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FUYUANPERLEIDUS DENGI GENG ET AL., 2012 (OSTEICHTHYES, ACTINOPTERYGII) FROM THE MIDDLE TRIASSIC OF YUNNAN PROVINCE, SOUTH CHINA

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Abstract. Two well preserved specimens of *Fuyuanperleidus dengi* Geng et al., 2012 are described from the Upper Member of the Guanling Formation (Pelsonian, Anisian, Middle Triassic) in Luoping County, Yunnan Province, South China. The attribution to Perleidiformes is confirmed according to a combination of features such as the general skull pattern, with the large preoperculum showing a prominent infraorbital process, the maxilla with deep posterior region and a dentition made of long and stout peg-like teeth with an acuminate apex, the deep mid-lateral flank scales and the caudal fin with epaxial fin rays. However, this taxon shows an unique arrangement of the squamation (here considered as autapomorphy) given by the insertion of several scales in each vertical row posterior to the pelvic fin, just below the scales carrying the lateral line, when their depth decreases abruptly. Owing to this unique character, and in spite of the very recent description of this genus, the authors considered necessary the erection of a new family, Fuyuanperleididae offering also new insights on the evolutionary trends and morphological specializations of the "subholosteans". A cladistic analysis of the well known perleidiformes, with this taxon included, supports a possible monophyly of the order, and matches well the paleobiogeographic relationships of the Gondwana fresh-water taxa. The specialized deep-bodied Gondwana and Tethyan perleidiformes are independently evolved, ascertained by the parsimony analysis.

Riassunto. Vengono descritti due esemplari ben conservati del perleidiforme *Fuyuanperleidus dengi* Geng et al., 2012, provenienti dal Membro Superiore della Guanling Formation (Pelsonico, Anisico, Trias Medio) nella Contea di Luoping (Provincia dello Yunnan, Cina Meridionale). L'appartenenza ai Perleidiformes viene confermata grazie alla combinazione di caratteri data dalla struttura generale del cranio (ampio preopercolo che mostra un processo infraorbitale ben sviluppato, mascellare con un'alta regione posteriore e dentatura fatta di lunghi e robusti denti a piolo con un apice acuminato) dalle alte scaglie mediolaterali e la pinna caudale che presenta raggi epaxiali. Questo taxon mostra tuttavia una disposizione unica delle scaglie (qui considerata come autapomorfia), data dall'inserzione di scaglie supplementari in ciascuna fila verticale posteriore alle pinne pelviche, appena sotto le scaglie della linea laterale, dove la loro altezza diminuisce bruscamente. Per questo carattere presente solo in questo taxon, e nonostante la recente descrizione del genere, si è ritenuta necessaria l'istituzione della nuova famiglia Fuyuanperleididae; vengono inoltre fornite nuove indicazioni sulle tendenze evolutive e le specializzazioni morfologiche dei "subolostei". Un'analisi cladistica dei perleidiformi già noti, incluso il taxon in oggetto, supporta una monofilia possibile dell'ordine, e si adatta perfettamente alle relazioni paleobiogeografiche dei taxa d'acqua dolce del Gondwana. I perleidiformi specializzati a corpo alto del Gondwana e della Tetide si sono evoluti in modo indipendente, come accertato dall'analisi di parsimonia.

Introduction

The term "subholosteans" was ever considered as an informal taxonomical name or grade level, since Brough (1936) first coined it, to lodge a possible unnatural assemblage of fossil fishes which possess mosaic characters of palaeoniscoids and higher actinopterygians e.g. holosteans (or basal neopterygians; Brough 1939; Schaeffer 1955, 1973). Seven orders (Parasemionotiformes, Redfieldiiformes, Pholidopleuriformes, Luganoiiformes, Cephaloxeniformes, Perleidiformes, Peltopleuriformes) have previously been proposed (Schaeffer 1973). However further taxonomic revisions proved that only if the "subholosteans" is severely restricted,

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can possibly synapomorphies be identified (Bürgin 1992; Gardiner et al. 1996). Nowadays, the "subholosteans", restricted to peltopleuriforms and perleidiforms, represent a morphologically distinct group which is characterized by the combination of a primitive skull-pattern with the maxilla strictly articulated to the preoperculum, a peculiar squamation made of deep anterior flank scales, an advanced dorsal and anal fin structure with lepidotrichia equal in number to their endoskeletal supports except for the last radial supporting more than one lepidotrichium (as for the basal neopterygians, see Tintori et al. 2010), and the hemiheterocercal caudal fin nearly reaching an external symmetry with the epaxial fin rays (Tintori & Lombardo 2005; Lombardo et al. 2011).

"Subholosteans", so far well recorded from the Middle Triassic of Northern Italy, Switzerland, Spain and China, are greatly morphologically specialized (Bürgin 1992, 1996; Lombardo 1999, 2001; Lombardo & Tintori 2004; Lombardo et al. 2008; Tintori & Lombardo 2005; Sun et al. 2008, 2009) because of their notably differentiated trophic adaptations. In the Late Triassic, "subholosteans" reached again a rather high level of morphological specializations, such as fins and vertebral column adapted to gliding (*Thoracopterus*, Tintori & Sassi 1992), powerful predatory dentition (*Gabanellia*, Tintori & Lombardo 1996) or fully durophagous one (*Endennia*, Lombardo & Brambillasca 2005).

The two fairly well-preserved specimens of *Fuyuanperleidus dengi* from the Middle Anisian (Middle Triassic) of the Luoping Fauna, Yunnan Province, Southern China, suggest to erect a new perleidiform family for this genus, and to provide further insights on the relationships of perleidiforms, especially regarding the arrangement of the flank scales. It must be pointed out that specimens described herein are from a quite different fossil assemblage in respect to the supposed one for the holotype of Geng et al. (2012).

Geological setting and age

The Luoping Fauna, from the Upper Member of the Guanling Formation (Pelsonian, Middle Triassic) of Yunnan Province in South China (corresponding to the Member II in Zhang et al. 2009), is a recently discovered fossil-Lagerstätte, which yields abundant and very well preserved fishes, marine reptiles, different arthropods (isopods, decapods, horseshoe crabs, mysidiaceans, etc.), molluscs (bivalves, gastropods, cephalopods), echinoderms, brachiopods and conodonts, as well as foraminifers, making it a complex marine ecosystem. The striking feature of the Luoping Fauna, in contrast to other Triassic marine vertebrate faunas of Southern China i.e. the Anisian Panxian Fauna, the Late Ladinian Xingyi Fauna, and the Early Carnian Guanling Fauna (Jiang et al. 2005; Li 2006; Motani et al. 2008), is that it yields, besides marine reptiles and invertebrates, a highly abundant fish assemblage, probably with more than 25 taxa of actinopterygians and crossopterygians. The good preservation and the high number of specimens, make the Luoping Fauna one of the most important finds in the last decades for Middle Triassic marine ichthyofaunas (Tintori et al. 2010). So far, already 12 species of 9 genera of fishes have been named and described (*Marcopoloichthys ani* Tintori et al. 2008; *Luopingichthys bergi* Sun et al. 2009; *Saurichthys dawaziensis* Wu et al. 2009; *Saurichthys yunnanensis* Zhang et al. 2010; *Gymnoichthys inopinatus* Tintori et al. 2010; *Habroichthys broughi* Lin et al. 2011; *Perleidus sinensis* Lombardo et al. 2011; *Sangiorgioichthys sui* López-Arbarello et al. 2011; *Sinosaurichthys longipectoralis* Wu et al. 2011; *Sinosaurichthys longimedialis* Wu et al. 2011; *Sinosaurichthys minuta* Wu et al. 2011; *Kyphosichthys grandei* Xu & Wu 2012).

The Guanling Formation of the Luoping County generally represents the Anisian deposits of the southwestern Yangtze Platform in the China Southern Block. The fossiliferous layers yielding the Luoping fauna belong to the Upper Member and were subdivided into two horizons, namely Lower and Upper Vertebrate Horizons (LVH and UVH, see also Sun et al. 2009) separated by 1.8 m thick, barren dolomitic limestones with chert nodules (Fig. 1D). The carbonate microfacies analysis suggests that the Upper Member of the Guanling Formation represents a shallowing-upward (regressive) depositional sequences in an interplatform basin (Huang et al. 2009).

The Luoping Fauna is supposed to be coeval to the Panxian Fauna (Sun et al. 2006, 2009; Huang et al. 2009). Actually, conodont biostratigraphy of the Upper Member of the Guanling Formation, exposed in both Luoping County (Yunnan Province) and adjacent Panxian County (Guizhou Province), ascertained the fossiliferous layers of these two marine vertebrate faunas within the same conodont *Nicoraella kockeli* zone, a definitive indicator of the Pelsonian in the Tethyan realm. However, it is almost impossible to compare in more detailed way the real relative age of the two sites.

Remarks. In this paper, following the Principle of Priority, we use the nomenclature adopted by Geng et al. (2012), but some clarifications are needed.

In erecting the taxon *Fuyuanperleidus dengi* Geng et al., 2012, the Authors indicate as Locality and Horizon: "Jiyangshan, Shibalianshan, Fuyuan County, Yunnan Province; Middle Triassic (Upper Ladinian) Zhuganpo Member of the Falang Formation" (Geng et al. 2012: 916). Following this indication, we cast doubt

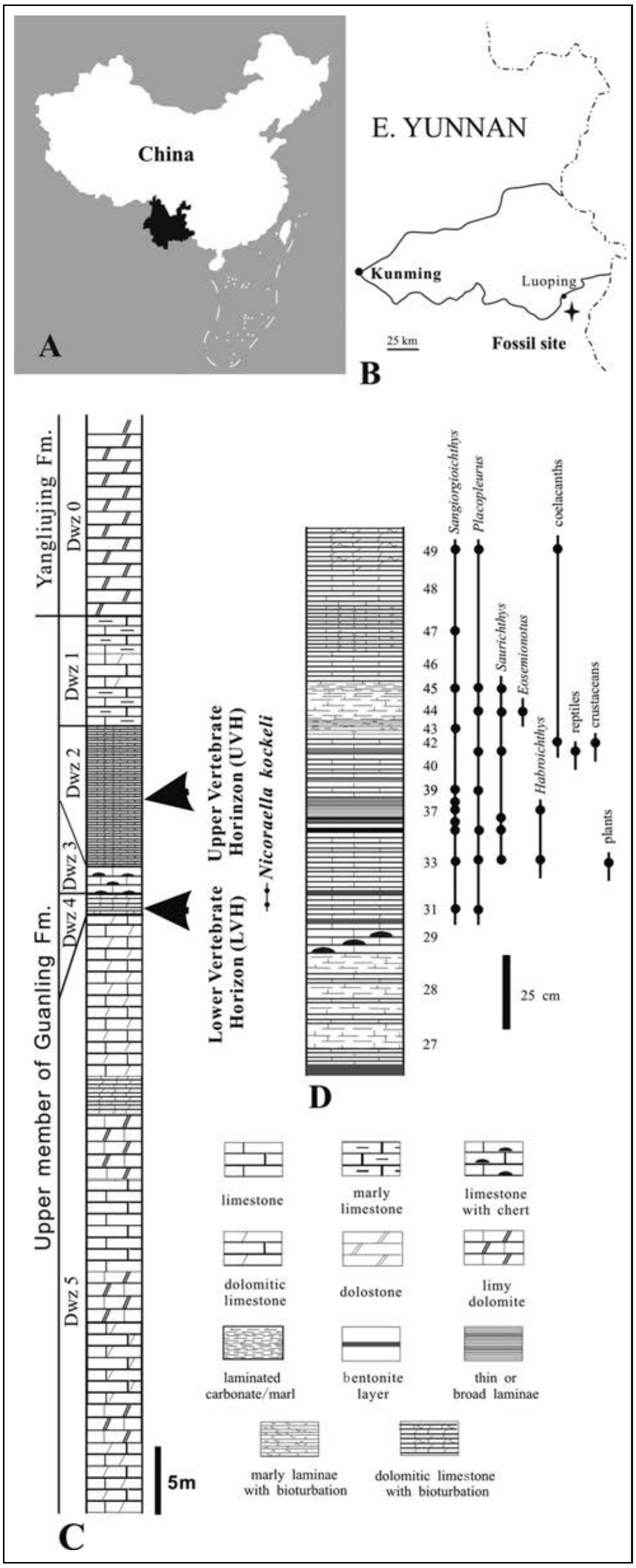


Fig. 1 - A, B, simplified maps indicating the site of the Luoping Fauna; C, D, simplified stratigraphic chart indicating the stratigraphic position of the Luoping Fauna and detailed sequence of the LVH, respectively (modified from Sun et al. 2009).

about the provenience, and therefore the dating, of the material described by Geng et al. (2012), on the basis of two main observations:

1) the holotype of *Fuyuanperleidus dengi* Geng et al., 2012, has the same kind of preservation shown by the material coming from the fossiliferous layers of the Luoping Fauna, as the specimens here described. The field experience of some of the Authors of this paper (Z.S., A.T., D.J., Y.S.) suggests that the fossils coming from Fuyuan have a kind of preservation completely different: therefore the provenience of the holotype of *Fuyuanperleidus dengi* Geng et al., 2012, from that locality and horizon is highly questioned.

2) The holotype of the species is, according to the Authors who erected it, Late Ladinian in age, while the specimens described in this paper come from Middle Anisian levels. The time span dividing these specimens, which undoubtedly belong to the same species, is at least suspicious, in particular if we take into consideration the explosive evolutionary radiation shown by the Middle Anisian ichthyofaunas, and the well-known extraordinary variability of the representatives of "subholosteans" (Lombardo et al. 2008, 2011; Sun et al. 2009; Lin et al. 2011; Geng et al. 2012). Furthermore, following the latest version of the International Chronostratigraphic Chart (International Commission on Stratigraphy – IUGS, July 2012), the time span between Middle Anisian and Upper Ladinian may be up to 10 My: this makes unlikely, according to us, the presence of the same species in levels several millions years apart. Moreover, the Late Ladinian fish fauna from Dinxiao-Wusha-Fuyuan is quite poor in "subholosteans" compared to the Anisian Luoping Fauna, being so far known only *Habroichthys orientalis* (Lin et. al. 2011) and *Peripeltopleurus* sp. n. (Jin 2006 and personal observations), both of them representing the youngest representatives for these genera.

Material and methods

In the section through the Guanling Formation, Dwz 2 and Dwz 4 comprise the fossiliferous layers of the Luoping Fauna (Fig. 1C, D); the specimens described herein were collected from the Dwz 4, and are now stored at the Geological Museum and Department of Geology, Peking University, Beijing, China (GMPKU). They were prepared mechanically by fine steel-needles under the binocular microscopes WILD M 8. Drawings were made by one of coauthors (C.L.)., with the help of a camera lucida and illustration software for digitalization.

The anatomical nomenclature of the skull are used according to Bürgin (1992). Concerning the terminology of the elements of the caudal fin, we follow Hutchinson (1973a), Gardiner (1988), Grande & Bemis (1998) and Lombardo (2001), referring the term "epaxial fin rays" to the caudal fin rays dorsal to the notochord or when the upper caudal fin rays elongate beyond the termination of the body axis (for further discussion see Lombardo 2001).

Abbreviations used in figures: afls, anal fin lateral scute; **ant**, antorbital; **bf**, basal fulcra; **br**, branchiostegal rays; **dpt**, dermopterotic; **dr**, distal radials; **cl**, cleithrum; **dsph**, dermosphenotic; **efr**, epaxial fin rays; **exsc**, extrascapular; **fr**, frontal; **hy**, hypurals; **ifo**, infraorbitals; **ldr**, last distal radial; **llj**, left lower jaw; **lls**, lateral line scales; **mx**, maxilla; **na**, nasal; **op**, operculum; **pa**, parietal; **pas**, parasphenoid; **pcl**, postcleithrum; **pfr**, pelvic fin rays; **pmx**, premaxilla; **pop**, preoperculum; **pr**, proximal radials; **pt**, posttemporal; **r**, radials; **rlj**, right lower jaw; **ro**, rostral; **sbo**, suborbital; **sc**, scales; **scl**, supracleithrum; **so**, supraorbital; **sop**, suboperculum; **vlr**, ventral lobe rays of the caudal fin.

Systematic paleontology

Osteichthyes Huxley, 1880

Actinopterygii Cope, 1887

Perleidiformes Berg, 1937

Fuyuanperleididae fam. n.

Diagnosis: Small Perleidiformes with peculiar squamation pattern: the number of scales in each vertical row increases behind the pelvic fins by addition of several scales ventral to the lateral lines scale row.

Discussion. The morphological characters of the "subholosteans" among perleidiforms and peltopleuriforms has already been remarked (Bürgin 1992; Tintori & Lombardo 1996; Lombardo & Tintori 2004; Mutter & Herzog 2004, among others). *Fuyuanperleidus* fits well with "Subholostean" morphologies: moreover, a combination of features that clearly makes it discriminate from the known representatives of the group can be proposed.

The dentition and the shape of the preoperculum are differentiated between perleidiforms and peltopleuriforms. The dentition of perleidiforms is generally made of peg-like marginal teeth and crushing inner ones (even if not highly specialized) (Bürgin 1992; Lombardo 2001) but deep-bodied forms show a more specialized dentition such as in *Felberia* (Lombardo & Tintori 2004) and *Stoppania* (Lombardo et al. 2008) from the western Tethys. Peltopleuriforms are often characterized by minute teeth or no tooth at all (e.g. *Habroichthys*, Bürgin 1992; *Peltopleurus*, Lombardo 1999). Perleidiforms often has a large and wedge-shaped preoperculum, while the preoperculum is much narrower and more vertically arranged among peltopleuriforms, except few genera, e.g. *Meridensia* or *Altisolepis,* whose preoperculum is quite narrow and vertical (Bürgin 1992; Mutter & Herzog 2004). The new taxon shows a large preoperculum with a well developed infraorbital process, and strong upper and lower jaws bearing long peg-like teeth with an acrodine cap, which is reminiscent of perleidiforms.

Of the postcranial anatomy, differences between perleidiforms and peltopleuriforms include the shape and arrangement of the flank scales, and the structure of the caudal fin. The flank scales are typically thin, narrow and high to very high along the body in peltopleuriforms, while those of perleidiforms are usually thick, somewhat higher than longer only in the anterior flank. Nevertheless, morphological variability of the flank scales (Hutchinson 1973a; Bürgin 1992; Tintori & Lombardo 1996; Lombardo 1999; Mutter & Herzog 2004) hinders the taxonomic significance of squamation for "subholostean" taxa. Especially in peltopleuriforms, the depth of the mid-lateral scales is highly variable, ranging from a depth equaling that of the whole flank (*Habroichthys*, Brough 1939; Bürgin 1990, 1992; Lin et al. 2011) to a complete absence (*Thoracopterus magnificus*, Tintori & Sassi 1992), through various intermediate stages (Lombardo 1999). The new taxon has two horizontal rows of high flank scales so that regarding the shape of the flank scales it is seemingly more similar to peltopleuriforms than to perleidiforms, however they are thick with ganoine rather than thin as that of peltopleuriforms. Moreover, flank scales are sometimes significantly higher also in the perleidiforms *Altisolepis* and *Luganoia* (Bürgin 1992, 2005; Mutter & Herzog 2004).

The presence of epaxial fin rays in the tail is a character shared by perleidiforms and peltopleuriforms, however it is highly variable in number. Among perleidiformes the number of epaxial fin rays ranges from about six (*Perleidus*) to 10 (*Cleithrolepis*) or 12 (*Gabanellia*) (Gardiner 1988; Gardiner & Schaeffer 1989; Tintori & Lombardo 1996; Lombardo 2001), as in the case of *Fuyuanperleidus* (10-12 epaxial fin rays).

Among the characters shared by "subholosteans", one of the most peculiar is the presence of sexual dimorphism usually shown by modified anal fins in male specimens (Bürgin 1990a; Lombardo 1999). As it is for the pattern of squamation, there is a variety of anal fin modifications, from a simple thinning of rays with small hooklets on the posterior part of the fin (e.g. in *Habroichthys*, Bürgin 1990 or *Thoracopterus*, C.L. pers. obs.) to complex structures, similar to the gonopodia of some living Cyprinodontida teleosts, as in *Peripeltopleurus* and *Peltopleurus* (Bürgin 1990b, 1992; Lombardo 1999). Nevertheless, sexual dimorphism is also present in some perleidid, *Gabanellia agilis* possessing a strongly dimorphic anal fin (Tintori & Lombardo 1996). Besides the modified fin rays, the male anal fin of sexually dimorphic "subholosteans" is often characterized by the presence of a large scute which covers the proximal ends of the lepidotrichia. A large scute present on specimen GMPKU-P-3009 of *Fuyuanperleidus* is thus interpreted as related to the sexual dimorphism rather than a simple pre-anal scale due to its shape and typical position. The other specimen GMPKU-P-3010 lacks this large scute, but instead its ventral scales has denticulations on the posterior margin while those of GMPKU-P-3009 have a smooth one. The mutually exclusive presence of a large anal scute and denticles on posterior margin of the scales can be therefore related to sexual dimorphism rather than to taxonomy.

Taking all characters mentioned above into considerations, the taxon here described is included within perleidiforms rather than peltopleuriforms, in particular based on the features of the skull pattern.

As a very successful order, the Perleidiformes currently include seven families: Gabanellidae, Cleithrolepidae, Polzbergiidae, Colobodontidae, Perleididae, Pseudobeaconiidae and Luganoiidae (Brough 1931; Hutchinson 1973a; Gardiner 1988; Bürgin 1992; Tintori & Lombardo 1996; Mutter 2004; Lombardo & Tintori 2004; Lòpez-Arbarello & Zavattieri 2008).

The Gabanellidae, a monotypic family represented by a single species, *Gabanellia agilis*, is typical for its numerous rows (about 95) of very thin scales and the powerful predatory dentition made of conical, radially striated, uneven teeth (Tintori & Lombardo 1996). All representatives of the deep-bodied perleidiform family Cleithrolepidiidae are characterized for their triangular maxilla, a narrow lower jaw devoid of tooth and the absence of posttemporal (Hutchinson 1973a; Gardiner 1988). The Pseudobeaconiidae are characterized by the presence of an incomplete dorsal ridge of spine-like scales between the skull and the dorsal fin and scales with straight posterior border, elevated central region and marginal concentric ridges of ganoine. The family Polzbergiidae includes deep-fusiform to deep-bodied representatives, which share the general skull pattern with an operculum smaller than the suboperculum, the premaxilla fused to the antero-dorsal edge of the maxilla, and the presence of the procumbent long anterior teeth (Griffith 1977; Lombardo & Tintori 2004; Lombardo et al. 2008; Sun et al. 2009). Colobodontidae are represented by large-sized perleidiforms which yield a rather conservative skull osteology, such as the presence of a small rostral followed by a large postrostral separating nasal bones, and among other characters, a hemidurophagous dentition and well ornamented scales (Bürgin 1996; Mutter 2004; Rusconi et al. 2007; Sun et al. 2008). The genus *Luganoia*, the only representative of the family Luganoiidae, shows the addition of one or two scale rows in correspondence of the main mid-lateral flank scales, the ones bearing the lateral line canal. *Luganoia* is however very derived for its skull pattern, for instance the maxilla is completely free from the large and broad preoperculum and the elements of the cheek show very distinctive morphology and arrangement (Brough 1939; Bürgin 1992). Although with a skull pattern very similar to that of the new taxon, among known Perleididae genera, none of them is characterized by a squamation with very deep mid-lateral scales as well as the insertion of additional scale rows posterior to the pelvic fins.

The unique pattern of squamation with the insertion of several scales in each vertical row after the pelvic fins, definitively discriminate the genus *Fuyuanperleidus* from the perleidiform families mentioned above: for this reason it is necessary to erect a new family based on this unique autapomorphy to accommodate it.

Remarks. Geng et al. (2012), erected the new genus *Fuyuanperleidus,* on the basis of a single, and, according to the Authors, only known specimen and they put it within the family Perleididae, together with other new taxa of perleidiforms, *Luopingperleidus* and *Diandongperleidus* based on following characters: "fishes of small size, the preoperculum nearly vertical, most of skull bones ornamented with tubercles or ridges, maxilla as in Palaeonisciformes, jaws toothed with conical teeth, nearly symmetrical caudal fin" (Geng et al. 2012: 925). According to us, with this choice Geng et al. (2012) underestimated the remarkable differences on body morphology, skull pattern and above all squamation between *Fuyuanperleidus* and the other genera described in the same paper (actually the three generic diagnosis are very similar to each other and quite uninformative), which, owing to their actual characters, cannot be ascribed to the same family. Taking into consideration the complexity of the order, also the comparison of the genus with the representatives of each family of Perleidiformes appears simplistic and hurried. *Fuyuanperleidus* is unique for the insertion of scales in each vertical row after the pelvic fins: similar addition among perleidiforms is known (although to a lesser degree) only on *Luganoia* (see above), but in the discussion Geng et al. (2012) do not mention it, limiting to cite a different scale pattern for the two taxa. According to the Geng et al. (2012), characteristic of *Fuyuanperleidus* is given by the deepened flank scales; for this reason they compare their new taxon with *Peltoperleidus* and *Altisolepis,* from which *Fuyuanperleidus* differs, among the other characters, also for "lower deepened flank scale row continued by five horizontal scale rows posterior to level of anal fin insertion" (Geng et al. 2012: 925), neglecting the importance of the peculiar addition of scales.

Fuyuanperleidus Geng, Jin, Wu & Wang, 2012

Type-species*: Fuyuanperleidus dengi* Geng, Jin, Wu & Wang, 2012

Diagnosis: As for the single species.
Geographic distribution: As for the species

Fuyuanperleidus dengi Geng, Jin, Wu & Wang, 2012

Figs 2-6

Diagnosis (emended): Among the following combination of characters, an asterisk (*) indicates possible apomorphies: deep-fusiform perleidiform up to 85 mm in standard length (SL); operculum slightly larger but narrower than the suboperculum; scales of the mid-lateral flank row, carrying the lateral line, highly deepened up to the level of the pelvic fins; *addition of up to four scales in the vertical

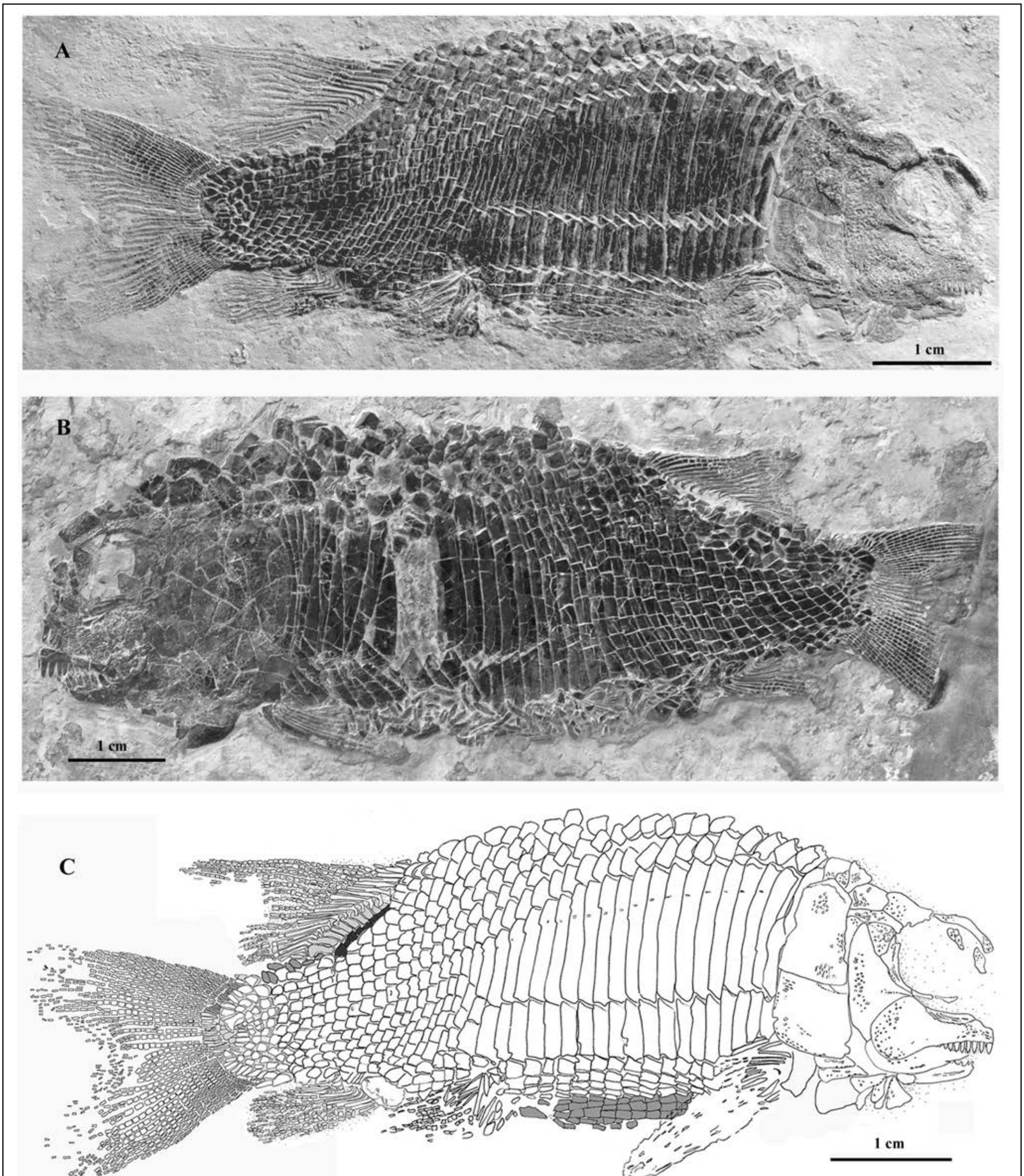


Fig. 2 - *Fuyuanperleidus dengi* Geng, Jin, Wu & Wang, 2012: A, GMPKU-P-3009; B, GMPKU-P-3010; C, drawing of GMPKU-P-3009. Scales visible in inner side are shaded.

rows behind the pelvic fins; ventral scales between the pectoral and pelvic fins very low, much longer than deep; *scales covering the caudal peduncle irregularly shaped. Triangular dorsal fin well posterior to the half-length of the body; *distal radials of the dorsal fin enlarged, with the last one bearing four lepidotrichia; caudal fin wide, with more than 40 closely arranged lepidotrichia of which 10 to 12 are referred to as epaxial fin rays.

Holotype: A nearly complete specimen, IVPP V16517, stored at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Peking.

Material: GMPKU-P-3009 (Fig. 2A, C): an almost complete specimen of 63 mm in standard length (SL). The snout region is missing and the skull roof is fragmentary. GMPKU-P-3010 (Fig. 2B): a fairly well-preserved fish of 85 mm in SL, with elements of the snout region

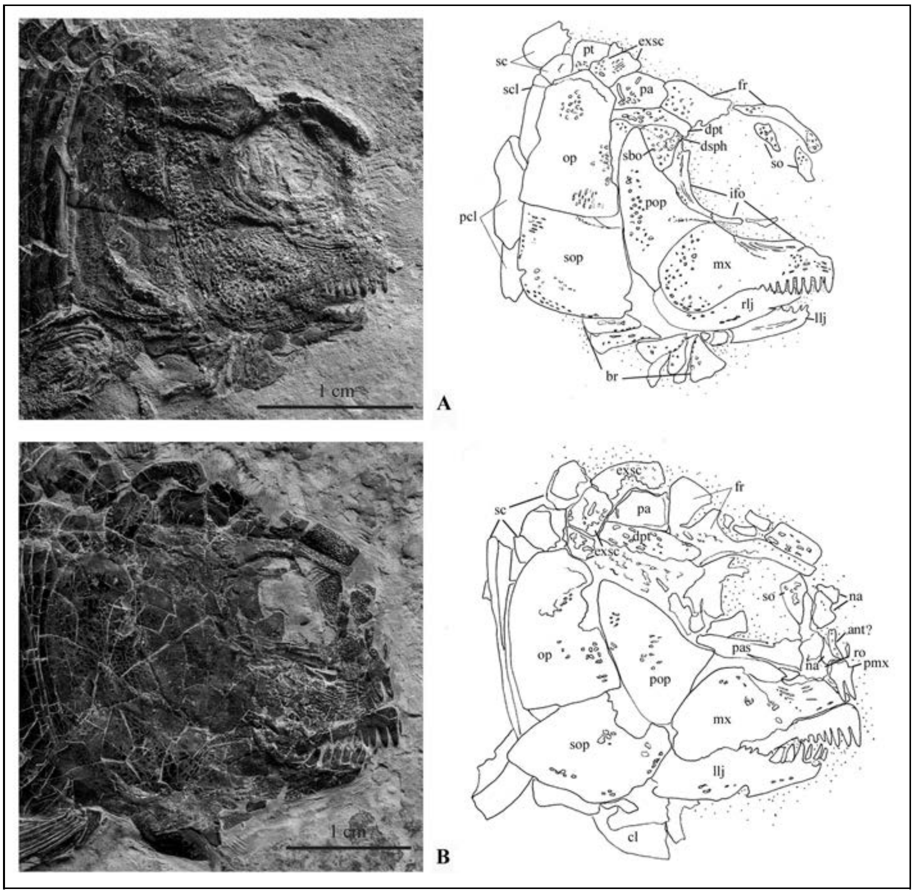


Fig. 3 - *Fuyuanperleidus dengi* Geng, Jin, Wu & Wang, 2012: drawings of the skull in A, GMPKU-P-3009; B, GMPKU -P-3010.

and the skull roof partially preserved. The scales along the belly and the dorsal ridge are scattered and two or three rows of deepened scales on the anterior flank are missing.

Locality and horizon: As mentioned above, the distribution of the species is limited to around Dawazi village of Luoping County, Yunnan Province, South China: Lower Vertebrate Horizon (LVH) of the Luoping Fauna, in the Upper Member of the Guanling Formation, Pelsonian (Middle Anisian, Middle Triassic). The presence of the species at Jiyangshan, Shibalianshan, Fuyuan County, Yunnan Province from the Upper Ladinian Zhuganpo Member of the "Falang Formation" as supposed by Geng et al. (2012) is not considered, even if the genus (and consequently the new family) took the name from that locality.

Description. The two fairly well-preserved specimens are deep-fusiform in shape, with total length/maximal body depth being about 3-3.5; specimen GMPKU-P-3009 seems to be a little deeper than GMPKU-P-3010. They are small-sized, with the SL up to 85 mm. The head length is about 29% of the SL. The peduncle is moderately deep, being 40% of the maximum body depth. The triangular dorsal fin is placed well posterior to the half-length of the body, four or five scale-rows behind that of the anal fin (Fig. 2). All skull bones are ornamented with small ganoine tubercles, somewhat homogeneously arranged on each element.

Skull. The bones in the ethmoidal region are completely missing on GMPKU-P-3009, while they are partially and scatteredly preserved on GMPKU-P-3010 (Fig. 3A, B). The nasals are rectangular in shape, dorso-ventrally elongated; the opening for the anterior nostril is well detectable on specimen GMPKU-P-3010. The pores of supraorbital sensory canal are longitudinally arranged with respect to the longest axis of the bone. A large convex element visible from the inside and partly covered by other bones is interpreted as the rostral. The frontal is partially preserved on both specimens: it is quite short, with a supraorbital narrow region longer than that of the expanded postorbital one. The pores of supraorbital sensory canal along the lateral margin are visible on GMPKU-P-3010; the postorbital region is broad but its outline is not clearly detectable, as well as the course of the interfrontal suture. The surface of the frontal is ornamented by small tubercles and patches of ganoine. The parietal is quadrangular, joined to the frontal through a sinuous suture and to the extrascapular bone in a rounded one, well visible on GMPKU-P-3009. Two pit lines are detectable on the posterior half of the bone. On the parietal the ornamentation is made of ganoine patches which tend to merge, making a quite homogeneous surface. The dermopterotic has a trapezoidal shape, antero-posteriorly; the strong ornamentation is made of flat ganoine tubercles and small pores of the temporal sensory canal are visible on the ventral region of this bone on GMPKU-P-3010. The extrascapular bones were displaced and partially overlapped by the operculum on GMPKU-P-3009. The trajectory of the supratemporal commissure can be identified by a groove crossing the ventral part of the extrascapular bone on GMPKU-P-3010.

Circumorbital series. At least two large supraorbital bones are clearly visible on the dorsal margin of the orbit of both specimens, but their shape and size are well detectable only on GMPKU-P-3010. The anteriomost one is triangular and very large: it probably forms the anterior margin of the orbit, contacting the nasal bones. The second is rectangular and occupies the antero-lateral margin of the frontal bone, for half of its length. Both are elongated antero-posteriorly and are strongly ornamented by small tubercles. Two additional small, rectangular fragments are visible on GMPKU-P-3010 behind the second element and, according to their position, they could represent a third and fourth element of the series. A small hourglass element, visible on GMPKU-P-3009 and lying behind the infraorbital bones and on suborbital is interpreted as the dermosphenotic, which is clearly displaced in respect to its original position. The ornamentation is made of small tubercles arranged longitudinally to the element. There is at least one suborbital, also visible on GMPKU-P-3009, placed between antero-dorsal margin of preoperculum and postero-dorsal border of the largest infraorbital and partly covered by dermosphenotic. The state of preservation and the strong ornamentation do not allow to state the precise outline of this element or if other similar bones were present. Of the infraorbital series only two elements, which border the postero-ventral edge of orbit, are well detectable. An elongate element, overlapping the dorsal margin of the maxilla, is interpreted as the first infraorbital; even if its ventral suture is not clearly defined, its shape can be outlined due to to the ornamentation pattern, with longitudinal ganoine ridges following the dorsal margin of the element and clearly different from that of the upper jaw, which consists of rounded ganoine tubercles. On GMPKU-P-3010 the same element seems to have a very large ventral region, covering most of the anterior part of the upper jaw, even if also in this specimen, its ventral margin is not detectable. Nevertheless the course of the pores of the infraorbital sensory canal which tends to bend clearly downwards, is well defined. The other infraorbital visible, bordering the whole posterior margin of the orbit, is sickle-shaped, with the dorsal limb slightly enlarged. The infraorbital sensory canal is visible along the median region of the element. A narrow elongated bone lying on the supposed rostral and carrying the pores of a sensory canal, probably represents the antorbital.

Cheek, opercular and branchiostegal series. The large and vertical preoperculum has its dorsal region nearly equal to the ventral one in size. It bears a very well-developed infraorbital process extending up to about the middle of the orbit. Its antero-ventral margin is concave, where it widely embraces the posterior edge of the maxilla. The operculum is a shield-like element, its depth being 1.5 times of the maximum width. It is slightly larger but narrower than the suboperculum and contacts the latter with a straight suture. The suboperculum is squarish, with a slightly rounded ventral margin. Both preoperculum and operculum are characterized by an ornamentation made of ganoine tubercles, more densely arranged on preoperculum. Between the postero-dorsal corner of preoperculum and antero-dorsal margin of operculum there is enough room to accommodate some bones (anteoperculum, dermohyal), however, owing to the state of preservation, it is not possible to be confidently ascertained. At least seven branchiostegal rays are present. They are triangular in shape and bear flat ganoine tubercles.

Jaws. The upper jaw consists of a maxilla with an expanded and rounded posterior region, and a narrower anterior one which is nevertheless stout. On GMPKU-P-3010 a median trapezoidal bone, carrying two large teeth that are similar in size to those borne by the anterior region of the upper jaw, is interpreted as the premaxilla. The dorsal border of the upper jaw is slightly concave. There are nine long and strong peg-like teeth with an acuminate acrodine apex, borne on the anterior half of the oral margin. They are gradually decreasing in length posteriorly. The lower jaw is a stout wedge-like bone, with a convex ventral margin. On GMPKU-P-3009 the oral margin of the lower jaw is only partially visible, being covered by the ventral margin of maxilla, making impossible to precisely describe the details of teeth. On GMPKU-P-3010 there are at least six peg-like teeth with an acrodine cap visible on the oral margin of the lower jaw.

Pectoral girdle. The posttemporal is rounded, with a smooth dorsal region and a slightly ornamented ventral one, where the pores of the sensory canal coming from the extrascapular bones are detectable on GMPKU-P-3009. The supracleithrum is narrow and deep, extending for 2/3 of the height of operculum; its surface is smooth and the passage of the lateral line is well detectable on its dorsal region. The postcleithrum has the same shape and size of the supracleithrum and it is placed at the level of the suture betwen operculum and suboperculum. The cleithrum is only visible by part of its ventral region, being covered by the suboperculum; its surface is ornamented by small ganoine tubercles.

Paired fins. The paired fins are incompletely preserved, making it impossible to describe the detailed structure of rays. Remnants of the pectoral fins include the proximal parts of the lepidotrichia of the right fin and the very distal region of those of the left one. Ten

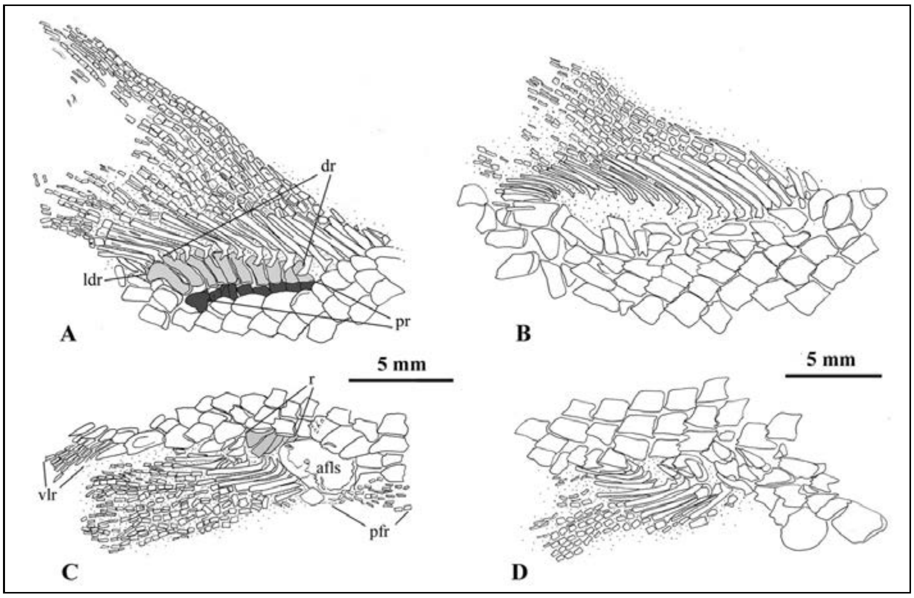


Fig. 4 - *Fuyuanperleidus dengi* Geng, Jin, Wu & Wang, 2012: drawings of the median fins in A (dorsal fin) and C (anal fin), GMPKU-P-3009; B (dorsal fin) and D (anal fin), GMPKU-P-3010. The endoskeletal elements are shaded (light grey: radials and distal radials; dark grey: proximal radials).

rays can be counted in the right pectoral fin. The pelvic fins, placed at the level of the 17/18th scale row, are preserved only in part and with the distal region scattered. On both pectoral and pelvic fins, the proximal bases are very long and the rays are preceded by few basal fulcra.

Unpaired fins. The dorsal fin (Fig. 4A, B) is large, triangular in shape. It is placed at the level of the 28th scale rows. There are about 20 lepidotrichia with long unsegmented proximal bases and the following small squared segments, preceded by three basal fulcra. The first lepidotrichium, segmented but unbranched, is rudimentarily developed, consisting of about ten segments on GMPKU-P-3009 and three on GMPKU-P-3010, and it is followed by rays which apparently increase abruptly in length. Each ray branches at least twice, beginning from the third one. Ganoine covering is restricted to the proximal elements of the anteriormost rays, and to the median region of the distal ones; on these latter, ganoine appears as minute patches or tubercles. No fringing fulcra are detectable.

The triangular anal fin (Fig. 4A, B) is placed at the level of the 23/24th scale rows; there are about 12 lepidotrichia branching at least twice. The ganoine covering is not homogeneous, being limited to the median part of the segments of the anteriormost lepidotrichia, like that of the dorsal fin. Neither basal nor fringing fulcra on the anterior margin of the fin are visible.

The caudal fin (Fig. 5A, B) is hemiheterocercal, with dorsal and ventral body lobes nearly symmetrical externally. It is wide, slightly forked and has about 43-46 very closely arranged lepidotrichia, of which 10 to 12 can be considered as epaxial fin rays. There are at least 6 unsegmented and unbranched lepidotrichia on the dorsal and five on ventral lobe on GMPKU-P-3009. Rays in front of the dorsal and ventral lobes are segmented from their bases, while between the two lobes rays show a slighly longer and slender proximal bases. The precise number of branching is unclear due to the incomplete preservation, however, the principal rays branch at least twice. Ganoine covering is present on both epaxial and hypaxial marginal rays and decreases gradually towards the central, where there are about ten central lepidotrichia devoid of any ganoine. The tip of the fin is delicate and partially preserved because the distal ends of all rays are made of thinner and more spaced elements which lack of ganoine. On GMPKU-P-3009 only one basal fulcrum in front of each lobe is present and fringing fulcra are absent, while on GMPKU-P-3010 both lobes are preceded by strong basal fulcra. Being incomplete in its posterior part, it is not possible to verify if fringing fulcra were present.

Endoskeletal elements. The bases of the median and caudal fins is partly uncovered by scales so that the endoskeletal elements can be observed. The median fins show distal and proximal radials (Fig. 4A): in the dorsal fin, the distal radials are large and rectangular, with thickened margins, of which each radial joins to one lepidotrichium, except that the last one supports at least four rays. The dorsal end of this last element is bending posteriorly. Ventrally, these elements contact the proximal radials, visible only in their dorsalmost region. In the anal fin, the distal radials seem to be smaller than those of the dorsal one, but they show their same structure. In the caudal fin only a small region between the two lobes is lacking scales, showing the distal ends of few hypurals.

Squamation. Up to 42 transversal scale rows have been counted, but the scales covering the caudal peduncle seems irregularly arranged, so that it is not possible

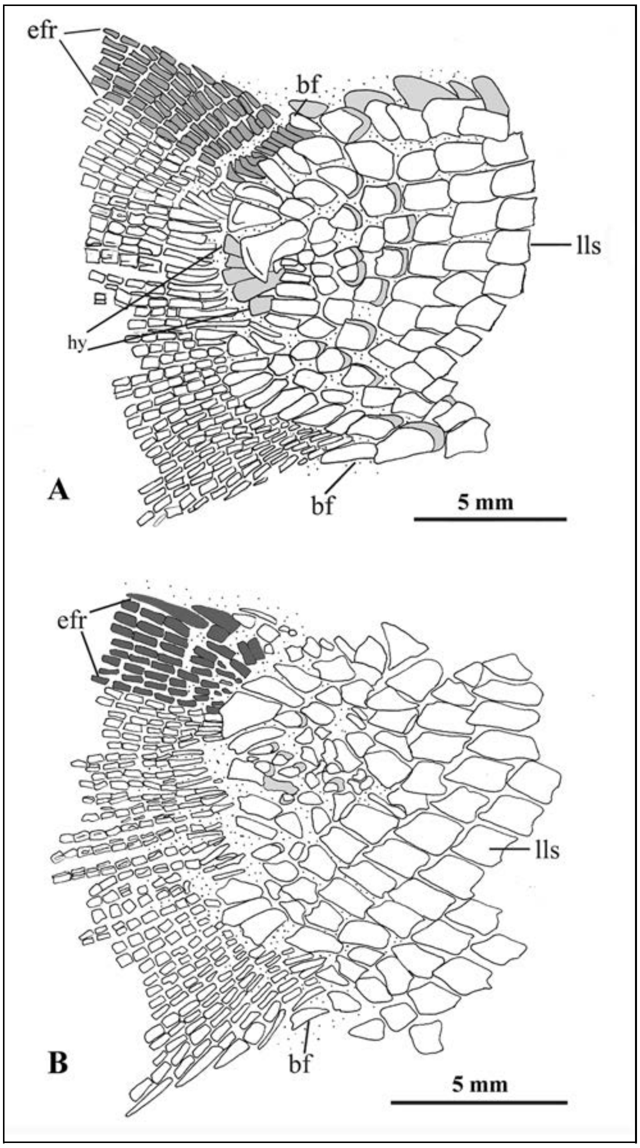


Fig. 5 - *Fuyuanperleidus dengi* Geng, Jin, Wu & Wang, 2012: drawings of the caudal fins in A, GMPKU-P-3009; B, GMPKU-P-3010. For a better localization, the hypural fin rays (light grey) and the epaxial fin rays (dark grey) have been shaded.

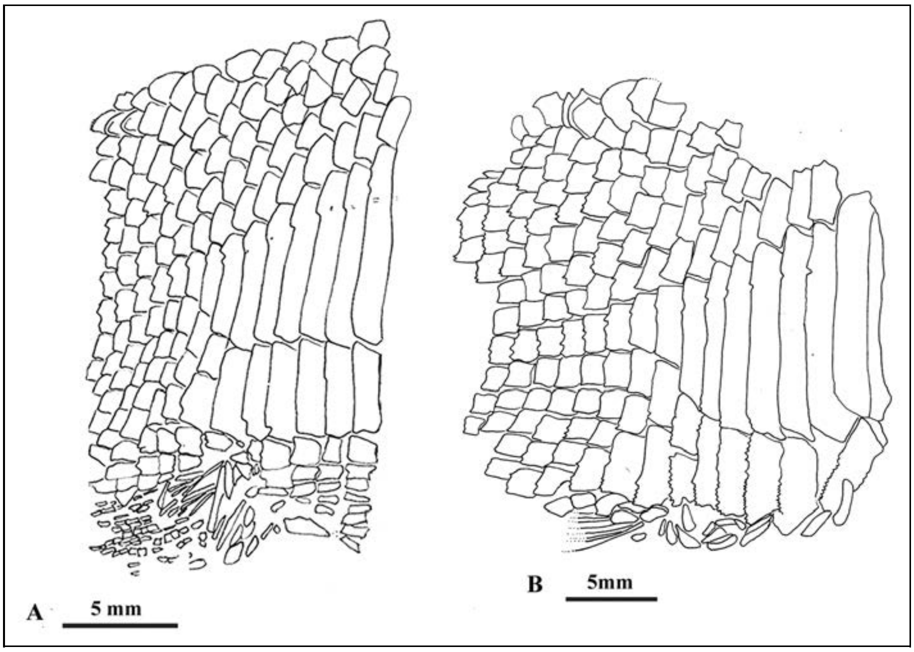
to precisely detect each vertical row in the posteriormost part of the body. The arrangement of the scales of this new taxon is peculiar: the scales on the mid-lateral flank (which bear the lateral line) are rectangular, highly deepened; their depth is quite the same until the mid-length of the body, where their depth abruptly decreases. The ventral flank scale-row which lies immediately below the mid-lateral row are made also by highly deepened scales, being about 1/3 of those of the mid-lateral row in depth (Fig. 2, 6). Along this scale row, the multiplication of the scales starts at the last two high deepened scales: on GMPKU-P-3009 the first one doubles, then triples proceeding posteriorly, while on GMPKU-P-3010 the first one doubles and keep this state for one scale-row, then triples proceeding posteriorly, each scale quickly decreasing in height (Fig. 6A, B). More ventrally, there are at least five horizontal rows, which are much longer than deep between the pectoral and pelvic fins (Fig. 2C). After these, all the scales become small and rhomboidal in shape. The scales on the dorsal region, although less evident, seem to be present the same horizontal multiplication of the scales seen for the ventral flank scale-row; although the anteriormost part of the dorsal region is not completely preserved, on GMPKU-P-3009 there is an evident displacement and insertion of additional scales rows beginning from the middle of the body to the insertion of the dorsal fin. Beginning from this region, the squamation appears homogeneous for shape, size and arrangement of the scales, being rhomboidal, slightly longer than deeper, except for those covering the caudal peduncle. Within the caudal peduncle, the scales of the median part are small and rounded, while those bordering the dorsal and ventral scaly lobes of the fin are antero-posteriorly elongated. On GMPKU-P-3009 these scales are regularly arranged on a single row, while on GMPKU-P-3010 they seem to be more irregularly set due to state of preservation. Two scutes cover the tip of the axial body lobe: the dorsalmost is triangular, while the ventral one has an axe shape. The course of the lateral line is visible transparently on the dorsal region of the high flank scales, traced by vertical slits on several scales of the posterior part of the body.

An anal scute, covering the proximal part of the lepidotrichia of the anal fin on GMPKU-P-3009 (Fig. 4A), is visible: it is rather large and oval in shape, with few ganoine on the central part of the element. On GMPKU-P-3010 there is no anal scute where they are alternated by the equivalents of few horizontal rows of very low scales. This difference is interpreted as related to the sexual dimorphism, herein. All scales are thick and smooth: on GMPKU-P-3009 their posterior margins are straight, while on GMPKU-P-3010 they are variable and bear several small denticulations, especially on scales of the ventral flank scale-row, where denticles are borne by most of the margin even if they are much denser in the ventral half. Sparse denticles are present also on the scales of most of the caudal region on GMPKU-P-3010.

Phylogenetic analysis

As already pointed out by López-Arbarello & Zavattieri (2008, p. 1047), perleidiforms had a wide stratigraphical range covering most of the Triassic, even if they concentrate mostly in the Middle and Late Triassic. It must be pointed out that what is considered by López-Arbarello & Zavattieri (2008) as "the most basal monophyletic group" made by *Perleidus*, *Meridensia*

Fig. 6 - *Fuyuanperleidus dengi* Geng, Jin, Wu & Wang, 2012: details of the arrangement of the flank scales in A, GMPKU-P-3009; B, GMPKU-P-3010.



and *Peltoperleidus* is not actually from the Late Triassic of Central Europe but it is yielded mainly by the Tethyan Middle Triassic sequence in the Southern Alps, in Northern Italy and Southern Switzerland, as well as in Southern China (Lombardo 2001; Lombardo et al. 2011).

López-Arbarello & Zavattieri (2008) discussed some of the Perleidiformes by performing a cladistic analysis to enlighten the interrelationships among them. Following their taxa and character selection, a further cladistic analysis was conducted to assess the phylogenetic relationships of *Fuyuanperleidus* with other "perleidiforms". In the new data matrix we established, several character statements were revised based on the direct observations on specimens of *Peltoperleidus*, *Dipteronotus* and *Ctenognathichthys* (A.T. and C.L. pers. obser.), as well as *Manlietta* following Wade (1935) and Hutchinson (1973a) contributions.

The new data matrix consists of 17 taxa and 27 characters (Tab. 1) and the parsimony analysis was performed using the exhaustive search command (Branch-and-bound) in PAUP* version 4.0b10 for Windows (Swofford 2002). All characters were equally weighted. Multistate characters were treated as unordered to allow all possible hypotheses of evolutionary relationship among the character states. The search resulted in three most parsimonious trees (MPT) (tree length, TL= 68 steps; consistency index, CI= 0.47; retention index, RI= 0.59). The strict consensus tree of these tree equally parsimonious trees was shown in Fig. 7. To assess clade supports, a non parametric bootstrap analysis was carried out in PAUP* using 500 replicates.

Regarding the paleoenvironmental and paleobiogeographic distribution of the perleidiforms, there seems to be a clear subdivision between the fresh-water dweller of the Gondwana and the marine Tethyan genera, with only *Dipteronotus* (Tintori 1990) that could be considered a possible continental taxon along the southern margin of the then northern continent. Thus, it is not correct to ascribe the "European" genera to the Laurasia (López-Arbarello & Zavattieri 2008: 1044) or considering the group as widely distributed in Pangea (López-Arbarello & Zavattieri 2008: 1048), as those were continental regions while almost all the non-Gondwanian taxa are fully marine. Furthermore, in the light of the new finds in Southern China, at the level of the genus the putative Tethyan taxa are no more limited to Western Tethys (now Europe) but are becoming known also in the Eastern Tethys, especially the Southern China Block. There, apart from the taxon described herein, we are also aware of the presence of *Colobodus* (Sun et al. 2008), *Luopingichthys* (Sun et al. 2009) and *Perleidus* (Lombardo et al. 2011) while *Peltoperleidus* and other undescribed perleidiform taxa are still under study by the research group at PKU (Beijing). It must also be pointed out that while the Triassic Gondwana fish faunas are somewhat related to the Tethyan marine faunas (Perleidiformes and maybe Redfieldiformes if the latter will prove to be related to Perleidiformes themselves) the Laurasia faunas are quite different (see for instance Xuand Gao 2011). That there are close relationships between some of the Tethyan faunas and the Gondwana fresh-water environments is also supported by the common presence of some isopod crustaceans in the Middle Triassic of southern China (Luoping Fauna) and Australia (Fu et al. 2010).

Our analysis matches well the paleobiogeographic relationships of the Gondwana fresh-water taxa (Fig. 7),

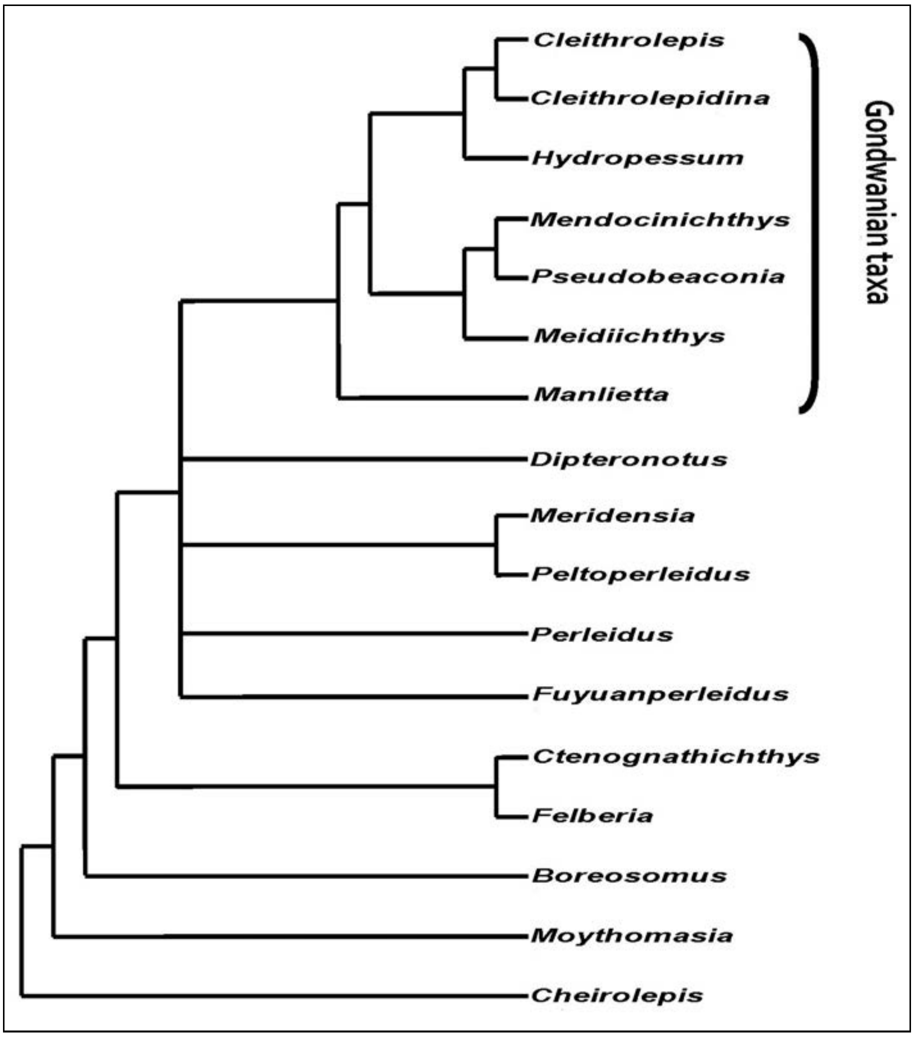


Fig. 7 - Consensus of 3 most parsimonious trees of 68 steps with a Consistency Index of 0.47 and a Retention Index of 0.59.

and the hypothesis of their monophyly appears plausible on the basis of our results, but the low bootstrap support value (18%) requires further validations. Among the Tethyan taxa, the very specialized *Ctenognathichthys* and *Felberia* forms a monophyletic group as the sister group of all the remaining perleidiforms; *Fuyuanperleidus* is more closely related to the Tethyan taxa *Dipteronotus*, *Perleidus*, and the clade containing *Meridensia* and *Peltoperleidus*, than the other perleidiforms. However these taxa form a polytomy, showing a unresolved relationship. The Gondwana deep-body perleidiforms (i.e. *Cleithrolepis*, *Cleithrolepidina*, *Hydropessum*) and the Tethys taxa (*Felberia* and *Dipteronotus*, for instance) does not form a sister group as in López-Arbarello & Zavattieri (2008) and the shared characters regarding the body depth should be a convergent acquisition rather than a phyletic reason.

We must point out that several other described perleidiforms have not been considered here, as this analysis is based on López-Arbarello & Zavattieri (2008) one. A complete revision of Perleidiformes, as well as the search to clarify the relationships with other “subholostean” groups is beyond the scope of this work. As we are working on further perleidiform material from the Middle Triassic of Southern China, we will consider for a complete phylogenetic analysis after the description of those new taxa. This will imply also changes in the character setting.

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APPENDIX 1

Characters used in the phylogenetic analysis (All characters are cited from López-Arbarello & Zavattieri 2008).

1. Relative length of the parietal bones: about twice the length of the postparietal bones or less (0); more than twice the length of the postparietal bones (1).

2. Quadratomandibular articulation: far behind the posterior border of the orbit (0); at about the posterior border of the orbit (1); well anterior to the posterior border of the orbit (2).

3. A bone separating the extrascapular bone from the dorsal border of the operculum ("accessory dermopterotic" of Hutchinson 1973b): absent (0); present (1).

4. Maxilla expanded posteroventrally: present (0); absent (1).

5. Lower jaw extremely slender: absent (0); present (1).

6. Nasal bones reach antorbitals ventrally: present (0); absent (1).

7. Number of supraorbital bones: two or three (0); more than three (1); supraorbitals absent (2).

8. Anterior supraorbital bone elongated anteriorly lateral to nasal bone: absent (0); present (1).

9. Suborbital bones: absent (0); present (1).

10. Supraorbital sensory canal entering postparietal bones: present (0); absent (1).

11. Marginal dentition: present (0); reduced or absent (1).

12. Marginal teeth very large and pencil- or fang-like: absent (0); present (1).

13. Crushing dentition: absent (0); present (1).

14. Preoperculum narrower ventrally than dorsally: present (0); absent (1).

15. Infraorbital process of preoperculum: absent (0); present (1).

16. Relative depth of the suboperculum: shorter than operculum (0); approximately as deep as the operculum (1); notably taller than the operculum (2).

17. Shape of flank scales: two to three times deeper than long (0); four or more times deeper than long (1).

18. Both dorsal and anal fins situated very close to the caudal fin: absent (0); present (1).

19. Epaxial fin rays: absent (0); present (1).

20. Number of epaxial fin rays: 10 or more (0); less than 10 (1).

21. Head approximately triangular, deepest posteriorly: absent (0); present (1).

22. Dorsal ridge of spine-like scales: absent (0); present (1); ridge scales gradually enlarged posteriorly (2).

23. Dorsal hump: absent (0); present (1).

24. Scales in pectoral region: normal (0); inverted (1).

25. Flank scales: ornamented with striae and /or tubercules (0); generally smooth, but with concentric ridges (1); completely smooth (2).

26. Posterior border of scales: serrated (0); smooth (1).

27. Skull bones: ornamented (0); smooth (1).

APPENDIX 2

Data matrix of 17 species and 27 morphological characters analyzed under parsimony criterium. "P" indicates that the taxon is polymorphic for states 0 and 1.

Taxa	0000000001	1111111112	2222222
	1234567890	1234567890	1234567
Cheirolepis	0000012?00	000000?00?	00000?0
Moythomasia	0010002?00	000100000?	0000000
Boreosomus	1000002?10	000110000?	0000000
Cleithrolepis	12111?0011	1001?21110	1011010
Cleithrolepidina	1111100?10	100112111?	1011010
Ctenognathichthys	010000011?	0100110011	0000000
Dipteronotus	1000000010	0000110111	1210210
Felberia	1100000100	0111111111	1010000
Hydropessum	12010?0011	1001011010	1010010
Manlietta	1001000101	0000110010	000?21P
Meidiicthys	11010??01?	0001120010	0000201
Meridensia	1000001010	001010001?	0000010
Mendocinichthys	??????????	??????0011	?10011?
Peltoperleidus	10000010P0	00P01?10?1	00002P0
Perleidus	1000000010	0010120011	0000200
Pseudobeaconia	0101110001	0001110011	0100111
Fuyuanperleidus	10000?011?	0001101110	00002P0