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# A new basal actinopterygian fish from the Anisian (Middle Triassic) of Luoping, Yunnan Province, Southwest China

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The new neopterygian fish taxon *Luoxiongichthys hyperdorsalis* gen. et sp. nov. is established on the basis of five specimens from the second member of the Guanling Formation (Anisian, Middle Triassic) from Daaozi Quarry, Luoping, Yunnan Province, Southwest China. The new taxon is characterized by the following characters: triangular body outline with a distinct apex located between skull and dorsal fin; free maxilla; slender preopercular almost vertical; three suborbitals; at least eight strong branchiostegals with tubercles and comb-like ornamentation on the anterior margin; clavicles present; two postcleithra; ganoid scales covered by tubercles and pectinate ornamentation on the posterior margin with peg-and-socket structure; hemiheterocercal tail slightly forked. Comparison with basal actinopterygians reveals that the new taxon has parasemionotid-like triangular symplectics, but a semionotid opercular system. Cladistic analysis suggests that this new genus is a holostean, and either a basal halecomorph or basal semionotiform.

**Key words:** Actinopterygii, Halecomorphi, Triassic, Anisian, Luoping, Yunnan Province, China.

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## Introduction

Actinopterygian fishes were severely affected by the end-Permian mass extinction (Benton and Twitchett 2003; Tong et al. 2006) and their recovery in the Early and Middle Triassic was slow, lasting some 10–15 Ma (Mutter 2004; Mutter and Neuman 2009). In Chinese sections, the Perleididae were the first actinopterygian family to recover, in the Lower Triassic, and the rarer Semionotidae, Parasemionotidae, and Saurichthyidae began to diversify in the Olenekian and Anisian (Wang and Jin 2007). Understanding the diversity and relative abundance of fish taxa during these critical intervals is crucial for understanding the nature of the Triassic recovery of fishes after the devastation of the end-Permian mass extinction.

One of the best and most complete ichthyofaunas that illustrates a late phase in the recovery process is the Luoping Biota, from Luoping County in NE Yunnan Province, China (Zhang and Zhou 2008b; Zhang et al. 2008, 2009; Hu et al. 2011). The Luoping biota is an exquisite Lagerstätte, yield-

ing well preserved invertebrates and vertebrates, including numerous fishes (Zhang and Zhou 2008a; Zhang et al. 2010). Initial identifications indicate nine families of fishes, and seven new species have been named: *Macropoloichthys ani* Tintori, Sun, Lombardo, Jiang, Sun, and Hao, 2007, *Luopingichthys bergi* Sun, Tintori, Jiang, Lombardo, Rusconi, Hao, and Sun, 2009, *Saurichthys dawaziensis* Wu, 2009, *Saurichthys yunnanensis* Zhang, 2010, *Gymnoichthys inopinatus* Tintori, Sun, Lombardo, Jiang, Sun, and Hao, 2010, *Sino-saurichthys longimedialis* Wu, 2011, and *Sinosaurichthys minuta* Wu, 2011.

Triassic bony fishes belong to several clades, the basal pholidopleuriforms and perleidiforms, outgroups to the major clade Neopterygii. Triassic neopterygians include semionotids, pycnodontids, macrosemiids, halecomorphs, and the first teleosts (Gardiner et al. 1996). In this paper we present the eighth new fish taxon from the Luoping biota, a basal neopterygian showing similarities to both semionotids and parasemionotids.

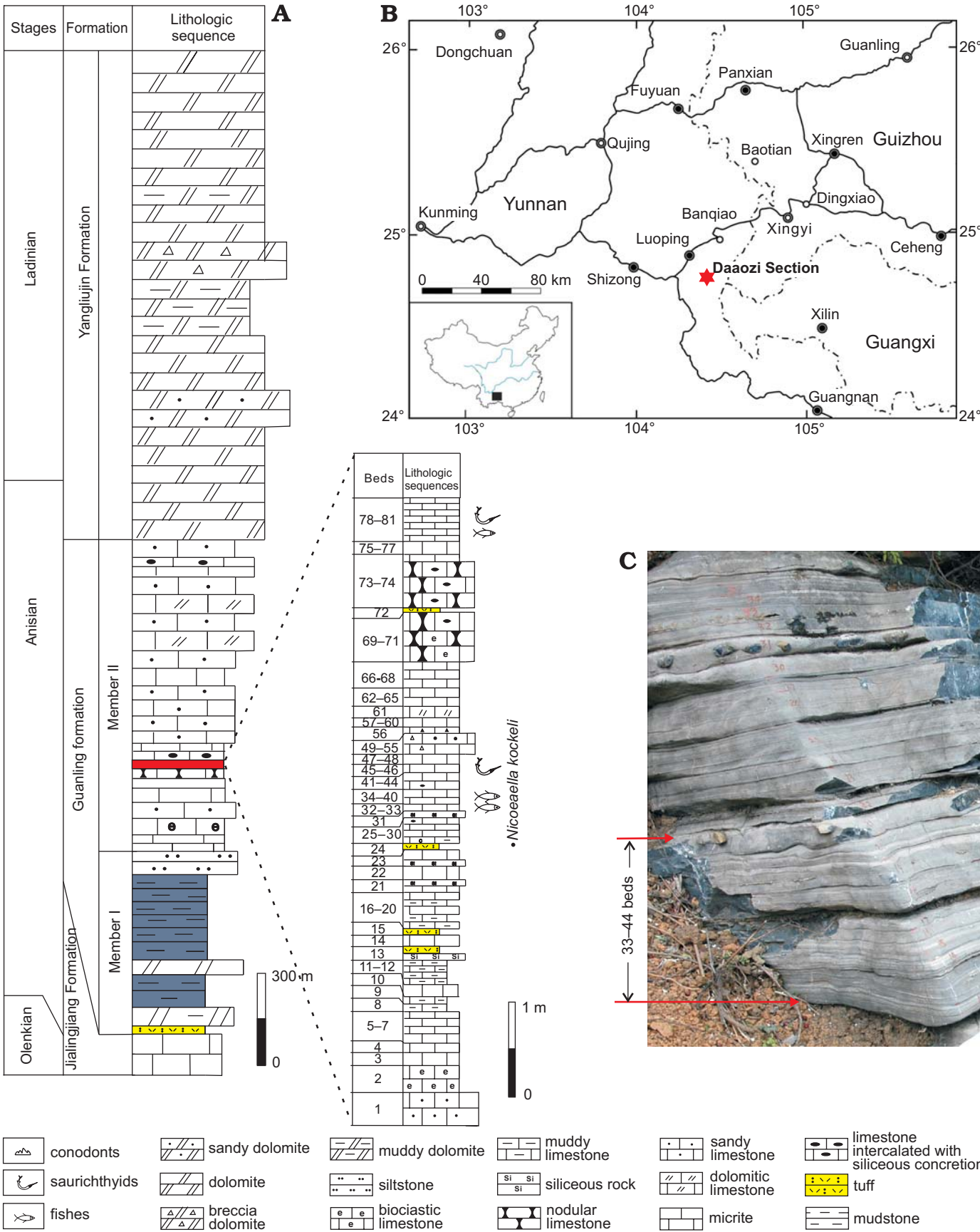


Fig. 1. **A.** Lithological sequence of the Daozi Section showing detail of Member II, with bed numbers, fossiliferous beds are shaded red. **B.** Location map (modified from Zhang et al. 2009). **C.** A photograph of fossiliferous beds 33–44.

**Institutional abbreviation.**—LPV, Luoping County Vertebrates, Chengdu Institute of Geology and Mineral Resources, Chengdu, China.

**Other abbreviations.**—CI, consistency index; HI, homoplasy index; L, length; RC, rescaled consistency index; RI, retention index; TBR, Tree-bisection-reconnection; TNT, Tree analysis using New Technology.

## Geological setting

The new material was collected from the early Middle Triassic sequence in the Daaози section, 25 km NE of Luoxiong town, Luoping County (Fig. 1). Here, the early Middle Triassic succession is assigned to the Guanling Formation, which is subdivided into two members. Member I is 333 m thick, and consists of calcareous silty mudstone and mudstone intercalated with muddy dolomite, indicating a transition from a restricted-evaporitic tidal flat environment to a shallow marine setting. A coarse-grained volcanic ash bed (green pisolite; Zhu 1994) is seen at the base (Fig. 1). This ash bed is widely distributed in Guizhou, Yunnan and Sichuan areas, Southwestern China, and is a pronounced marker for the basal Guanling Formation and widely used in regional stratigraphic correlation (Zhu 1994; Wan 2002; Xiao and Hu 2005). This unit yields abundant conodont and bivalve faunas, which suggest an early Anisian age throughout South China (Wang et al. 2005).

Member II, source of the Luoping Biota, is a 580-m-thick ramp facies succession comprising dark grey medium- to thick-bedded nodular micritic limestone, muddy limestone and cherty micritic limestone interbedded with dolomite, yielding abundant and diverse marine vertebrates (reptiles and fishes), invertebrates (shrimps) and plant fossil assemblages (Zhang et al. 2008). Most of the fossil reptiles, shrimps, fishes, invertebrates and plants are exceptionally preserved and extremely abundant and diverse. They were termed the Luoping biota by Zhang et al. (2008).

The overlying unit, the Yangliujing Formation, comprises 1204 m of peritidal facies dolostone and dolomitic limestone intercalated with limestone breccias that are characterized by pseudomorphs of gypsum- and evaporite-solution breccias. This unit is equivalent to the Yangliujing Formation in neighbouring parts of Guizhou Province. This dolomite succession was constrained as earliest Ladinian in age (Wang and Chen 2009).

The Luoping biota is preserved in the middle part of Member II, in a succession approximately 16 m thick, at some richly fossiliferous localities near the village of Daaози, and delimited at the bottom and top by bioturbated limestone and silty limestone, respectively (Zhang et al. 2008, 2009). This fossiliferous horizon consists mainly of thinly laminated micritic limestone alternating with thin- to moderately thick-bedded silty limestone. Lower units (Beds 2–66) are dark grey, medium- to thick-bedded, laminated micritic limestone

with siliceous concretions (Fig. 1). A 40-mm-thick dark grey claystone (Bed 15) and a 50-mm-thick grey-yellow, thin-bedded silty mudstone (Bed 24) are pronounced in the lower units. A highly diverse fish assemblage has been recovered mainly from Beds 33 and 44. Most saurichthyid fish fossils are found in Bed 48. The conodonts associated with the Luoping biota from Member II were assigned to the *Nicoraella kockeli* Zone, which points to a late Pelsonian (middle–late Anisian) age (Zhang et al. 2008, 2009). Accordingly, the new fish material described below is middle–late Anisian in age.

## Material and methods

This study is based on five specimens. The holotype and the paratypes are well preserved. All specimens were mechanically prepared with sharp needles under the stereomicroscope. The circumorbital bones are poorly preserved in the holotype, but they are well preserved in the paratype. This large specimen shows many dermal bones not seen in the holotype, especially the opercular system and circumorbital bones in dorsal view. The drawings were based on outlines taken from photographs and completed with direct observation of specimens under a Leica M125 microscope. All specimens are deposited in LPV.

## Systematic palaeontology

Class Osteichthyes Huxley, 1880

Infraclass Neopterygii Regan, 1923

Subdivision Halecomorphi Cope, 1872

Family indet.

Genus *Luoxiongichthys* nov.

*Type species:* *Luoxiongichthys hyperdorsalis* sp. nov.; see below.

*Etymology:* The genus name is based on the town Luoxiong, where the fossils were collected.

*Diagnosis:* As for species.

*Luoxiongichthys hyperdorsalis* sp. nov.

Figs. 2–4.

*Etymology:* From Greek *hyperdorsalis*, over—of the back, the species name is derived from its unique feature, the elevated “hump” in front of the dorsal fin.

*Type material:* Holotype: LPV-10144, a nearly complete specimen (Fig. 2). Paratype: LPV-10120, a 170 mm-long specimen, showing the major part of the skull in dorsal view (Fig. 3B).

*Type horizon:* Member II, Guanling Formation, Middle Triassic (*Nicoraella kockeli* Zone, late Pelsonian, middle–late Anisian).

*Type locality:* Daaози Village, Luoxiong Town, Luoping County, Qujing City, Yunnan Province, China (GPS: N 24°46'24.7"; E 104°19'24.7"; Fig. 1).

*Material.*—LPV-10625, a specimen lacking most of the dorsal fin and the whole anal fin (Fig. 3A); LPV-6868 A and LPV-6868B, part and counterpart of the same fossil showing



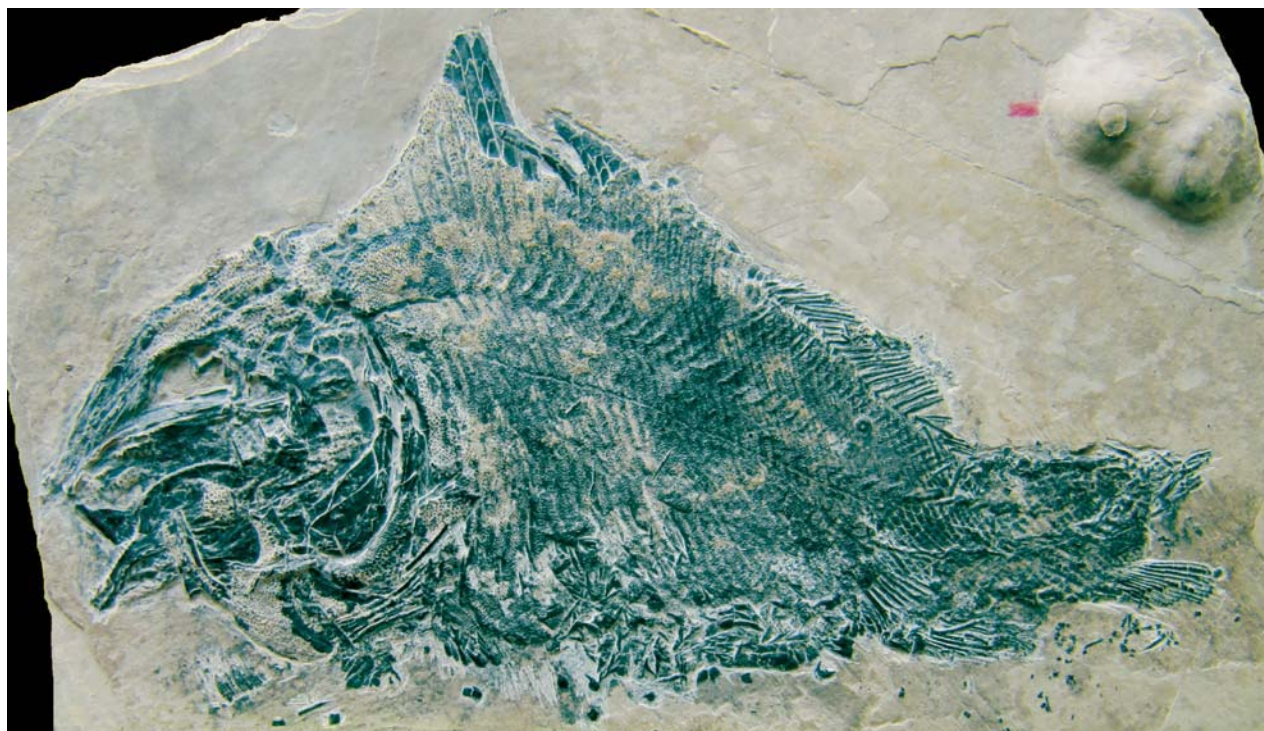
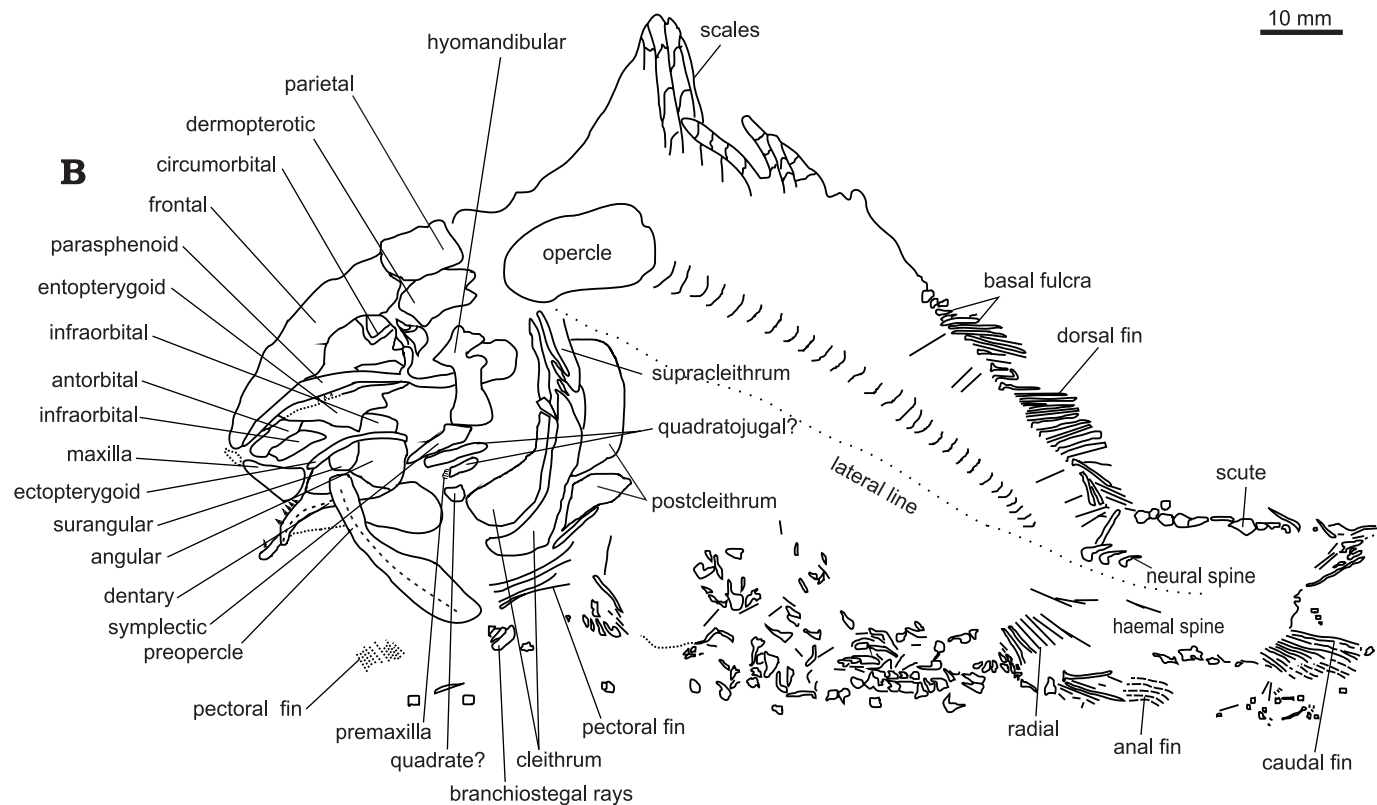
**A****B**

Fig. 2. Holotype of the basal actinopterygian fish *Luoxiongichthys hyperdorsalis* gen. et sp. nov., LPV-10144, Guanling Formation, Anisian, Middle Triassic; Daozi Quarry, Luoping, Yunnan Province, Southwest China; in lateral view (A), interpretive drawing (B).

the body outline; LPV-11817, complete fin system with scattered skull bones.

**Diagnosis.**—Middle-sized fishes, laterally compressed. The outline is triangular, with the apex of the triangle formed by a

pointed “hump” in the dorsal region. Opercular series comprising opercle, subopercle, interopercle, and preopercle; subopercular has long ramus anterior to opercular; subopercular a little less than half the size of the opercular; preo-

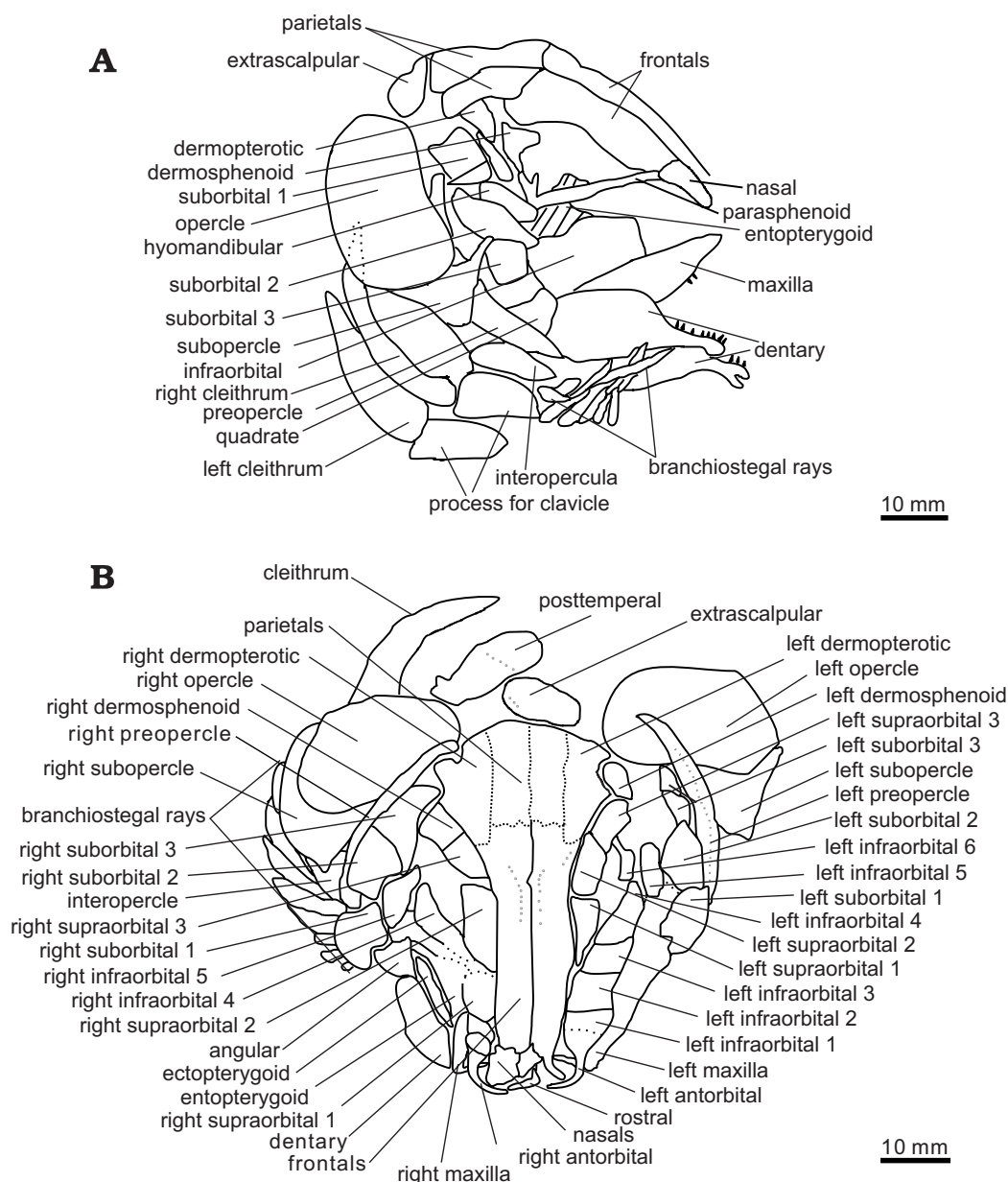


Fig. 3. Skull of the basal actinopterygian fish *Luoxiongichthys hyperdorsalis* gen. et sp. nov., Guanling Formation, Anisian, Middle Triassic; Daaiozi Quarry, Luoping, Yunnan Province, Southwest China. **A.** LPV-10625 in dorso-lateral view. **B.** LPV-10120 in dorsal view.

percular almost vertically oriented, with slender dorsal limb; three square-like suborbitals; at least eight branchiostegal rays with tubercles on the surface and comb-like ornament on their anterior margin; strong lower jaw has coronoid process; pointed grasping teeth in upper jaw, lower jaw, parasphenoid and entopterygoid; articulation of jaw immediately below posterior margin of orbit; cleithrum is strong, with ridge ornament on surface of upper part; supracleithrum is large, nearly half the depth of the cleithrum, the lower end is somewhat pointed; two postcleithra lie behind the cleithrum; clavicle present; hemiheterocercal tail slightly forked; each radial supports one lepidotrichium in unpaired fins; all rays segmented from middle part and bifurcated distally; fringing fulcra on anterior margin of all fins; enlarged fulcra before

anal fin and caudal fin; the whole body is covered with ganoid scales with tuberculate ornament; scales contact each other by peg-and-socket structure.

### Description

*Luoxiongichthys hyperdorsalis* has many characteristics of Neopterygii. For example, many cartilages become ossified during ontogeny, the maxilla is no longer hinged with the preopercular, the mandible has a coronoid process, the dorsal branch of the preopercular is slender, but it is also almost vertical, the interopercular is present (Hurley 2007), each radial supports one lepidotrichium, the tail is hemiheterocercal (= externally almost symmetrical), and the scales are ganoid (Gardiner et al. 2005). Among those characters, the



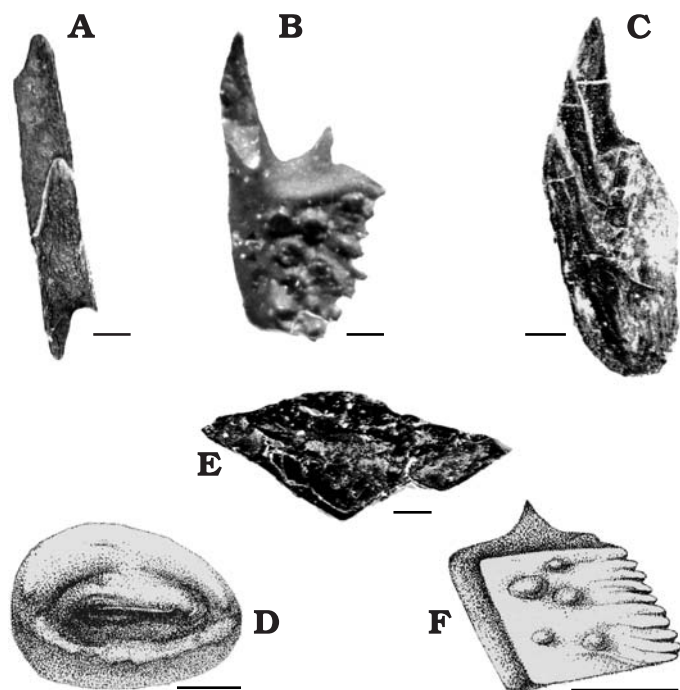


Fig. 4. Scales of the basal actinopterygian fish *Luoxiongichthys hyperdorsalis* gen. et sp. nov., Guanling Formation, Anisian, Middle Triassic; Daaazi Quarry, Luoping, Yunnan Province, Southwest China. Scales in the dorsal region: inner (A) surface. Scales in the Ventral region: outer (B) and inner (C) surface. Large fulcrum scale from in front of the dorsal fin (E) and anal fin (D). Rhombic scale from the caudal peduncle (F). Scale bars 1 mm.

compound coronoid process, vertical suspensorium, mobile maxilla, interopercle present, and the unpaired fin rays about equal in number to their supports are considered as synapomorphies of neopterygians (Olsen and McCune 1991). However, the new fish is distinguished from all other neopterygians by its unique high dorsal region, double jaw joint and thick tuberculous scales all over its body.

The total length is almost four times the head length, and body depth is twice the head length.

**Skull.**—The skull is triangular in lateral view (Fig. 2). The roof of the skull is poorly preserved in the holotype, but is better seen in LPV-10120 and LPV-10625 (Fig. 3). The elements include a long frontal and an oblong parietal. The parietals are rectangular and almost twice as long as wide, and they suture anteriorly with the frontals, and laterally with the oblong dermopterotics. The frontals are three times as long as the parietals. The narrowest part of the frontal is just above the orbit, and anterior and posterior parts are slightly widened to a similar extent. The dermopterotic bones are relatively long, approximately rectangular, and extend anteriorly lateral to the frontals. They are about 2.7 times longer than deep and about 1.2 times longer than the parietals. The extrascapular bones are poorly preserved and their number is unknown.

The opercle (Fig. 3) is large, the ventral side a little longer than the dorsal. It is an oblong element, 1.8 times as deep as long. At the anteroventral corner of the subopercle there is a long and narrow triangular interopercle in LPV-10625 (Fig.

3A). The preopercular is elongated, with a slender dorsal ramus, curving ventrally. A sensory canal runs along the posterior margin of the preopercle. There are five branchiostegals in LPV-10625 (Fig. 3A). The hyomandibular is well preserved in the holotype (Fig. 2): it is a triradiate element, comprising a dorsal head, a ventral shaft, and a prominent opercular process. There is an isolated hyomandibular in LPV-11817. The triangular symplectic lies right beside the hyomandibular. As in *Parasemionotidae*, the symplectic is very large and bears a head for the articular. In LPV-10625, the quadrate lies right behind the mandible, indicating that both the symplectic and quadrate contributed to the jaw joint. This is characteristic of *Halecomorphi*. The two splint-like bones probably are fragments of quadratojugal (Fig. 2B). In front of the margin of the shorter bone, there is a small bone bearing five pencil-shaped teeth. There are three small pores distributed on the anterior margin. These traits indicate that the small bone is a fragment of the premaxilla.

The gape is relatively small. The articulation of the lower jaw is below the posterior margin of the orbit. The dentary has a gently elevated coronoid process. The strong mandible comprises dentary and angular. Both of these participate in the coronoid process. The articular cannot be seen in the holotype. The dentary bears powerful pointed teeth. The upper jaw comprises maxilla and premaxilla, but in the holotype (Fig. 2), only an impression of the premaxilla is preserved. The parasphenoid is well preserved in both LPV-10144 and LPV-10625, and it is 30 mm long in LPV-10144. It has a very broad end. Pencil-like teeth are also seen on the entopterygoid and parasphenoid in the holotype. In LPV-10625 (Fig. 3A), the maxilla also has pointed grasping teeth. A line of pores appears along the dentary and continues to the angular, representing the mandibular canal.

Large nasal bones can be seen in LPV-10120. The right nasal is not complete, and has moved to contact the left nasal (Fig. 3B). The rostral bone is also not complete; it is a V-shaped element, but the right one has eroded away.

There are three supraorbital bones bordering the dorsal margin of the orbit (Fig. 3B), but these cannot be counted in other specimens. The anteriormost supraorbital is triangular and contacts three infraorbital bones ventrally, closing the circumorbital series. There are four infraorbitals, and two additional infraorbitals forming the anterior border of the orbit. The first three infraorbitals are deeper than long. The postero-ventral corner is occupied by a very large infraorbital. Its dorsal margin is slightly curved. The outlines of the last two infraorbitals are not so clear. The antorbital is approximately triangular, narrowing anteriorly, like a slim tail. The dermosphenotic takes part in the circumorbital system and occupies the posterodorsal corner of the orbit. There are three suborbital bones on both sides, and they are not in their original places. They all differ in shape: the lower two suborbitals are roughly square in shape, and they are almost of the same size, but the uppermost one is larger on the left side and smaller on the right. The shapes of the suborbitals are cautiously taken as characteristic for the ge-

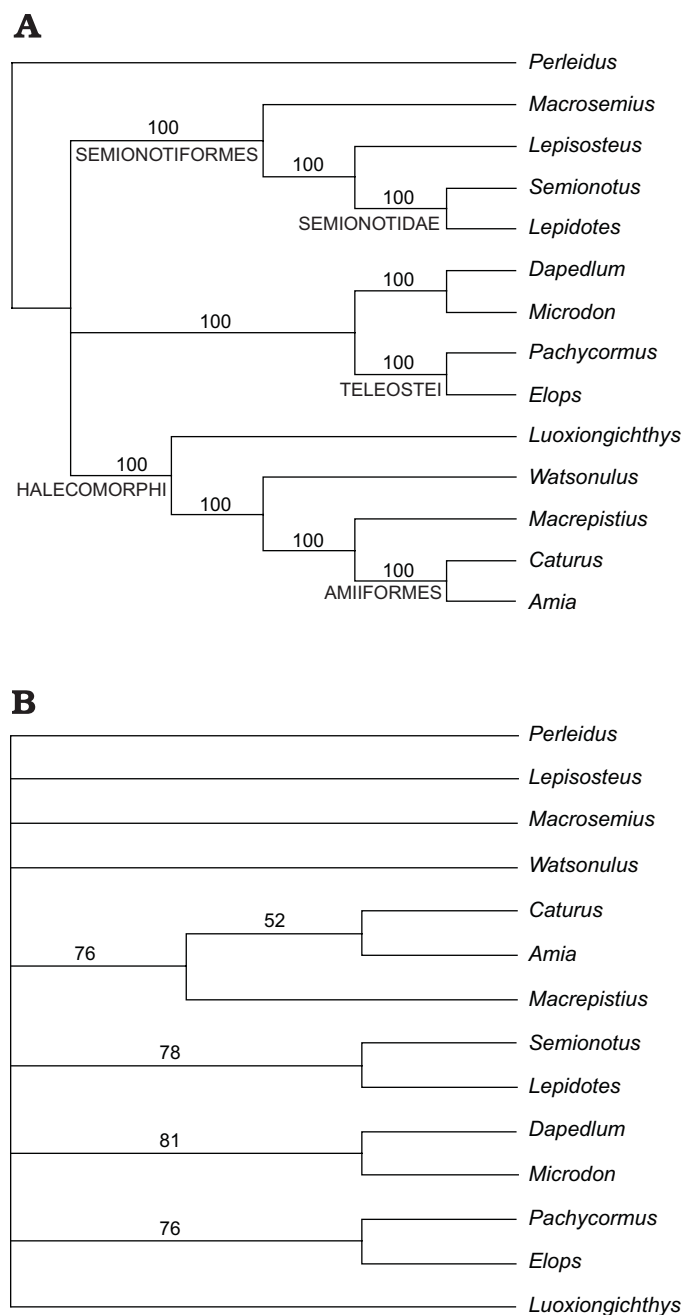


Fig. 5. Cladograms showing the phylogenetic position of *Luoxiongichthys*, as a basal neopterygian, and possible halecomorph, based on the data matrix from Gardiner et al. (1996). **A.** The strict consensus of two most parsimonious trees. **B.** Consensus phylogeny, showing how most nodes collapse when only the bootstrap values (1000 replicates) over 50% are shown. Other nodes, including that linking *Luoxiongichthys* to Halecomorphi, are not robust.

nus. On the left side of the paratype, the entopterygoid and ectopterygoid can be seen.

The opercle is high, up to 1.8 times as high as long. It has a round anteroventral corner, in front of which there is a well-developed long ramus of the subopercle. The dorsal ramus is narrow and relatively high, almost the same height as the subopercle. The subopercle is a little less than half the size of the opercle. Ventrally, the opercle overlaps the dorsal

margin of the subopercle, which seems to be dorsally concave. The triangular interopercle articulates anterior to the subopercle and is lightly overlapped by the ventral portion of the preopercle. There are at least four branchiostegal rays in the holotype (Fig. 2), five in LPV-10625, and eight in LPV-10120 (Fig. 3). They are strong and covered by tubercles and comb-like ornamentation on the anterior margin.

The preopercle is slender, and the slim dorsal ramus appears to be vertically oriented. The lower portion is curved ventrally. Its posterior margin is slightly convex and contacts the opercle and subopercle. The anterior margin of the preopercle is overlapped by suborbital bones. The sensory canal runs along the posterior margin of the preopercle.

**Pectoral girdle:** The elements that can be observed in the pectoral girdle of the holotype include the cleithrum, supracleithrum, and postcleithrum (Fig. 2). The cleithrum is the largest and longest paired element in the pectoral girdle, with many tubercles. Its lower end is bent forward and expanded a little. The upper part is ornamented with ridges, but is fragile and overlaps the supracleithrum a little. The supracleithrum is relatively large, nearly half the depth of the cleithrum, and the lower end is somewhat pointed. Two postcleithra lie behind the cleithrum. In LPV-10120, based on the presence of three pores of the sensory canal, one of the extrascapulars can be identified. It is oval in shape. The sensory canal runs along the lower margin. Behind the extrascapular is the large posttemporal. The sensory canal crosses the posttemporal and extends to the trunk (Fig. 3B).

It seems that there is a prominent triangular plate that lies immediately anterior to the cleithrum in LPV-10625 (Fig. 3A), LPV-11817 and 6868(A), and it is especially prominent in the first two, but not well preserved in the last. If this triangular plate is a separate bone, its position indicates it might be the clavicle. However, it is strange that this bone shows no ornamentation on its surface. It is clear that this condition is original and not a result of preparation damage. As a result, it is much more like a process for articulation of the clavicle, which still means that the clavicle was still present in this taxon. In LPV-11817, the situation is the same. This is a primitive character, as seen in *Watsonulus eugnathoides* (Olsen 1984), but unusual in what otherwise seems to be a neopterygian.

**Axial skeleton.**—Owing to the rather heavy scale covering, the axial skeleton is poorly known, but some information is available from the caudal region. The vertebrae are not ossified. The vertebral column is surrounded by neural and haemal arches. About 31 vertebrae can be counted. We can see three neural and four haemal spines in the region between the dorsal fin and anal fin due to the displacement of the scales. In the caudal region of LPV-6688, the neural spines bend sharply backward and the haemal spines are expanded to support the caudal fin.

**Paired fins.**—Little can be said about the pectoral fins in the holotype, which shows seven lepidotrichial rays. However, in LPV-10120 and LPV-11817 the pectoral fins are well pre-



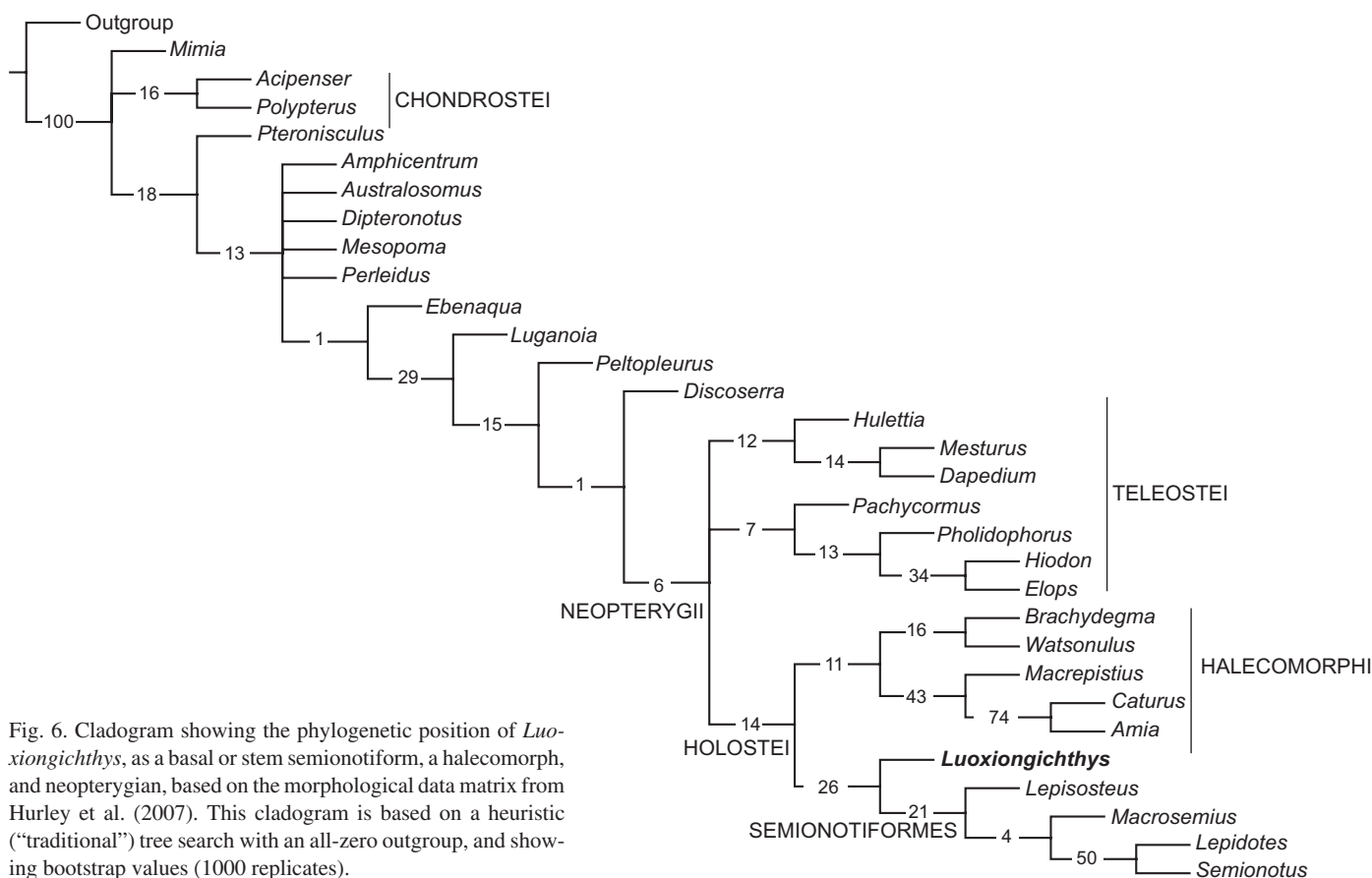


Fig. 6. Cladogram showing the phylogenetic position of *Luoxiongichthys*, as a basal or stem semionotiform, a halecomorph, and neopterygian, based on the morphological data matrix from Hurley et al. (2007). This cladogram is based on a heuristic ("traditional") tree search with an all-zero outgroup, and showing bootstrap values (1000 replicates).

served, and they are seen to insert rather low. There are more than ten lepidotrichial rays in LPV-11817, and 13 in LPV-10120, the first of which bears numerous fringing fulcra. These rays begin to be segmented from the middle part and are bifurcated distally.

The pelvic fins are only preserved in LPV-11817, which shows their relative position and points of insertion. The pelvic fins are very small, with an unknown number of lepidotrichia, and placed closer to the anal fin than the pelvic fins.

**Unpaired fins.**—The dorsal fin lies in a very posterior position, opposite the anal fin (Fig. 2). The dorsal fin originates posterior to the pelvic fins and anterior to the anal fin, and is markedly larger than the latter, the end of the dorsal fin being slightly anterior to the end of the anal fin. In the dorsal and anal fin, each lepidotrichium is supported by one radial, a synapomorphy of Neopterygii. The lepidotrichial ray is ornamented by two longitudinal rows of tubercles. Both dorsal and anal fins are segmented and bifurcated distally. The dorsal fin contains about 28 lepidotrichia, the anal fin about 12 in the holotype.

The caudal fin is hemiheterocercal, with an equilobate outline. It is incompletely preserved in all available specimens, so it is reconstructed here (Fig. 6) from all specimens we have. The upper lobe of the caudal fin is covered by ganoid scales. The lepidotrichial ray is still segmented and bifurcated distally.

**Scales.**—The whole body is covered by finely tuberculate scales (Figs. 2A, 4). The scale-type is 60 14/17. The scales differ from one another in size and shape in different regions. They are deeper than wide and vary from quadrangular to rhombic in shape, as is usual in basal actinopterygians. There appear to be 50–60 scale rows between the cleithrum and dorsal fin, about 35 scale-rows anterior to the dorsal fin, and 38 in front of the anal fin.

In the uppermost region between the skull and dorsal fin, the scales (Fig. 4C, G) are largest, and they are 2.5 times as deep as wide: these cover the characteristic dorsal "hump". Scale proportion decreases downwards and backwards. Dorsally and in the caudal region the scales are smallest, and rhombic in shape (Fig. 4A, E).

There are two basal fulcra respectively preceding the dorsal fin and anal fin. Many slender fringing fulcra are well-developed on all fins. In front of the dorsal lobe of the caudal fin, there is a large unpaired fulcra (Arratia 2009) on the holotype (Fig. 2) and LPV-11817. These rhombic fulcra are six times larger than other caudal peduncle scales. Dorsal ridge scales are not well-developed in our specimens.

Scales in the ventral region are smaller (Fig. 4B, F). In front of the anal fin, there is a large fulcrum in LPV-11817 (Fig. 4D), with a protuberant ridge in the middle.

A trace of the lateral line is visible on about 60 scales in both LPV-10144 (Fig. 2) and LPV-10625. The median surface of the lateral line scales is longitudinally traversed by a

Table 1. Measurements of the specimens of *Luoxiongichthys hyperdorsalis* (mm).

Specimen number	LPV-10144	LPV-10625	6868(A, B)	LPV-10120	LPV-11817
Total length	150	?	155	220	145
Head length	38	55	40	60	35
Orbit length	12	14	12	?	?
Rostrum length	15	?	?	22	?
Distance head-dorsal fin	85	105	?	120	70
Distance head-anal fin	92	?	?	?	87
Body depth	75	98	80	?	75
Caudal penduncle depth	17	?	?	?	20

Table 2. Differences between *Luoxiongichthys* and *Lepidotes*.

Genus	<i>Luoxiongichthys</i> gen. nov.	<i>Lepidotes</i>
Preopercular	nearly vertical, curving ventrally, the ventral ramus is slightly anterior	“L”-like shape, the ventral ramus points forward, and forms a horizontal ramus
Fulcra	not well developed	well developed
Clavicle	present	absent
Scales	on the antero-dorsal side, a long process as long as the depth of the scale	both the dorsal and ventral anterior side extend short spines
Antorbital	has a long narrow part	triangle

groove, and the scales are excavated posteriorly. They bend sharply downwards in the dorsal fin region.

The outer scale surface is decorated by round or oval tubercles with pectinate ornament on the posterior margin. At the level of the anal fin and in the peduncle region, the serration is reduced. These serrations are very delicate and difficult to see. A process extends from the antero-dorsal side of the scale. As the scale deepens, the spine lengthens, and the spine is as long as the depth of the scale. The inner surface of the scale is smooth, with a peg-and-socket structure, and this articulation also exists in the scales of the caudle peduncle (Fig. 4H).

**Remarks.**—Several characteristics demonstrate that *Luoxiongichthys* is a neopterygian, for example, the presence of an interopercular bone, supraorbitals, the shape and separation of the maxilla from the preopercular, the presence of a coronoid process on the lower jaw, widely separated fin rays, and the hemiheterocercal tail fin (Hurley et al. 2007).

Further, the new taxon appears to be a member of the clade Halecomorphi identified by Gardiner et al. (1996), based on the V-shaped rostral, squared parietal, and double jaw joint (Li 2009). *Luoxiongichthys* also shows the classic halecomorph apomorphy (Grande and Bemis 1998) of an elongated symplectic forming part of the double articulation with the lower jaw, but the other two features noted by those authors, a notch or concavity in the posterior margin of the maxilla and the single supramaxillary bone, cannot be determined.

However, *Luoxiongichthys* has some unique features that differentiate it from other halecomorphs. Owing to poor preservation of the skull, the family cannot be determined, but it may be identified as a new genus and species. The head length of the new species is about 50% the length of its body depth and 25% the length of total length. The new genus has a “hump” anterior to the dorsal fin, which is similar to that of

the Triassic pycnodontid fish *Gibbodon*, but they differ from each other in teeth and dermal bones of the skull. For example, *Gibbodon* has bifid teeth and its opercular system is not complete (Tintori 1981).

The circumorbital bone is of semionotid type (López-Arbarello 2008). According to the characteristics of the opercular system and suborbital, this new genus resembles *Lepidotes*, because *Semionotus* only has one suborbital, but *Lepidotes* has more than one suborbital (McCune 1986; Olsen and McCune 1991; Qian and Zhu 1997). However, many differences between *Luoxiongichthys* and *Lepidotes* can be summarized in the preopercular, fulcra, clavicle, antorbital, and scales (McCune 1986; Jin 1987) (Table 2).

The preopercular of *Luoxiongichthys* resembles that of *Asialepidotus* in being nearly vertical, curving ventrally, and with the ventral ramus slightly forward, a primitive structure (Su 1959). The relative positions of the opercle and subopercle are also very like those in *Asialepidotus*. However, a marked difference between the two genera lies in the scales: *Luoxiongichthys* has scales with numerous tubercles on the surface, and fulcra are not well developed, with only a few fulcra in front of the dorsal lobe of the caudal fin, whereas the scales of *Asialepidotus* are smooth and the posterior margin is very finely pectinate, and there are small fulcra in front of all fins. Moreover, *Lepidotes jurongensis* also has smooth scales, which are quite different from those of *Luoxiongichthys hyperdorsalis* (Qian and Zhu 1997).

Judging from the characteristics of the scales, there are some similarities between *Luoxiongichthys* and *Neolepidotes*. The scales are large and rectangular in the trunk region. They decrease gradually in size backwards and become rhombic (Zhang and Zhou 1974). In *Neolepidotes liaodongensis*, the scales are rhombic and smooth. The flank scales unite with a

peg-and-socket articulation, and with their overlapped margin extended forwards at the antero-dorsal margin as prongs (Jin 1987; Su 1996). The scales of *Luoxiongichthys* also have the same structure. In the holotype, some isolated scales can be seen. The peg-and-socket structure is prominent in the ventral region, but seems not to be typical in the dorsal region. Here, the scales are more “teleost-like” in that they articulate with each other by overlapping, rather than by a peg-and-socket structure. In *Neolepidotes*, the extended spine is as long as the depth of the scale, and as the scale becomes deeper, the spine lengthens. Further, the scales of *Neolepidotes liaodongensis* are smooth.

Because *Luoxiongichthys* is from the Anisian, it is no surprise that both the number of suborbitals and the ornamentation of the scales are different from *Lepidotes*, which is a Jurassic–Cretaceous taxon. *Lepidotes* from the late Mesozoic has more suborbitals.

The dermal shoulder girdle of *Luoxiongichthys hypdorsalis* has a clavicle like *Watsonulus eugnathoides*, a parasemionotid fish from the Early Triassic (Olsen 1984; Gardiner et al. 1996). But *Watsonulus eugnathoides* has a preopercular with a typical broad dorsal limb (Olsen 1984), which is different from *Luoxiongichthys hypdorsalis*. Another difference between the new genus and Parasemionotidae is the shape of the rostral: it is tube-like in the former, and V-shaped in the latter (Lombardo 2001).

*Geographical and stratigraphical distribution.*—Type locality and horizon only.

Cladistic analysis

Two cladistic analyses were conducted to establish the phylogenetic position of *Luoxiongichthys*. In the first analysis, the data matrix of Gardiner and Maisey et al. (1996: appendix 1) was used, with the new taxon coded according to the 37 characters, of which only 20 could be coded (Table 3). The cladistic analysis, conducted using the branch-and-bound method in PAUP 4.0b10 (Swofford 1998) with all default settings produced two trees of length (L) 133 steps, and with consistency index (CI) 0.61, homoplasy index (HI) 0.39, retention index (RI) 0.58, and rescaled consistency index (RC) 0.36. These two trees differ in the relative placements of the three clades Semionotiformes, (Pycnodontiformes + Teleostei), and Halecomorphi. *Luoxiongichthys* emerges as a basal member of Halecomorphi, including *Watsonulus*, *Macrepistius*, and Amiiiformes (*Caturus* + *Amia*). The identification of Semionotiformes as including *Lepisosteus*, as well as *Lepidotes* and *Semionotus* (Fig. 5A)

confirms the earlier finding by Olsen and McCune (1991), Brito (1997), and Cavin and Suteethorn (2006), but not Gardiner et al. (1996), who placed *Lepisosteus* as a basal neopterygian well outside Semionotiformes. However, many of these nodes are not robust, and the cladogram largely collapses when bootstrap values (1000 replicates) are assessed (Fig. 5B), and even those five nodes with bootstrap values over 50% (Amiiiformes, 52%; Amiiiformes + *Macrepistius*, 76%; Teleostei, 76%; Semionotidae, 78%; *Dapedium* + *Microdon*, 81%) all show values less than 85%.

The result (Fig. 5A) differs from those reported by Gardiner et al. (1996: fig. 1) in the inclusion of *Lepisosteus* in Semionotiformes, as sister to Semionotidae, rather than as a basal neopterygian taxon. A re-run of their data matrix, excluding *Perleidus* and *Luoxiongichthys*, yielded four trees (L = 114; CI = 0.65; HI = 0.35; RI = 0.60; RC = 0.39), one of which is the same as they showed. However, the strict consensus removes the basal structure, making a polytomy among the five clades *Lepisosteus*, *Macrosemius*, Halecomorphi, Semionotidae, and (*Dapedium* + *Microdon* + Teleostei). Note that it is not clear how the cladogram in Gardiner et al. (1996: fig. 1) was generated, as they offer very different tree statistics (L = 131; CI = 0.362; RI = 0.578) from those we obtained, and they do not report their exact methods.

In our second cladistic analysis, we used the data set from Hurley et al. (2007: supplement). First, we replicated the result reported by Hurley et al. (2007: fig. 2), running a “traditional” search (heuristic search, parsimony ratchet; TBR, 2000 replications) in TNT (Goloboff et al. 2008), and finding 116 trees with trees of 234 steps. Adding our new codings for *Luoxiongichthys* (Table 3: line 2; 37 of 70 characters coded; 53%) and an all-zero outgroup, found the tree identified by Hurley et al. (2007: fig. 2). In our phylogenetic analysis (Fig. 6; strict consensus of 12 trees of 241 steps; CI = 0.46; RI = 0.71), clades identified include Chondrostei, Neopterygii, Holostei, Teleostei, Halecomorphi, and Semionotiformes, and *Luoxiongichthys* is inserted at the base of Semionotiformes, within Holostei. None of these nodes is robust, however, and bootstrap values (1000 replicates) are remarkably low: only two clades shows values above 50% (*Lepidotes* + *Semionotus*, 50%; *Caturus* + *Amia*, 74%), and these values are still far from indicating robust relationships.

Our conclusion is that the systematics of basal neopterygians is still in modest turmoil, and some key elements of the phylogeny have yet to be resolved. Indeed, the general lack of resolution that we have found in our phylogenetic analyses is typical of earlier work (e.g., Olsen and McCune 1981; Gardiner and Maisey et al. 1996; Cavin and Suteethorn 2006; Hurley et al. 2007), which highlighted major debates about relationships of basal Neopterygii. However, one common ele-

Table 3. Character codings for *Luoxiongichthys*: first line, for the 37 characters given in “Data Matrix 1” of Gardiner et al. (1996: 144); second line, for the 70 characters given in the “Data Supplement” of Hurley et al. (2007). Character codings are grouped in fives for ease of comparison.

<i>Luoxiongichthys</i>	????? ???? 10??? 11222 13113 21?0? ?100? 00
<i>Luoxiongichthys</i>	????? ????1 ???? ????1 ????1 11111 11121 ?0231 1111? ?1110 0?11 1101? 04?11 ?????



ment in nearly all studies has been the identification of Halecomorphi and Holostei as a clade, and we confirm that here, and the new bony fish from Luoping, *Luoxiongichthys*, appears to be a holostean, and either a basal halecomorph or a basal semionotiform, but the conclusion is not robust.

## Reconstruction and function

The reconstruction of *Luoxiongichthys hyperdorsalis* (Fig. 7) is based primarily on the holotype, LVP-10144 (Fig. 2). The body outline, scalation, position and shapes of the fins, as well as the broad skull outline are all clear in this specimen. The skull was reconstructed from the holotype, but with additional information from LVP-10625 (Fig. 3A) and LVP-10120 (Fig. 3B). Distal parts of the fins were reconstructed from those of related Triassic fishes.

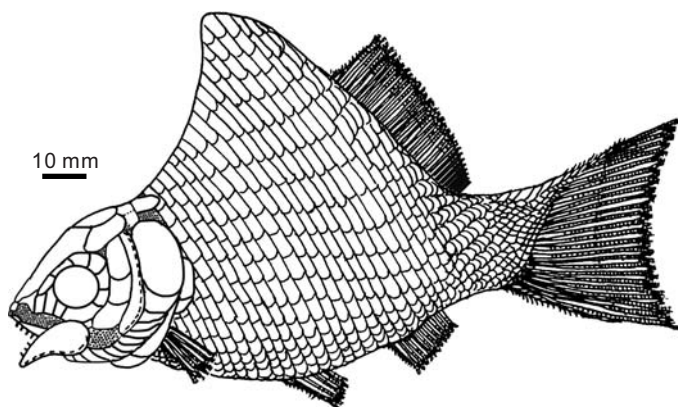


Fig. 7. Reconstruction of the basal actinopterygian fish *Luoxiongichthys hyperdorsalis* gen. et sp. nov., Guanling Formation, Anisian, Middle Triassic; Daaazi Quarry, Luoping, Yunnan Province, Southwest China; in lateral view.

The reconstruction highlights the extraordinary triangular shape of the fish in lateral view and its high antero-dorsal “hump”, which is shaped like a “reverse shark’s dorsal fin” with a smoothly rising, convex postero-dorsal body contour, but a clearly convex antero-dorsal margin. The anterior margin of the “hump” is narrow from side to side, so this component of the body was like a cut-water, and would not have presented a great deal of resistance to forward movement. However, the unusual shape was presumably more for display than for defense or speed, and would have required constant trimming movements to keep the fish vertically positioned from subtle movements of the paired and unpaired fins and the tail. The form of the body and fins and position of unpaired fins indicates are characteristic for reef-dwelling fishes, or those living in a structured environment.

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