

Research paper

# A new antiarch fish from the Upper Devonian Zhongning Formation of Ningxia, China

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Received 2 April 2009; received in revised form 8 December 2009; accepted 9 February 2010

Available online 17 February 2010

## Abstract

A new antiarch, *Ningxialepis spinosa* n. gen. n. sp., is described from the Zhongning Formation (Famennian, Late Devonian) of Shixiagou, Qingtongxia, Ningxia, northwestern China. It is characterized by the presence of X-shaped pit-lines, long obstatic margins, high dorsal median spine of the trunk armour formed from the anterior and posterior median dorsal plates, prominent dorsolateral and ventrolateral ridges of the trunk armour, and the anterior median dorsal plate partly overlapping the anterior dorsolateral plate.

*Ningxialepis* is placed as the sister taxon to *Jiangxilepis* in the Family Jiangxilepididae from South China, based on a phylogenetic analysis of the Euantiarcha. The Jiangxilepididae is redefined. The close affinity between *Ningxialepis* and *Jiangxilepis* further corroborates the geographic proximity between the North China and South China blocks in the Late Devonian.

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**Keywords:** Antiarcha; Placodermi; Late Devonian; Phylogeny; Paleogeography

## 1. Introduction

Pan et al. (1980) first reported Devonian vertebrates in Ningxia, and described two antiarchs (*Bothriolepis niushoushanensis* and *Remigolepis zhongningensis*) from the Shixiagou section (Fig. 1), which used to be an area of Zhongning County, and now belongs to the neighboring Qingtongxia city. Since

then, abundant fish fossils (mainly antiarchs and petalichthyids) were recovered from four main Devonian Sections in Ningxia, i.e., the Shixiagou and Dadaigou sections of Qingtongxia, the Shanghongya Section of Zhongning, and the Hongshiwan Section of Zhongwei (Fig. 1; Pan et al., 1987). In the past decade, we have organized several expeditions to the Devonian outcrops of Ningxia and neighboring areas, and collected more vertebrate fossils including the first Devonian tetrapod from Asia (*Sinostega*, Zhu et al., 2002) and abundant sarcopterygian fish remains.

This paper describes one of the new antiarchs from the *Sinostega*-bearing bed, i.e., the uppermost part of the Zhongning Formation in the Shixiagou section (Pan et al., 1987, figs. 1 and 3). Associated fossils include the plants *Leptophloeum rhombicum* and *Sublepidodendron mirabile*, land plant spores, the antiarchs *Remigolepis*, *Sinolepis* (Pan et al., 1987) and *Bothriolepis*, and some arthrodire remains, in addition to *Sinostega* (Zhu et al., 2002).

## 2. Geological setting and stratigraphy

Pan et al. (1987) documented the exposure of Devonian rocks in Ningxia, and gave a detailed description of four main fish-

**Abbreviations:** ADL, anterior dorsolateral plate; AMD, anterior median dorsal plate; AVL, anterior ventrolateral plate; Bo, Bothriolepididae; Cd<sub>1</sub>, dorsal central Plate 1; Cd<sub>2</sub>, dorsal central Plate 2; csl, central sensory line; d.end, opening of canal for endolymphatic duct; dl<sub>2</sub>, posterior oblique dorsal sensory line groove; dlr, dorsolateral ridge of the trunk-armour; dp, external groove above crista transversalis interna posterior; Jx, Jiangxilepididae; L, lateral plate; lc, lateral corner of the PMD plate; leg, main lateral line groove; Ml<sub>2</sub>, lateral marginal Plates 2; Mm<sub>2</sub>, mesial marginal Plates 2; MV, median ventral plate; nm, obstructed nuchal area; Nu, nuchal plate; OG, outgroup; om, obstatic margin; PDL, posterior dorsolateral plate; plc, posterolateral corner of PMD; PM, postmarginal plate; PMD, posterior median dorsal plate; PNu, paranuchal plate; Pp, postpineal plate; proc, preobstatic corner of the head shield; PVL, posterior ventrolateral plate; SM, submarginal plate; socc, supraoccipital cross-commissural pitline groove; vlr, ventrolateral ridge of trunk-armour.

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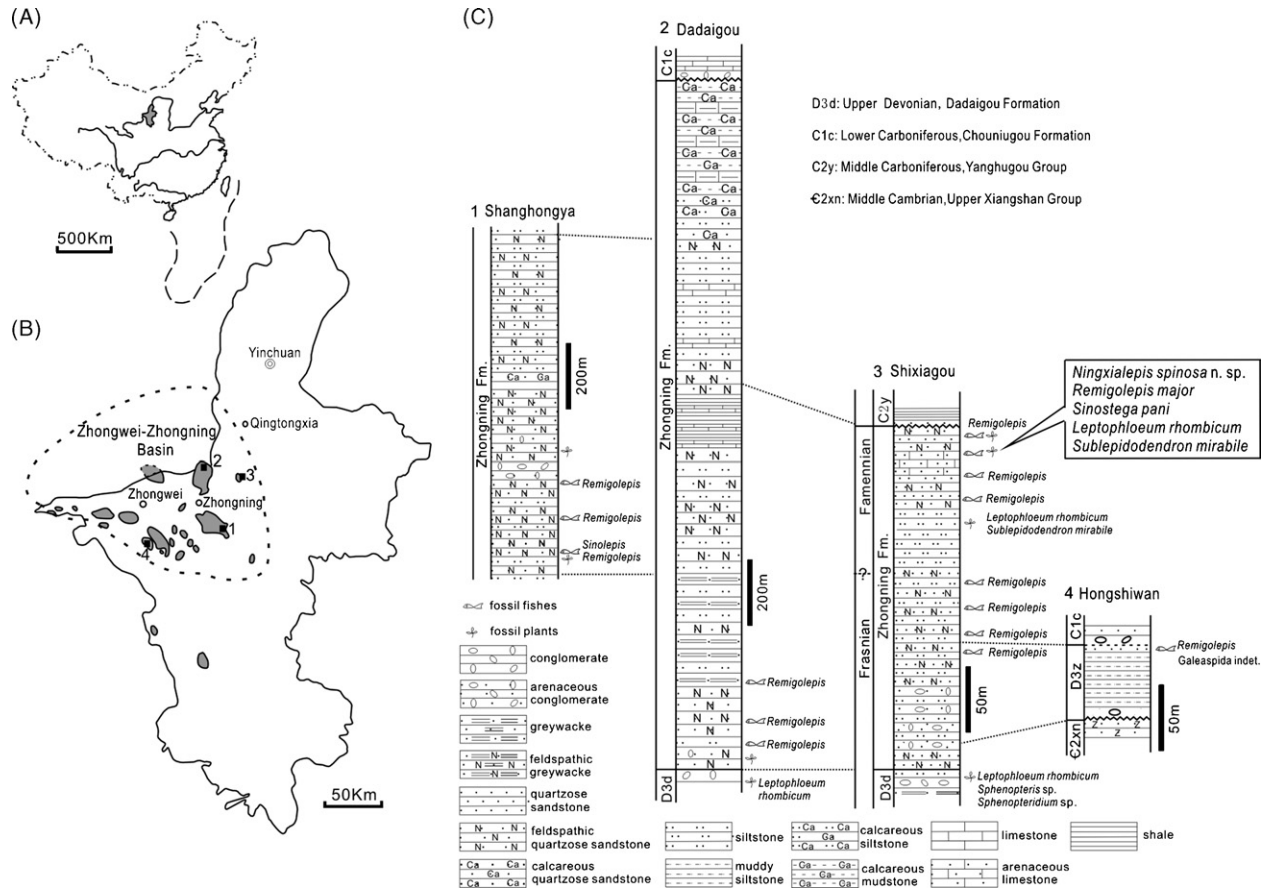


Fig. 1. Correlation of four selected sections of Zhongning Formation. (A) Geographic location of Ningxia Hui Autonomous Region. (B) Devonian outcrops in Ningxia (after Pan et al., 1987, fig. 2), 1–4 represent the section numbers in (C). (C) Correlation of the Zhongning Formation in four selected sections (stratigraphic data mainly based on Pan et al., 1987).

bearing sections (Fig. 1). The Devonian strata in Ningxia are subdivided into three formations in ascending order, the Shixiagou, Dadaigou and Zhongning formations. They are deposits of the Zhongwei-Zhongning Basin, which tectonically is referred to the Hexi Corridor Transition Belt of the Qilian Fold System (Pan et al., 1987). An angular unconformity exists between the Shixiagou Formation and the Dadaigou Formation. The Middle Devonian age of the Shixiagou Formation is based on its fish fauna, which closely resembles that of the Haikou Formation in Yunnan, southwestern China. Plant remains, such as *L. rhombicum*, *Sphenopteris* sp., and *Sphenopteridium* sp., suggest a Frasnian (Late Devonian) age for the Dadaigou Formation. Based on the faunal assemblage, miospores, and stratigraphic sequence, Pan et al. (1987) assigned the age of the overlying Zhongning Formation to the Famennian. The Zhongning Formation yields the plants *Leptophloeum* and *Sublepidodendron*, the antiarchs *Sinolepis*, and at least six species of *Remigolepis* (Pan et al., 1980, 1987). A similar biota, including the antiarchs *Sinolepis*, *Jiangxilepis* and *Remigolepis*, the macroplants *L. rhombicum* and *S. mirabile*, and a miospore assemblage with *Retispora lepidophyta*, was found from the upper part of the Wutung Formation in Jiangsu, the upper part of the Sanmentan Formation in Jiangxi, and the Hsikuangshan Formation in Hunan (Liu and Pan, 1958; Zhang and Liu, 1991), which were referred to the Famennian with little doubt.

Ritchie et al. (1992) compared the *Sinolepis*-*Jiangxilepis* fauna of South China to the *Grenfellaspis* fauna of southeastern Australia, and suggested a similar age (late Famennian) for these two faunas. Meanwhile, they proposed that a somewhat older age is likely for the Zhongning Formation based on the spore list in Pan et al. (1987). Blicek et al. (2007) followed this proposal, and provisionally considered the Zhongning Formation as Frasnian in age, based on personal communication from two palynologists. Pan et al. (1987) compared the miospore assemblage of the Zhongning Formation to that of the Zhangtong Formation of Tibet, with shared spores including *Apiculiretusispora plicata*, *A. granulata*, *A. septalata* var. *minor*, *Geminospora parvibasilaris*, *G. lemurata*, *Archaeozonotriletes variabilis*, *Calamospora atava*, *C. nigrata*, *Verrucosiporites omalus*, *Stenozonotriletes conformis*, and *Aneurospora greggsii*. They pointed out the absence of *R. lepidophyta* and *Vallatisporites pusillites* in the Zhongning Formation (yet presence in the Zhangtong Formation), but still considered the age of the Zhongning Formation as Famennian. *R. lepidophyta* and *V. pusillites* are index miospores from the Fa2d of Belgium (*pusillites-lepidophyta* Zone, uppermost Famennian), and their absence in the Zhongning Formation is not inconsistent with the age of the formation as Famennian, if not latest Famennian. The downward extension of the formation to the Frasnian is likely, but new palynomorph analysis is needed to complement or testify the only spore list from the for-

mation. Thus far, a Famennian age of the Zhongning Formation, especially for its upper part, cannot be excluded.

In the Shixiagou Section, a disconformity exists between the Zhongning Formation and the overlying Yanghugou Group, of early Late Carboniferous (Bashkirian) age. In the Dadaigou and Hongshiwan sections, the Zhongning Formation is overlain by the Chouniugou Formation, of middle Early Carboniferous (Viséan) age. Within the whole depositional basin (Zhongwei-Zhongning Basin, Fig. 1), the thickness of the Zhongning Formation varies from 55 m (Hongshiwan Section close to the basin margin, Fig. 1) to 2160 m (Dadaigou Section at the basin center). This is attributed to differential rates of deposition from the basin center to the margin, and the gap extension between the Zhongning Formation and the overlying strata. Based on the depositional sequence and assemblage, we provide a tentative correlation of four sections in the Zhongwei-Zhongning Basin (Fig. 1). We suggest that the upper part of the Zhongning

Formation in the Dadaigou Section is missing in the Shixiagou Section. The *Sinostega-Ningxialepis* bed, although at the uppermost part of the Zhongning Formation in the Shixiagou Section, is probably older than the latest Famennian (*pusillites-lepidophyta* Zone). The Zhongning Formation in the Hongshiwan Section is very thin, and bears *Lepidophloeum rhombicum*, *Remigolepis zhongweiensis*, *R. xiangshanensis*, and a galeaspid agnathan. It is likely that the Zhongning Formation in the Hongshiwan Section roughly corresponds to the lower part of the Zhongning Formation in Shixiagou and Dadaigou sections, and is Frasnian in age. In this case, the Frasnian age of the galeaspid agnathan in North China would be consistent with the generally accepted stratigraphical distribution of ‘ostracoderms’ (Bleick et al., 2007). Better definition of the Frasnian/Famennian boundary in the Zhongning Formation of the Shixiagou section needs further biostratigraphic research.

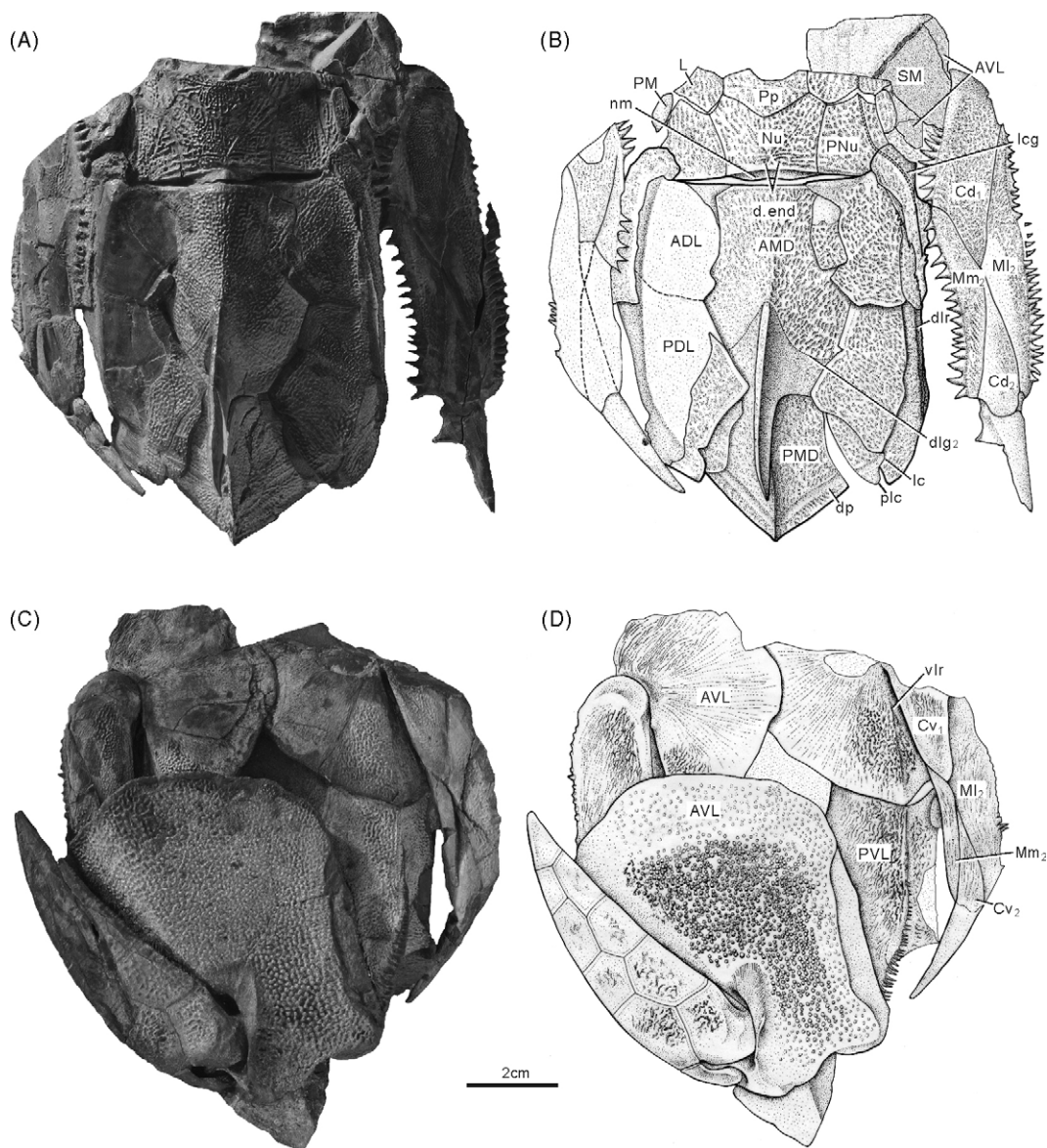


Fig. 2. *Ningxialepis spinosa* n. gen. n. sp. (A and B) Holotype in dorsal view. (C and D) Holotype in ventral view.

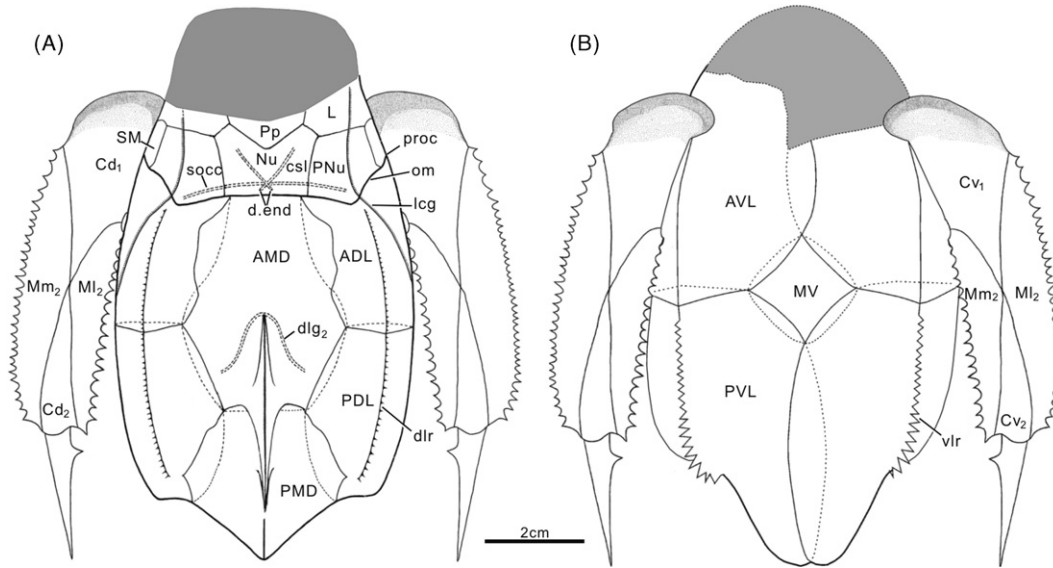


Fig. 3. *Ningxialepis spinosa* n. gen. n. sp. (A) Restoration in dorsal view, based on Fig. 2A. (B) Restoration in ventral view, based on Fig. 2C.

Blieck et al. (2007) argued that the age estimate of about 355 Ma would put the bed in the lowest Carboniferous, but Zhu et al. (2002) were using the estimate for the Devonian-Carboniferous boundary at that time, of about 354 Ma. More recent timescales (e.g., Gradstein et al., 2004) place the boundary at about 360 Ma; so, on that estimate a late Famennian age would be about 362 Ma.

### 3. Systematic paleontology

Class Placodermi M'Coy, 1848

Order Antiarcha Cope, 1885

Family Jiangxilepididae Zhang et Liu, 1991

**Diagnosis:** Anterior and posterior margins of the anterior median dorsal (AMD) plate broad. Dorsal median spine of the trunk armour developed. Tergal angle of the AMD plate centrally placed. Axillary foramen small. Pectoral appendages elongate, extending beyond the posterior margin of the trunk armour. Proximal segment of the pectoral appendage narrow and long with a breadth/length (B/L) index about 29, with marginal spines. Length of its distal segment about a third that of the proximal segment. Dorsal central Plates 1 and 2 (Cd<sub>1</sub>, Cd<sub>2</sub>) in contact, separating the mesial and lateral marginal Plates 2 (Mm<sub>2</sub>, MI<sub>2</sub>). Posterior oblique dorsal sensory line groove (dlg<sub>2</sub>) on the trunk armour developed. Ornamentation of mature individuals reticulate.

**Remarks:** The above is modified from Zhang and Liu (1991), to incorporate the data of the new antiarch from Ningxia. Our phylogenetic analysis suggests that the new form is closely related to *Jiangxilepis* from South China, and belongs to the family Jiangxilepididae (Zhang and Liu, 1991). *Ningxialepis* n. gen. **Etymology:** After Ningxia, the fossil locality. **Diagnosis:** As for the type species (by monotypy).

*Ningxialepis spinosa* n. sp. (Figs. 2–4)

**Etymology:** From the Latin *spinus*, by reference to conspicuous small spines along the dorsolateral and ventrolateral ridges of the trunk armour.

**Holotype:** A nearly complete trunk armour, naturally associated with pectoral appendages and incomplete head shield (IVPP V14714). Part of its ventral wall is covered by the trunk armour of *Remigolepis*.

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

**Locality and horizon:** Zhongning Formation, Late Devonian, Famennian; Shixiagou, Qingtongxia, Ningxia, northwestern China.

**Diagnosis:** A medium-sized jiangxilepid antiarch characterized by the pointed dorsal median spine formed from the AMD and

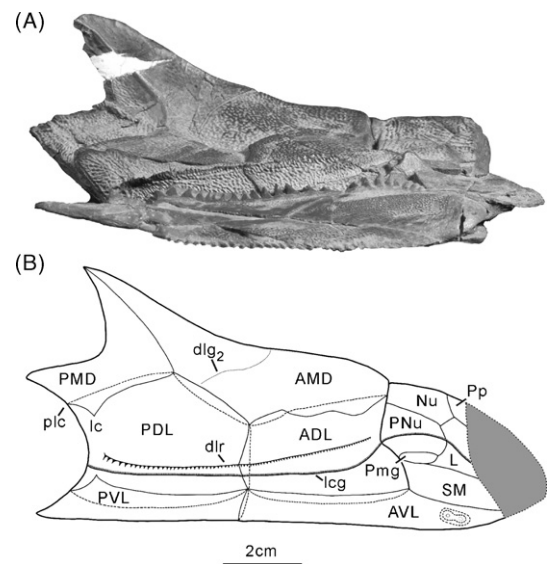


Fig. 4. *Ningxialepis spinosa* n. gen. n. sp. (A) Holotype in lateral view. (B) Restoration in lateral view.

the posterior median dorsal (PMD) plates, the AMD plate partly overlapping the anterior dorsolateral (ADL) plate and partly overlapped by the ADL plate, small spines along prominent dorsolateral and ventrolateral ridges (dlr, vlr) of the trunk-armour, no small spines along the margins of the distal segment of the pectoral appendage, and the presence of X-shaped pit-lines.

*Remarks:* *Ningxialepis* shares with the Bothriolepidoidei its elongate  $Ml_2$  relative to the trunk armour. It shares with the Bothriolepidoidei excluding *Luquanolepis* Zhang et Young (1992) in the lateral lamina of the posterior ventrolateral (PVL) plate as high as or higher than the lateral lamina of the anterior ventrolateral (AVL) plate. It shares with the Bothriolepidoidei excluding *Luquanolepis* and *Nawagiaspis* Young (1990b) in the absence of the posterior lateral plate. Among the Bothriolepidoidei, *Ningxialepis* closely resembles *Jiangxilepis* Zhang et Liu (1991) in its elongate pectoral appendages, reticulate ornamentation, centrally placed tergal angle of the AMD plate, and the developed dorsal median spine of the trunk armour.

However *Jiangxilepis* differs from the new genus in its dorsal median spine formed solely by the AMD plate, the AMD plate totally overlapping the ADL plate, no spines along the dorsolateral and ventrolateral ridges of the trunk armour, small spines along both sides of the distal segment of the pectoral appendages, and the absence of X-shaped pit-lines.

### 3.1. Description

#### 3.1.1. Head shield

The head shield (Fig. 2) is incompletely preserved, missing the part anterior to the postpineal plate (Pp, Fig. 2). As judged from the preserved part, the Pp plate was relatively short and wide. It sutures with the lateral plate (L, Fig. 2), separating the nuchal plate (Nu, Fig. 2) from the orbital fenestra. In this regard, the new form resembles *Jiangxilepis* and the Asterolepidoidei. The Nu plate is completely preserved, with a length/width index of 54. It is broadest at the level of the lateral corners, which are anteriorly positioned. Posteriorly, the Nu plate exhibits an extensive obteched nuchal area (nm, Fig. 2). The paranuchal plate (PNu, Fig. 2) is of moderate breadth, and pentagonal in shape. Posterior to the L plate and lateral to the PNu plate, a small, ellipse-shaped plate represents the postmarginal (PM, Fig. 2) plate. The PM and PNu plates form a long obstantic margin of the head shield (om, Fig. 3), which faces posterolaterally. The preobstantic corner of the head shield (proc, Fig. 3) is well anterior to the posterior extremity of the head shield. Noteworthy is a large dermal plate, which is lateral to the L and PM on the right side of the specimen. This plate is also dorsal to the AVL plate, and presumably represents the submarginal plate (SM, Fig. 2A and B).

The sensory canal system of the head shield shows that the central sensory line (csl, Fig. 3) on the Nu plate does not reach the anterior lateral margin of the plate, this being a difference from that of *Bothriolepis*. Posteriorly, this line is continuous with the middle pit-line. The X-shaped pit-lines, comprising the middle and posterior pit-lines as in the Yunnanolepidoidei (Zhu, 1996), *Pterichthyodes* (Hemmings, 1978), and *Bothriolepis* (Young, 1988), are in confluence with the endolymphatic duct openings

(d.end, Fig. 2). The supraoccipital cross-commissural pitline groove (socc, Fig. 3) is a long transverse groove issued from the principal section of the infraorbital sensory line.

#### 3.1.2. Trunk armour

The nearly complete trunk armour (Fig. 2) has a maximum length of about 79 mm in dorsal view. The anteriormost portion of the ventral wall is not preserved, including the semilunar plate and part of the AVL plates. In addition, part of the left half of the ventral wall is covered by a trunk armour of *Remigolepis*. The median ventral (MV, Fig. 2) plate is also missing; however, the space encircled by the neighbouring plates indicates a small rhombic plate. The posterior extremities of the dorsal and ventral walls are of the same level.

The AMD plate (Fig. 2) is long and narrow (B/L index 72). It is hexagonal in shape. The anterior and posterior margins of the AMD plate are broad, and the posterior margin is slightly broader than the anterior margin. Along the anterodorsal margin, the AMD plate overlaps the ADL plate anteriorly and then is overlapped by the latter. The AMD plate is totally overlapped by the PMD plate and the posterior dorsolateral (PDL, Fig. 2) plate. The posterior oblique dorsal sensory line groove (dlg<sub>2</sub>, Fig. 2) is developed on the AMD plate, but does not reach the posterior lateral margin of the plate.

The PMD plate (Fig. 2) is polygonal in shape, with straight postero-lateral margins, and the lateral corners (lc, Fig. 2) forming acute angles. The external groove above the crista transversalis interna posterior (dp, Fig. 2) is present. The dorsal median spine of the trunk armour (Figs. 2 and 3) is well developed to form a high ridge, which comprises parts of the AMD and PMD plates.

The ADL plate (Fig. 2) is moderately broad. Its dorsal lamina is about 1.3 times as long as broad. The breadth of the dorsal lamina is about 2 times the height of the lateral lamina. The PDL plate (termed ‘mixilateral plate’ in Zhang and Liu, 1991) is overlapped by the ADL plate and has the same length and width as the ADL plate. We suggest that the loss of the PL plate (like the loss of the AL plate) rather than the fusion of the PL and PDL plates to form the mixilateral plate involves less *ad hoc*. The prominent dorsolateral ridge (Figs. 2 and 3) extends longitudinally through the trunk armour, and is ornamented with a row of small spines.

The flat ventral wall of the trunk armour (Fig. 2) is represented by the AVL and PVL plates. The MV and semilunar plates are not preserved. The right PVL and part of the right AVL plate are invisible externally, for they are covered by the AVL plate and pectoral appendage of a *Remigolepis*.

The AVL plates (Figs. 2 and 3) are incompletely preserved, and lack most of the subcephalic lamina. The articulation region with the pectoral appendage is well preserved on the right side. The right AVL plate overlaps the left one.

The exposed portions of the PVL plates show that the left overlaps the right. The lateral lamina of the right PVL plate is visible, with the prominent ventrolateral ridge (vlr, Figs. 2 and 3). Like the dorsolateral ridge, the ventrolateral ridge extends longitudinally through the trunk armour. The small spines along the ridge become larger posteriorly.

### 3.1.3. Pectoral appendages

The pectoral appendages (Figs. 2 and 3) are long and jointed, with the distal end approaching the level of the posterior margin of the trunk armour. The proximal and distal segments of both sides are preserved.

The proximal segment is comparatively slender, about 3.4 times as long as it is broad, and bears small spines on both margins. The  $Ml_2$  plate is elongate relative to the trunk armour, with its distal end beyond the center of the MV plate when adducted. The  $Cd_1$  and  $Cd_2$  plates form a pointed connection, as in the Asterolepidoidei excluding *remigolepids*. The distal segment is much narrower and shorter than the proximal segment, and bears only one thorn-like mesial spine. Bone sutures in the distal segment are indistinct.

### 3.1.4. Ornamentation

The dermal bones show reticular ornamentation, as in *Jiangxilepis* (Zhang et Liu, 1991). However, the dorsal median spine and distal segments of the pectoral appendages are deficient of the reticulate ridges, i.e., smooth.

## 4. Phylogenetic analysis of the Euantiaracha

A phylogenetic analysis of the Euantiaracha was performed based on a matrix of 48 characters (all treated as unordered, weighted equally) scored for 25 taxa (see Appendices 1 and 2). The yunnanolepiform *Parayunnanolepis* (Zhang et al., 2001), and sinolepids *Grenfellaspis* and *Dayaoshania* (Ritchie et al., 1992) were selected as outgroups, with 22 euantiarch taxa as the ingroup. The character data entry and formatting were performed with Mesquite version 2.5.

We analyzed the data set with the heuristic algorithms of PAUP version 4.0b 10 (Swofford, 2003). MacClade 4.0 was used to trace the character transformation in the selected cladogram. The analysis generated seven most parsimonious (MP) trees (tree length = 110; CI = 0.4818; RI = 0.7397). The strict consensus tree (Fig. 5A) shows two polytomies within the Bothriolepidoidei and the Asterolepidoidei, respectively. One polytomy remains in the 50% majority consensus tree (Fig. 5B). Two major monophyletic groups of the Euantiaracha are clearly shown in the cladogram, i.e., the Asterolepidoidei (Fig. 6, Node 4) and Bothriolepidoidei (Fig. 6, Node 13). All the seven MP trees place *Ningxialepis* as the sister group of *Jiangxilepis*, and the monophyly of the Jiangxilepidae is supported by five synapomorphies (Fig. 7, Appendix 3, Node 16). One of the MP trees is selected to trace the character changes (Fig. 6, Appendix 3).

In our analysis, the monophyly of the Bothriolepidoidei (Miles, 1968) is supported by three synapomorphies including one ambiguous character (elongate  $Ml_2$  plate relative to the trunk armour, unpaired semilunar plate, anteriorly placed tergal angle of the AMD plate). In this regard, the new cladogram differs from Zhu's (1996) cladogram, in which the paraphyly of the Bothriolepidoidei was suggested. In both analyses, the Bothriolepididae (Fig. 7, Node 19) and the Microbrachiidae (Fig. 7, Node 22) are well supported. However, the other groupings are weakly supported. A heuristic search made for all trees of length of 111 or less resulted in recovery of 110 trees, and suggested the unstable phylogenetic positions of many bothriolepidoid taxa such as *Luquanolepis*, *Nawagiaspis*, and *Dianolepis*. The lower Bremer decay index for the Bothriolepidoidei indicates that further morphological studies should be done to resolve the monophyly or paraphyly of the Bothriolepidoidei.

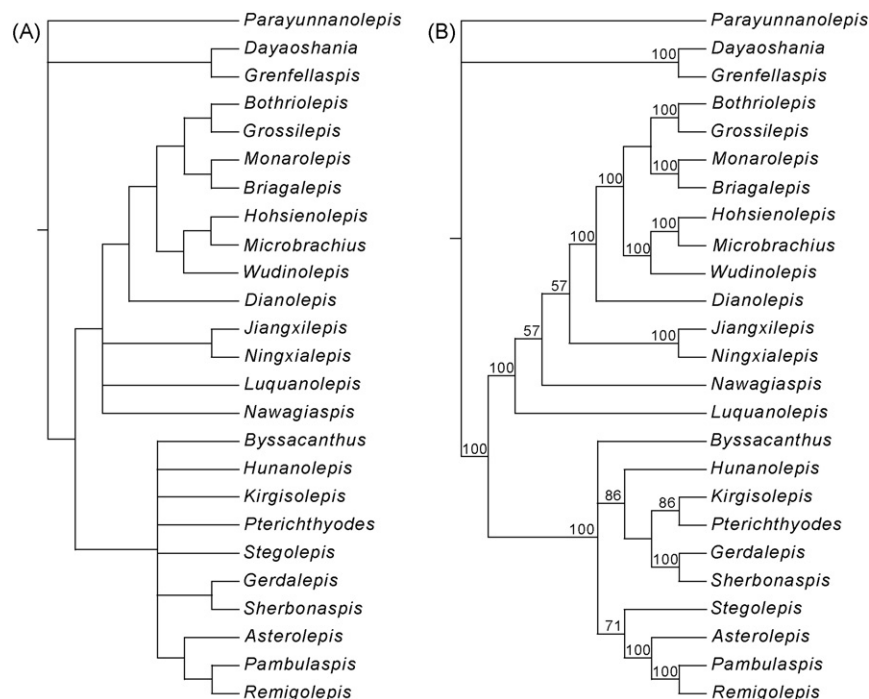
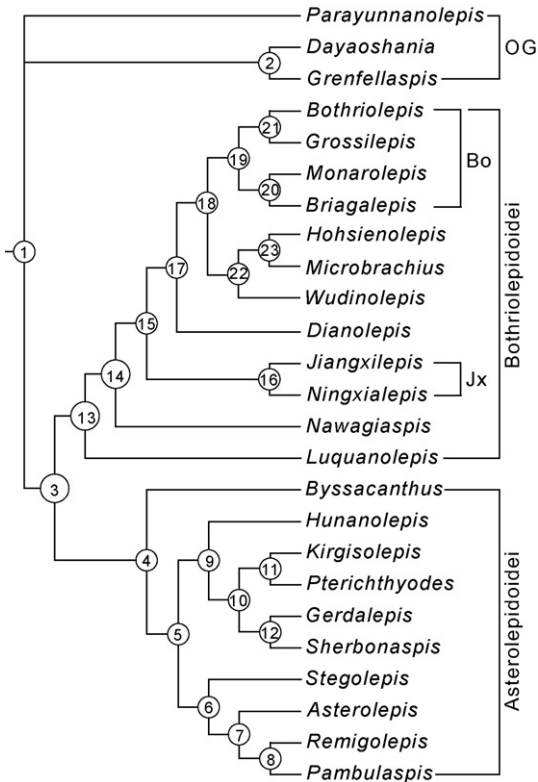


Fig. 5. Strict (A) and 50% majority-rule (B) consensus trees of 7 MP trees with the length  $\leq 110$ . Numbers alongside nodes in B represent percentage support values.



**5. Paleogeographic significance**

The antiarch placoderms with high endemism have contributed a lot to research on Siluro-Devonian paleogeography (Young, 1981, 1984, 1990a). Mainly based on the endemic galeaspid agnathans and yunnanolepiform antiarchs from South China, Young (1981) proposed the ‘galeaspid-yunnanolepid province’ as one of the five major vertebrate faunal provinces for the Early Devonian. The discovery of galeaspids in the Tarim Basin (Wang et al., 1996) and Ningxia (Pan et al., 1987) corroborates the presence of the Pan-Cathaysian Landmass Group (the South China, Tarim, and North China blocks) during the mid-Palaeozoic (Zhao and Zhu, 2007). The paleogeographic connection between the South China and Tarim blocks is also supported by sinacanthids and mongolepids from the Silurian of both blocks (Zhu and Wang, 2000). Tông-Dzuy et al. (1996) reported a yunnanolepiform antiarch from the Middle Devonian of central Vietnam. The yunnanolepiforms, as a highly endemic group of antiarchs, were previously known from the Silurian and Lower Devonian of South China and northern Vietnam. The yunnanolepiform occurrence in central Vietnam suggested close links between the Indochina and South China blocks in the Middle Devonian, and extended the scope of the ‘galeaspid-yunnanolepid province’.

The antiarchs from the Middle and Upper Devonian exhibit more cosmopolitan characteristics, and reflect the enhanced faunal exchange or biotic dispersal between various provinces

Fig. 6. One of the MP trees (tree length = 110; CI = 0.4818; RI = 0.7397).

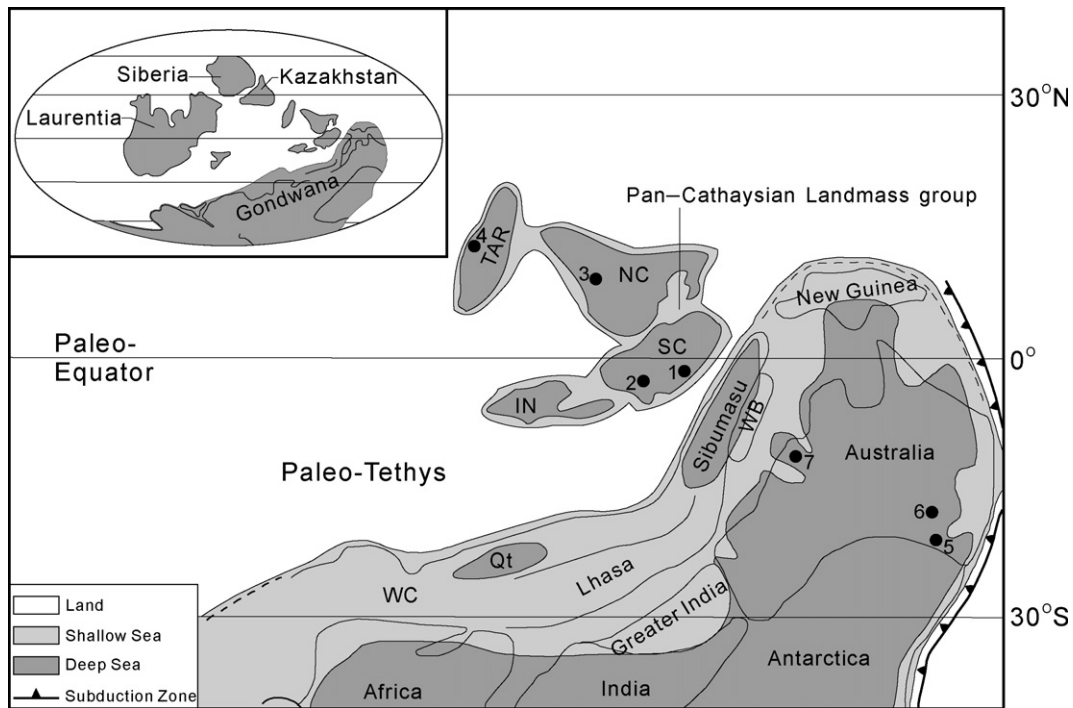


Fig. 7. Paleogeographic reconstruction of eastern Gondwana and China for the Late Devonian (based on Metcalfe, 1998; Fig. 6). Black dots represent the Late Devonian antiarch localities in China and Australia: (1) Nanjing of Jiangsu Province (*Sinolepis macrocephala*, *S. wutungensis*, Liu and Pan, 1958); (2) Yudu, Chongyi and Quannan of Jiangxi Province (*Jiangxilepis longibrachius*, Zhang and Liu, 1991); (3) Zhongning, Zhongwei and Qingtongxia of Ningxia Autonomous Region (*R. zhongningensis*, Pan et al., 1980; *Remigolepis major*, *R. microcephala*, *R. xiangshanensis*, *R. xixiaensis*, *R. zhongweiensis*, *Sinolepis szei*, Pan et al., 1987; *Ningxialepis spinosa*); (4) Tarim Basin of Xinjiang (Antiarcha gen. et sp. indet., Wang et al., 1997); (5) Mt. Howitt, Victoria (*Bothriolepis cullodenensis*, Long, 1983); (6) Grenfell, New South Wales (*Grenfellaspis branagani*, Ritchie et al., 1992); (7) Canning Basin, Western Australia (*Bothriolepis* sp., Young, 1984). Abbreviations: IN, Indochina Block; SC, South China Block; NC, North China Block; Qt, Qiangtang; TAR, Tarim Block; WB, Western Climmerian Continent; WC, West Burma.

(Young, 1981, 1984, 1990a). The sinolepids are a group of antiarchs with unique biogeographic interest (Long, 1983; Pan et al., 1987; Young, 1990a; Ritchie et al., 1992). They were originally known from the Upper Devonian of Jiangsu (Liu and Pan, 1958). Their occurrence in Ningxia (Pan et al., 1987) and Australia (Long, 1983; Ritchie et al., 1992) not only suggests close connection between the South China and North China blocks, but also corroborates that the Pan-Cathaysian Landmass Group was close to eastern Gondwana during Devonian time.

The distribution (Fig. 7) of a sister pair of antiarchs (*Ningxialepis* from North China, *Jiangxilepis* from South China) is also of biogeographic interest. It provides additional evidence to support the geographic proximity between the South China and North China blocks. Whether the Jiangxilepididae has a wider distribution needs further investigation, for instance, in the Grenfell fauna of Australia (Ritchie et al., 1992).

### Acknowledgements

This is a contribution to IGCP 491. We thank G.C. Young, J. Lu and T. Qiao for discussions, M.W. Yang and J.L. Huang for illustrations. We also thank G.C. Young and an anonymous reviewer for their comments on and improving the manuscript. This work was supported by the Knowledge Innovation Program of the Chinese Academy of Sciences (KZCX2-YW-156), the Major State Basic Research Projects (2006CB806400), the State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing, 083115), the CAS/SAFEA International Partnership Program for Creative Research Teams, and the National Natural Science Foundation of China (40602005).

### Appendix 1. Character list used in the phylogenetic analysis

1. Premedian plate: short and broad (0); long and narrow (1).
2. Anterior margin of the premedian plate: convex (0); slightly concave (1).
3. An unornamented shelf and rostrocaudal groove on the premedian plate: absent (0); present (1).
4. Rostral width/orbital width index of the premedian plate: smaller (0); large than 200 (1).
5. Lateral plate: narrow (0); broad (1).
6. Preorbital depression: present (0); absent (1).
7. Preorbital depression: extending laterally onto the lateral plate (0); restricted to the premedian plate (1).
8. Preorbital recess: absent (0); restricted to the premedian plate (1); extending laterally to the lateral plate (2).
9. Nasal opening: at the anterolateral corners of the rostral plate (0); at the anterior margin of the rostral plate (1).
10. Orbital fenestra: large (0); small (1).
11. Relative position of the orbital fenestra: anterior (0); slightly anterior (1); slightly posterior (2); posterior (3).
12. Postpineal and nuchal plates: long and narrow (0); short and broad (1).
13. Pronounced postpineal thickening: absent (0); present (1).
14. Nuchal plate: without orbital facets (0); with orbital facets (1).
15. Obstantic margin: long (0); short (1).
16. Submarginal articulation: absent (0); present (1).
17. Endocranial postorbital process: short (0); extending in front of the orbital notch (1).
18. Prelateral plate: present (0); absent (1).
19. Mental plates of both sides: separated (0); meeting in the mid-line (1).
20. Central sensory-line groove: present (0); absent (1).
21. X-shaped pit-line grooves: present (0); absent (1).
22. Branch of the infraorbital groove diverging on lateral plate: present (0); absent (1).
23. Semicircular pit-line groove: absent (0); present (1).
24. Middle pit-line groove issued from the infraorbital groove: absent or short (0); long and extending onto the nuchal plate (1).
25. Trunk-shield: low and elongated (0); high and short (1).
26. Pectoral appendage: short (0); elongate (1).
27. Pectoral appendage: unjointed (0); jointed (1).
28. Cd<sub>1</sub> and Cd<sub>2</sub> plates: in contact (0); separated (1).
29. Ml<sub>2</sub> plate relative to the trunk-shield: short (0); elongate (1).
30. Ml plate of the distal segment: three (0); two (1).
31. Helmet-shaped branchial process and pars pedalis: rudimentary and without pars pedalis (0); Helmet-shape (1).
32. Axillary foramen: small (0); large (1).
33. Index between width of anterior margin and maximum width of the AMD plate: > 55 (0); 35-55 (1); 15-35 (2); < 15 (3).
34. Tergal angle of AMD plate: centrally placed (0); anteriorly placed (1).
35. AMD plate overlapping the ADL plate: completely (0); partly (1).
36. AMD plate: underlapping or partly overlapping the PDL plate (0); completely overlapping the PDL plate (1).
37. AMD plate: partly or completely overlapping the PDL plate (0); underlapping the PDL plate (1).
38. Anterior ventral process and pit on the AMD plate: present (0); absent (1).
39. Dorsal median spine of the trunk armour: absent (0); present (1).
40. Crista transversalis interna posterior: lying laterally to the posterior ventral pit and process of the PMD plate (0); lying behind the posterior ventral pit and process of the PMD plate (1).
41. PL plate: present (0); loss (1).
42. Lateral lamina of PVL: lower than lateral lamina of AVL plate (0); as high as or higher than lateral lamina of AVL plate (1).
43. Lateral lamina of PDL: as deep as or shallower than lateral lamina of ADL plate (0); deeper than lateral lamina of ADL plate (1).
44. Semilunar plate: paired (0); unpaired (1).
45. A large rectangular aperture on the ventral wall of trunk-shield: absent (0); present (1).
46. Reticular adult ornamentation: absent (0); present (1).



47. Ridged adult ornamentation on the dorsal wall of the trunk-shield: absent (0); present (1).  
 48. Subparallel ridged adult ornamentation on the dorsal wall of the trunk-shield: absent (0); present (1).

**Appendix 2. Data matrix of 48 characters for 25 antiarch genera. ? = unavailable character; – = logical impossibility; X = 0/1.**

	0000000001111111112222222222333333333344444444
	123456789012345678901234567890123456789012345678
<i>Parayunnanolepis</i>	0000100?0000?0000?01 00000000—300000000000000—
<i>Grenfellaspis</i>	00011011010000000?1 11000?100000110100001100100—
<i>Dayaoshania</i>	0001101?010100000?1 110000100000210100001100100—
<i>Luquanolepis</i>	?00?????0? ?????????? ????001?1? 10110?001 0001000—
<i>Wudinolepis</i>	1000100?00300?0?0?0 1101001?1? 110100100111010010
<i>Hohsienolepis</i>	1000100?0030000????0 110?001??? 1?0100100111010011
<i>Microbrachius</i>	10001000003000010?0? 1101001?0? 110100100111010011
<i>Dianolepis</i>	100011–2002100010?0? 11000010?? 10110010011101000—
<i>Nawagiaspis</i>	100001–?00310??10001 ????1?1??? 1011???001 0101000—
<i>Briagalepis</i>	?00???–?0? ???1?1???1 100?0?1??? 1?011010011101000—
<i>Monarolepis</i>	?00???–?0? ??????????0 1??0?11?? 10011010011101000—
<i>Grossilepis</i>	100011–20121010110?0001001111111010100011101000—
<i>Bothriolepis</i>	100011–2012101011000001001111111010010011101010—
<i>Gerdalepis</i>	000001–10000?01??1?1 110110100010100011011011000—
<i>Sherbonaspis</i>	010001–100?1001001?1 1??1101000 10200011011010000—
<i>Jiangxilepis</i>	100001–20021000?0?0?1 1?0001101? 10100011111101010—
<i>Kirgisolepis</i>	100000–10021?00?0?1?0 00111?1??? 1010101?111011000—
<i>Stegolepis</i>	110001–10011?01??1?1 110110100?102000011100000X0
<i>Byssacanthus</i>	100001–10020001001?1 1111101001 10100001110000000—
<i>Pterichthyodes</i>	100001–1002100100111010110100010100011011010000—
<i>Hunanolepis</i>	100001–10031001001?1 1101101011101000110110100010
<i>Asterolepis</i>	011001–11011001001111101001001103000101011010000—
<i>Pambulaspis</i>	011001–11011101?01?1 110100?00?10300011010000000—
<i>Remigolepis</i>	011001–1101110100111110100000?10300001010000000—
<i>Ningxialepis</i>	????????? ?1000?0?0?1 01?001101?1?10001?11110?010—

**Appendix 3. Apomorphy list of a selected most parsimonious tree (Fig. 7)**

Ambiguous character states resolved using DELTRAN are marked with an asterisk, reversals are prefixed with a minus sign (–).

- Node 1: 21(0), 22(0), 27(0), 33(3).  
 Node 2: 4, 7, 10, 34\*, 36, 41, 42, 45.  
 Node 3 (Euantiarcha): 1, 5(0), 6, 11(2), 30\*, 31\*, 40.  
 Node 4 (Asterolepidoidei): 15, 48\*, 24, 25, 38.  
 Node 5: 12\*, 19\*.  
 Node 6: 2, 11(2)\*.  
 Node 7: 1(0), 3, 9, 25(0), 33(3).  
 Node 8: 13.  
 Node 9: 37, 41, 43.  
 Node 10: 30(0).  
 Node 11: 21(0).  
 Node 12: 1(0).  
 Node 13 (Bothriolepidoidei): 29, 34\*, 44.  
 Node 14: 12\*, 16\*, 42.  
 Node 15: 8(2), 37\*, 41.  
 Node 16 (Jiangxilepididae): 26, 34(0), 38, 39, 46.  
 Node 17: 5, 20(0).

- Node 18: 33(0).  
 Node 19 (Bothriolepididae): 14, 22(0), 28\*.  
 Node 20: 10\*, 17\*, 21(0), 23, 26\*, 32\*.  
 Node 21: 35.  
 Node 22 (Microbrachiidae): 6(0), 11(3), 12(0), 32\*, 47.  
 Node 23: 48.

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