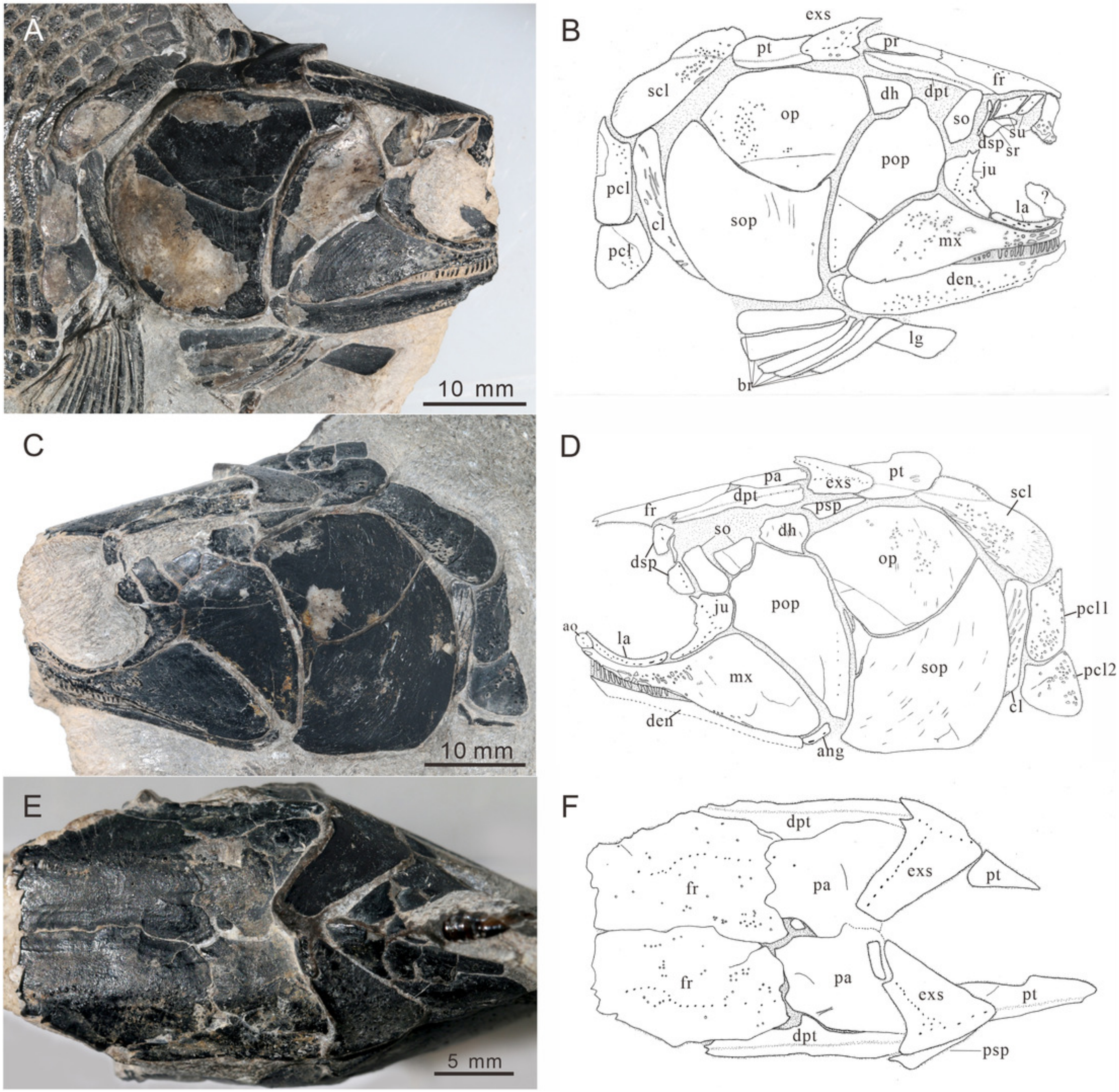


Figure 4

Skull and pectoral girdle of holotype from right, left and skull roof view of CUGM K2-E2601 (holotype).

(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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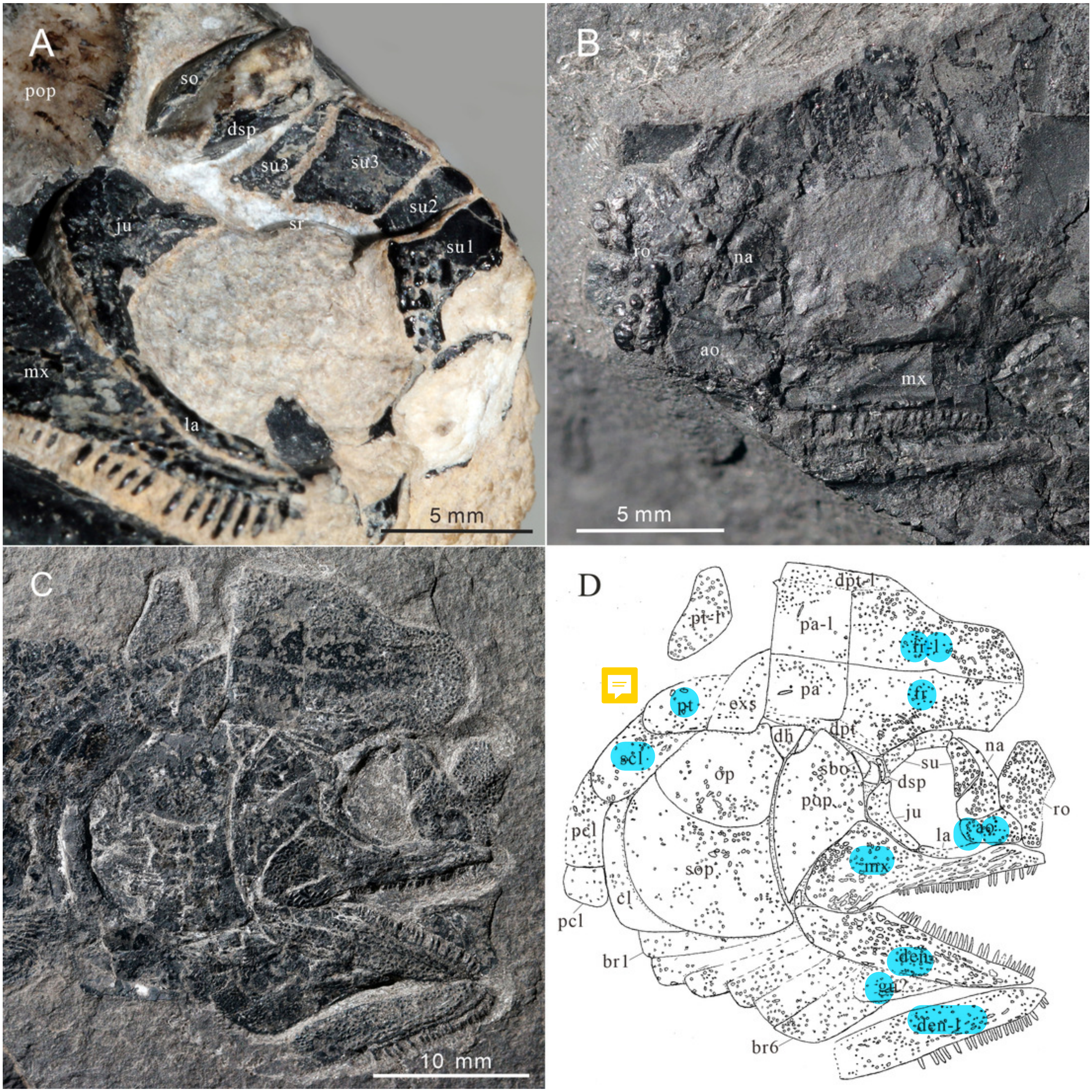
ang
E
5 mm
F
dpt
fr
pa
exs
pt
fr
pa
exs
pt
dpt
psp

Figure 5

Skull and pectoral girdle of *Guiyangichthys elegans* gen. et 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.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pa-l
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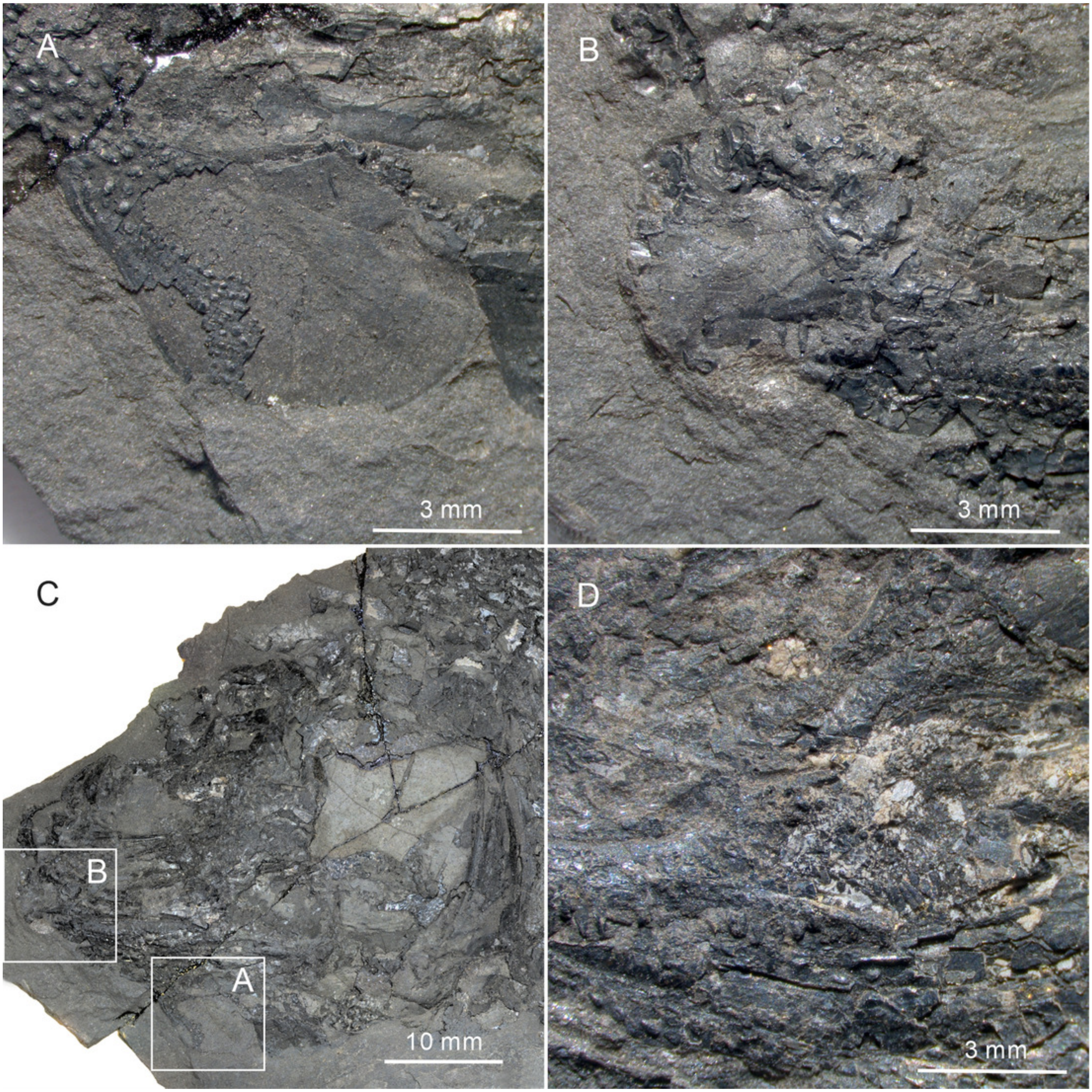
Figure 6

Gular, premaxilla and molariform teeth of *Guiyangichthys elegans* gen. et sp. nov.

(A-C) CUGM K2-E2607; (A) Gular, (B) premaxilla, (C) Head. (D) CUGM K2-E2602, molariform teeth.


A
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3 mm
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A
10 mm
D
3 mm

Figure 7

Reconstruction of skull and pectoral girdle of *Guiyangichthys elegans* gen. et sp. nov.

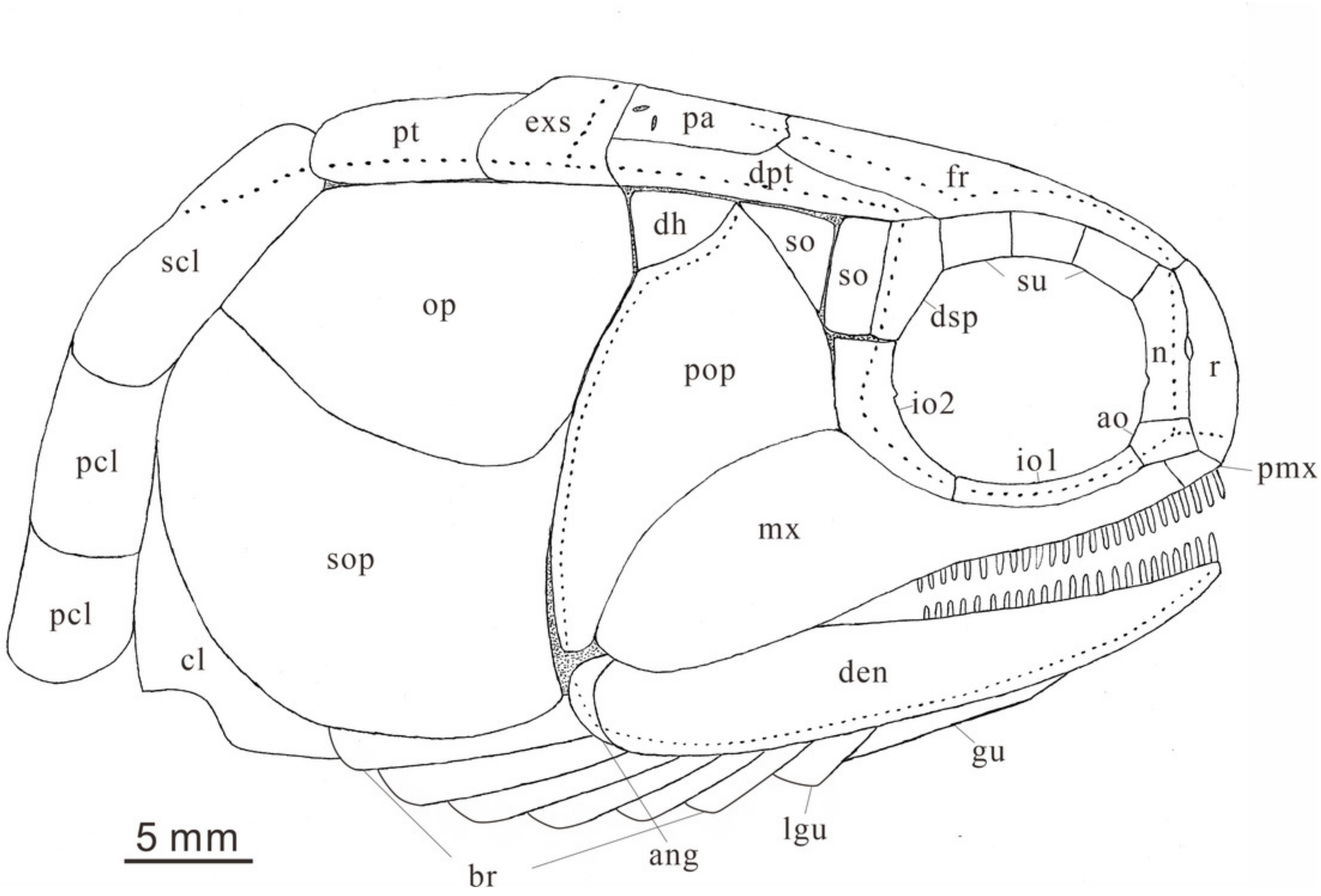


Figure 8

Fins of *Guiyangichthys elegans* gen. et sp. nov. of CUGM K2-E2601 (holotype).

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

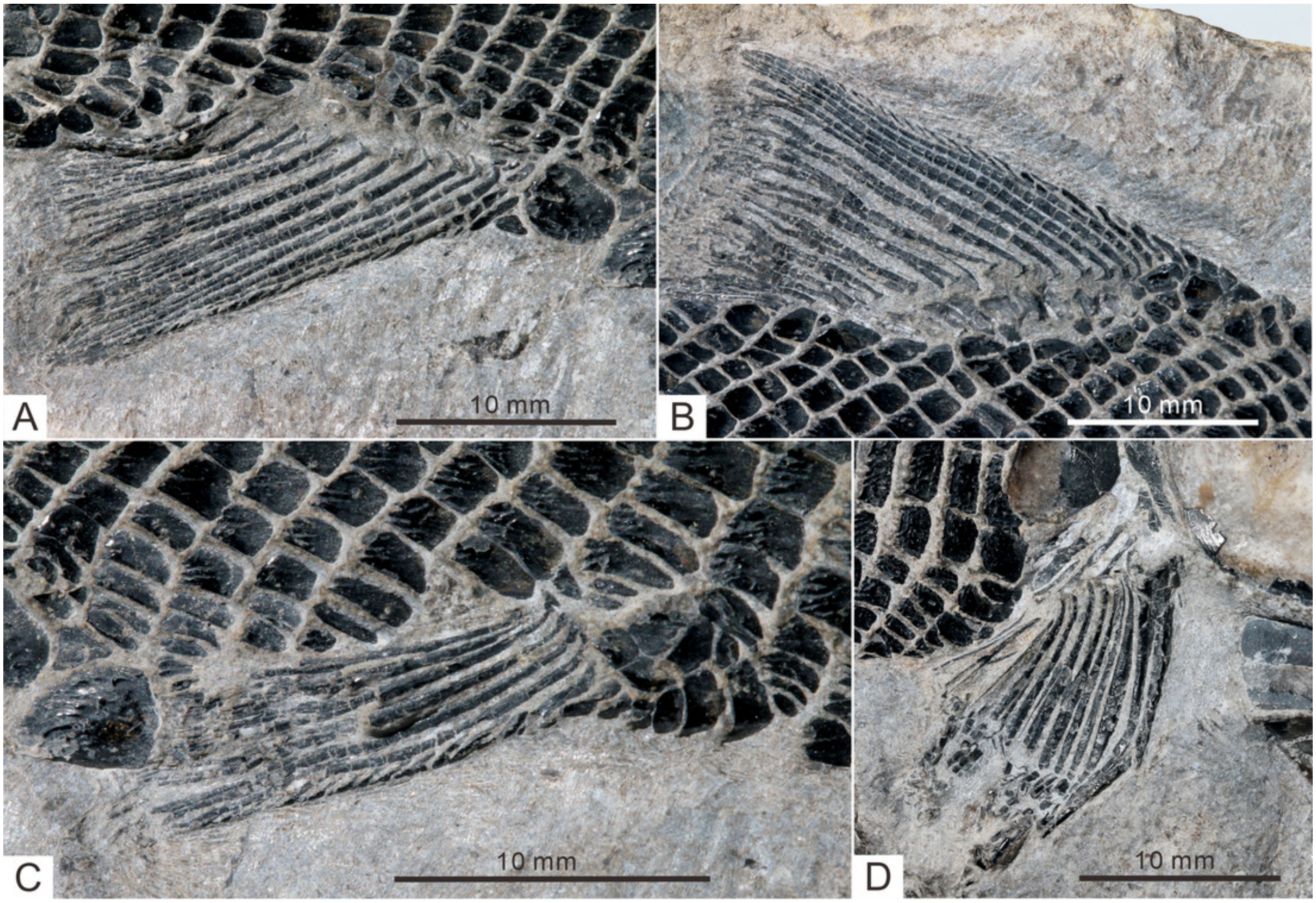
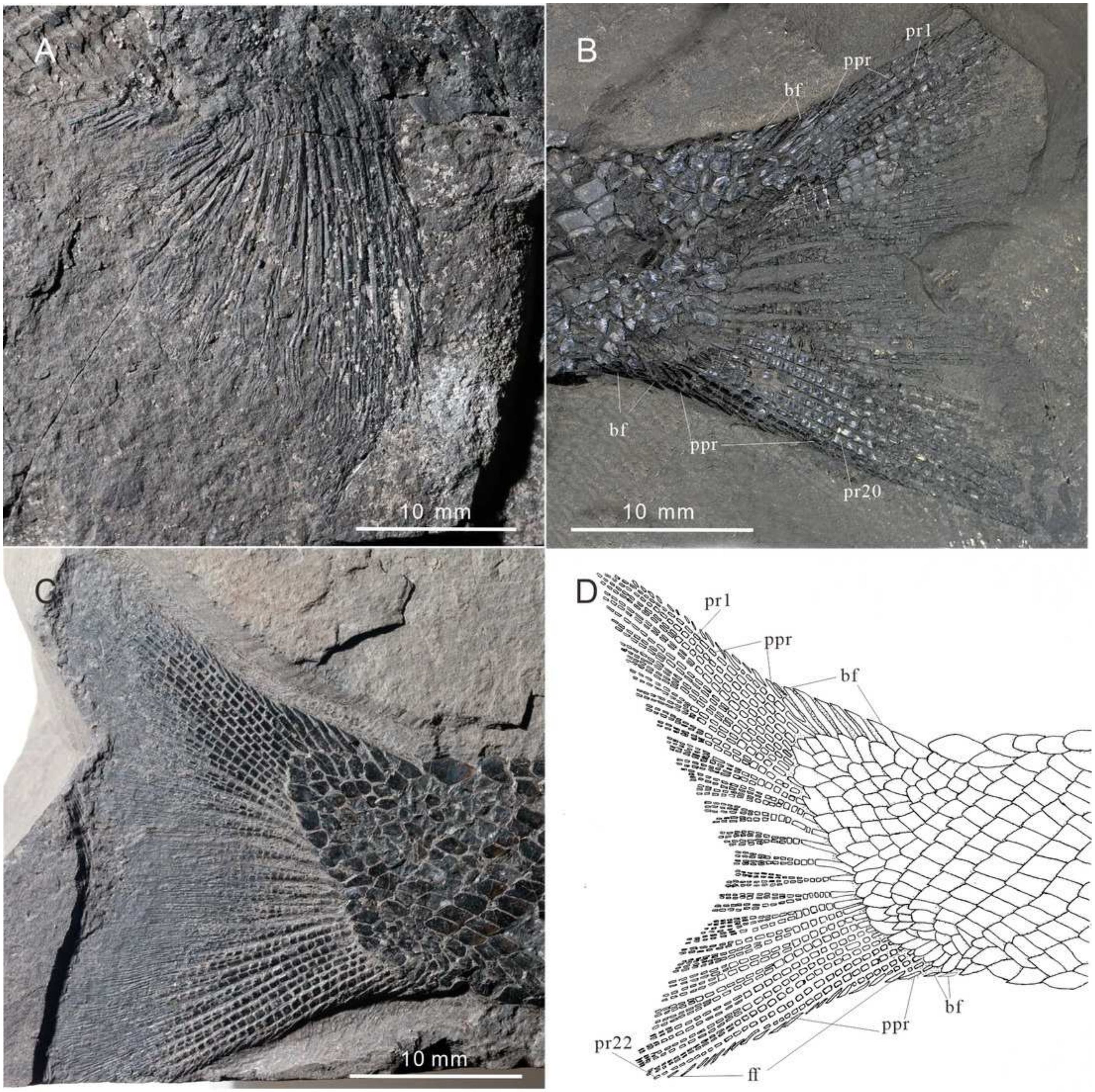


Figure 9

Pectoral fin and Caudal fin of *Guiyangichthys elegans* gen. et 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.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pr20
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C
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D
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pr22
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Figure 10

Strict consensus of most parsimonious trees.

Strict consensus of 90 most parsimonious trees (tree length = 463 steps, consistency index = 0.420, retention index = 0.755), illustrating the phylogenetic position of *Guiyangichthys elegans* gen. et sp. nov. within the Actinopterygii. Numbers above nodes indicate Bremer decay indices.

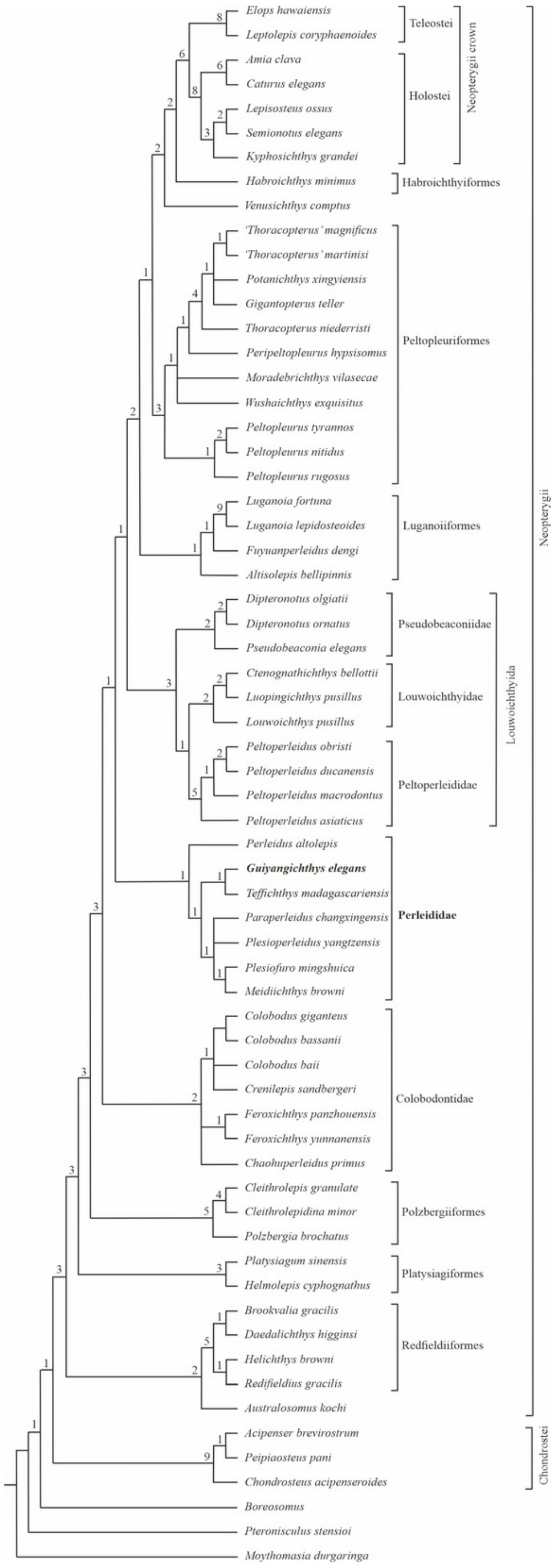
Elops hawaiensis
Leptolepis coryphaenoides
Amia clava
Caturus elegans
Lepisosteus ossus
Semionotus elegans
Kyphosichthys grandei
Habroichthys minimus
Venusichthys comptus
'Thoracopterus' magnificus
'Thoracopterus' martinisi
Potanichthys xingyiensis
Gigantopterus teller
Thoracopterus niederristi
Peripeltopleurus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

Figure 11

The paleogeographic distribution of Perleididae in Early 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.

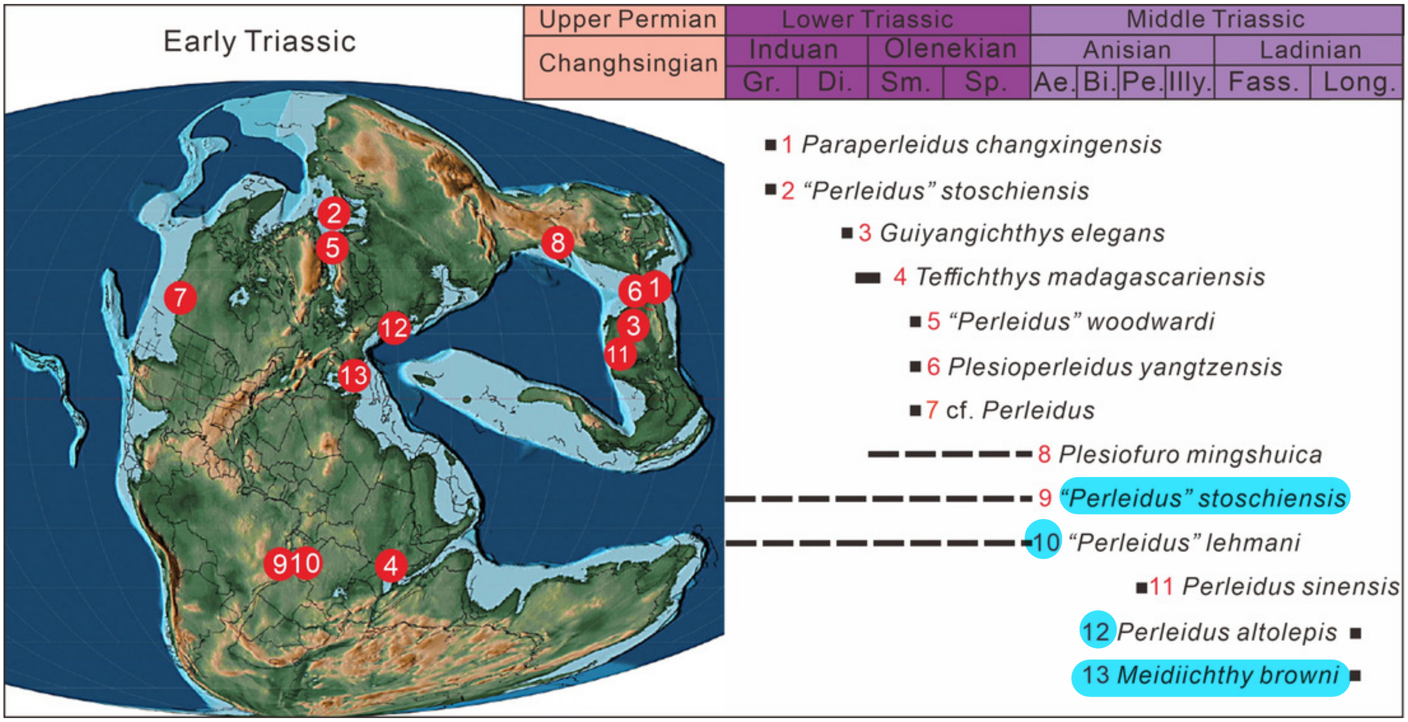

Table 1(on next page)

Summary of characters used to differ members of Perleididae.

Data from Lombardo, 2001; Marrama et al., 2017; Zhao and Lu, 2007; Jin, 2003; Xu, 2015; Brough, 1931. *Paraperleidus* and *Plesioperleidus* is based on personal observation. 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
Guiyangichthys elegans	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)