

## A NEW PERLEIDID FROM THE SPATHIAN (OLENEKIAN, EARLY TRIASSIC) OF CHAOHU, ANHUI PROVINCE, CHINA

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**Key words:** New taxon, Perleidiformes, Early Triassic, Spathian, South China.

**Abstract.** A new actinopterygian genus and species, *Chaohuperleidus primus* gen. n. sp. n., is described from the Upper Member of the Nanlinghu Formation (Spathian, Olenekian, Early Triassic) at Majiashan (Majia Hill), Chaohu City, Anhui Province, Southeast China. The new taxon is assigned to the order Perleidiformes on the basis of a combination of features: large wedge-like preoperculum with expanded infraorbital process and the sensory canal running almost vertical along the posterior margin of the preoperculum itself; flank scales somewhat higher than long in the trunk region; presence of epaxial rays in the caudal fin. Among Perleidiformes, the new taxon belongs to the Perleididae, being very similar to *Perleidus* in the general body shape, pattern of the skull bones, dentition made of peg-like marginal teeth, and number of epaxial rays. The new genus is characterized by the presence of a very large antero-dorsal process on the suboperculum, a high number (about 55) of transversal scale rows and rather posterior dorsal and anal fins. Dating back to the Spathian, *Chaohuperleidus* gen. n. represents the oldest record of the order Perleidiformes.

**Riassunto.** Viene descritto il nuovo attinotterigio *Chaohuperleidus primus* gen. n. sp. n. su esemplari rinvenuti nel Membro medio della Nanlinghu Formation (Spathiano, Olenekiano, Triassico Inferiore) sulla Collina di Majia (Majiashan, Chaohu City, Provincia di Anhui, Cina). Il nuovo taxon appartiene ai subholostei in quanto presenta raggi epaxiali nella pinna caudale. La sua appartenenza ai Perleidiformi è confermata da un insieme di caratteri quali i denti a piolo, un preopercolo ampio, con un evidente processo infraorbitale, e con il canale sensoriale verticale lungo il margine posteriore dell'osso, le scaglie della regione anteriore del fianco più alte che lunghe. L'aspetto generale del corpo, la struttura anatomica del dermatocranio, la dentatura non specializzata e il numero di raggi epaxiali ha permesso l'attribuzione di *Chaohuperleidus primus* gen. n. sp. n. alla famiglia Perleididae. Il nuovo taxon è caratterizzato dalla presenza di un ampio e arrotondato processo antero-dorsale del subopercolo, un numero elevato di file di scaglie (circa 55) e dalla posizione relativamente posteriore delle pinne

dorsale ed anale. *Chaohuperleidus* gen. n. rappresenta il più antico perleidiforme conosciuto e prova l'origine dei perleidiformi già verso la fine del Triassico Inferiore.

### Introduction

The well-known Triassic Early Fish Faunas (TEFF, Tintori et al. 2013) of Madagascar, Greenland, Spitzbergen and West Canada (Antunes et al. 1990; Lehman 1952; Piveteau 1934; Schaeffer & Mangus 1976; Stensiö 1921, 1932) are not younger than the end-Smithian. Those assemblages are composed of primitive neopterygians (Parasemionotiformes) and basal actinopterygians that include some specialized taxa (*Saurichthys* and *Bobasatrania*) already appeared in the latest Permian (Liu & Wei 1988; Tintori & Lombardo 2007). A few taxa were also ascribed to *Perleidus* following Stensiö (1921) (see Antunes et al. 1990; Lehman 1952; Piveteau 1934): though, according to Lombardo (2001), they lack the epaxial rays characterizing the subholosteans, so their attribution to perleidiforms had therefore to be questioned. All the TEFFs range from the Induan to the end of the Smithian. The youngest fishes are probably those found in southeastern China at Qinshan in Jurong County (Jiangsu Province) and Majiashan near Chaohu City (Anhui Province): they can be placed just below the Smithian/Spathian boundary (Tong et al. 2006). A few taxa have been described from these two major Chinese sites as well as from other sparse localities in southern China (Su 1981; Su & Li 1983; Qian et

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al. 1997; Liu et al. 2002; Jin et al. 2003; Tong et al. 2006; Zhao & Lu 2007), with taxa often erected on single specimens. The general assemblage in these Chinese localities is rather poor of species compared with the other worldwide sites. It comprises only a few parase-mionotiforms and the coelacanth *Chaouichthys* (Tong et al. 2006) other than a number of species now ascribed to *Plesio-perleidus* by Tong et al. (2006). This poverty may be ascribed either to the fact that in the end-Smithian a new crisis deeply affected at least the marine environment (Galfetti et al. 2007a, b) or to a somewhat different paleoenvironment, since Majiashan is thought to have been farther from the coast than other sites like, for instance, the NW Madagascar localities (Beltan 1996).

At Majiashan, a complete Early Triassic sequence (Fig. 1) was exposed in a large quarry exploited for road constructions and cement-making limestone rocks. After the Anhui Provincial administration in 2011 stopped the commercial quarrying to allow detailed scientific researches, it was possible to investigate the whole series bed by bed. Search for vertebrates focused on the Smithian/Spathian boundary, where the well-known level of fish-bearing nodules crops out (Tong et al. 2006), as well as on the middle-upper Spathian. Here, as first reported by Chen (1985), *Saurichthys* and few specimens of the basal ichthyosaur *Chaobusaurus* had

been collected during the quarrying works. During our preliminary 2010 field campaign in Majiashan some fish remains, here described, were collected together with few fragmentary specimens of *Chaobusaurus*. The major field works were carried out in 2011 and 2012, when several specimens of reptiles (Jiang et al. 2012) and fishes were collected and are now under study. Most fishes come from the uppermost Smithian nodule level (top of the Helongshan Formation), but not all the collected fishes were preserved in nodules. A few specimens were also found in the Spathian Nanlinghu Formation, together with *Chaobusaurus*. This represents the first fish assemblage of this age. Though most material is poorly preserved and fragmentary, we are confident in ascribing it to a very restricted number of taxa. The assemblage thus appears quite scanty: so far only one perleidid genus and two or three non-perleidid genera have been preliminary recognized. The perleidid genus is the object of the present paper.

## Material and methods

Specimens herein described are preserved in light grey calcareous marls whose faint lamination hardly splits, so that the fossils are usually visible in section as the rock is broken. Furthermore, in the Majiashan quarry layers are almost vertically arranged; the wall left by the former commercial quarrying is rather high, making the fossils difficult to reach and collect. The material used for this study includes only two complete specimens and four fragmentary ones. Preliminary preparation was done by air-chisels; subsequently, thin steel tools under stereomicroscope were used. Photos were taken by means of Nikon D3100 camera and Nikkor F60 microlens. Drawings were made through camera lucida on a WILD M8 stereomicroscope and later digitalized using Adobe Photoshop 6.0 graphic software.

**Abbreviations:** GMPKU-P, Geological Museum Peking University paleontological collections; ant, antorbital; br, branchiostegal; cl, cleithrum; dhy, dermohyal; dpt, dermopterotic; dsph, dermosphenotic; exsc, extrascapular; fr, frontal; io, infraorbital; iopr, infraorbital process of the preoperculum; mx, maxilla; md, mandible; na, nasal; op, operculum; pa, parietal; pcl, postcleithrum; pmx, premaxilla; pop, preoperculum; pt, posttemporal; ro, rostral; sc, scale; scl, supracleithrum; sbo, suborbital; sop, suboperculum.

## Systematic Palaeontology

The subholosteans are here considered as specialized non neopterygian actinoptery-

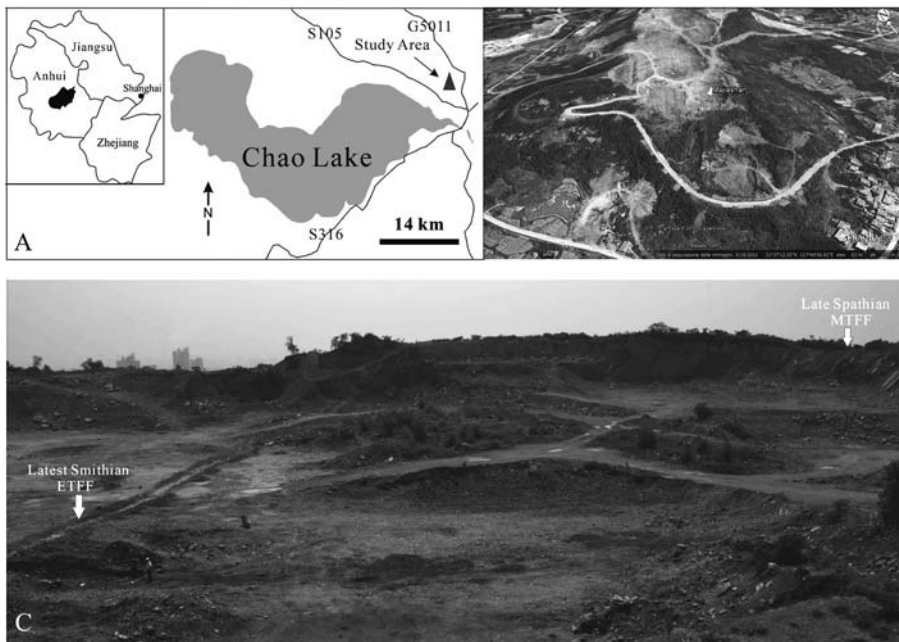


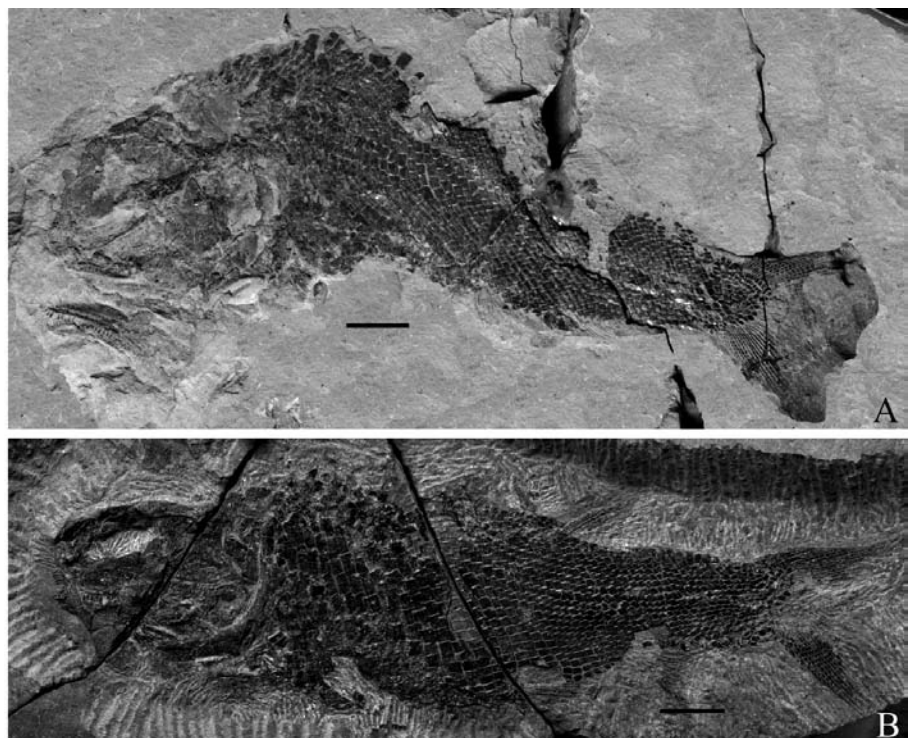
Fig. 1 - A, B) Localization of Majiashan quarry in Chaohu City, Anhui Province, South China. ▲ makes the position of Majiashan Quarry. C) The Majiashan Quarry seen from West toward East. The picture was taken almost perpendicular to the vertical beds of the Helongshan Formation (foreground) and Nanlinghu Formation well visible in the background and making most of the quarry bottom. People in the foreground at left are at the top of the Helongshan Formation in the small trench corresponding to the level yielding the fossiliferous nodules with fishes. In the background at right the wall remaining after the commercial quarrying was stopped: from that spot come most of the *Chaobusaurus* and the associated fish remains, mostly *Chaouperleidus* gen. n.

gians following the early interpretation by Brough (1931, 1939) and Schaeffer (1955, 1973); though, they definitely need a complete phylogenetic analysis. This is an interesting fish group that bloomed in the Triassic seas since the latest Early Triassic, as proved in this paper. They show somewhat derived characters in the postcranial skeleton respect to the paleonisciforms for instance (caudal fin more or less symmetrical and reduced number of radials in the dorsal and anal fins) beside a more conservative dermal skull pattern where the maxilla remained fixed to the preoperculum and the interoperculum was still missing. In the last years, subholosteans have been usually considered either in this same way (Bürgin 1992; Lombardo 2001; Lombardo & Tintori 2004; Lombardo et al. 2008) or as neopterygians or stem group neopterygians (Gardiner et al. 2005; Hurlley et al. 2007; Xu & Wu 2012). The latter hypothesis is mainly due to the alleged free maxilla of *Luganoia* (Bürgin 1992). However, *Luganoia* has a rather specialized overall skull pattern and its maxilla is not totally free from the preoperculum, especially if the postmaxillaries of Bürgin (1992) are considered as anamestic part of the preoperculum. Moreover, the separation of the maxilla from the preoperculum also concerns other basal actinopterygians, such as *Bobasatrania* (Nielsen 1952) or another subholostean, *Habroichthys* (Lin et al. 2011). However, all the above mentioned actinopterygians lack the interoperculum, whose appearance was considered by Patterson (1973) as directly related to the separation of the maxilla from the preoperculum among neopterygians. Another widely-accepted neopterygian apomorphy, the one-to-one relationship between radials

and rays of the dorsal and anal fins, needs to be reconsidered. Most subholostean and basal neopterygian taxa which show the endoskeleton of the median fins, i.e. *Marcopoloichthys*, *Gymnoichthys*, *Kyphosichthys*, *Placopleurus*, *Thoracopterus*, *Fuyuanperleidus*, *Peltopleurus*, indicate that the putative one-to-one relationship is not totally achieved because at least the last radial of both fins articulates two to five rays (Tintori et al. 2008, 2010, 2012; Sun et al. 2012; pers. obs.). Furthermore, the subholosteans and the basal non teleostean neopterygians acquire the external symmetry of the caudal fin through different ways. In the former the body lobe becomes very short, but not fully dorsal as the vertebral column does not sharply bend, so that epaxial (dorsally inserted) rays are present (hemiheterocercal caudal fin). In neopterygians the body lobe becomes shorter (abbreviated heterocercal caudal fin) with all the rays inserted ventral to the vertebral column. Anyway, the thorough interpretation and phylogenetic analysis of subholosteans are far from being settled, and are beyond the aim of this paper; we refer to Sun et al. (2012) for the Perleidiformes interrelationships.

Perleidiformes, together with Peltopleuriformes, are the largest subholostean orders. They are characterized by flank scales deeper than long, vertical or almost vertical preoperculum, usually still connected to the posterior end of the maxilla – but see Lin et al. (2011) for *Habroichthys* and Bürgin (1992) for *Luganoia* – lack of the interoperculum and by the presence of epaxial rays in the caudal fin. The meaning of subholostean fishes is far from being fixed and nobody ever attempted a general phylogenetic analysis. Though a few different

Fig. 2 - *Chaohuperleidus primus* gen. n. sp. n. A) The holotype, specimen GMPKU-P-1120. B) Specimen GMPKU-P-3074. Nanlinghu Formation (Spathian, Early Triassic) of Majiashan quarry, Chaohu City, Anhui Province, China. Scale bars = 10 mm.



orders have been assigned to the subholosteans during the last 70 years, we think at present only Perleidiformes and Peltopleuriformes are thoroughly consistent with the above cited characters and are herein considered.

Class **Osteichthyes** Huxley, 1880  
 Subclass **Actinopterygii** Cope, 1887  
 Order **Perleidiformes** Berg, 1937  
 Family Perleididae Brough, 1931  
 Genus *Chaohuperleidus* gen. n.

**Diagnosis:** As for the type and only known species.

**Etymology:** From Chaohu, the city which the Majiashan quarry belongs to, and where the studied specimens come from, and from *Perleidus*, the type genus of the subholostean Perleididae.

***Chaohuperleidus primus* gen. n. sp. n.**

Figs 2-7

**Diagnosis:** (A unique combination of primitive and derived characters; \*autapomorphies.) Medium-sized perleidid (up to 125 mm in standard length) with a quite elongate fusiform body. Preoperculum with narrow, elongated infraorbital process, covered by infraorbitals. Suboperculum with large, rounded, antero-dorsal process\*. Dermal skull bones ornamented with scattered small round tubercles, quite larger on the jaws. About 55 transversal scale-rows along the lateral line\*. Anterior flank scales at least twice deeper than long. Scales denticulated on the posterior margin; anterior scales showing faint longitudinal ridges. Large scale in front of the anal fin. Field of smaller scales in front of the ventral lobe of the caudal fin\*. Sensory canal of the lateral line with few transversal pores opening in the dorsal half of the scales. Pectoral fin made of 15 rays, pelvic made of ten. Dorsal fin short and made of 12 rays\*. Dorsal fin inserted in the posterior half of the body, starting at about 70% of the s. l.\*. Anal fin inserted at about 78% of the s. l.\*. Ten to eleven epaxial rays, seven of them, segmented but unbranched, bearing small fringing fulcra\*. Pterygial formula:

$$\frac{D \ 35}{P \ 17-18 \ A \ 30-31 \ C \ 47} \ 55$$

**Etymology:** From the Latin word *primus*, meaning first, as this is the first (and oldest) true perleidid described from Early Triassic.

**Holotype:** GMPKU-P-1120, a complete specimen with standard length of 125 mm.

**Paratypes:** GMPKU-P-1121, 3074, 3075, 3076, 3077.

**Type horizon and locality:** The Upper Member of the Nanlinghu Formation (Spathian, Early Triassic) of Majiashan quarry, Chaohu City, Anhui Province, China.

**Description.** The standard length of the complete specimens is 115 mm and 125 mm and the skull is 32 and 35 mm long respectively. Also the fragmentary specimens should have a similar size as a complete skull (GMPKU-P-3075) measures 36 mm in length. They are rather elongate fusiform fishes: the ratio between the maximum body depth and the total length is about 25%.

**Skull.** The median sub-exagonal rostral is somewhat longer than wide, with a rounded ventral part

that looks slightly convex. The median region is squarish; along the lateral margins there are two notches for the anterior nostrils. The dorsalmost part seems to be narrower and the dorsal margin almost semicircular. The rostral is well ornamented by round tubercles, of which those located between the nostrils are much larger than the others. The nasals are rectangular and border the rostral and are somewhat shorter. The sensory canal can be traced by several small pores: it entered the nasal close to the antero-medial corner, then crossed the bone obliquely toward the latero-dorsal corner. Also the nasals are ornamented by scattered tubercles.

The paired frontals are rectangular in shape, with a shallow embayment at the orbit level: their length is about twice the maximum width. The median suture seems straight, while the suture with the parietals is quite indented. The supraorbital sensory canal was deeply embedded in the bone and it gave rise to a ridge on the inner surface: it entered the frontals almost in the middle of each bone. The surface shows small and scattered tubercles.

The paired parietals are squarish: they seem to be very large laterally, so that it possibly fused with the dermopterotics, even if we can see no trace of the infraorbital sensory canal. The supraorbital sensory canals entered the bone at about 1/3 from the lateral margin and reached at least the mid-length. Nothing can be said about the actual outline of the extrascapulars, except that their shape was probably subtriangular, as shown in specimen GMPKU-P-3075.

Each upper jaw is made of a maxilla and, most probably, a premaxilla; though, this latter has never been found in anatomical connection but only as toothed fragments around the anterior end of the maxilla. A possible premaxillary bone is visible in specimens GMPKU-P-3075: there are at least six teeth being the same size as those of the maxilla. The maxilla shows a low anterior part bearing a minimum of 14 peg-like teeth, backward decreasing in length, and a very high triangular posterior plate, with an almost straight oral margin. The anterior tip is smooth and a little depressed, as if it yielded the premaxilla: six teeth are borne in this region and they possibly lay medially to the premaxilla teeth. The remaining part of the maxilla is covered by large and dense tubercles.

The lower jaws are elongate, with an almost straight oral margin. Owing to the poor preservation and the dense ornamentation, their single bones cannot be detected. Teeth are approximately all the same length, but the posterior elements are stouter than the anterior ones. These latter are similar in size and shape to the anterior elements of the upper jaws, but their tips bend slightly inward, giving these teeth a sigmoidal shape. There are at least 22 peg-like teeth on each side

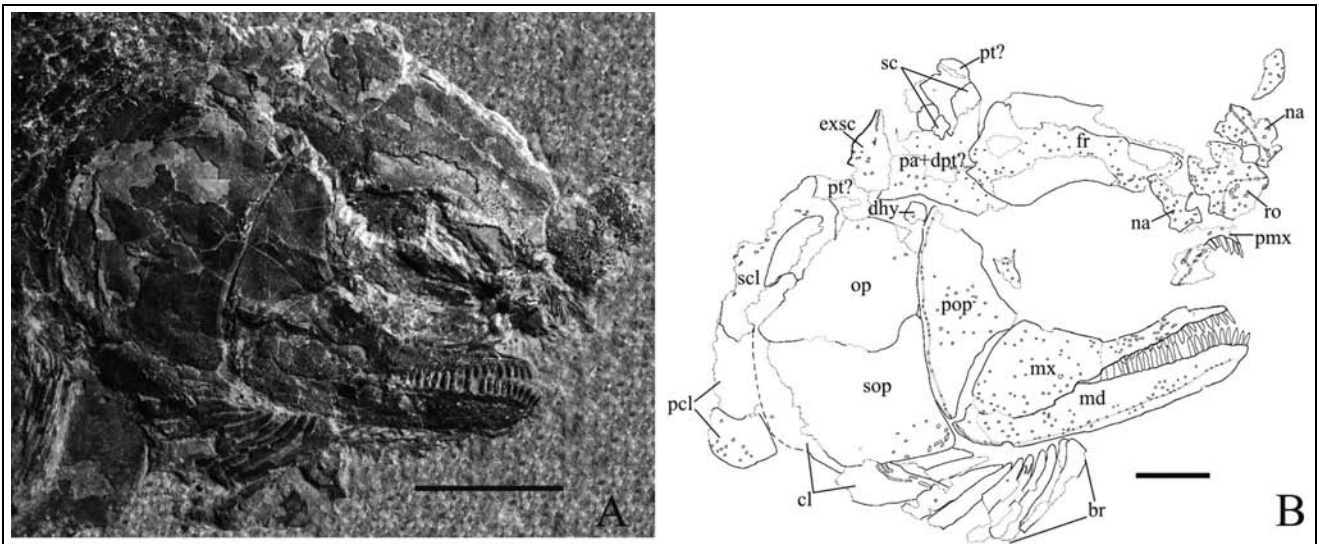


Fig. 3 - *Chaohuperleidus primus* gen. n. sp. n. A) GMPKU-P-3075, fish 1. B) Drawing of the skull of the same. Scale bar = 10 mm.

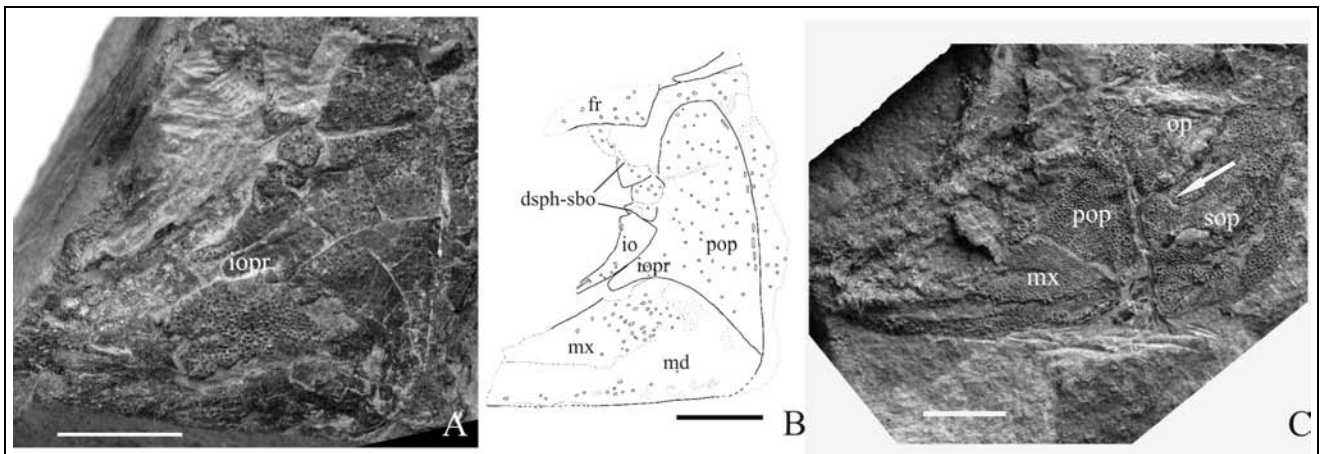


Fig. 4 - *Chaohuperleidus primus* gen. n. sp. n. A) Specimen GMPKU-P-3076. B) Drawing of the same. C) Specimen GMPKU-P-3077. The arrow points to the large anterodorsal process of the suboperculum. Scale bars = 5 mm.

of the lower jaws, but further inner tooth rows were probably present: teeth fragments are visible in between the teeth of the external row.

The elements of the circumorbital series are partially preserved on specimen GMPKU-P-3076 (Fig. 4) where a crescent-shaped jugal infraorbital is located at the posteroventral corner of the orbit. The sensory canal ran close to its anterior margin. In this specimen there are three more bone fragments dorsally to the jugal infraorbital: on the grounds of their position they may be regarded as parts of the postorbitals and/or the dermosphenotic.

The preoperculum embraces the posterior plate of the maxilla: its ventral region is triangular and in specimen GMPKU-P-3076 there is a well-developed infraorbital process with a rounded anterior tip. Because most of the process is smooth, it was probably covered by the jugal element of the infraorbitals series. The dorsal region is much more expanded, with the dorsal mar-

gin gently rounded. The position of the sensory canal is marked by very small pores at the rear edge of the bone: it ran vertical and gently bent forward in the dorsalmost part. The surface is completely smooth except for very rare small ganoine tubercles

The operculum is made of broad opercular and subopercular bones, the former being only somewhat larger than the latter. The suture between the two elements is antero-ventrally gently forward inclined and a large and rounded antero-dorsal process is well detectable. The surface of the two bones shows only very rare small ganoine tubercles. Ten branchiostegal rays are placed ventrally to the suboperculum. In the first three rays the antero-ventral edge overlaps the preceding ray; the fourth ray is overlapped on both sides because there is a reversal of the overlapping so that in the five anterior rays the most antero-ventral edge is covered by the posterior margin of the preceding ray. No clear traces of a gular element can be detected.

*Girdles.* The cleithrum is almost totally hidden by the opercular bones, except for some areas covered by ganoine ridges, dorso-ventrally elongated. Supracleithrum is quite large and there are probably two post-cleithral bones: all of them have a few ganoine ridges antero-caudally directed.

*Paired and median fins.* All the fins yield small fringing fulcra: those on the dorsal edge of the caudal fin are borne by at least seven segmented rays, which is a quite unusual high number of fringing fulcra yielding rays.

The pectoral fins have a triangular outline; each fin is made of about 15 rays, showing a long unsegmented proximal base and several distal segments.

The pelvics are small, triangular in outline. They are made of only 6-7 rays and inserted at approximately the 16<sup>th</sup> scale row, about half of the body total length.

The dorsal fin is inserted rather posteriorly, well in the second half of the body, around the 70% of the s. l., at the 34-35<sup>th</sup> scale row. It is small, its shape is a triangle with a short base. It comprises only 10-11 rather short lepidotrichia which branch once or twice.

The anal fin is also small in size and triangular in shape. It has almost the same number of rays as the dorsal one, but they appear much stouter and possibly branch up to three times. It is posterior to the dorsal as it inserts around 78% of the s. l., even if it starts at about the 30<sup>th</sup> scale row.

The caudal fin is almost symmetrical externally and has about 34 segmented rays, of which 10-11 are considered as epaxial rays (Fig. 5). There are at least seven short segmented fin rays, both dorsal and ventral to the leading fin rays. Epaxial and major ventral rays are abutting to each other, whereas two or three median rays are broadly spaced. The ganoine covering of the lepidotrichia is heterogeneous: patches are present on the proximal segments but not distally.

*Squamation.* At least 55 transversal scale rows are present, counted along the lateral line canal. The anterior flank scales are twice as deep as long both dorsally and ventrally to the deepest scales of the row where the lateral line ran. All the scales have a denticulated posterior margin: about 15 denticles in the highest anterior flank scales, about five at the beginning of the caudal region and one or two just before the caudal fin. Anterior scales show faint ridges in correspondence with each denticle: though, the ridges disappear after only five to seven transversal rows, and beyond that point most scales are smooth, just covered by a thin layer of ganoine. A large oval anal scale is present in front of the anal fin. A short field of smaller scales, compared to those around them, is at the base of the tail ventral lobe. The short body lobe ends with two rows of nine rectangular scales each, well distinct from the preceding

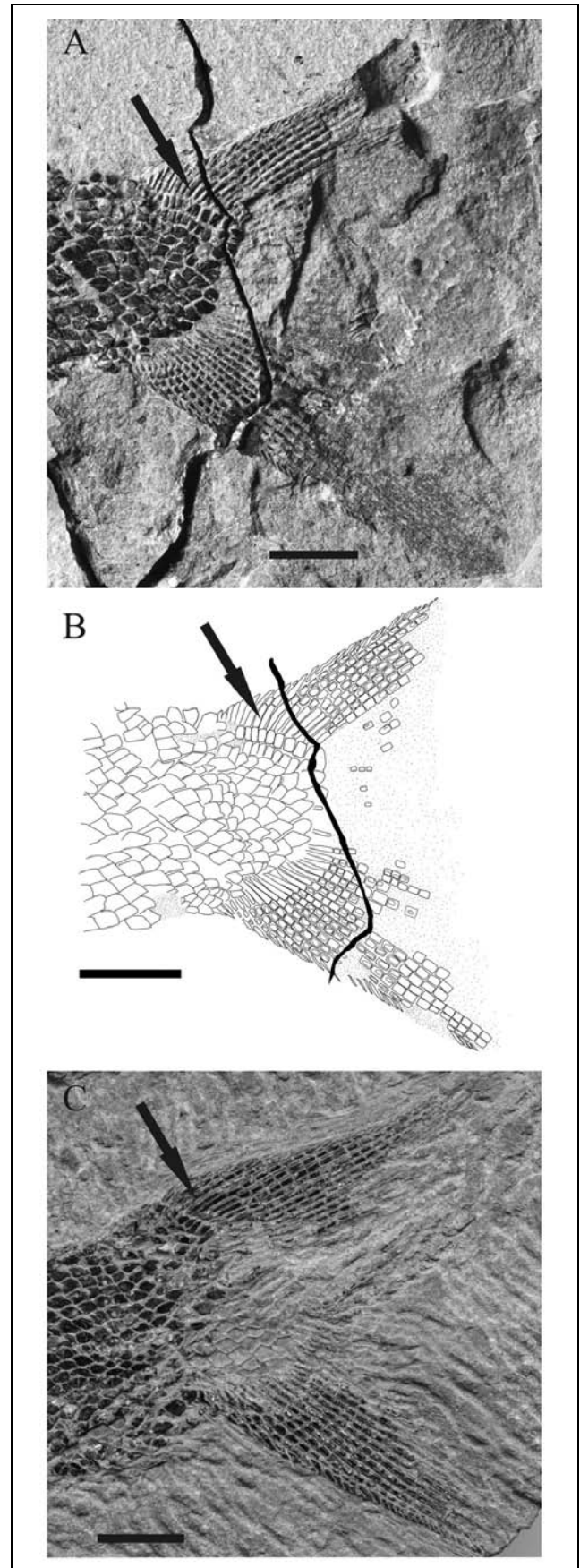


Fig. 5 - *Chaohuperleidus primus* gen. n. sp. n. Caudal fin. A) The holotype GMPKU-P-1120. B) The drawing of the same. C) Specimen GMPKU-P-3074. Arrows point to epaxial rays. Scale bars = 5 mm.

rhombic ones. The pores of the lateral line sensory canal are very few and they appear as vertical slits.

**Discussion.** *Chaohuperleidus primus* gen. n. sp. n. displays features typical of the subholosteans as above defined, such as the presence of a vertical or almost vertical preoperculum still connected to the posterior end of the maxilla, the lack of an interoperculum, the presence of epaxial rays in the caudal fin, and flank scales deeper than long.

Among subholosteans, it is clearly more similar to Perleidiformes than to Peltopleuriformes, owing to its dentition made of peg-like marginal teeth, large and wedge-like preoperculum, thick flank scales just deeper than long in the trunk region, numerous (at least ten) epaxial rays. The order Peltopleuriformes on the other hand is characterized by minute teeth or no teeth at all, narrower and vertical preoperculum, flank scales typically thin, narrow and much deeper than long along most of the body flank.

The families currently recognized in the order Perleidiformes are Cleithrolepidae, Polzbergidae, Gabanellidae, Luganoidae, Pseudobeaconiidae, Colobodontidae, Perleididae and Fuyuanperleididae (Lombardo et al. 2011; Sun et al. 2012).

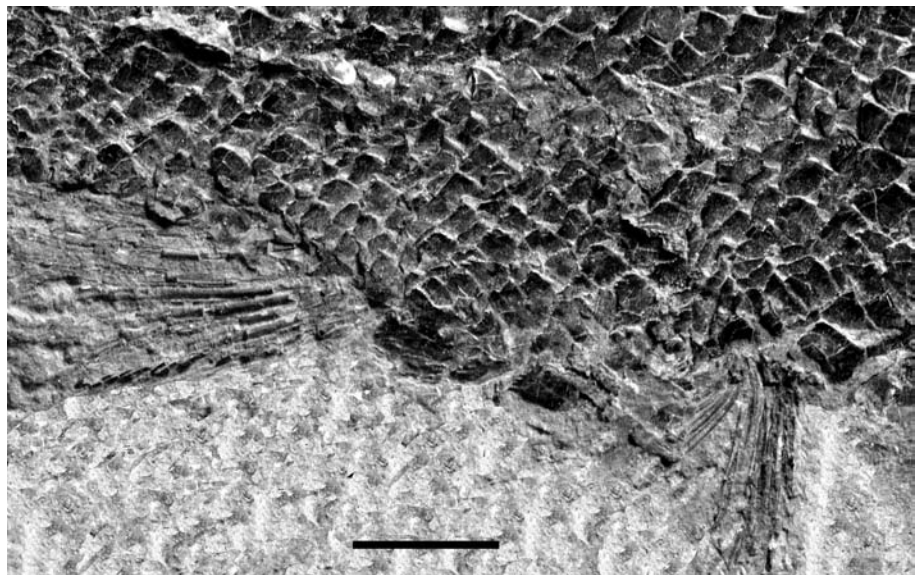
The new taxon is different from Cleithrolepidae and Polzbergidae (Lombardo et al. 2008), which are deep-fusiform or deep-bodied perleidiforms. Cleithrolepidae are characterized also by a triangular maxilla, a narrow lower jaw devoid of teeth and the absence of posttemporal (Hutchinson 1973; Gardiner 1988), while Polzbergidae show the premaxilla fused to the anterodorsal edge of the maxilla and the presence of long procumbent anterior teeth (Griffith 1977; Lombardo & Tintori 2004; Lombardo et al. 2008; Sun et al. 2009). None of these characters are present in *Chaohuperleidus* gen. n.

Gabanellidae show very thin scales arranged in very numerous rows and a predatory dentition (Tintori & Lombardo 1996): both characters are absent in the new taxon. The major synapomorphy of Luganoidae is a unique pattern of the cheek region, where the preoperculum is still in contact with the posterior region of the maxilla, even if for a short length (Bürgin 1992). *Chaohuperleidus* gen. n. shows a wide contact between the preoperculum and the posterior edge of the maxilla. Pseudobeaconiidae (López-Arbarelo & Zavattieri 2008) have a gently rounded posterior edge of most scales and spinous mid-dorsal scales, contrasting with the subrectangular and pectinated scales of the new taxon herein described. Colobodontidae are represented by large fishes, even longer than 50 cm, with a rather conservative dermal skull pattern, such as the presence of a small rostral followed by a large postrostral separating nasal bones, and peculiar scale ornamentation (Sun et al. 2008). No postrostral has been detected in *Chaohuperleidus* gen. n.

Fuyuanperleididae comprise small perleidiforms with a 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 line scale row (Sun et al. 2012). *Chaohuperleidus* gen. n. evidently differs from this last family, as it has no additional longitudinal scale rows.

Perleididae is by far the most diverse family within its order. Besides the type genus, *Perleidus*, it contains several genera, ranging from the Middle Triassic to the Norian: *Meridensia*, *Aetheodontus*, *Peltoperleidus*, *Dipteronotus*, *Ctenognathichthys*, *Daninia*, *Endennia* (Bürgin 1992; Mutter & Herzog 2004; Tintori 1990; Tintori 1998; Lombardo 2001; Lombardo & Brambillasca 2005). The new taxon here described is manifestly different from all the cited taxa. Compared to *Meridensia*,

Fig. 6 - *Chaohuperleidus primus* gen. n. sp. n. Specimen GMPKU-P-3077. The region between pelvic fins (to the right) and anal fin (to the left) showing the anal scales. Scale bar = 5 mm.



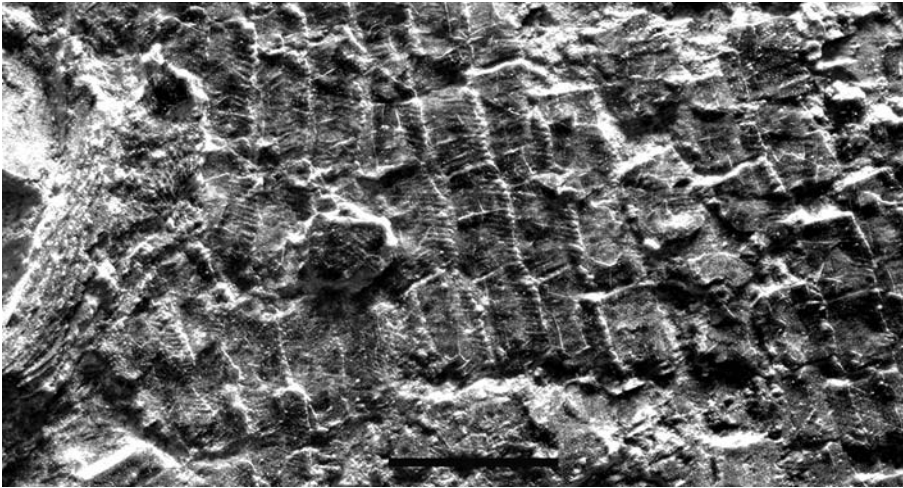


Fig. 7 - *Chaohuperleides primus* gen. n. sp. n. Specimen GMPKU-P-3074. The anterior trunk scales to show the posterior denticulation and the thin longitudinal ridges on their surface. Scale bar = 5 mm.

this genus remarkably differs in the shape of both preoperculum and maxillary, and in the morphology of scales in the dorsal region, above the deepest ones. A particular squamation, made of minute scales, is characteristic also of *Aetheodontus*, which moreover has a peculiar dentition made of very small teeth on the oral margin of the jaws and also on the palatal bones, where they are mostly low and stout. *Peltoperleides* is different in the skull roof, made of a single fused bone plate, in the pattern of cheek bones, in the shape of the posterior region of the maxilla and in the dentition (Bürgin 1992; Mutter & Herzog 2004). Even more evident is the difference with *Dipteronotus*, whose body is rather deep and bearing a dorsal ridge-scales row projecting above the hump. Both *Ctenognathichtys* and *Endennia* present a highly specialized dentition, besides remarkable differences in the skull pattern (especially in the preopercular shape) (Tintori 1990; Tintori 1998; Lombardo & Brambillasca 2005). Also the small and fusiform *Daninia* is different in the general body morphology and squamation and in the kind of dentition (Lombardo 2001).

On the contrary, *Chaohuperleides* sp. n. is similar to *Perleides*; the two taxa show a comparable pattern of the dermal skull bones and a similar dentition, which is of a non-specialized kind in both cases. Scales share a well denticulated posterior margin and faint longitudinal ridges on the scales of the most anterior rows. Nevertheless, we can observe some differences in the skull, mainly in the suboperculum, which has a large and rounded antero-dorsal process, totally lacking in *Perleides*. The major differences concern the body. The general outline, in fact, is more elongated in the new taxon than in *Perleides*, and its dorsal fin is much further posteriorly inserted (70% of the s.l. vs 57%). The anal fin starts about five scale rows before the beginning of the dorsal fin, while in *Perleides* they are inserted more or less at the same row. Finally, the new taxon has 10-11 epaxial rays in the caudal fin, approxi-

mately four more than *Perleides altolepis*, the type species of the genus (Lombardo 2001).

Other genera described as perleiidids, such as *Plesioperleides* (Su & Li, 1983), *Zhangina* (Liu et al., 2002), *Paraperleides* (Zhao & Lu, 2007) from the pre-Spathian Early Triassic, lack epaxial rays in the caudal fin. Lombardo (2001) had clearly shown that the absence of epaxial rays prevent any taxon from being ascribed not only to the Perleiididae but also to the Perleiidiformes; thus we cannot compare them with our new material.

All these evidences support the erection of a new taxon inside the Perleiididae, because it is more similar to *Perleides* than to any other genus of the order Perleiidiformes.

## Conclusions

The subholosteans were previously supposed to be the first actinopterygians to radiate intensively after the end-Permian crisis, in Late Anisian/Early Ladinian of Middle Triassic, followed by the neopterygians later on, in the Norian (Tintori 1998). Evidence to this hypothesis mainly came from the ichthyofaunas of the western Tethys, especially those yielded by the Besano Formation and the Meride Limestone, in the Monte San Giorgio area. Recently, new finds in the Panxian (Guizhou Province) and Luoping (Yunnan Province) Counties, indicate that both neopterygians and subholosteans intensively radiated during the Middle-Late Anisian (Sun et al. 2008, 2009, 2012; Tintori et al. 2008, 2010; Lin et al. 2011; López-Arbarello et al. 2011; Lombardo et al. 2011; Wen et al. 2012; Xu & Wu 2012) even with several morphologically specialized forms, on the whole making the Triassic Middle Fish Fauna (TMFF, Tintori et al. 2013). However, we do not know of any good late Early Triassic or Early Anisian fish-faunas: this time-gap needs to be fully understood in order to definitely state when the TMFF actually bloomed (Tintori et al.



2013) after its appearance in the Spathian, proved by this new Perleidiformes genus. Certainly, the Chaohu fish assemblage from the Spathian Nanlinghu Formation is still poorly known. Further field collecting will be necessary to learn the actual composition of this fish fauna.

Once more, our models of radiation and/or evolution inside a group such as the actinopterygians fishes (Tintori 1998; Tintori et al. 2013) prove to be deeply influenced by the preservation windows and by the discovery of new sites and fossil assemblages. Certainly, the paleontological record is strictly related to the geological setting and to the rather uncommon possibility of vertebrates to be preserved. Detailed collecting, like

the new bed by bed excavation in the Majiashan quarry, is fundamental to improve the paleontological record.

Finally, we want to emphasize that the rising of the TMFF happened together with the appearance of several marine reptile groups, just about 3 million years after the P/Tr crisis.

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