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Research paper

A basal antiarch (placoderm fish) from the Silurian of Qujing, Yunnan, China

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Abstract

A new basal antiarch, *Silurolepis platydorsalis* n. gen. n. sp., represented by a large-sized trunk armor and a disassociated anterior median dorsal plate (AMD), is described from the Ludlow (Silurian) of Qujing, Yunnan, southwestern China. It is characterized by its AMD overlapping the posterior median dorsal plate, broad anterior margin of the AMD, and crest-shaped dorsolateral ridge of the trunk armor. As the oldest known articulated placoderm fish to date, the new fish provides new insights into the early evolution of antiarchs.

Keywords: Antiarcha; Placodermi; Silurian; Phylogeny; China

1. Introduction

Among the jawed vertebrates, the Antiarcha are considered either a subgroup of the Placodermi (Goujet, 1984; Young, 1986, 2008; Janvier, 1996; Zhu, 1996) or the sister group to the clade comprising the crown-group Gnathostomata (i.e., Chondrichthyes, Acanthodii and Osteichthyes) and the non-antiarch placoderms (Johanson, 2002; Brazeau, 2009), mainly dependent on how the Artiarcha and the Arthrodira are interrelated. The antiarch fishes have a fossil record dating back to the Wenlock of the Silurian (Wang, 1991a; Zhu, 1996; Zhu and Wang, 2000; Zhao and Zhu, 2010), suggesting an early split between antiarchs and the rest of the jawed vertebrates. *Shimenolepis graniferous* and an indeterminate form referred to the Chuchinolepidae, from the Xiaoxiyu Formation of Lixian, Hunan, represent the earliest representatives of placoderm fishes (Wang, 1991a; Qu et al., 2010). In addition to these two forms, Wang (1993) reported a new antiarch from the Upper part of the Kuanti Formation (also known as Guandi Formation) of Qujing, Yunnan (Fig. 1; Fang et al., 1985), but gave no description and thus rendered it a *nomen nudem* (*Silurolepis platydorsalis*). The same applies to '*Wangolepis*', a basal placoderm from the Yuejiashan Formation of Xundian and Qujing, Yunnan, and the Xiaoxiyu Formation of Sangzhi, Hunan (Pan, 1986; Pan and Dineley, 1988; Zhu and Wang, 2000).

In this paper, the Silurian antiarch fish reported by Wang (1993) is described. The type specimen, a part of the trunk armor comprising the dorsal and lateral walls, was collected from a Silurian site near the Xiaoxiang Reservoir in the suburb of Qujing by S.T. Wang in 1970s. Later from the same site, N.Z. Wang collected several disassociated placoderm remains including an anterior median dorsal plate described here. This new fish, although younger than *Shimenolepis*, represents the oldest articulated placoderm fish described thus far, and adds a new member to the Silurian Xiaoxiang Fauna that includes the oldest known articulated osteichthyan *Guiyu* (Zhu et al., 2009).

2. Systematic palaeontology

Class Placodermi McCoy, 1848.
Order Antiarcha Cope, 1885.
Silurolepidae n. fam.
Silurolepis n. gen.

Diagnosis: as for the type species (by monotypy).
Type species: *Silurolepis platydorsalis* n. sp.
Etymology: alluding to the Silurian fish.
Remarks: *Silurolepis platydorsalis*, the only species of the genus, is one of the largest antiarchs from the Silurian and

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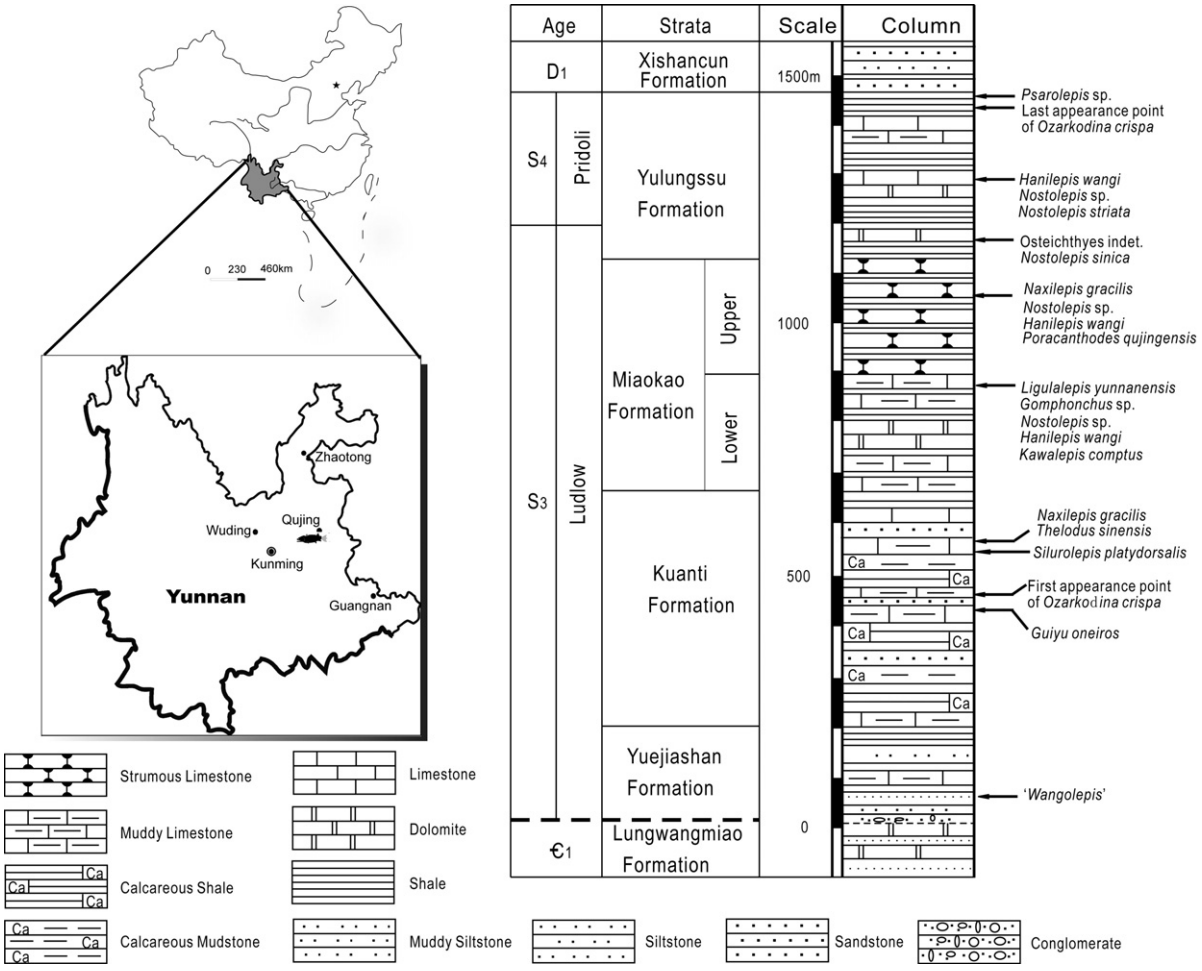

Fig. 1. The summary Silurian sequence in Qujing (Yunnan, China), showing the stratigraphic positions of *Silurolepis platydorsalis* n. gen. n. sp. and other early vertebrates (modified from Zhu et al., 2009).

Lower Devonian, with its mid-dorsal length of the trunk armor attaining at least 123 mm. It is referred to the Antiarcha based on its anterior median dorsal plate (AMD) larger than the posterior median dorsal plate (PMD). It resembles the Yunnanolepiformes in its tubercular ornament, separate posterior lateral plate (PL), the crista transversalis interna posterior lateral to the posterior ventral process of the PMD, and putative simple pectoral fin articulation. However, it differs in its AMD overlapping the anterior dorsolateral (ADL) and PMD plates, the AMD with a broad anterior margin, and the crista transversalis interna anterior of the ADL with a strong posterior extension. The broad anterior margin of the AMD is also found in the basal antiarch *Minicrania* (Zhu and Janvier, 1996), the Sinolepidae (Ritchie et al., 1992) and many euantiarchs (Denison, 1978), and is assumed to be plesiomorphic for antiarchs (Zhu, 1996). The new form is distinguishable from *Minicrania* by its AMD overlapping the PMD, and large adult size.

Silurolepis platydorsalis n. sp.
(Figs. 2–4).

1993 *Silurolepis platydorsalis* (*nomen nudem*) – Wang, p. 255.
2000 *Silurolepis platydorsalis* (*nomen nudem*) – Zhu and Wang, pp. 161, 165, 166.

Diagnosis: A large-sized antiarch with a mid-dorsal length of the trunk armor attaining at least 123 mm. The trunk armor is broad and low, with a maximum breadth/length (B/L) index about 80, and without a median dorsal ridge. The dorsolateral ridge of the trunk armor bears a low crest with two rows of tubercles. The AMD plate has a broad anterior margin (nearly half of its total width) and overlaps all neighboring trunk armor plates including the PMD plate; B/L index about 90; lateral corner posteriorly situated; levator fossa undeveloped. The PMD length is approximately 1/4 of the mid-dorsal length of the trunk armor; lateral corner developed and close to the posterior margin of the plate; crista transversalis interna posterior lateral to the posterior ventral process. The ADL plate has a narrow dorsal lamina; about 1.6 times the posterior dorsolateral plate (PDL) in length. The crista transversalis interna anterior is developed in the ADL, and extends backwards along the suture between the ADL and AMD plates. The posterior lateral plate (PL) plus the lateral lamina of the PDL plate have the same depth as the lateral lamina of the ADL. The lateral laminae of the anterior ventrolateral and posterior ventrolateral plates (AVL, PVL) are long and low.

Holotype: A part of the trunk armor comprising the dorsal and lateral walls (IVPP V 11680.1).

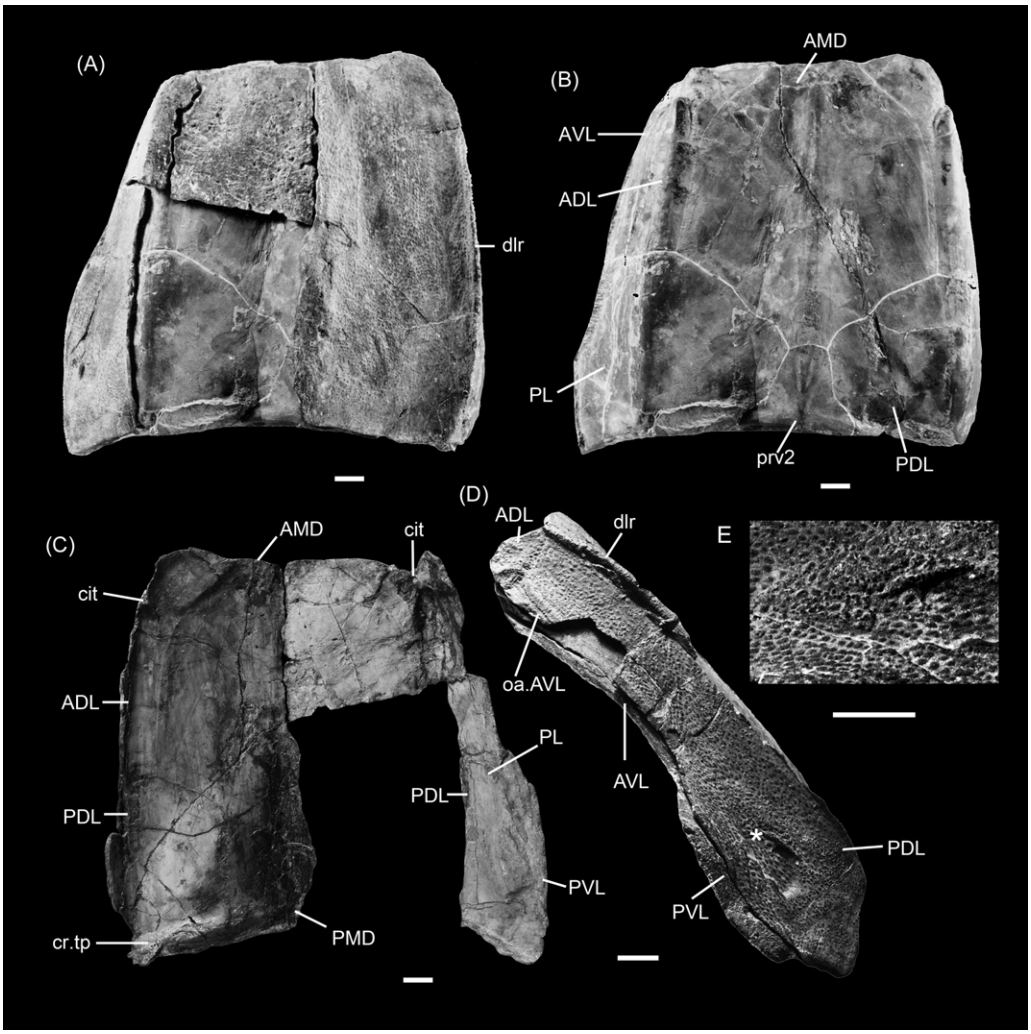

Fig. 2. *Silurolepis platydorsalis* n. gen. n. sp. Holotype (IVPP V 11680.1) showing the dorsal and lateral walls of the trunk armor: (A) in dorsal view; (B) internal mould in dorsal view; (C) in ventral view; (D) in left lateral view; (E) close-up of the tubercular ornament, indicated by the asterisk (*) in D. Scale bars = 1.0 cm. *Abbreviations*: ADL, anterior dorsolateral plate; AMD, anterior median dorsal plate; AVL, anterior ventrolateral plate; cit, crista transversalis interna anterior; cr.tp, crista transversalis interna posterior; dlr, dorsolateral ridge; oa.AVL, area overlapped by anterior ventrolateral plate; PDL, posterior dorsolateral plate; PL, posterior lateral plate; PMD, posterior median dorsal plate; prv2, posterior ventral process of PMD; PVL, posterior ventrolateral plate.

Referred material: A complete AMD plate in ventral view (IVPP V 11680.2).

Etymology: From *platy* (Gr.), broad, and *dorsalis* (Lat.), dorsal, alluding to the broad dorsal wall of the trunk armor.

Locality and horizon: Kuanti Formation, Late Ludlow, Silurian, Xiaoxiang Reservoir, Qujing, China.

Fossil repository: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences.

Description: The holotype (Fig. 2) has preserved nearly complete dorsal and lateral walls of the trunk armor, which is broad and low. The maximum length of the trunk armor as preserved (along the dorsolateral ridge) is about 137 mm, and the mid-dorsal length as preserved is about 123 mm. The maximum breadth of the trunk armor (between the dorsolateral ridges) is about 118 mm, with a maximum B/L index about 80. Thus, the new form is among the large-sized antiarchs. The yunnanolepiforms are usually small- or medium-sized (Zhang, 1978, 1984; Zhu, 1996), and the largest representative of the group is *Heteroyunnanolepis* (Wang, 1994; Zhu, 1996), whose mid-dorsal length of the trunk armor is up to 65 mm. The large-sized individuals occurred in later antiarchs, including the sinolepid *Xichonolepis* (P'an and Wang, 1978; Ritchie et al., 1992; Zhang, 1980) and many euantiarchs (Johanson, 1997; Long, 1983; Pan et al., 1987; Young, 1988).

The dorsal wall of the trunk armor is slightly convex along the dorsal median line, but lacks a crest or median ridge. The dorsal wall is broadest posteriorly across the lateral corners. The posterior margin is straight or slightly concave, without a posterior median process. The dorsolateral margin of the trunk armor is developed as a low crest, ornamented by two rows of tubercles (dlr, Fig. 2A). As inferred from the low lateral wall, the dorsal wall of the trunk armor is narrower than the ventral wall, which is not preserved in the holotype. The trunk armor plates are fused, with the bone sutures obscured by the tubercular ornament on the external surface. However, most sutures are distinct on the internal side of the plates (Fig. 2C) or on the internal mould of the trunk armor (Fig. 2B). The sensory canals of the trunk armor are not developed.

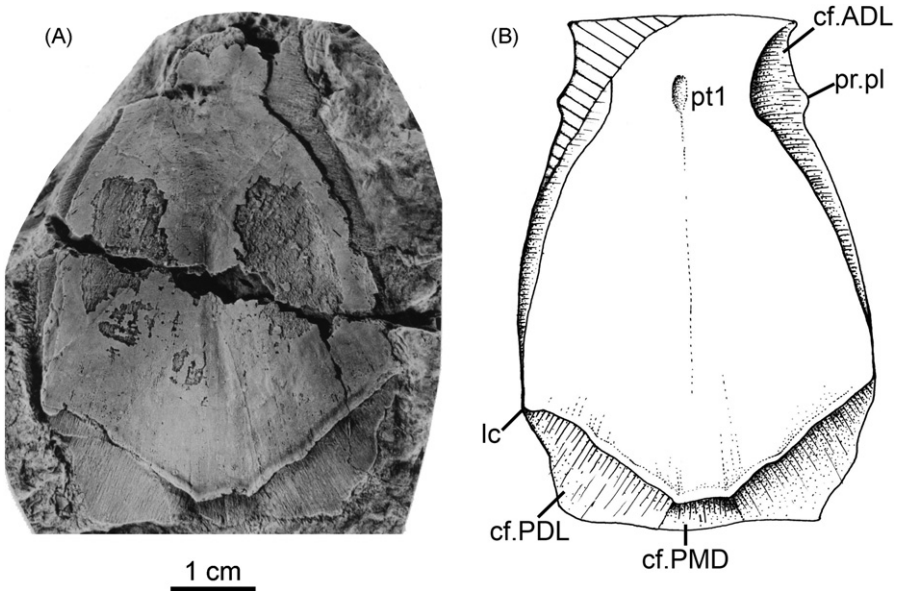

Fig. 3. *Silurolepis platydorsalis* n. gen. n. sp. An anterior median dorsal plate, IVPP V 11680.2: (A) in ventral view and (B) illustrative drawing. Abbreviations: cf.ADL, area overlapping ADL; cf.PDL, area overlapping PDL; cf.PMD, area overlapping PMD; lc, lateral corner of AMD; pr.pl, external postlevator process of AMD; pt1, anterior ventral pit of AMD.

The AMD plate (Figs. 2–4) is urn-shaped, with the lateral corners situated at three quarters of the length from the anterior margin. The AMD of the holotype is a long and broad bone, about 113.5 mm long and 92.6 mm wide (B/L index 81.6). Externally, the anterior margin (about 28.4 mm wide) is narrower than the posterior margin (about 71 mm). However, in internal aspect, the anterior margin is broader than the posterior margin. The overlap relationships between the AMD and neighboring plates are distinct in V11680.2 (Fig. 3), demonstrating that the AMD plate overlaps all the neighboring plates including the ADL, PDL and PMD plates (cf.ADL, cf.PDL, cf.PMD). In other antiarchs, the AMD plate is always overlapped by the PMD plate. Thus, the AMD overlapping the PMD in *Silurolepis* is exceptional for antiarchs. The AMD totally overlapping the PDL is also seen in the Sinolepidae and asterolepids except *Remigolepis*, possibly a primitive condition (Ritchie et al., 1992). The ventral structure of the AMD is clearly shown in V11680.2. The postlevator thickening is not developed, leaving no definite levator fossa.

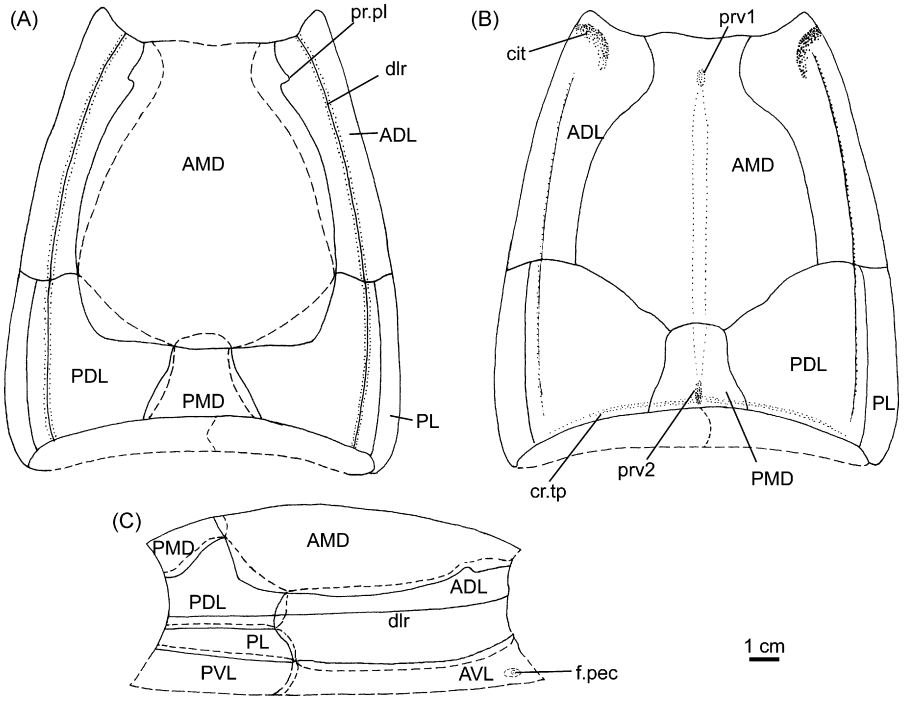

Fig. 4. *Silurolepis platydorsalis* n. gen. n. sp. The restoration of the trunk armor in dorsal (A), and lateral (C) views. (B) Internal mould of the trunk armor in dorsal view. Abbreviations as in Figs. 2 and 3.

This might be a primitive condition, as the weak levator fossa is also present in the Yunnanolepiformes (Zhu, 1996) and Sinolepidae (Ritchie et al., 1992). The anterior ventral process and pit are situated anteriorly at the one fifth of the length (Fig. 3). Posteriorly, the median ventral ridge and groove appear weak or absent.

The PMD plate (Fig. 2A–C) is about 30.5 mm long and 42 mm wide (B/L index 138). It is much smaller than the AMD plate, and about one fourth of the length of the AMD. The anterior margin of the PMD is slightly convex, yet lacks the anterior corner. The posterior margin is straight, and without the posterior process. The plate gets broader posteriorly with strong lateral corners near the posterior end, which gives it a bell shape. In ventral view, the median ventral ridge and groove are weak or absent. The small posterior ventral process and pit are positioned between the crista transversalis interna posterior (ct.tp, Fig. 2B), as present in the Yunnanolepiformes (Zhu, 1996), *Minicrania* (Zhu and Janvier, 1996), and the Sinolepidae (Ritchie et al., 1992). The posterior marginal area is very short.

The ADL plate (Figs. 2 and 4) is well preserved in the holotype, shown by the bone proper and the internal mould. The plate is divided into the dorsal and lateral laminae by the strong dorsolateral ridge. The angle between two laminae is obtuse, indicating that the ventral wall of the trunk armor was broader than the dorsal wall. The dorsal lamina of the plate is long and narrow, about 1/9 of the trunk armor in width, which is the narrowest among the antiarchs. In ventral aspect, the dorsal lamina is widest anteriorly, with a length of 79 mm and a width of 13 mm (B/L index 16.5). Because the anterior extremity of the trunk armor is missing, the condition of the obstanic process is unknown. The lateral lamina of the plate is long and low, with a length of 64.6 mm and a height of 25 mm (height/length index 38.7). The area overlapped by the AVL plate is clearly shown in the left ADL plate of the holotype (oa.AVL, Fig. 2D). The crista transversalis interna anterior (cit, Fig. 2C) is well developed on the internal side of the lateral lamina; dorsally this crista does not extend medially into the AMD plate, but backwards to form a low buttress. In the internal mould, this indistinct buttress forms a shallow depression on the dorsal lamina of the plate (cit, Fig. 4B).

The PDL plate (Figs. 2 and 4) is very broad with a prominent dorsal corner. The dorsal lamina is about 48 mm wide, and 62.8 mm long (B/L index 76.4). The length of the anterodorsal margin (overlapped by the AMD plate) is about 1.6 times the length of the posterodorsal margin (overlapped by the PMD plate). The lateral lamina is long and low (with a depth of about 10 mm), and forms an obtuse angle with the dorsal lamina. Internally, the crista transversalis interna posterior is well developed, and situated close to the posterior margin of the plate.

The PL plate (Figs. 2 and 4) is a long and narrow bone on the lateral wall of the trunk armor. It is overlapped by the PDL plate dorsally and the PVL plate ventrally. Together with the lateral lamina of the PDL plate, it occupies about the same height as the lateral lamina of the ADL plate.

The AVL plate was broken from the holotype; however, it has left part of the internal mould on the left lateral wall (Fig. 2B and D). Judged from the complete lateral lamina of the PVL plate, the lateral lamina of the AVL should be very low, leaving a very limited space for the pectoral fin articulation, which might have been as small and simple as in the Yunnanolepidae and *Minicrania* (Zhu and Janvier, 1996).

The ornament of *Silurolepis* consists of crowded round or oval tubercles (Fig. 2E), with no obvious alignment into rows except for the dorsolateral ridges.

3. Relationships of *Silurolepis*

Although the skull, the pectoral appendage, and the ventral wall of the trunk armor are not preserved in *S. platydorsalis*, the incorporation of an extra median dorsal plate (PMD, which is smaller than the AMD plate) into the trunk armor and the absence of the anterior lateral plate is sufficient for the new form to be assigned to the Antiarcha (Denison, 1978; Janvier and Pan, 1982; Young, 1984; Zhu, 1996). The undescribed basal placoderm '*Wangolepis*' also has two median dorsal plates (personal examination); however, its AMD plate is much smaller than the PMD plate, resembling the extrascapular and median dorsal plates of the petalichthyid *Eurycaraspis* (Liu, 1991). Among antiarchs, the PMD larger than the AMD is uniquely present in the euantiarch *Hunanolepis* (Wang, 1991b), and should be an autapormorphy of this Middle Devonian taxon. The preserved portion of the AVL plate suggests a possible simple pectoral fin articulation as in the Yunnanolepidae and *Minicrania* (Zhu, 1996). The anterior margin of the AMD plate is broad in *Silurolepis*. In this regard, it resembles *Minicrania* (Zhu and Janvier, 1996) and the Sinolepidae (Ritchie et al., 1992), but differs from the Yunnanolepiformes, which have an anteriorly pointed AMD plate. Zhu (1996) suggested that the broad anterior margin of the AMD is a primitive antiarch character.

The crista transversalis interna posterior lateral to the posterior ventral process of the PMD plate, which is shared by *Silurolepis*, the Yunnanolepiformes, *Minicrania* and the Sinolepidae, should be another primitive antiarch character. In the Euantiarcha, the crista is situated behind the posterior ventral process and pit (Young, 1988). The AMD plate totally overlapping the ADL plate is shared by *Silurolepis*, the Sinolepidae, and asterolepids except *Remigolepis*, and Ritchie et al. (1992) considered it as a possible primitive condition for antiarchs. Based on the above character combination of *Silurolepis*, we are tempted to place it in the basal antiarchs.

Silurolepis differs from all other antiarchs in its unique overlap relationship between the AMD and PMD plates. Thus far known in antiarchs, the AMD plate is overlapped by the PMD plate without exception. In *Silurolepis*, the overlap relationship between the AMD and PMD plates is reversed, like that of dorsal ridge scales (the anterior overlapping the posterior). The same overlap relationship is seen between the extrascapular and median dorsal plates of arthrodires (Goujet, 1973) and petalichthyids (Liu, 1991). With the reference to the antiarch cladogram of Zhu and Janvier (1996), we suggest *Silurolepis* as the sister taxon to the other antiarchs that have evolved the PMD plate overlapping the AMD plate (Fig. 5), although the additional characters, especially those from the skull, are needed to test this assignment.

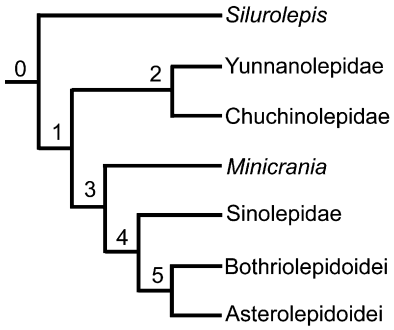

Fig. 5. Simplified cladogram of antiarch interrelationships (modified from Zhu and Janvier, 1996), showing the position of *Silurolepis*. Taxa and selected synapomorphies: Node 0, Antiarcha, incorporation of an extra median dorsal plate in the trunk armor, pectoral fenestra enclosed within a single plate, pectoral appendage covered with small dermal plates, antiarchan skull-roof pattern (the latter two characters unknown in *Silurolepis*); Node 1, Antiarcha crownward of *Silurolepis*, AMD overlapping PMD; the other nodes referring to Zhu and Janvier (1996, fig. 12).

4. Conclusions

The discovery of *S. platydorsalis* is remarkable as it represents the first articulated placoderm fish from the Silurian, and amplifies the range of morphological disparity among early antiarchs. On the basis of the available data, the new form is parsimoniously placed at the most basal position of the Antiarcha. It differs from the other antiarchs including yunnanolepiforms in its unique overlap relationship between the AMD and PMD plates, and should represent a new family of antiarchs (Silurolepidae n. fam.).

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