

New perleidid fishes from the Middle Triassic strata of Yunnan Province

记云南中三叠世新的裂齿鱼类

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Abstract: Three new genera and species of perleidid fishes from the Middle Triassic strata of Yunnan Province, i.e., *Fuyuanperleidus dengi* gen. et sp. nov., *Luopingperleidus sui* gen. et sp. nov., and *Diandongperleidus denticulatus* gen. et sp. nov., are described in this paper. *Fuyuanperleidus dengi* is distinguishable from other perleidids by the shape of the maxilla, the big teeth, the ornamentation of the skull bones, maxilla fused with the first infraorbital and the deepened flank scales. *Luopingperleidus sui* is distinguishable from other perleidids by the following features: the triangular main branchiostegal rays, four horizontal rows of deepened flank scales anterior to the pelvic fin, and three anal scales. *Diandongperleidus denticulatus* is distinguishable from other perleidids by the following features: the anterior border of some anterior fin rays of both the paired fins and the dorsal and anal fins bearing denticles, and posterior strongly serrated scales. The new discoveries not only add to the diversity of perleidid fishes in South China, but also shed new light on the radiation of Triassic perleidid fishes in the world.

Key words: perleidid fishes; Middle Triassic; Yunnan

摘要: 记述了产自云南中三叠世的裂齿鱼类 3 个新属种——邓氏富源裂齿鱼(*Fuyuanperleidus dengi* gen. et sp. nov.)、苏氏罗平裂齿鱼(*Luopingperleidus sui* gen. et sp. nov.)和小齿滇东裂齿鱼(*Diandongperleidus denticulatus* gen. et sp. nov.)。邓氏富源裂齿鱼区别于其它裂齿鱼的特征,包括上颌骨形状、上下颌牙齿大小及形状、头骨纹饰、上颌骨与第一眶下骨愈合、高鳞片。苏氏罗平裂齿鱼区别于其它裂齿鱼的特征,包括三角形的鳃条骨、腹鳍前有 4 列水平方向的高鳞片、3 个臀鳞。小齿滇东裂齿鱼区别于其它裂齿鱼的特征,包括胸鳍、腹鳍、背鳍和臀鳍前面鳍条的前缘具有小锯齿,鳞片后缘具有许多小锯齿。裂齿鱼类的新发现不仅丰富了中国华南裂齿鱼类的多样性,而且提供了裂齿鱼类在三叠纪全球辐射的新信息。

关键词: 裂齿鱼; 中三叠世; 云南

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1 Introduction

The order Perleidiformes is an important group of the "Subholostei" with high diversity. It is a heterogeneous group of fishes known from Triassic sediments. Seven families are currently recognized in the order: Platysiagidae, Luganoiidae, Gabanellidae, Cleithrolepididae, Colobodontidae, Perleididae and Polzbergiidae^[1-7].

Previous records of perleidid fishes from the Upper Yangtze region include *Luopingichthys bergi* and *Perleides sinensis* from Guanling Formation of Luoping, Yunnan, South China^[8-9], *Colobodus ball* from Guanling Formation of Panxian, Guizhou, South China^[10], which were assigned to the families Polzbergiidae and Colobodontidae respectively.

Here we describe three new perleidid fishes (*Fuyuanperleides dengi* gen. et sp. nov., *Luopingperleides sui* gen. et sp. nov., and *Diandongperleides denticulatus* gen. et sp. nov.). *Fuyuanperleides dengi* gen. et sp. nov. is collected from Jiyangshan, Shibilianshan, Fuyuan County, Yunnan Province; *Luopingperleides sui* gen. et sp. nov. and *Diandongperleides denticulatus* gen. et sp. nov. are collected from Dawazi, Luoxiong, Luoping County, Yunnan Province (Fig.1). They are all ascribed to the family Perleididae.

2 Systematic Paleontology

Perleidiformes Berg, 1940^[11]

Perleididae Brough, 1931^[1]

Fuyuanperleides gen. nov.

Etymology:"Fuyuan" refers to the locality where the fossil was collected; "perleides" is the type genus of the family Perleididae.

Type species:*Fuyuanperleides dengi* gen. et sp. nov.

Diagnosis: A fusiform, relatively small sized perleidid fish. Most of skull bones ornamented with tubercles and ridges. Suboperculum smaller than operculum, and preoperculum with a large fan-shaped infraorbital process. Jaws toothed with conical teeth.

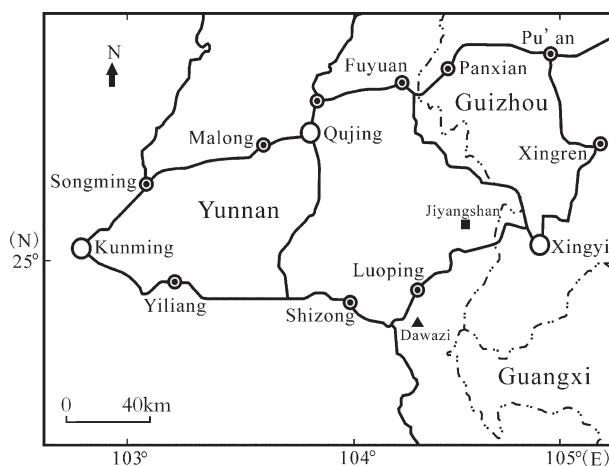


Fig. 1 The locality of fossil fish from Yunnan Province

Maxilla deep and in a triangular shape, and fused with the first infraorbital. Dorsal and anal fins set relatively far back on the body, and their posterior rays more widely spaced than the anterior ones. Caudal fin deeply forked and almost symmetrical. About 38 transversal scale rows. Two horizontal rows of deepened flank scales well developed before pelvic fin, the upper row deeper than the lower one, and the lower flank scale row continued by five horizontal scale rows after pelvic fin. One big anal scale.

Fuyuanperleides dengi gen. et sp. nov.

(Figs. 2-3)

Etymology:The species name is dedicated to Mr. Deng Kewen, who donated the only specimen of this new perleidid fish.

Holotype:A nearly complete specimen, IVPP V16517.

Locality and horizon:Jiyangshan, Shibilianshan, Fuyuan County, Yunnan Province; Middle Triassic (Upper Ladinian) Zhuganpo Member of the Falang Formation.

Diagnosis:As for genus (monotypic).

Description:The holotype and only known specimen of *Fuyuanperleides dengi* gen. et sp. nov. is a relatively small fish (Fig.2). The fish is fusiform with a blunt head. The standard length is approximately 90mm. The maximum depth, just behind the pectoral fin, is estimated to be 30mm. The length of the head

is about 28mm. The dorsal and anal fins are located far posteriorly, well behind the middle of the body; and the dorsal fin is opposing the space between the pelvic and anal fins.

Snout—The snout is formed by a single medial rostral bordered laterally by a pair of nasals (Fig.2). The rostral portion is difficult to observe since it is poorly preserved. The right nasal (Fig.2, Fig.3) is preserved very well. It is a small and nearly rectangular bone, with a large opening of the anterior nostril. The nasal is ornamented with small tubercles.

Skull roof—The skull roof is smooth (Fig.3), as in *Meidiichthys* and *Pseudobeaconia*^[1,2]. The anterior border is gently rounded. The frontals are the main elements of the skull roof, with a length approximately three times that of the parietals. The frontals are elongated and the length is more than twice than the width. The suture between the frontals is irregular. It has a narrower anterior portion and wider posterior portion, and a curved lateral margin. The narrowest of the frontal is just above the orbit. The anterior part of the frontal is ornamented with small tubercles and ridges. The posterior lateral part of the frontal is ornamented with some ridges. The supraorbital sensory canal runs nearly along the lateral margin of the frontal. The parietals are roughly rectangular, and joined together along the cranial midline through an irregular suture. The suture with the frontals is sinuous. The posterior edge of the parietals is nearly straight, which are overlapped by the extrascapulars. The dermopterotic (Fig.3) is slightly longer and narrower than the parietal, meeting the frontal and parietal in a variably sinuous suture and extending more posteriorly laterally than medially. Its ganoine-free posterior edge is overlapped by the anterior edge of the extrascapulars. The extrascapular (Fig.3), only the right bone being partially preserved, is rectangular, with a larger width than its length. The extrascapular joins with the parietal and dermopterotic anteriorly.

Circumorbital series—The circumorbital series (Fig.3) are well preserved and consist of supraorbitals, infraorbitals, and dermosphenotic. There are three

quadrangular supraorbitals (Fig.3). The dorsal part of these bones runs along the border of the frontals, and the posterior supraorbital contacts the dermosphenotic. The first supraorbital is the biggest and the length is two times of the width. The second supraorbital is a small bone and is about 1/3 the length of the first supraorbital. The third supraorbital is about 2/3 the length of the first supraorbital. The dermosphenotic (Fig.3) is a small bone. It contacts the frontal dorsally and an infraorbital ventrally. Three infraorbitals (Fig.3) are preserved. The first infraorbital is the biggest. It is fused with the maxilla. The suture between the two bones is difficult to observe. The second infraorbital is an elongate, slightly curved bone. The third infraorbital is an elongate bone. All the supraorbitals are externally ornamented with short ridges. The anterior two infraorbitals are ornamented with long ridges, and the third infraorbital is ornamented with short ridges.

Jaws—The upper jaw (Fig.3) is formed by a rather smaller premaxilla and a larger maxilla. The premaxilla should bear at least two long, pointed teeth. The maxilla consists of a long, bar-like dentigerous part merging into a dorsally expanded and rounded posterior plate. It bears at least 9 long teeth. The maxillary teeth are sharp, conical, and appear to be arranged in one row. Most of the teeth show a tiny enameloid cusp. The maxilla is ornamented with big tubercles.

The lower jaw (Fig.3) is short and powerful. The dentary (Fig.3) is similar to most perleidid fish. It bears 7 teeth. Teeth on the dentary are arranged in one row and appear to be as robust as the teeth of the maxilla and premaxilla. The cusp of some teeth is not preserved. The ventral part of the dentary is ornamented by short ridges.

Operculum series—The preoperculum (Fig.3) is nearly vertical and the depth is larger than the length, with a triangular projection wedged between the suboperculum and maxilla. The preoperculum is ornamented with big tubercles. The depth of the operculum (Fig.3) is larger than the length. Its anterior border is concave and the posterior border is strongly convex. Anteriorly, it contacts the preoperculum. Its

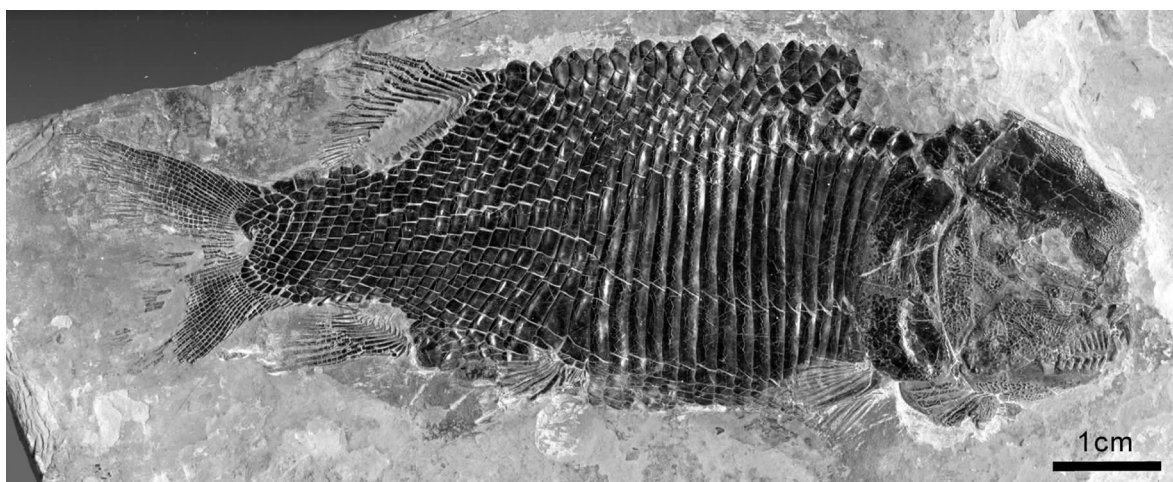


Fig. 2 *Fuyuanperleidus dengi* gen. et sp. nov., holotype in right lateral view

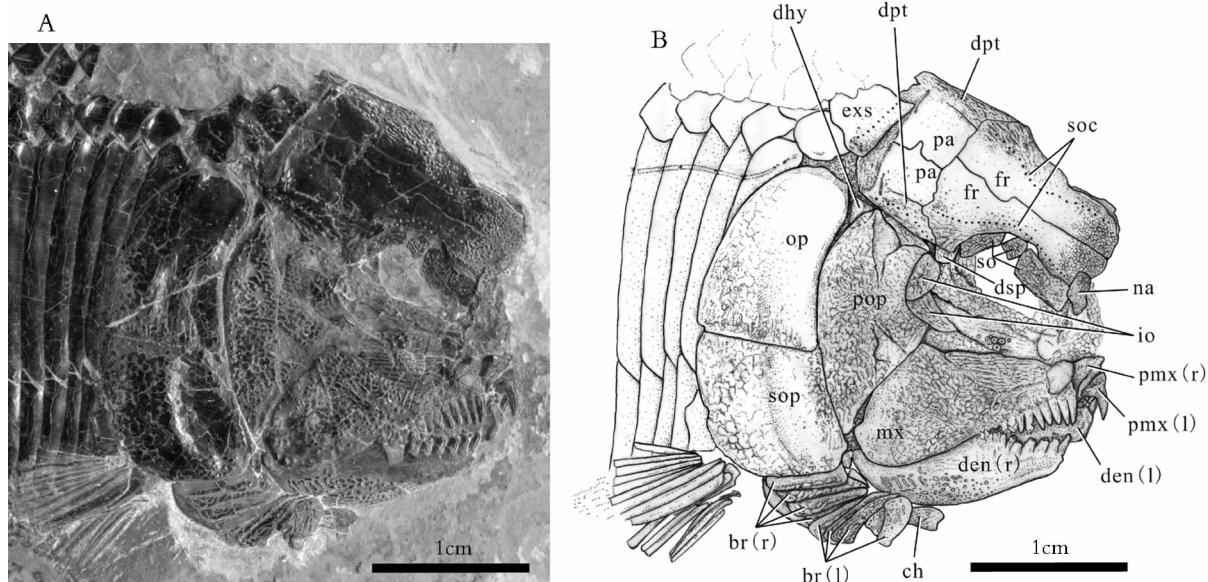


Fig. 3 *Fuyuanperleidus dengi* gen. et sp. nov., holotype. Photograph (A) and drawing of the skull (B)

Abbreviations: br(l), left branchiostegal rays; br(r), right branchiostegal rays; den(l), left dentary; den(r), right dentary; dhy, dermohyal; dpt, dermopterotic; dsp, dermosphenotic; exs, extrascapular; fr, frontal; io, infraorbitals; mx, maxilla; na, nasal; op, operculum; pa, parietal; pmx(l), left premaxilla; pmx(r), right premaxilla; pop, preoperculum; ch, ceratohyal; so, supraorbitals; soc, supraorbital sensory canal; sop, suboperculum

dorsal border reaches the dermal roof, whereas its ventral straight border abuts the suboperculum. The suboperculum (Fig.3) is shorter than the operculum, as in *Mendocinichthys*^[13]. Its anterior and dorsal border is slightly straight. Its posterior and ventral border is rounded. Four rectangle branchiostegal rays (Fig.3) are present as in most perleidid fishes. They show the same strong ornamentation of the preoperculum. The der-

mohyal(Fig.3) is a small triangular bone. It contacts the dermopterotic dorsally, the operculum posteriorly, and the preoperculum anteriorly.

Paired fins—The shoulder girdle is not preserved. The pectoral fin (Fig.2) is not well preserved. There are 10 fin rays at least. The distal parts of the fin rays are missing. The first ray is not greatly lengthened.

The pelvic fin (Fig.2), placed at the position of

the 17th scale row, included at least 8 long fin rays and 3 spine-like rays. The distal parts of the fin rays are missing.

Unpaired fins—The dorsal and anal fins (Fig. 2) are set relatively far back on the body, as in *Ctenognathichthys*^[4]. The dorsal fin is situated at about scale row 28. It is composed of about 20 distally segmented fin rays, all of which are distally branching except the first anterior one. The anterior eight fin rays are completely preserved; the basal and distal parts of the posterior twelve fin rays are not preserved. The leading edge is preceded by at least three basal fulcra. The endoskeletal supported the unpaired fins are visible, and they are same in number with the fin rays.

The anal fin is situated at about scale row 23. It is smaller than the dorsal fin but with the same character. It is composed of about 15 distally segmented fin rays and all are distally branching except the first anterior three.

Caudal fin—The well developed, almost symmetrical caudal fin (Fig. 2) is composed of at least 44 segmented fin rays, of which the more central ones are distally branched. Both dorsal and ventral margins bear at least one basal fulcrum.

Scales—There are about 38 rows of scales. The scales are smooth and are absent of any kind of ornamentation as in *Meidiichthys*, *Peltoperleidus*, and *Perleidus*^[11, 14–15]. The posterior border of the scales is not serrated, as in *Meridensia*, *Mendocinichthys*, and *Pseudobeaconia*^[12–13, 16]. There are two horizontal rows of deepened flank scales before the pelvic fin, of which the upper row is deeper than the lower one. The lower row is continued by five horizontal scale rows after the pelvic fin, as in *Luganoia*^[16]. But in *Luganoia* only the lateral line scale row is marked by the presence of highly deepened flank scales. The lateral line scales are easily recognized by the presence of a well-marked notch on their posterior portion. There is a big anal scale on the front base of the anal fin.

***Luopingperleidus* gen. nov.**

Etymology: "Luoping" refers to the locality

where the fossil was collected; "perleidus" is the type genus of the family Perleididae.

Type species: *Luopingperleidus sui* gen. et sp. nov.

Diagnosis: A fusiform, relatively small sized perleidid fish. All skull bones ornamented with tubercles and ridges. Suboperculum bigger than operculum, preoperculum with a large fan-shaped infraorbital process, and main branchiostegal triangle. Jaws toothed with conical teeth, and maxilla deep and triangular. Dorsal and anal fins set relatively far back on the body, and their posterior rays more widely spaced than the anterior ones. Caudal fin forked and hemiheterocercal. About 47 transversal scale rows, the biggest scale about 5 times deeper than long. Four horizontal rows of deepened flank scales developed before pelvic fin, and the second to fourth flank scale rows continued by two horizontal scale rows after pelvic fin. Three anal scales.

***Luopingperleidus sui* gen. et sp. nov.**

(Figs. 4–5)

Etymology: The specific name is in honour of Prof. Su Dezhao, who initially worked on the marine Triassic fishes from South China.

Holotype: A nearly complete specimen, IVPP V16518.

Locality and horizon: Dawazi, Luoxiong, Luoping County, Yunnan Province; Middle Triassic (middle-late Anisian) Guanling Formation.

Diagnosis: As for genus (monotypic).

Description: The holotype and only known specimen of *Luopingperleidus sui* gen. et sp. nov. is almost complete (Fig. 4). The fish is fusiform, with the total and standard length up to 83 mm and 68 mm. The deepest part of the body is in front of the dorsal fin, with a depth of 20 mm. The head length is 20 mm. The dorsal and anal fin located far posteriorly, well behind the middle of the body.

Snout—The snout (Fig. 5) is poorly preserved. The shape of the medial rostral can not be identified. The paired nasals are small elongated bone, forming the anterior margin of the orbit. The nasal is ornamented

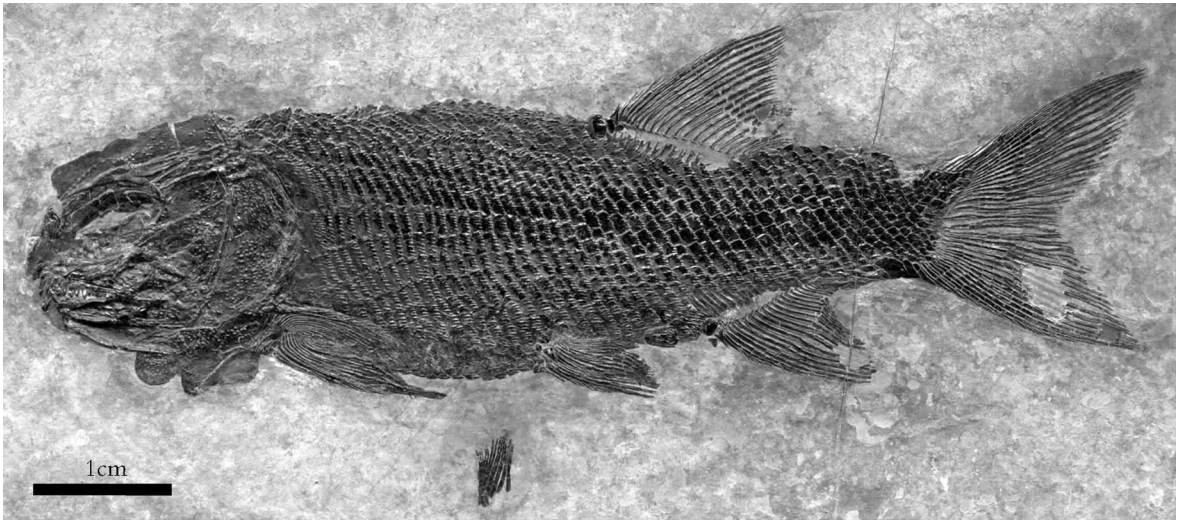


Fig. 4 *Luopingperleidus sui* gen. et sp. nov., holotype in left lateral view

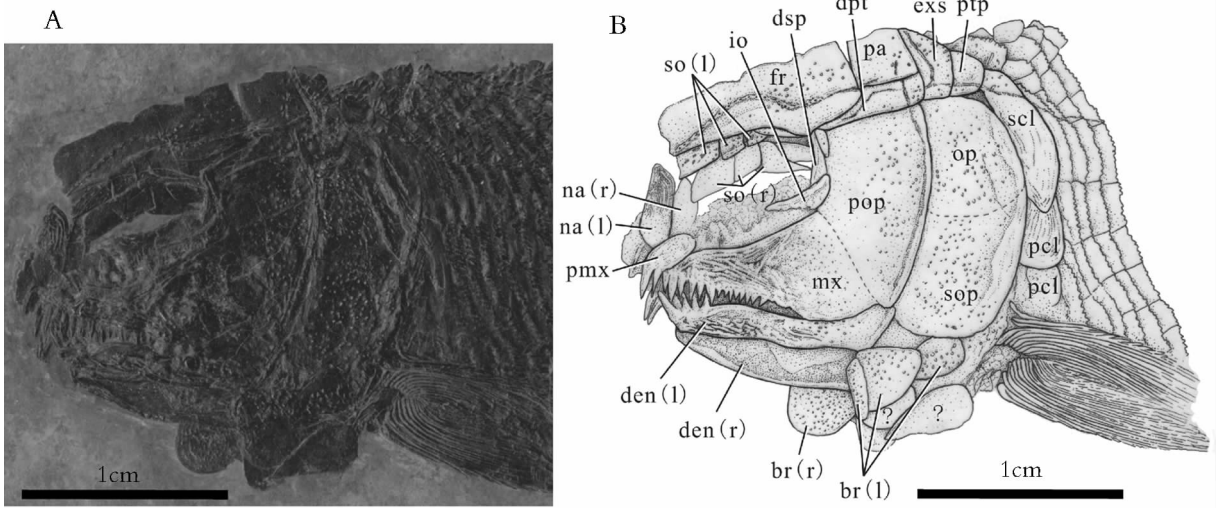


Fig.5 *Luopingperleidus sui* gen. et sp. nov., holotype. Photograph and drawing of the skull

Abbreviations: br(l), left branchiostegal rays; br(r), right branchiostegal rays; den(l), left dentary; den(r), right dentary; dpt, dermopterotic; dsp, dermosphenotic; exs, extrascapular; fr, frontal; io, infraorbitals; mx, maxilla; na(l), left nasal; na(r), right nasal; op, operculum; pa, parietal; pcl, postcleithrum; pmx, premaxilla; pop, preoperculum; ptp, posttemporal; scl, supracleithrum; so(l), left supraorbitals; so(r), right supraorbitals; sop, suboperculum

with ganoid ridges.

Skull roof—All the skull roof bones are ornamented with tubercles, as in *Ctenognathichthys*, *Luopingichthys*, *Meridensia*, *Peltoperleidus* and *Perleidus*^[4,8,14–16]. Only the left part of the skull roof(Fig.5) is preserved. The frontal is main part of the skull roof, approximately three times the length of the parietal. The anterior border of the frontal is gently sinuous,

but the posterior border is more or less straight. The lateral border of the frontal forms a pointed process behind the posterior margin of the orbit. The supraorbital sensory canal runs along the lateral margin of the bone. The parietal is a small and roughly square-shaped bone. The posterior border of the parietal is straight, which is overlapped by the anterior edge of the extrascapular. The dermopterotic is slightly

longer and narrower than the parietal, meets the frontal and parietal in a variably sinuous suture and extends more posteriorly laterally than mesially. Its ganoine-free posterior edge is overlapped by the anterior edge of the extrascapular. The extrascapular is rectangular, and connects anteriorly with the parietal and the dermopterotic, and posteriorly with the posttemporal. The posttemporal is subtriangular, and smaller than the extrascapular.

Circumorbital series—The circumorbital series (Fig.5) is partly preserved and consists of supraorbitals, infraorbitals and dermosphenotic. All the bones are ornamented with small ridges or tubercles. There are four quadrangular supraorbitals. The first supraorbital is the biggest, twice as long as wide. The second is smaller, about 1/2 length of the first. The third is further smaller than the second, about 1/3 length of the first. The fourth is covered by frontal, preoperculum and can not be observed. The shape of the dermosphenotic can not be observed. The total number of infraorbital elements cannot be determined.

Jaws—The upper jaw (Fig.5) is formed by a premaxilla and a maxilla. The contact between the premaxilla and the maxilla can not be observed. The premaxilla is small, and should bear at least three long, pointed teeth. The maxilla is a large triangular bone, and consists of a long, bar-like dentigerous part merging into a dorsally expanding, rounded posterior plate. There are about 11 long and sharply pointed teeth, most of them show a tiny enameloid cusp. The anterior part of the maxilla is ornamented by short ridges, and the poster part is ornamented by tubercles.

The lower jaw (Fig.5) is short and powerful. The dentary is wedge-like, and bears some teeth of similar shape and size to those of the upper jaw. The dentary is ornamented with short ridges and big tubercles.

Operculum series—This series is formed by operculum, suboperculum, preoperculum and branchiostegal rays, and all the bones are ornamented with small tubercles (Fig.5). The depth of the operculum (Fig.5) is larger than the length. Its posterior and ventral border is slightly convex, and the anterior border is

slightly concave. The dorsal border of the operculum reaches the dermal roof, whereas its ventral border is slightly concave and abuts the suboperculum. The suboperculum is bigger than the operculum, as in most perleidid fishes. Its posterior and ventral border is convex, and the anterior border is slightly concave. The contact between the operculum and the suboperculum cannot be observed clearly. The preoperculum is nearly vertical and has a triangular projection wedged between the suboperculum and maxilla. Only the posterior border of the preoperculum can be observed. There are at least two nearly rounded branchiostegal rays.

Paired fins—The shoulder girdle (Fig.4) is incompletely preserved. The supracleithrum is a large and subrectangular bone. The postcleithrum is similar to the supracleithrum. Only part of the cleithrum is preserved.

The pectoral fin (Fig.4) is well preserved. There are at least 12 fin rays. The leading edge of the pectoral fin is preceded by prominent fringing fulcra.

The pelvic fin (Fig.4), placed at the position of the 15th scale row, includes at least 13 fin rays. All fin rays are distally segmented, with the exception of the most anterior three ones. The leading edge of the pectoral fin is preceded by the prominent fringing fulcra.

Unpaired fins—The dorsal fin (Fig.4) is situated at about scale row 28. There are at least 22 fin rays. All fin rays are distally segmented, with the exception of the anteriormost three ones. All fin rays are distally branching, with the exception of the six anterior ones. The leading edge of the dorsal fin is preceded by two basal fulcra and prominent fringing fulcra. The endoskeletal supports of the dorsal fins are visible, and they agree in number with the fin rays.

The anal fin (Fig.4) is situated at about scale row 26. It has about 25 distally segmented fin rays, with the exception of the anteriormost two ones. The leading edge of the anal fin is preceded by one basal fulcra and prominent fringing fulcra.

The well-developed, hemiheterocercal caudal fin

(Fig.4) is composed of about 36 segmented fin rays, of which the more central ones are distally branched once or twice. The ventral margin of the caudal fin bears at least two basal fulcra. Both the dorsal and ventral leading edges are preceded by a series of fringing fulcra.

Scales—There are about 47 scales along the main lateral line. The scales are covered by ganoine, and their posterior margin is serrated as in *Meidiichthys*, *Ctenognathichthys* and *Perleidus*^[1,4,15]. Only some of the scales of the caudal peduncle and at the base of the caudal fin have smooth posterior border. There are at least four horizontal rows of deepened flank scales before the pelvic fin, and the lateral line scales are the deepest. The anteriormost scale is largest, and is almost fifth as high as wide. Posteriorly, scales become gradually less deep towards the tail region, and after the dorsal fin the scales are diamond-shaped. The second to the fourth deepened flank scale rows are continued by two scale rows. The rear part of the anterior 21 scales is ornamented with small ridges. Posteriorly, the scales are smooth. The scales of the lateral line are easily recognized by the presence of a well-marked notch on their posterior portion. There are three anal scales at the front base of the anal fin.

***Diandongperleidus* gen. nov.**

Etymology: "Diandong" refers to the locality where the fossil was collected; "perleidus" is the type genus of the family Perleididae.

Type species: *Diandongperleidus denticulatus* gen. et sp. nov.

Diagnosis: A fusiform, relatively small size perleidid fish. Most of skull bones ornamented with tubercles and ridges. Nasal and parietal bones small, and frontals being the main element of skull roof. Suboperculum bigger than operculum, preoperculum with a large fan-shaped infraorbital process, and main branchiostegal triangle. Jaws toothed with conical teeth, and maxilla deep and triangular. Anterior border of some anterior fin rays of both paired fins and dorsal and anal fins bearing denticles. About 36 transversal scale rows, the biggest scale about 4 times the depth

to the length. Scales strongly serrated posteriorly.

***Diandongperleidus denticulatus* gen. et sp. nov.**

(Figs. 6–7)

Etymology: "denticulatus" (Latin) –denticle, refers to the anterior border of the anterior fin rays bears denticles.

Holotype: An incomplete specimen, IVPP V16519.

Locality and horizon: Dawazi, Luoxiong, Luoping County, Yunnan Province; Middle Triassic (middle–late Anisian) Guanling Formation.

Diagnosis: As for genus (monotypic).

Description: The holotype and only known specimen of *Diandongperleidus denticulatus* gen. et sp. nov. (Fig.6) is a fusiform fish of medium size, and about 95 mm in standard length. The fish is strongly contorted and slightly disarticulated. The head length is about 1/4 of the standard length. The dorsal fin is placed at about the midpoint of the body. Most of the head bones and scales are preserved in medial view. Head bones, fin rays and scales are covered with ganoine.

Snout—The snout is composed of a rostral and a pair of nasals, which are not well preserved (Fig.7). The rostral has a lateral indentation for anterior nostril. The nasal is irregular in shape. The medial edge of the nasal has a small indentation for anterior nostril. The supraorbital sensory canal passes through the nasal.

Skull roof—The skull roof is partially preserved (Fig.7). The paired frontals are the main element of the skull roof. The anterior border of the frontal is unclear and the posterior border is covered by the hyomandibular. The contact of the frontal with the parietal can not be observed. The lateral margin of frontal is produced into a pointed process behind the posterior margin of the orbit. The suture between the frontals is almost straight. The supraorbital sensory canal passes through the frontals. Most portion of the parietal is covered by the hyomandibular and scales, so it is impossible to identify its shape. The dermopterotic is a long and narrow bone. It meets the frontal and parietal in a variably sinuous suture. The middle part of the dermopterotic is covered by the

hyomandibular. The extrascapular is a triangular bone.

Circumorbital series –The circumorbital series is poorly preserved (Fig.7). The supraorbitals are covered by the frontal and scales, and there are at least three plate-like supraorbitals preserved dorsally along the

lateral border of the frontal. The dermosphenotic is partially visible, and is a quite elongate bone. The infraorbitals are slender bones, and their number cannot be determined.

Jaws –The maxilla (Fig.7) is a large triangular

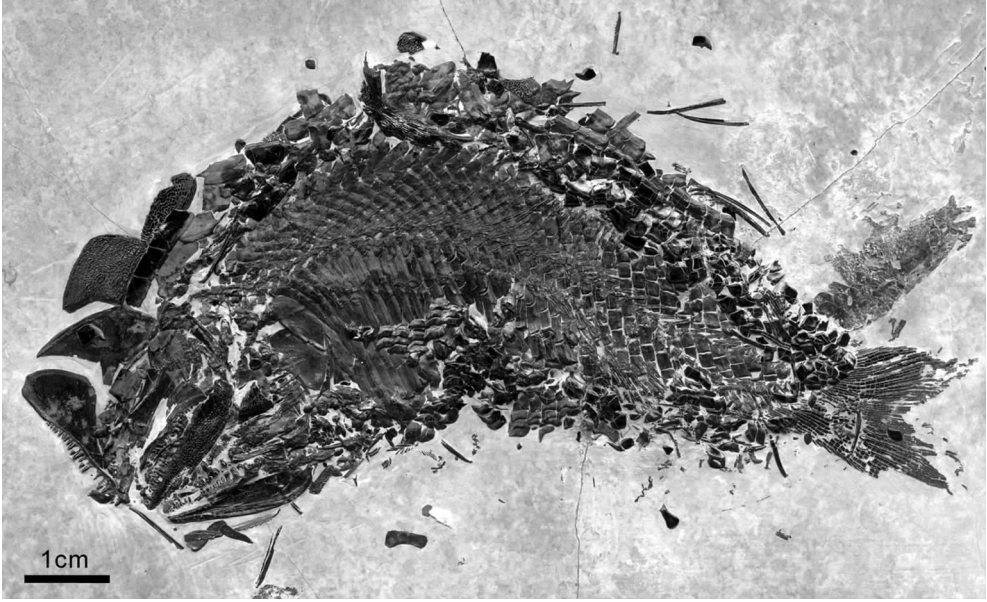


Fig. 6 *Diandongperleidus denticulatus* gen. et sp. nov., holotype in right lateral view

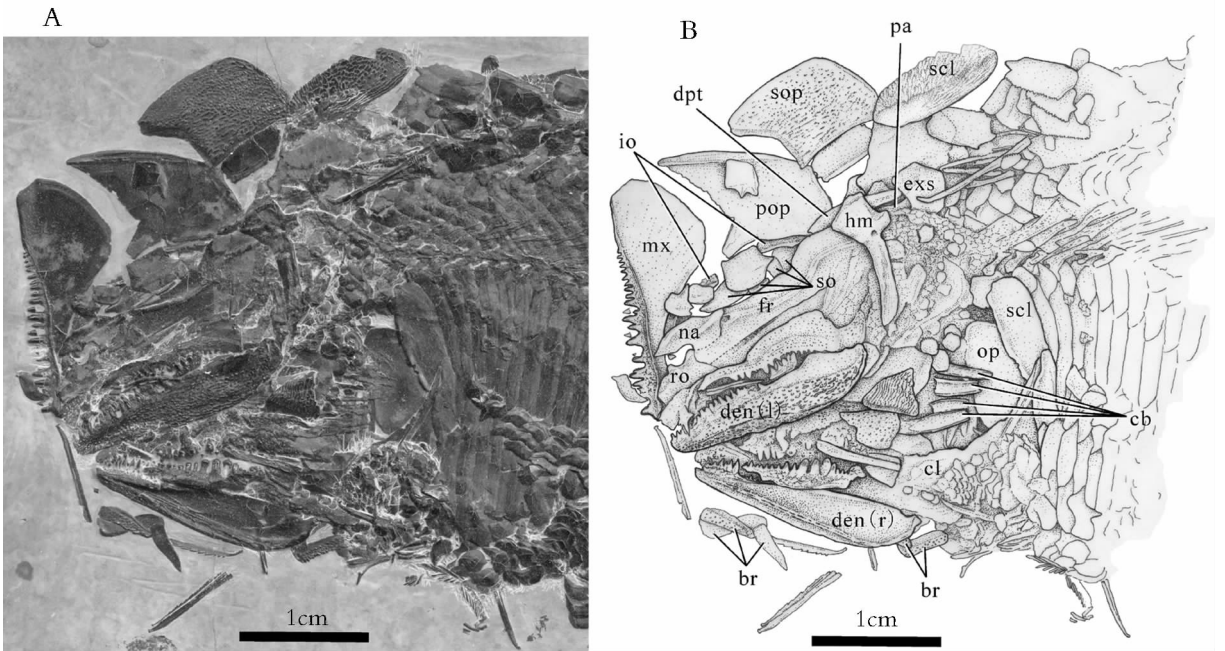


Fig. 7 *Diandongperleidus denticulatus* gen. et sp. nov., holotype. Photograph and drawing of the skull
 Abbreviations: br, branchiostegal rays; cb, ceratobranchials; cl, cleithrum; den(l), left dentary; den(r), right dentary; dpt, dermosphenotic; exs, extrascapular; fr, frontal; hm, hyomandibular; io, infraorbitals; mx, maxilla; na, nasal; op, operculum; pa, parietal; pop, preoperculum; ro, rostral; scl, supracleithrum; sop, suboperculum; so, supraorbitals

bone, and consists of a long, bar-like dentigerous part merging into a dorsally expanded, rounded posterior plate. There are at least 21 long and sharply pointed teeth present, most of which show a tiny enameloid cusp.

The lower jaw is short and slender (Fig.7). The dentary is wedge-like, and bears more than 18 teeth which are similar in shape and size to those of the maxilla. The lower jaw is ornamented with many short ridges and big tubercles. The dentary sensory canal is clearly visible, and there is a series of small pores along the ventral margin of the dentary.

Operculum series—The posterior margin of the operculum is covered by supracleithrum and cleithrum (Fig.7), and its shape cannot be identified. The anterior margin of the operculum is slightly straight. The preoperculum (Fig.7) is nearly vertical, and has a sharp and long infraorbital process that extends anteriorly. Its dorsal border is nearly straight, and its posterior border is convex. The preoperculum sensory canal passes along the posterior margin of the preoperculum. The suboperculum (Fig.7) is bigger than the operculum, with a slightly convex posterior and ventral border, and a concave dorsal border. The suboperculum is ornamented with many small tubercles and ridges. Six branchiostegal rays (Fig.7) are preserved, but the exact number of these elements is unknown. The branchiostegal rays are ornamented with many small tubercles.

Hyoid and branchial arches—The hyomandibular and four fragmented ceratobranchials are preserved (Fig.7). The hyomandibular is a slender bone, almost vertically oriented. The bone has an expanded dorsal and a narrow ventral extremity. There is no evidence of a nerve foramen in the vertical shaft.

Axial skeleton—the vertebrae are not ossified. The neural arches and spines are well ossified. The hemal arches and spines are not well ossified. The number of vertebrae is about 34.

Paired fins—The shoulder girdle (Fig.6) is incompletely preserved. The supracleithrum is a long, plate-like bone. The anterior part of the

supracleithrum is ornamented with long ridges, and the posterior part is ornamented with many small tubercles. The sickle-shaped cleithrum is divided by a lateral, longitudinal ridge into a smooth anterior and an ornamented posterior part. The dorsal tip of the cleithrum is sharply pointed. The ornamentation of the posterior part consists of long ridges. The only one postcleithrum is partially visible. The endoskeletal elements of the shoulder girdle are not preserved.

The pectoral fin (Fig.6) is poorly preserved. It has at least 11 fin rays. The anterior border of the anterior fin rays bear denticles. The leading edge of the pectoral fin is preceded by prominent fringing fulcra.

The pelvic fin is not preserved.

Unpaired fins—The dorsal fin (Fig.6) is poorly preserved. It is situated at about scale row 21/22. Only 6 fin rays are present, and their distal portion is missing. The anterior border of the anterior fin rays also bear denticles as in the pectoral fin. At least fourteen endoskeletal supporting of the dorsal fin are present, and they agree in number with the fin rays.

The anal fin (Fig.6) is poorly preserved.

The well-developed, hemiheterocercal caudal fin (Fig.6) is composed of about 28 segmented fin rays, of which the more central ones are distally branched once or twice. Both the dorsal and ventral leading edges are preceded by a series of fringing fulcra.

Scales—There are about 36 scales along the main lateral line (Fig.6). The scales are covered by ganoine, and their posterior margin is strongly serrated. In the anterior region of the body, the scales are larger and higher. The largest scale's height is almost fourth the length. Posteriorly, the scales become diamond-shaped.

3 Discussion

The three fishes described herein show a suite of characters commonly found in the perleidiforms: skull pattern, almost vertical preoperculum, almost symmetrical caudal fin with epaxial rays, unevenly segmented, long based fin rays, one to one relationship between dorsal and anal fin rays and radials, and scales deeper

than long in the anterior portion of the flank. Therefore they are referred to the order Perleidiformes.

Fuyuanperleidus dengi gen. et sp. nov., *Luopingperleidus sui* gen. et sp. nov., *Diandongperleidus denticulatus* gen. et sp. nov. differ much from all genera of the family Platysiagidae in nearly symmetrical caudal fin and the shape of the maxilla. They differ much from all genera of the family Luganoiidae in the fusion of skull-roof elements, the relation between the maxilla and the preoperculum, and the scale pattern. They differ much from all genera of the family Gabanellidae in the fusiform body, the skull morphology, and the size of the operculum. They differ much from all genera of the family Cleithrolepididae in the elegantly fusiform body, the shape of the maxilla, and the presence of posttemporal. They differ much from all genera of the family Colobodontidae in the body size and snout pattern. They differ from all genera of the family Polzbergiidae in the upper jaws and the anterior teeth of the jaws. Consequently, *Fuyuanperleidus dengi* gen. et sp. nov., *Luopingperleidus sui* gen. et sp. nov., *Diandongperleidus denticulatus* gen. et sp. nov. are provisionally referred to the family Perleididae based on 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.

Fuyuanperleidus dengi gen. et sp. nov. is characterized by the deepened flank scales. In perleidids, *Peltoperleidus* and *Altisolepis* also possess this character, but *Fuyuanperleidus dengi* gen. et sp. nov. is distinguishable from them in the shape of the maxilla, the big teeth, the ornamentation of the skull bones, the suboperculum smaller than the operculum, maxilla fused with the first infraorbital, the upper deepened scale row two times deeper than the lower one, the lower deepened flank scale row continued by five horizontal scale rows posterior to level of anal fin insertion, and the almost symmetrical caudal fin^[4, 17-18].

Luopingperleidus sui gen. et sp. nov. is obviously distinguished from the known forms of perleidids

in the following characters: the main branchiostegal triangle, four horizontal rows of deepened flank scales before the pelvic fin, deepened flank scales becoming gradually less deep towards the tail region, the second to fourth deepened scale rows continued by two scale rows, and three anal scales. Among perleidids, *Luopingperleidus sui* gen. et sp. nov. is similar to *Peltoperleidus ducanensis* in the fish size, the teeth of the jaws, the shape of the operculum and suboperculum, the hemiheterocercal caudal fin, the ventral margin of the caudal fin with two basal fulcra, deepened scale rows taper toward the caudal peduncle^[14, 17]. However, it differs from *Peltoperleidus ducanensis* in several other features: the maxillar shape, counts of the deepened flank scale rows, the vertical scale rows and the horizontal scale rows, scales with posterior denticles, three anal scales.

Diandongperleidus denticulatus gen. et sp. nov. is clearly distinguished from the known perleidids on the basis of following characters: scales strongly serrated posteriorly, the anterior border of some anterior fin rays of both the paired fins and the dorsal and anal fins bearing denticles^[2-4, 5, 7-10, 12, 19-20].

We have compared the three new species to each other, and compared them with other perleidid fishes (*Luopingichthys bergi*, *Colobodus ball*, *Perleidus sinensis*) reported from Upper Yangtze region.

Fuyuanperleidus dengi gen. et sp. nov. has three supraorbitals, as in *Luopingichthys bergi*^[8]. In *Fuyuanperleidus dengi* gen. et sp. nov., the maxilla fused with the first infraorbital; different from the five perleidid fishes^[8-10]. The teeth of *Fuyuanperleidus dengi* gen. et sp. nov. is bigger than *Luopingperleidus sui* gen. et sp. nov., *Diandongperleidus denticulatus* gen. et sp. nov., *Colobodus ball*, *Perleidus sinensis*, but similar to *Luopingichthys bergi*^[8-10]. The lower jaw of *Fuyuanperleidus dengi* gen. et sp. nov. is stronger than *Luopingperleidus sui* gen. et sp. nov., *Diandongperleidus denticulatus* gen. et sp. nov., *Colobodus ball*, *Perleidus sinensis*^[9-10]. The operculum is bigger than the suboperculum in *Fuyuanperleidus dengi* gen. et sp. nov., but in other perleidid fishes, the opercu-

lum is smaller than the suboperculum^[8-10]. The deepened flank scales of *Fuyuanperleidus dengi* gen. et sp. nov. are more than five times deeper than long. This condition is different from that of other perleidid fishes^[8-10]. In *Fuyuanperleidus dengi* gen. et sp. nov., the scales are smooth, and with smooth posterior border. Among the five perleidid fishes, only *Luopingichthys bergi* and *Diandongperleidus denticulatus* gen. et sp. nov. have smooth scales^[8-10].

Luopingperleidus sui gen. et sp. nov. has four supraorbitals, as in *Diandongperleidus denticulatus* gen. et sp. nov.. Furthermore, *Luopingperleidus sui* gen. et sp. nov. has a slender lower *Luopingperleidus sui* gen. et sp. nov. shows a triangle branchiostegal, but the branchiostegal in other perleidid fishes is rectangle^[8-10]. *Luopingperleidus sui* gen. et sp. nov. has four horizontal rows of deepened flank scales before the pelvic fin, deepened flank scales becoming gradually less deep towards the tail region, the second to fourth deepened scale rows continued by two scale rows. This condition is different from that of other perleidid fishes^[8-10]. *Luopingperleidus sui* gen. et sp. nov. shows serrated posterior border scales, as in *Luopingichthys bergi*, *Colobodus ball*, *Perleidus sinensis*^[8-10]. *Luopingperleidus sui* gen. et sp. nov. has three anal scales, as in *Luopingichthys bergi*^[8].

Diandongperleidus denticulatus gen. et sp. nov. shows scales strongly serrated posteriorly, and the anterior border of some anterior fin rays of both the paired fins and the dorsal and anal fins bearing denticles. These conditions are different from that of other perleidid fishes^[8-10]. The shape of the lower jaw is similar to *Luopingperleidus sui* gen. et sp. nov., *Colobodus ball*, *Perleidus sinensis*^[9-10].

In China, perleidid fishes were found from the Early Triassic of the Lower Yangtze region and the Middle Triassic of the Upper Yangtze region. Only three species (*Plesioperleidus yangtzensis*, *Plesioperleidus jiangsuensis*, *Paraperleidus changxingensis*) were reported from the Early Triassic of the Lower Yangtze region^[19, 21-26]. Together with the new discoveries in this paper, Six perleidid fishes have been re-

ported from the Middle Triassic of the Upper Yangtze region in South China^[8-9]. The perleidid fishes from the Lower Yangtze region show a low taxonomic diversity, and The perleidid fishes from the Upper Yangtze region show a high taxonomic diversity. The new discoveries made a high taxonomic diversity of the perleidid fishes from the Upper Yangtze region. High taxonomic diversity of perleidid fishes in the Middle Triassic the Upper Yangtze region indicates that the Middle Triassic was an important period for the adaptive radiation of perleidid fishes in the world.

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