




A new antiarch placoderm from the Emsian (Early Devonian) of Wuding, Yunnan, China

Zhaohui Pan, Min Zhu, You'An Zhu & Liantao Jia


To cite this article: Zhaohui Pan, Min Zhu, You'An Zhu & Liantao Jia (2018) A new antiarch placoderm from the Emsian (Early Devonian) of Wuding, Yunnan, China, *Alcheringa: An Australasian Journal of Palaeontology*, 42:1, 10-21, DOI: [10.1080/03115518.2017.1338357](https://doi.org/10.1080/03115518.2017.1338357)

To link to this article: <https://doi.org/10.1080/03115518.2017.1338357>

 View supplementary material 

 Published online: 07 Aug 2017.

 Submit your article to this journal 

 Article views: 114

 View Crossmark data 

A new antiarch placoderm from the Emsian (Early Devonian) of Wuding, Yunnan, China

ZHAOHUI PAN , MIN ZHU , YOU'AN ZHU  and LIANTAO JIA 

PAN, Z., ZHU, M., ZHU, Y. & JIA, L., August 2017. A new antiarch placoderm from the Emsian (Early Devonian) of Wuding, Yunnan, China. *Alcheringa* 42, 10–21. ISSN 0311-5518.

Wufengshania magniforamini, a new genus and species of the Euantiarcha (Placodermi: Antiarcha), is described from the late Emsian (Early Devonian) of Wuding, Yunnan, southwestern China. The referred specimens were three-dimensionally preserved in black shales, allowing a high-resolution computed tomography reconstruction of anatomical details. The new euantiararch is characterized by a large orbital fenestra, an arched exoskeletal band around the orbital fenestra and a developed obteched nuchal area of the skull roof. Maximum parsimony analysis, using a revised data-set of antiarchs with 44 taxa and 66 characters, resolves *Wufengshania* gen. nov. as a member of the Bothriolepididae, which is characterized by the presence of the infraorbital sensory canal diverging on the lateral plate, and the nuchal plate with orbital facets. New analysis supports a sister group relationship between *Dianolepis* and the Bothriolepididae. *Luquanolepis*, a coeval euantiararch from the neighboring site of the new form, is referred to the Asterolepidoidei and represents the basalmost and earliest member of the Asterolepidoidei.

Zhaohui Pan* [panzhaohui@ivpp.ac.cn], Min Zhu* [zhumin@ivpp.ac.cn], You'an Zhu† [zhuyouan@ivpp.ac.cn] and Liantao Jia [jialiantao@ivpp.ac.cn] Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing 100044, PR China. *Also affiliated with University of Chinese Academy of Sciences, Beijing, 100049, PR China. †Also affiliated with Uppsala University, PO Box 256, 751 05 Uppsala, Sweden. Received 12.1.2017; accepted 31.5.2017.

Key words: Antiarcha, Placodermi, Early Devonian, HRCT scanning, morphology.

THE ANTIARCHA is currently recognized as the most basal group of gnathostomes or jawed vertebrates (Brazeau 2009, Davis *et al.* 2012, Zhu *et al.* 2012, 2013, Dupret *et al.* 2014, Trinajstić *et al.* 2014, Zhu 2014, Giles *et al.* 2015, Long *et al.* 2015, Qiao *et al.* 2016, Zhu *et al.* 2016a, Zhu *et al.* 2016b), and its origin and early evolution have long been a spotlight issue in the study of early vertebrates (Stensiö 1948, Janvier & Pan 1982, Goujet 1984b, Young 1984, 1986, Ritchie *et al.* 1992, Janvier 1996, Johanson 2002, Arsenault *et al.* 2004, Young 2010, Zhu *et al.* 2012, Long *et al.* 2015). Recent field investigations on the Silurian marine red beds in northwestern Hunan Province indicate that the age of the earliest known antiarch *Shimenolepis graniferus* (Wang, 1991) is the late Ludlow rather than the Wenlock (Zhao *et al.* 2016). Hence, the geological age of antiarchs ranged from the late Ludlow to the end of the Devonian (Zhu 1996, Lukševičs 2001, Olive 2015).

All major groups of antiarchs have been documented in China (Zhao & Zhu 2010). The Antiarcha comprises yunnanolepidoids, *Minicrania*, sinolepids and euantiarchs (Zhu 1996, Zhu & Janvier 1996). Yunnanolepidoids, the earliest known members of the antiarchs, are only known in southern China and northern Vietnam (Liu 1963, Zhang 1978a, Zhang 1980b, Tông-Dzuy & Janvier 1987, Pan &

Dineley 1988). *Minicrania* from the Lower Devonian of Yunnan is a tiny yunnanolepidoid-like form that bears both a preorbital depression and a preorbital recess (Zhu & Janvier 1996). Sinolepids, phylogenetically intermediate between *Minicrania* and euantiarchs, were described from the Middle and Upper Devonian of China and eastern Australia (Liu & P'an 1958, Pan *et al.* 1987, Ritchie *et al.* 1992). Euantiarchs, comprising the Bothriolepidoidei and the Asterolepidoidei, are defined by the well-developed or helmet-shaped brachial process (Young & Gorter 1981, Janvier & Pan 1982, Zhu 1996, Zhu & Janvier 1996). Most of the euantiarchs have a worldwide distribution, especially *Bothriolepis* and *Remigolepis*.

The antiarch *Wudinolepis weni* is the first taxon described from the Early Devonian Jiucheng Formation of Wuding, Yunnan (Zhang 1965) (Fig. 1). However, compared with the diversified arthrodires from the Jiucheng Formation (Wang 1984, Wang & Zhu 1995, Zhu *et al.* 2016b), the rich antiarch specimens have not been studied except the first preliminary report by Zhang (1965) and the study of *Luquanolepis* by Zhang & Young (1992). Here we present a new antiarch from the Jiucheng Formation, *Wufengshania magniforamini* gen. et sp. nov., based on the specimens collected by the present authors in the summer of 2014. *Wufengshania* resembles *Dianolepis* (Zhang, 1965) with large orbital fenestra bordered by convex skull bones. In other regards (e.g., the presence of the branch of the infraorbital sensory canal diverging on the lateral plate

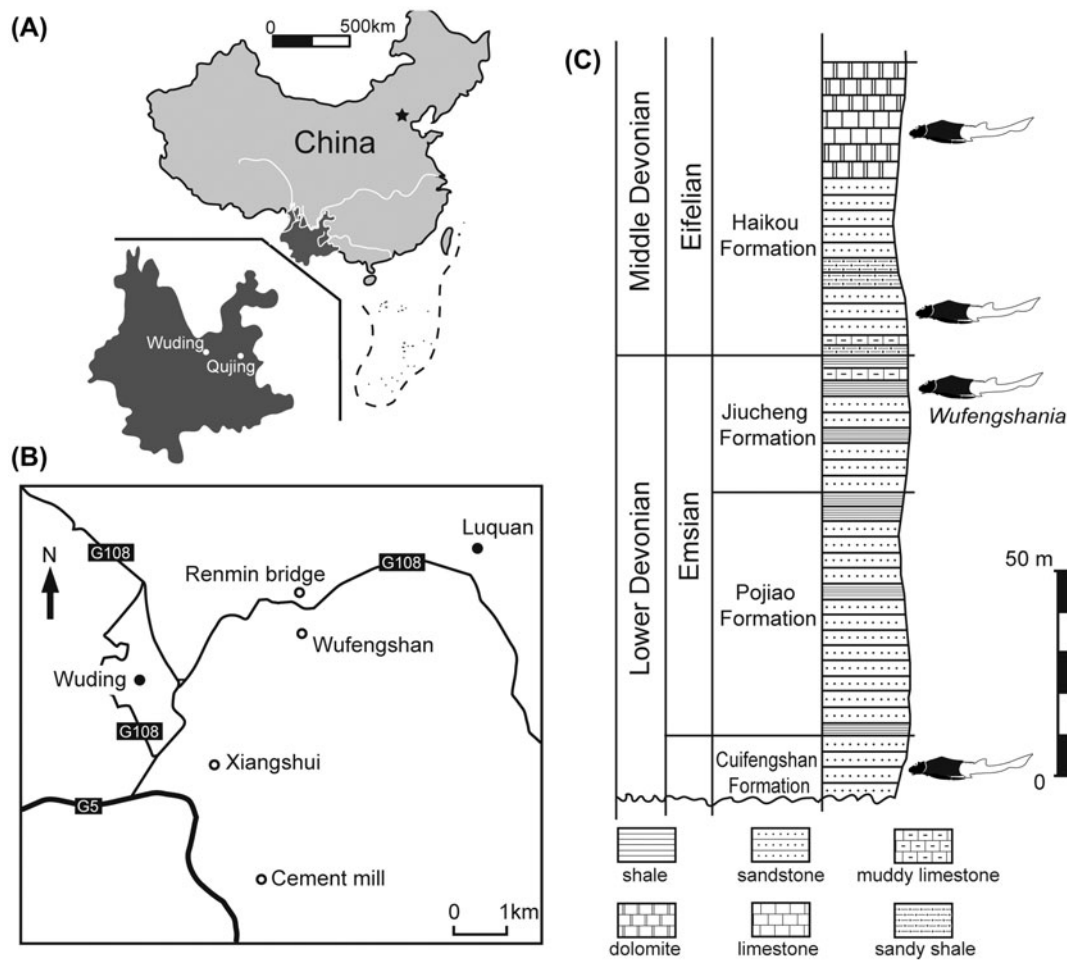


Fig. 1. A, Map of China, with emphasis on Yunnan province. B, Geographic map showing the section locality of the fish-bearing strata around Wuding, Yunnan Province. C, Early Devonian sequence in Wuding area (Yunnan, China), showing the stratigraphic position of *Wufengshania magniforaminis*.

and the nuchal plate with orbital facets), it is more *Bothriolepis*-like. The main goals of the present study are to provide a detailed description of *Wufengshania magniforaminis* gen. et sp. nov. and to discuss its phylogenetic position within the Euanthropia.

Material and methods

The holotype and the paratype of *Wufengshania magniforaminis* were collected from the black shale of the Jiucheng Formation exposed on Wufengshan (Wufeng Hill in Chinese, 25°32'30"N, 102°25'57"E), Wuding, Yunnan. The fish-bearing horizon is referred to the late Emsian in age (Wang 1984, Wang & Zhu 1995, Zhao & Zhu 2010).

A continuous fossiliferous Devonian succession, comprising the Cuifengshan, Pojiao, Jiucheng and Haikou formations in ascending chronological order, is well exposed in Wuding, Yunnan (Fig. 1). The succession contains many placoderm fossils, mainly from the Jiucheng and Haikou formations as well as rich invertebrate and plant remains (Liu & Wang 1973, Wang & Zhu 1995). The fossil fishes from the Jiucheng Formation include *Wudinolepis weni* (Zhang, 1965), *Exutaspis*

megista (Pan & Dineley, 1988), *Jiuchengia longocipita* (Wang & Wang, 1983), *Ynostius major* (Wang & Wang, 1984, Zhu *et al.*, 2016b), *Holonema* sp. (Wang, 1984) and *Xiangshuiosteus wui* (Wang, 1992). The fossil fishes from the Haikou Formation include *Bothriolepis tungseni* (Zhang, 1965), *Hunanolepis tieni* (P'an *et al.*, 1978), *Xichonolepis qujingensis* (Zhang, 1980a, Ritchie *et al.*, 1992), *Dianolepis liui* (Zhang, 1965) and some sarcopterygians (Wang & Zhu 1995).

The specimens were not prepared mechanically. We scanned the specimens directly using the 225 kV high-resolution computed tomography (HRCT) apparatus (developed by the Institute of High Energy Physics, Chinese Academy of Sciences) at the Key Laboratory of Vertebrate Evolution and Human Origins, Chinese Academy of Sciences (CAS), with a voltage of 150 kV and current of 120 mA, at a resolution of 14.11 µm per pixel. All scans were using a 360° rotation with a step size of 0.5° and an unfiltered aluminum reflection target. A total of 720 transmission images were reconstructed in a matrix of 1536 slices each measuring 2048 × 2048 pixels, using two-dimensional reconstruction software (IVPP225KVCT Reconstruction) developed by the Institute of High Energy Physics, CAS. Three-dimensional

reconstructions were then generated using Mimics (Materialize version 18), and images of reconstructions were exported from Mimics and finalized in Adobe Photoshop and Adobe Illustrator.

To explore the phylogenetic position of *Wufengshania*, we conducted a phylogenetic analysis using a modified data-set with 66 characters and 44 taxa (see supplementary data). This data-set is based on that of Zhu (1996) and Jia *et al.* (2010). The data matrix was composed by Mesquite version 2.73 (Maddison & Maddison 2008). *Kujdanowiaspis* was designated as out-group for state character polarization (Goujet 1984a, Dupret 2010). The data-set was subjected to the maximum parsimony analysis in TNT software package version 1.5 (Goloboff *et al.* 2008). The analysis was conducted using a traditional search strategy, with default settings apart from the following: 10 000 maximum trees in memory and 1000 replications. MacClade 4.0 (Maddison & Maddison 2000) was used to trace the character transformation in the selected cladogram.

Anatomical abbreviations. **alc**, anterolateral angle of skull roof; **aSM**, attachment area for submarginal plate; **aSO**, attachment area for suborbital plate; **a1SM**, anterior attachment area for submarginal plate; **a2SM**, posterior attachment area for submarginal plate; **cr.pm**, paramarginal crista of skull roof; **cr.pto**, postorbital crista of skull roof; **cr.tv**, transverse nuchal crista of skull roof; **cs1**, central sensory canal; **d.end**, opening of canal for endolymphatic duct; **fe.orb**, orbital fenestra; **fm**, unpaired insertion fossa on skull roof for levator muscles; **g**, pit on postpineal plate; **gr**, groove on postpineal plate; **gr.asc**, groove for ridge bordering anterior semicircular canal; **gr.psc**, groove for ridge bordering posterior semicircular canal; **ifc**, infraorbital sensory canal on skull roof; **ifc1**, principal section of infraorbital sensory canal on skull roof; **ifc2**, branch of infraorbital sensory canal diverging on lateral plate; **L**, lateral plate; **lpr**, lateral process of skull roof; **me**, median elevation inside rostral margin of premedian plate; **mpl**, middle pit line; **mr**, middle ridge of postpineal plate; **nm**, obtected nuchal area of skull roof; **npri**, prelateral notch of skull roof; **Nu**, nuchal plate; **occ**, occipital cross-commissure; **per**, perichondral bone; **PM**, postmarginal plate; **PNu**, paranuchal plate; **PP**, postpineal plate; **ppl**, posterior pit line; **prh**, preorbital recess of skull roof; **PrM**, premedian plate; **pr.nm**, obtected nuchal process of skull roof; **pr.po**, depression on skull roof for dorsal face of endocranial postorbital process; **ri**, oblique premedian ridge of skull roof; **sg**, spiracle groove; **soa**, suborbital area of skull roof; **soc**, anterior section of supraorbital sensory canal on premedian plate; **so**, supraotic thickening of skull roof.

Systematic palaeontology

ANTIARCHA Cope, 1885

EUANTIARCHA Janvier & Pan, 1982

BOTHRIOLEPIDIDAE Cope, 1886

Wufengshania gen. nov.

Wufengshania magniforaminis sp. nov.

Holotype. IVPP V 23293 (Fig. 2A), a near-complete skull with a minor part of the right half missing.

Paratype. IVPP V 23294 (Fig. 2B), a near-complete skull with part of the right lateral plate missing.

Etymology. Genus is named from Wufengshan, the fossil site. The specific epithet is derived from *magnus* (Latin, large) and *foraminis* (Latin, fenestra or hole), referring to the large orbital fenestra of the species.

Type locality and horizon. Wufengshan (close to Wufengshan cemetery), Wuding, Yunnan Province, China; Jiucheng Formation; late Emsian, Early Devonian.

Diagnosis. A bothriolepid antiarch of small size, with length of skull roof less than 15 mm; breadth/length ratio of skull roof nearly 1.00; length ratio between orbital fenestra and skull roof about 0.52; preorbital recess semicircular in shape, and roof of preorbital recess convex; postpineal plate arched and large; breadth/length ratio of premedian plate about 1.20; dorsal surface of nuchal plate with X-shaped domed ridges; supraorbital sensory canal developed as a short groove disjoined from infraorbital sensory canal; occipital cross-commissure short; obtected nuchal area of skull roof developed; skull roof ornamented by irregularly arranged tubercles.

Remarks. *Wufengshania* gen. nov. differs from *Bothriolepis* and *Monarolepis* which have a weakly development obtected nuchal area of the skull. *Wufengshania* differs from *Dianolepis* by the presence of the supraorbital canal and the infraorbital sensory canal branching on the lateral plate. *Wufengshania* is distinct from *Wudinolepis* in its large size of the orbital fenestra relative to the skull roof and irregularly distributed tubercles. Thus, the assignment of the new material to a new bothriolepidoid genus is here justified.

Description. The skull roof of *Wufengshania magniforaminis* is known from two specimens as molds. The HRCT reconstruction of the holotype (IVPP V23293) (Figs 3A, 4A) exhibits most of its dorsal surface and ventral structures in part. The HRCT reconstruction of the paratype (IVPP V23294) (Fig. 4B) shows some details in ventral view and the ornamentation of the premedian plate. Combining these two specimens, we restored the skull roof of the new fish in its dorsal and ventral aspects (Figs 3B, 4C). The skull roof has a maximum length of 14.6 mm, and the length along the midline is 14.1 mm. The breadth/length ratio of the skull roof is about 1.03, comparable with that of *Dianolepis liui* (Zhang, 1965).

The ornament of the skull roof is composed of irregularly arranged tubercles. The skull roof is arched both

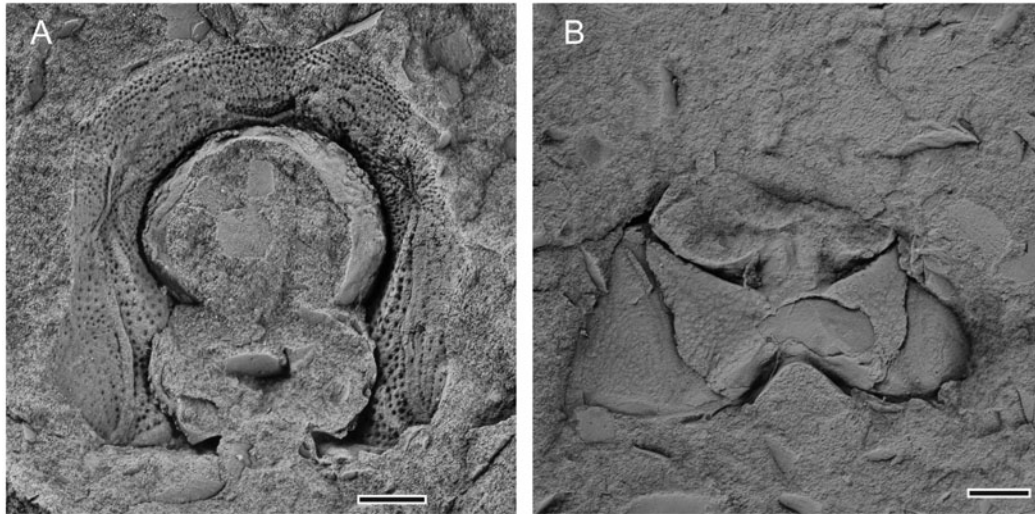


Fig. 2. *Wufengshania magniforamini* gen. et sp. nov., Wuding, Yunnan, China, late Emsian. Scale bars: 2 mm. **A**, Photo of the holotype IVPP V 23293. **B**, Photo of the paratype IVPP V 23294.

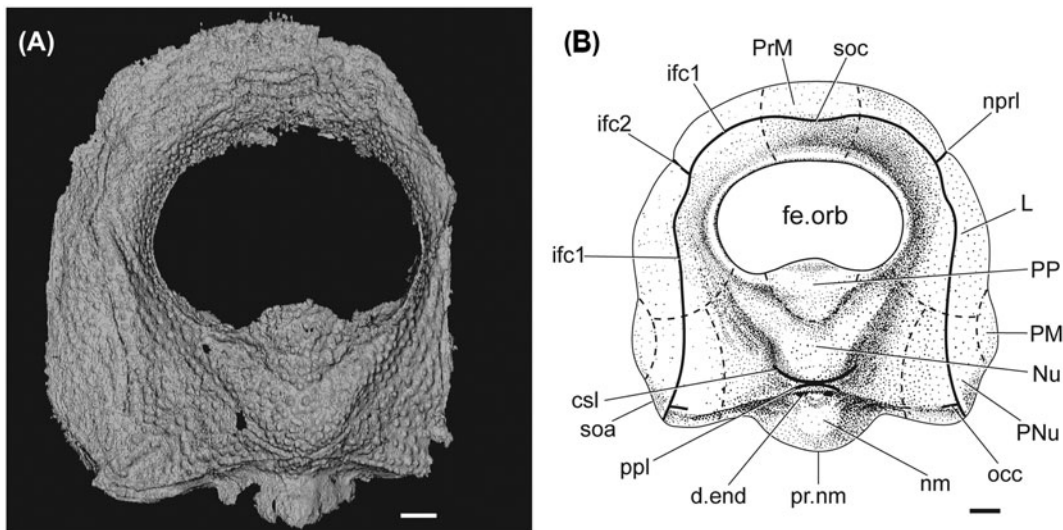


Fig. 3. Reconstructions of *Wufengshania magniforamini*, Wuding, Yunnan, China, late Emsian. Scale bars: 1 mm. **A**, 3D reconstruction of the paratype in the dorsal view. **B**, Illustrative restoration of the skull roof in the dorsal view.

rostrocaudally and transversely. Its sagittal section shows the greatest convexity on the nuchal and post-pineal plates (Fig. 3A, B). The rostral margin is straight to gently convex and lacks a rostral angle. The large orbital fenestra (fe.orb, Fig. 3A, B) is oval in shape, with a maximum length of 4.7 mm and a maximum breadth of 7.5 mm.

The orbital fenestra occupies an anterior position on the dorsal surface of the skull roof, unlike that of *Bothriolepis* (Miles, 1968, Young, 1988) which is somewhat posteriorly set. The narrow band of the skull roof forming the anterior margin of the orbital fenestra is arched, as in *Dianolepis* (Zhang, 1965) and *Bothriolepis* (Gross, 1933, Stensiö, 1948), and roofs the preorbital recess (prh, Figs 3B, 6). The tubercles on this band are denser and smaller than those on the rest of the skull roof. The anterolateral angle (alc, Fig. 3B) and lateral

process (lpr, Fig. 3B) of the skull roof are barely developed. The prelateral notch (npr, Fig. 3B) is similar to that in *Bothriolepis* (Miles, 1968).

The sutures between the premedian and lateral plates are indistinct in dorsal view. However, the premedian plate occupies an area corresponding to the median elevation (me, Fig. 4C) on the ventral side of the skull roof, which is delimited by the oblique premedian ridges of the skull roof (ri, Fig. 4C).

The postpineal plate has a length/breadth index of 82. It possesses a convex orbital margin that projects into the orbital fenestra. The orbital margin processes a raised crest as in some other antiarchs. Neither unornamented shelf nor rostrocaudal groove could be identified on the premedian plate.

The nuchal plate exhibits two pairs of oblique ridges in dorsal view, which correspond to the underlying

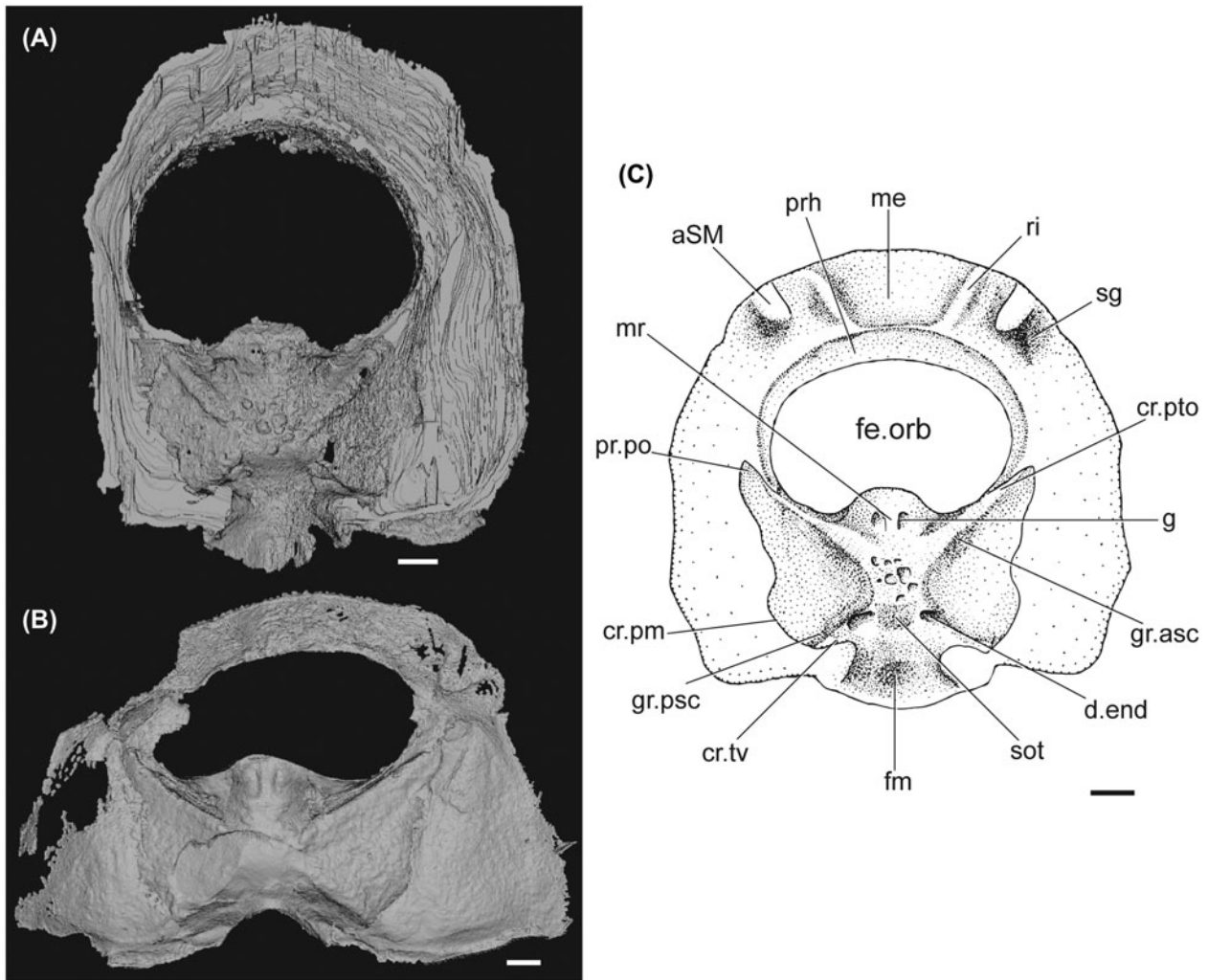


Fig. 4. Reconstructions of *Wufengshania magniforamini*, Wuding, Yunnan, China, late Emsian. Scale bars: 1 mm. **A**, 3D reconstruction of the dorsal view of the holotype. **B**, 3D reconstruction of the ventral view of the paratype. **C**, Illustrative restoration of the skull roof in the ventral view.

semicircular ridges of the braincase topologically (gr.asc, gr.psc, Fig. 4C). These dorsal ridges were known in the antiarch *Minicrania lirouyii* (Zhu & Janvier, 1996), as well as in arthrodiros (e.g., *Szealepis*, *Dicksonosteus*, Liu, 1979, Goujet, 1984a) and petalichthyids (e.g., *Diandongpetalichthys*, Zhu, 1991). The endolymphatic ducts in the skull roof can be traced by segmentation. They ascend dorsally through the nuchal plate and have their exits on the dorsal surface (d.end, Fig. 5) immediately behind the posterior pit lines and the highly developed supraotic thickening of the skull roof (sot, Fig. 4C). The nuchal plate has short orbital facets. At the posterior end of the nuchal plate, the obtected nuchal area of the skull roof (nm, Fig. 4A) is fairly large with a domed surface. Posteriorly, this area steps down to an unornamented lamina, which is termed the posterior descending lamina of the nuchal plate in petalichthyids (Liu 1991, Pan *et al.* 2015). The posterior process of the skull roof (pr.nm, Fig. 3A) is well developed.

The suborbital area of the skull roof (soa, Fig. 3B) is constrained in the paranuchal plate. The

obtected area on the paranuchal plate is steeply inclined with respect to the external bone surface. The post-marginal plate is small and lozenge-shaped.

The sensory canals are evident in the HRCT reconstruction of the skull roof (Fig. 3A). The pattern of sensory canals in *Wufengshania* resembles that in *Bothriolepis* (Miles, 1968, Young, 1988). The infraorbital sensory canal (ifc1, Fig. 3B) is exposed as a narrow groove, but its lateral branch is less distinct (ifc2, Fig. 3B). The supraorbital sensory canal (soc, Fig. 3B) is continuous with the infraorbital sensory canal and presents a shallow groove near the midline of the premedian plate. The occipital cross-commissure (occ, Fig. 3B), which was termed as the middle pit line in antiarchs (Stensiö 1948, Miles 1968, Young 1988), extends posteromedially from the infraorbital sensory canals. No circular sensory canal can be identified. The central sensory canals (csl, Fig. 3B) are restricted in the central part of the nuchal plate. They converge posteriorly and meet the posterior pit lines (ppl, Fig. 3B), which used to be termed as the supraoccipital cross-commissure in antiarchs (Stensiö 1948, Miles 1968,

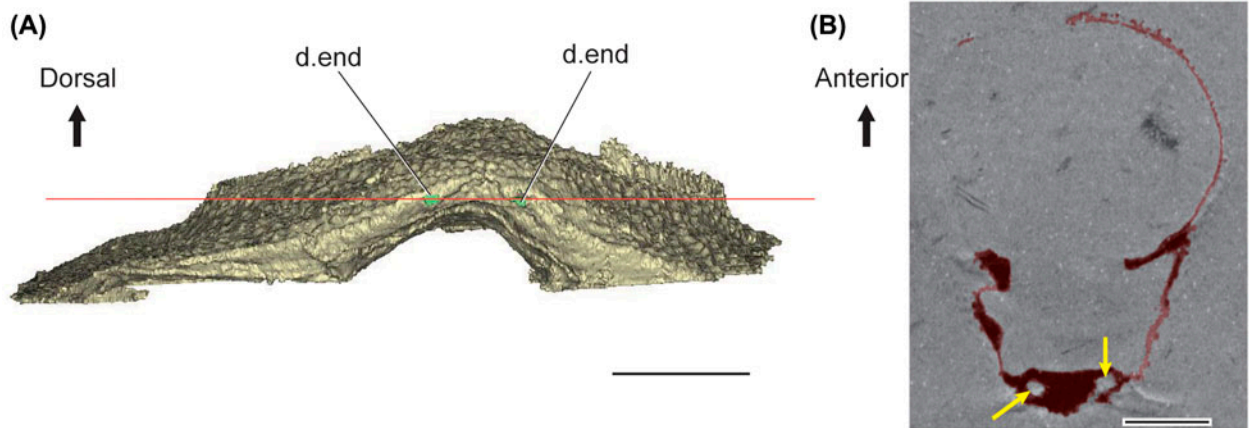


Fig. 5. Illustration of the openings of endolymphatic ducts. Scale bars: 2 mm. **A**, Posterior view of the 3D reconstruction of the holotype. Red line points to the position of the tomographic image presented in **B**. **B**, Tomographic image of the holotype. Yellow arrows point to the positions of the endolymphatic ducts.

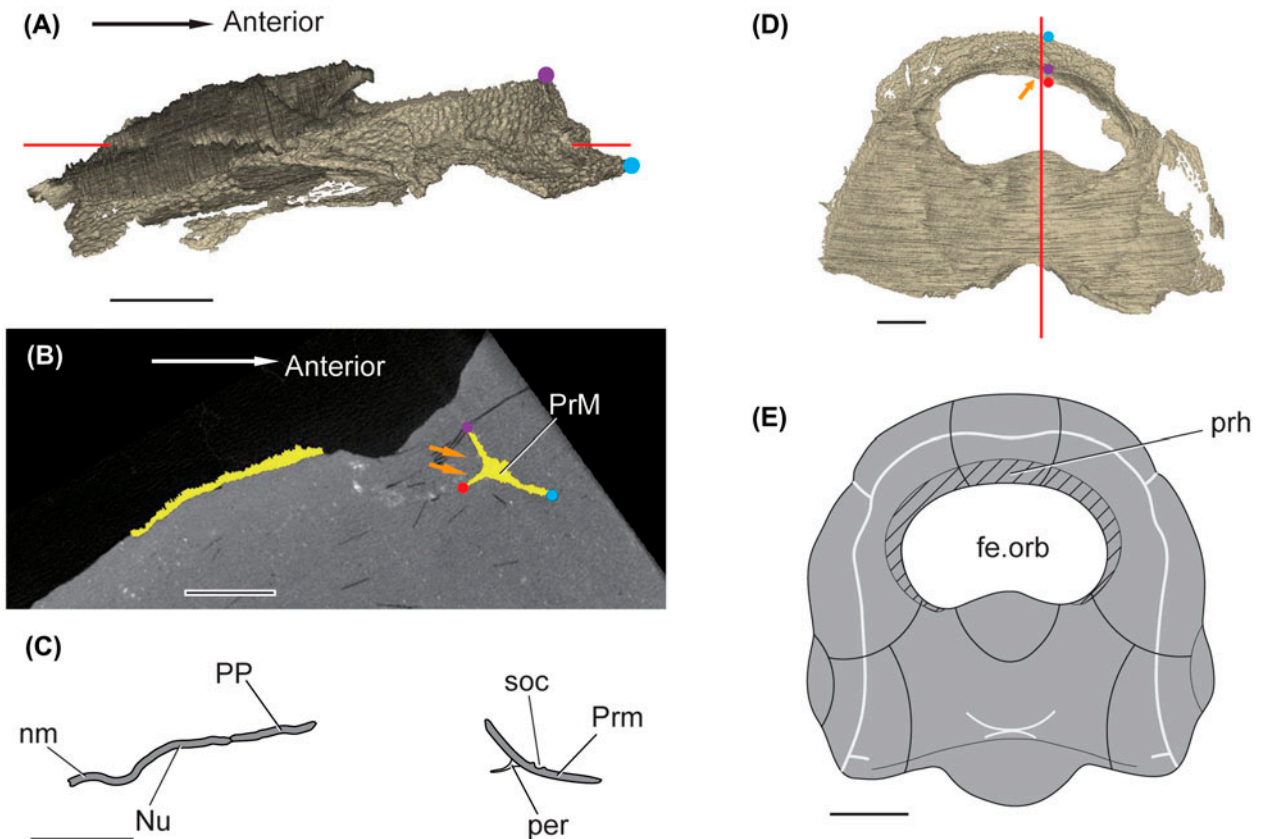


Fig. 6. Illustration of the preorbital recess. Scale bars: 2 mm. **A**, Lateral view of the 3D reconstruction of the paratype. Red line points to the position of the tomographic image presented in **B**. **B**, Tomographic image of the holotype. **C**, Interpretative drawing of the preorbital recess situated within a reconstructed cross-section of the skull. **D**, Dorsal view of the 3D reconstruction of the paratype. Red line points to the position of the tomographic image. **E**, Preorbital recess positioned in a silhouette of the skull.

Young 1988). The posterior pit lines of both sides diverge posteriorly and terminate in front of the obstructed nuchal area.

The visceral surface of the skull roof (Fig. 4) is partly restored owing to the incomplete preservation. The median rostral elevation (me, Fig. 4C) is weakly developed. The orbital fenestra is well defined. The preorbital recess of *Wufengshania* (Figs 4C, 6) is similar to that of *Micro-*

brachius chuandongensis (Wang & Zhang, 1999) in its narrow shape and extension (i.e., extending laterally onto the lateral plates). Two asymmetrical pits are separated by a median ridge on the postpineal plate. The shape of the otico-occipital depression, which corresponds to the otico-occipital region of the braincase, is similar to that of *Bothriolepis* (Stensiö, 1948, Miles, 1968, Young, 1988, Moloshnikov, 2004). This depression is characterized by

a pair of grooves, corresponding to the ridges bordering anterior and posterior semicircular canals of the labyrinth. The transverse nuchal crista (cr.tv, Fig. 4C) is well developed. The anterior part of the otico-occipital depression is preserved to show the structures housing a pair of postorbital processes (pr.po, Fig. 4C), which extend anterolaterally and almost level with the halfway of the orbital fenestra. The anterior margin of the otico-occipital depression is bounded by the postorbital crista (cr.pto, Fig. 4C). The supraotic thickening is present. The lateral margin of the otico-occipital depression is bounded by the paramarginal crista (cr.pm, Fig. 4C). The endolymphatic duct openings are conspicuous as large and deep cavities (d.end, Fig. 5). In the posterior region of the visceral surface, an unpaired insertion fossa (fm, Fig. 4B) is developed for levator muscles. The articular area for the submarginal plate (aSM, Fig. 4C) is represented by an anterolaterally extending thickening in front of the spiracular groove (sg, Fig. 4C).

Discussion

Comparison with Dianolepis. In *Dianolepis* (Fig. 7A, B), the sutures of the skull roof plates are distinct. The premedian plate of *Dianolepis* is similar to that of *Wufengshania* in shape, with its length ratio relative to the skull roof evidently shorter than that of *Bothriolepis* (Stensiö, 1948, Miles, 1968, Young, 1988). The prelateral notch of the lateral plate is not developed. The posterolateral corners and the anterolateral angle of the skull roof are absent. The oval-shaped orbital fenestra relative to the skull roof is larger than that of *Bothriolepis* but smaller than that of *Wufengshania* (Fig. 8). The proportion of the orbital fenestra area to the skull roof area is about 16.0% in *Wufengshania*, which is the largest in the known antiarchs. Like the other euantiarchs, the orbital fenestra in *Wufengshania* and *Dianolepis* is situated more posteriorly than that in *Yunnanolepis* (Fig. 8). An arched exoskeletal band encircles the orbital fenestra in *Dianolepis*, but it is not as developed as that of *Wufengshania*. The postpineal plate of *Dianolepis* is comparable with that of *Wufengshania* in forming the posterior margin of the orbital fenestra. The orbital facet of the nuchal plate is absent in *Dianolepis* but is present in *Bothriolepis* and *Wufengshania*. Unlike that of *Wufengshania*, the obtected nuchal area of the nuchal plate (nm, Fig. 7B) is short in *Dianolepis*.

The sensory canals of *Dianolepis* are distinguishable. However, neither semicircular pit line nor supraorbital sensory canal can be identified. The infraorbital sensory canal (ifc, Fig. 7B) does not branch on the lateral plate. The occipital cross-commissure (occ, Fig. 7B) is visible. The central sensory canal (csl, Fig. 7B) is much longer than that of *Wufengshania*, but it is still limited on the nuchal plate. It extends postero-medially and meets the posterior pit line (ppl, Fig. 7B).

In visceral view (Fig. 7C, D), the skull roof of *Dianolepis* bears a narrow obtected area anteriorly, which represents an attachment for the suborbital plate (aSO, Fig. 7D). Unlike that of *Bothriolepis* (Stensiö, 1948, Young, 1988), the articular area for the submarginal plate is subdivided into two segments. The first articular area (a1SM, Fig. 7D) is supported by a transverse prelateral crista, whereas the second articular area (a2SM, Fig. 7D) extends along the lateral margin of the skull roof. The first articular area in *Wufengshania* is much more developed than that in *Dianolepis*. As the corresponding part for the second articular area is missing in *Wufengshania*, it is unknown whether *Wufengshania* has one or two articular areas for the submarginal plate. The depression for the postorbital process does not extend to the anterior margin of the orbital fenestra in *Dianolepis*, unlike that in *Bothriolepis*.

The preorbital recess of *Dianolepis* can be traced in front of the orbital fenestra in visceral view. Both *Dianolepis* and *Wufengshania* possess the simple semicircular preorbital recess as defined by Long (1983) and Young (1988). However, the proportion of the preorbital recess of *Dianolepis* is much larger than that of *Wufengshania*.

Remarks on the data-set. Zhu (1996) compiled the matrix of antiarchs with 66 characters, 40 antiarch taxa and two outgroup taxa. Here we expanded the data-set of Zhu (1996) with the addition of three taxa (*Parayunnanolepis*, *Ningxialepis*, and *Wufengshania*), deleted an unnamed taxon and revised some codings. The expanded data-set with 44 taxa and 66 characters is the most comprehensive morphological matrix for antiarchs constructed to date.

Phylogenetic analysis. Janvier and Pan (1982) proposed the first phylogeny of the Antiarcha and grouped the sinolepids, bothriolepidoids and asterolepidoids in the Euantiarcha, which was characterized by the presence of a brachial process. Ritchie *et al.* (1992) proposed that the pectoral articulation of sinolepids is represented by a primitive structure, which pivoted around a single axis passing through the articulation. It is very different from the brachial articulation of bothriolepidoids and asterolepidoids, which bears a large helmet-shaped brachial process, with the dorsal and ventral articulations developed as deep hemispherical grooves separated anteriorly by the narrow *pars pedalis* of the brachial process. As such, they placed sinolepids outside euantiarchs, and this classification was followed by Janvier (1996) and Zhu (1996). To date, the most comprehensive phylogenetic study of antiarchs is proposed by Zhu (1996), which proposed three types of pectoral fin articulation: simple type, sinolepid type and euantiarch type. By outgroup comparison, the simple type in yunnanolepidoids is plesiomorphic for antiarchs. The sinolepid type is suggested to be derived from the simple one with a simple

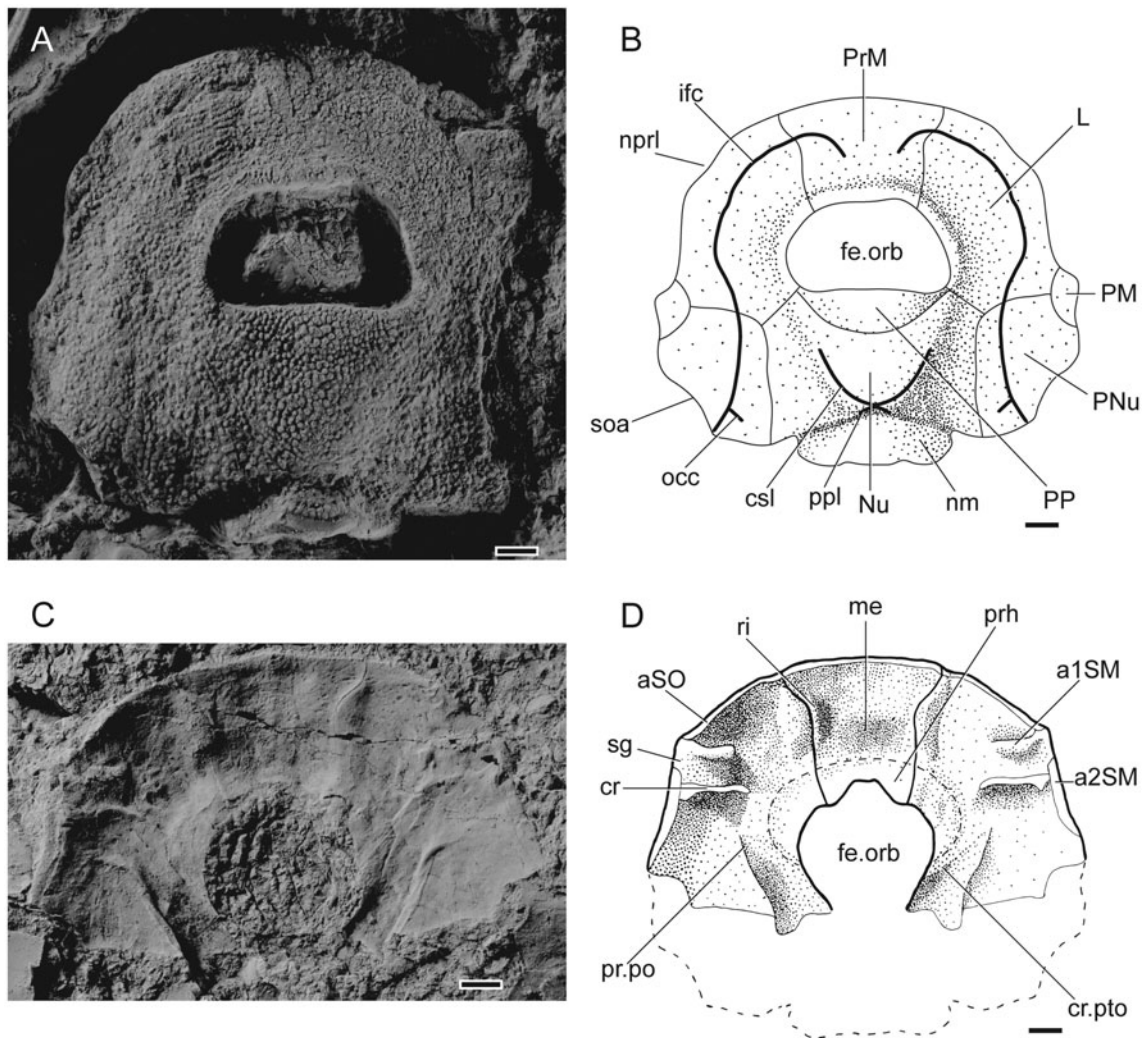


Fig. 7. *Dianolepis liui*, Wuding, Yunnan, China, Eifelian. Scale bars: 5 mm. **A**, Photo of IVPP V 2966.1. **B**, Illustrative restoration of the skull roof in dorsal view, IVPP V 2966.1. **C**, Photo of IVPP V 2966.3. **D**, Illustrative restoration of the skull roof in ventral view, IVPP V 2966.3.

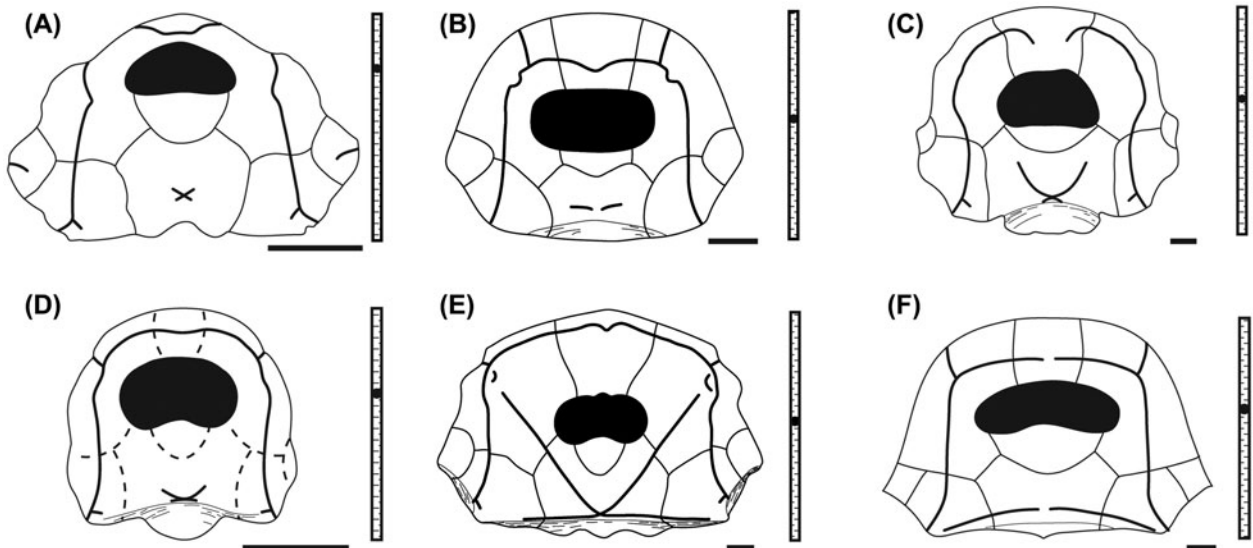


Fig. 8. Comparison of the orbital fenestra in euantriarchs. Scale bars: 5 mm. **A**, *Yunnanolepis parvus* (after Zhang, 1980b). **B**, *Tenizolepis rara* (after Moloshnikov 2012). **C**, *Dianolepis liui*. **D**, *Wufengshania magniforamini* gen. et sp. nov. **E**, *Bothriolepis canadensis* (after Stensiö, 1948). **F**, *Jiangxilepis longibrachius* (after Zhang, 1991). The vertical bar shows the relative lengths of the regions that make up the skull, and the small circle denotes the center of the orbital fenestra.

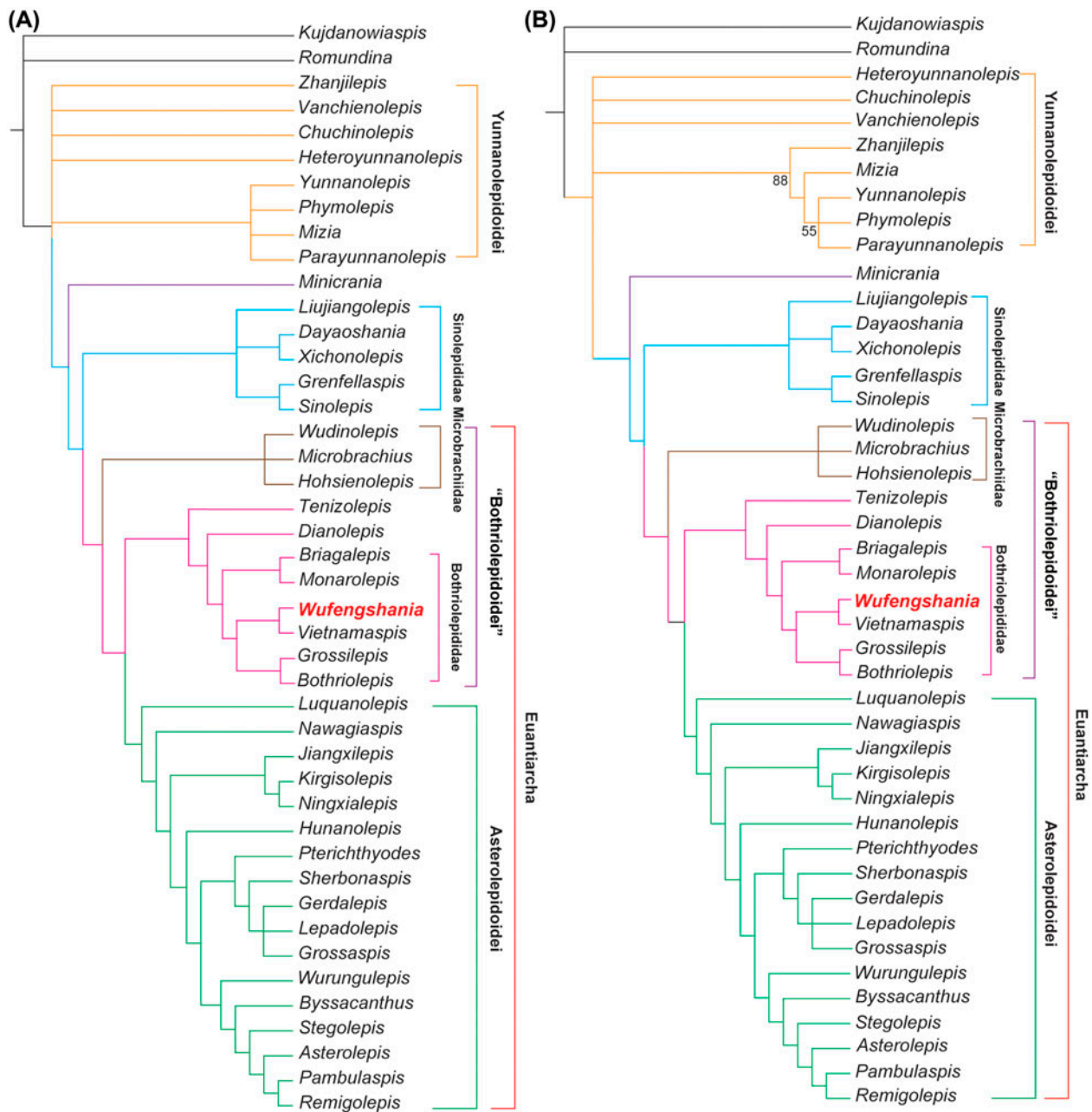


Fig. 9. **A**, Strict consensus tree of the 18 most parsimonious trees based on the data-set revised from Zhu (1996). **B**, 50% majority-rule consensus tree of the 18 most parsimonious trees. Numbers on branches indicate the percentage of most parsimonious trees that contain a particular clade (100% unless otherwise indicated).

brachial process. The euantiarcho type is more advanced with a helmet-shaped brachial process.

In order to resolve the systematic position of *Wufengshania magniforamini* within antiarchs and the relationship between *Dianolepis* and *Wufengshania*, a TNT-based phylogenetic analysis was performed. The maximum parsimony analysis using the revised data-set produces 18 most parsimonious trees of 168 steps [CI = 0.4405; HI = 0.5595; RI = 0.7707; RC = 0.3395]. These trees are summarized as a strict consensus tree (Fig. 9A) and a 50% majority-rule consensus tree (Fig. 9B). One of the 18 most parsimonious trees is selected to illustrate inferred character transformations at various nodes (Supplementary Data).

In the new scenario, *Luquanolepis* (Zhang & Young, 1992) is considered to be a member of the Asterolepidoidei with the support of the index between the width of the anterior margin and the maximum width of the anterior median plate ranging from 35 to 55, the narrow lateral plate and the long anterior process of the post-suborbital plate.

Our analysis consistently corroborates the paraphyly of the Bothriolepidoidei (Zhu 1996). *Grossilepis* is placed as the sister group of *Bothriolepis* with the support of the large axillary foramen, the small orbital fenestra and the endocranial postorbital process extending in front of the orbital fenestra. *Monarolepis* (Young & Gorter, 1981, Young, 1988) is placed as the sister group

of *Briagalepis* (Long *et al.*, 1990) with the support of the anterior median dorsal plate partly overlapping the anterior dorsolateral plate, and the absence of X-shaped canals.

Wufengshania is placed as the sister group of *Vietnamaspis* (Long *et al.*, 1990) with the support of the presence of the supraorbital sensory canal, and a long and narrow premedian plate. *Dianolepis* is placed as the sister group of the Bothriolepididae with the support of the presence of central sensory canals.

Wudinolepis, *Microbrachius* and *Hohsienolepis* are included in the Microbrachiidae, a monophyletic group supported by six synapomorphies: the large axillary foramen, the adult ornamentation ridged on the dorsal wall of trunk-shield, the presence of central sensory canals, the occipital cross-commissure issued from the infraorbital sensory canal extending on the nuchal plate, the preorbital recess restricted to the premedian plate, and the posterior position of the orbital fenestra. The Microbrachiidae is considered to be the most basally clade of the Euantriarcha. However, the taxa in the Microbrachiidae fall into a polytomy, and the restudy of *Wudinolepis weni* Zhang, 1965 will help to resolve the interrelationships of the Microbrachiidae. *Minicrania* is assigned to the sister group of the Sinolepididae plus the Euantriarcha. The interrelationships of the Yunnanolepidoidei are unsolved in the cladogram. This unsolved clade calls for further morphological descriptions of many yunnanolepidoids, such as *Phymolepis* (Zhang, 1978a, 1978b) and *Parayunnanolepis* (Zhang *et al.*, 2001, Zhu *et al.*, 2012).

Conclusions

Wufengshania magniforamini gen. et sp. nov. from Wuding, Yunnan, China represents a new member of the Euantriarcha with the arched exoskeletal band around the orbital fenestra. The skull roof of *Wufengshania* shows typical bothriolepidid characters such as the presence of the preorbital recess and the nuchal plate with orbital facets. With respect to the visceral surface of the skull roof, *Wufengshania* resembles *Dianolepis* rather than *Bothriolepis* in the endocranial postorbital process not extending in front of the orbital fenestra.

An expanded data-set with 44 taxa and 66 characters, which is the most comprehensive morphological matrix for antiarchs constructed to date, is presented. The phylogenetic analysis based on the revised data-set confirms the Bothriolepidoidei as a paraphyletic group. It also resolves *Dianolepis* as the sister group of Bothriolepididae, *Wufengshania* as the sister group of *Vietnamaspis* and *Luquanolepis* as a basal member of the Asterolepidoidei. There are still some unsolved clades (e.g., the Yunnanolepidoidei) in the current analysis, partly because the visceral morphologies of the dermal bones are unknown. Luckily, the non-destructive technologies in the fossil investigation, such as high-resolution computed

tomography and X-ray synchrotron radiation microtomography, make it easy to extract further morphological information, which would be helpful for solving the antiarch interrelationships.

Acknowledgements

We thank W. J. Zhao, Z. K. Gai and Y. J. Wang, for discussions, and Y. M. Hou, for HRCT scanning.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This research was funded by National Natural Science Foundation of China [grant number 41530102], [grant number 41672006], [grant number 41572108]; Key Research Program of Frontier Sciences of CAS [grant number QYZDJ-SSW-DQC002]; Strategic Priority Research Program of CAS (grant number XDPB05); CAS Funds for Paleontology Fieldwork and Fossil Preparation.

Supplemental material

The supplemental material for this paper is available online at <https://doi.org/10.1080/03115518.2017.1338357>

ORCID

Zhaohui Pan  <http://orcid.org/0000-0003-4321-3834>
 Min Zhu  <http://orcid.org/0000-0002-4786-0898>
 You'An Zhu  <http://orcid.org/0000-0002-6911-540X>
 Liantao Jia  <http://orcid.org/0000-0002-7018-7996>

References

- ARSENAULT, M., DESBIENS, S., JANVIER, P. & KERR, J., 2004. New data on the soft tissues and external morphology of the antiarch *Bothriolepis canadensis* (Whiteaves, 1880) from the Upper Devonian of Miguasha, Quebec. In *Recent Advances in the Origin and Early Radiation of Vertebrates*. ARRATIA, G., WILSON, M.V.H. & CLOUTIER, R., eds, Verlag Dr. Friedrich Pfeil, München, 439–454.
- BRAZEAU, M.D., 2009. The braincase and jaws of a Devonian 'acanthodian' and modern gnathostome origins. *Nature* 457, 305–308.
- COPE, E.D., 1885. The position of *Pterichthys* in the system. *American Naturalist* 19, 289–291.
- COPE, E.D., 1886. An interesting connecting genus of Chordata. *American Naturalist* 20, 1027–1031.
- DAVIS, S.P., FINARELLI, J.A. & COATES, M.I., 2012. *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes. *Nature* 486, 247–250.
- DUPRET, V., 2010. Revision of the genus *Kujdanowiaspis* Stensiö, 1942 (Placodermi, Arthrodira, "Actinolepida") from the Lower Devonian of Podolia (Ukraine). *Geodiversitas* 32, 5–63.
- DUPRET, V., SANCHEZ, S., GOUJET, D., TAFFOREAU, P. & AHLBERG, P.E., 2014. A primitive placoderm sheds light on the origin of the jawed vertebrate face. *Nature* 507, 500–503.
- GILES, S., FRIEDMAN, M. & BRAZEAU, M.D., 2015. Osteichthyan-like cranial conditions in an Early Devonian stem gnathostome. *Nature* 520, 82–85.
- GOLOBOFF, P.A., CARPENTER, J.M., ARIAS, J.S., ESQUIVEL, D. & ESQUIVEL, M., 2008. Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics* 24, 758–773.
- GOUJET, D.F., 1984a. *Les poissons placodermes du Spitsberg. Arthrodira Dolichothoraci de la Formation de Wood Bay (Dévonien*

- inférieur*). In Vol. 15. Paris Editions Centre National Recherche Scientifique, Cahiers de Paléontologie, Paris, 1–284.
- GOUJET, D.F., 1984b. Placoderm interrelationships: A new interpretation, with a short review of placoderm classifications. *Proceedings of the Linnean Society of New South Wales* 107, 211–243.
- GROSS, W., 1933. Die Fische des baltischen Devons. *Palaeontographica Abteilung A* 79, 1–74.
- JANVIER, P., 1996. *Early vertebrates*. Clarendon Press, Oxford.
- JANVIER, P. & PAN, J., 1982. *Hyrceanaspis blickei* n. g. n. sp., a new primitive euantriarch (Antiarcha, Placodermi) from the Middle Devonian of northeastern Iran, with a discussion on antiarch phylogeny. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 164, 364–392.
- JIA, L.T., ZHU, M. & ZHAO, W.J., 2010. A new antiarch fish from the Upper Devonian Zhongning Formation of Ningxia, China. *Palaeoworld* 19, 136–145.
- JOHANSON, Z., 2002. Vascularization of the osteostracan and antiarch (Placodermi) pectoral fin: similarities, and implications for placoderm relationships. *Lethaia* 35, 169–186.
- LIU, Y.H., 1963. On the Antiarchi from Chutsing, Yunnan. *Vertebrata Palasiatica* 7, 39–46.
- LIU, Y.H., 1979. On the arctolepid Arthrodira from Lower Devonian of Yunnan. *Vertebrata Palasiatica* 17, 23–34.
- LIU, Y.H., 1991. On a new petalichthyid, *Eurycaraspis incilis* gen. et sp. nov., from the Middle Devonian of Zhanyi, Yunnan. In *Early Vertebrates and Related Problems of Evolutionary Biology*. CHANG, M.M., LIU, Y.H. & ZHANG, G.R., eds, Science Press, Beijing, 139–177.
- LIU, T.S. & P'AN, K., 1958. Devonian fishes from Wutung Series near Nanking, China. *Palaeontologica Sinica, new series C* 141, 1–41.
- LIU, Y.H. & WANG, J.Q., 1973. Discussion of several problems regarding the Devonian of eastern Yunnan. *Vertebrata Palasiatica* 11, 17.
- LONG, J.A., 1983. New bothriolepid fish from the Late Devonian of Victoria, Australia. *Palaeontology* 26, 295–320.
- LONG, J.A., BURRETT, C.F., NGAN, P.K. & JANVIER, P., 1990. A new bothriolepid antiarch (Pisces, Placodermi) from the Devonian of Do Son peninsula, northern Vietnam. *Alcheringa* 14, 181–194.
- LONG, J.A., MARK-KURIK, E., JOHANSON, Z., LEE, M.S., YOUNG, G.C., ZHU, M., AHLBERG, P.E., NEWMAN, M., JONES, R., BLAAUWEN, J.D., CHOO, B. & TRINAJSTIC, K., 2015. Copulation in antiarch placoderms and the origin of gnathostome internal fertilization. *Nature* 517, 196–199.
- LUKŠEVIČS, E., 2001. Bothriolepid antiarchs (Vertebrata, Placodermi) from the Devonian of the north-western part of the East European Platform. *Geodiversitas* 23, 489–609.
- MADDISON, W.P. & MADDISON, D.R., 2000. *MacClade. Interactive analysis of phylogeny and character evolution, version 4.0*. Sinauer Associates, Sunderland, MA.
- MADDISON, W.P. & MADDISON, D.R., 2008. *Mesquite. A modular system for evolutionary analysis, version 2.5*. <http://mesquiteproject.org>.
- MILES, R.S., 1968. The old red sandstone antiarchs of Scotland: Family bothriolepididae. *Palaeontographical Society Monographs* 122, 1–130.
- MOLOSHNIKOV, S.V., 2004. Crested antiarch *Bothriolepis zadonica* H.D. Obrucheva from the Lower Famennian of Central European Russia. *Acta Palaeontologica Polonica* 49, 135–146.
- MOLOSHNIKOV, S.V., 2012. Middle-Late Devonian Placoderms (Pisces: Antiarchi) from Central and Northern Asia. *Paleontological Journal* 46, 1097–1196.
- OLIVE, S., 2015. Devonian antiarch placoderms from Belgium revisited. *Acta Palaeontologica Polonica* 60, 711–731.
- P'AN, K., WANG, S.T., GAO, L.D. & HOU, J.P., 1978. The devonian system of South China. In *Symposium on the Devonian System of South China*. Chinese Academy of Geological Sciences ed., Geological Publishing House, Beijing, 240–269.
- PAN, J. & DINELEY, D.L., 1988. A review of early (Silurian and Devonian) vertebrate biogeography and biostratigraphy of China. *Proceedings of the Royal Society of London Series B-Biological Sciences* 235, 29–61.
- PAN, J., HUO, F.C., CAO, J.X., GU, Q.C., LIU, S.Y., WANG, J.Q., GAO, L. & LIU, C., 1987. *Continental devonian system of Ningxia and its biotas*. Geological Publishing House, Beijing, 1–237.
- PAN, J. & DINELEY, D.L., 1988. A review of early (Silurian and Devonian) vertebrate biogeography and biostratigraphy of China. *Proceedings of the Royal Society of London Series B-Biological Sciences* 235, 29–61.
- PAN, J., HUO, F.C., CAO, J.X., GU, Q.C., LIU, S.Y., WANG, J.Q., GAO, L. & LIU, C., 1987. *Continental devonian system of Ningxia and its biotas*. Geological Publishing House, Beijing, 1–237.
- PAN, Z.H., ZHU, M., ZHU, Y.A. & JIA, L.T., 2015. A new petalichthyid placoderm from the Early Devonian of Yunnan, China. *Comptes Rendus Palevol* 14, 125–137.
- QIAO, T., KING, B., LONG, J.A., AHLBERG, P.E. & ZHU, M., 2016. Early gnathostome phylogeny revisited: Multiple method consensus. *PLoS ONE* 11(9), e0163157.
- RITCHIE, A., WANG, S., YOUNG, G.C. & ZHANG, G., 1992. The Sinolepidae, a family of antiarchs (placoderm fishes) from the Devonian of South China and eastern Australia. *Records of the Australian Museum* 44, 319–370.
- STENSIÖ, E.A., 1948. On the Placodermi of the Upper Devonian of East Greenland. II. Antiarchi: Subfamily Bothriolepinae. With an attempt at a revision of the previously described species of that subfamily. *Meddelelser om Grønland* 139, 1–622.
- TÔNG-DZUY, T. & JANVIER, P., 1987. Les vertébrés dévoniens du Vietnam. *Annales de Paléontologie (Vertébrés-Invertébrés)* 73, 165–194.
- TRINAJSTIC, K., BOISVERT, C., LONG, J., MAKSIMENKO, A. & JOHANSON, Z., 2014. Pelvic and reproductive structures in placoderms (stem gnathostomes). *Biological Reviews* 90(2), 467–501.
- WANG, J.Q., 1984. Geological and paleogeographical distribution of Devonian fishes in China. *Vertebrata Palasiatica* 22, 219–229.
- WANG, J.Q., 1991. The Antiarchi from Early Silurian of Hunan. *Vertebrata Palasiatica* 29, 240–244.
- WANG, J.Q., 1992. New discovery of early Middle Devonian brachytroracid (placoderm fish) from Wuding region of Yunnan. *Vertebrata Palasiatica* 30, 111–119.
- WANG, J.Q. & WANG, N.Z., 1983. A new genus of Coccosteidae. *Vertebrata Palasiatica* 21, 1–8.
- WANG, J.Q. & WANG, N.Z., 1984. New material of Arthrodira from the Wuding region, Yunnan. *Vertebrata Palasiatica* 22, 1–7.
- WANG, J.Q. & ZHANG, G.R., 1999. New material of *Microbrachius* from Lower Devonian of Qujing, Yunnan, China. *Vertebrata Palasiatica* 37, 200–211.
- WANG, J.Q. & ZHU, M., 1995. Age of the Jiucheng formation of Wuding, Yunnan. *Journal of Stratigraphy* 19, 20–24.
- YOUNG, G.C., 1984. Reconstruction of the jaws and braincase in the Devonian placoderm fish *Bothriolepis*. *Palaeontology* 27, 635–661.
- YOUNG, G.C., 1986. The relationships of placoderm fishes. *Zoological Journal of the Linnean Society* 88, 1–57.
- YOUNG, G.C., 1988. Antiarchs (placoderm fishes) from the Devonian Aztec siltstone, southern Victoria Land. *Antarctica. Palaeontographica Abt. A* 202, 1–125.
- YOUNG, G.C., 2010. Placoderms (Armored Fish): Dominant vertebrates of the Devonian period. *Annual Review of Earth and Planetary Sciences* 38, 523–550.
- YOUNG, G.C. & GORTER, J.D., 1981. A new fish fauna of Middle Devonian age from the Taemas/Wee Jasper region of New South Wales. *Bulletin of the Bureau of Mineral Resources Geology and Geophysics Australia* 209, 85–147.
- ZHANG, G.R., 1965. New antiarchs from the Middle Devonian of Yunnan. *Vertebrata Palasiatica* 9, 1–9.
- ZHANG, G.R., 1978a. The antiarchs from the Early Devonian of Yunnan. *Vertebrata Palasiatica* 16, 147–186.
- ZHANG, G.R., 1978b. Antiarchs from Early Devonian of Cuifengshan, Yunnan. In *Symposium on the Devonian System of South China*, Chinese Academy of Geological Sciences ed., Geological Publishing House, Beijing, 292–297.
- ZHANG, G.R., 1980a. New material of *Xichonolepis qujingensis* and discussion on some of its morphological characteristics. *Vertebrata Palasiatica* 18, 272–280.
- ZHANG, M.M., 1980b. Preliminary note on a Lower Devonian antiarch from Yunnan, China. *Vertebrata Palasiatica* 18, 179–190.

- ZHANG, G.R., 1991. A new antiarch from the Upper Devonian of Jiangxi, China. In *Early Vertebrates and Related Problems of Evolutionary Biology*. CHANG, M.M., LIU, Y.H. & ZHANG, G.R., eds, Science Press, Beijing, 179–194.
- ZHANG, G.R. & YOUNG, G.C., 1992. A new antiarch (placoderm fish) from the Early Devonian of south China. *Alcheringa* 16, 22.
- ZHANG, G.R., WANG, J.Q. & WANG, N.Z., 2001. The structure of pectoral fin and tail of Yunnanolepidoidei, with a discussion of the pectoral fin of chuchinolepids. *Vertebrata Palasiatica* 39, 9–19.
- ZHAO, W.J. & ZHU, M., 2010. Siluro-Devonian vertebrate biostratigraphy and biogeography of China. *Palaeoworld* 19, 4–26.
- ZHAO, W.J., ZHU, M., LIU, S., PAN, Z.H. & JIA, L.T., 2016. A new look at the Silurian fish-bearing strata around the Shanmen reservoir in Lixian, Hunan province. *Journal of Stratigraphy* 40, 341–350.
- ZHU, M. 1991. New information on *Diandongpetalichthys* (Placodermi: Petalichthyida). In *Early Vertebrates and Related Problems of Evolutionary Biology*. CHANG, M.M., LIU, Y.H. & ZHANG, G.R., eds, Science Press, Beijing, 179–194.
- ZHU, M., 1996. The phylogeny of the Antiarcha (Placodermi, Pisces), with the description of Early Devonian antiarchs from Qujing, Yunnan, China. *Bulletin du Muséum national d'Histoire naturelle* 18, 233–347.
- ZHU, M., 2014. Bone gain and loss: Insights from genomes and fossils. *National Science Review* 1, 490–497.
- ZHU, M. & JANVIER, P., 1996. A small antiarch, *Minicrania lirouyii* gen. et sp. nov., from the Early Devonian of Qujing, Yunnan (China), with remarks on antiarch phylogeny. *Journal of Vertebrate Paleontology* 16, 1–15.
- ZHU, M., YU, X.B., CHOO, B., WANG, J.Q. & JIA, L.T., 2012. An antiarch placoderm shows that pelvic girdles arose at the root of jawed vertebrates. *Biology Letters* 8, 453–456.
- ZHU, M., YU, X.B., AHLBERG, P.E., CHOO, B., LU, J., QIAO, T., QU, Q.M., ZHAO, W.J., JIA, L.T., BLUM, H. & ZHU, Y.A., 2013. A Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature* 502, 188–193.
- ZHU, M., AHLBERG, P.E., PAN, Z.H., ZHU, Y.A., QIAO, T., ZHAO, W.J., JIA, L.T. & LU, J., 2016a. A Silurian maxillate placoderm illuminates jaw evolution. *Science* 354, 334–336.
- ZHU, Y.A., ZHU, M. & WANG, J.Q., 2016b. Redescription of *Yinostius major* (Arthrodira: Heterostiidae) from the Lower Devonian of China, and the interrelationships of Brachythoraci. *Zoological Journal of the Linnean Society* 176, 806–834.