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广西下泥盆统南极鱼类(盾皮鱼纲:节甲鱼目)一新属[1)]

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摘要:依据采自广西平果早泥盆世郁江组中部的化石材料,记述了盾皮鱼纲节甲鱼目南极鱼科的一新属、新种——小眼坡塘鱼(*Potangaspis parvoculatus* gen. et sp. nov.)。该新属的眶孔很小,且为颅顶甲骨片所完全包围;中点线沟发育,与眶上感觉沟、中心感觉沟和后点线沟一起共同向颈片的骨化中心辏合。系统发育分析表明新属和发现于南极洲中泥盆统的南极鱼属构成姐妹群关系,支持了南极鱼科位于节甲鱼目最基干位置的假说,同时为早埃姆斯期东冈瓦纳大陆与中国南方之间的古地理密切联系提供了新的证据。

关键词:广西,下泥盆统,盾皮鱼纲,节甲鱼目,南极鱼类,系统发育,古生物地理

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A NEW ANTARCTASPID ARTHRODIRE (PLACODERM FISH) FROM THE LOWER DEVONIAN OF GUANGXI, CHINA

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Abstract *Potangaspis parvoculatus*, a new genus and species of the Antarctaspidae (Placodermi: Arthrodira), is described from the early Emsian (Yukiang Formation, Early Devonian) of Pingguo, Guangxi, China. This new form is characterized by small orbits enclosed by skull roof, and long, narrow nuchal plate on which the central and supraorbital sensory canals, middle and posterior pit-lines converge. Phylogenetic analysis corroborates the basal position of the family Antactaspidae amongst the Arthrodira, and suggests a sister group relationship between the new form and *Antarctaspis mcmurdoensis* from the Middle Devonian of Antarctic, thus providing additional evidence to support the biogeographic proximity between South China and East Gondwana during the early Emsian.

Key words Guangxi, China; Lower Devonian; Placodermi; Arthrodira; artarctaspids; phylogeny; paleobiogeography

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1 Introduction

The antarctaspids are a very peculiar group of the Placodermi (Silurian-Devonian), which are currently considered as the sister group of all other jawed vertebrates (Acanthodii, Chondrichthyes and Osteichthyes) (Janvier, 2007; Brazeau, 2009). The family Antarctaspidae was erected by White (1968) on the poorly known genus *Antarctaspis* White, 1968 from the Antarctic Aztec Siltstone, which was interpreted as an alluvial plain deposit of Middle Devonian (Young et al., 1992; Young, 1993). Based on the radiating structure of the bone in the holotype, White (1968) inferred that the paired central plates are separated by the elongate nuchal plate in *Antarctaspis*. However, this inference was rejected by Denison (1978), who suggested a very long paranuchal plate, and no central plates in *Antarctaspis*. Based on this new interpretation, which was also followed by Long (1984), Denison (1978) placed the family in a new suborder Antarctaspinae within the order Phyllolepida. Young and Goujet (2003) described another antarctaspid genus *Toombalepis* from the Dulcie Sandstone (Emsian-early Eifelian) of the Georgina Basin in northern Australia, and corroborated White's (1968) original identification regarding the presence of the central plates in *Antarctaspis*. They further suggested that *Yujiangolepis* from the Naokaoling Formation (Pragian) of Liujing, Guangxi, China, which was originally referred to the Phlyctaeniidae by Wang et al. (1998), is also an antarctaspid fish, and provided additional example of the biogeographic proximity between South China and East Gondwana during the Devonian.

Dupret et al. (2009) redescribed the morphology of *Yujiangolepis*, and supported its assignment to the family Antarctaspidae. Their phylogenetic analysis showed that the family, although paraphyletic, occupied the most basal position within the Arthrodira, and highlighted a Chinese origin of the Antarctaspidae. However, this 'center of origin' assumption is still weak partly due to scanty fossil records of the family. Here we describe a new antarctaspid fish, *Potangaspis parvoculatus* gen. et sp. nov., collected from the middle part of the Yukiang (Yujiang) Formation (early Emsian) in Potang village, Tonglao, Pingguo County, Guangxi (Fig. 1). The fossil horizon is the black microlite limestone, and represents a normal marine depositional environment. The new discovery conforms to the assumption of a fish migration episode from South China to East Gondwana at the end of the Pragian (E'Em bioevent, Zhu, 2000; Dupret et al., 2009).

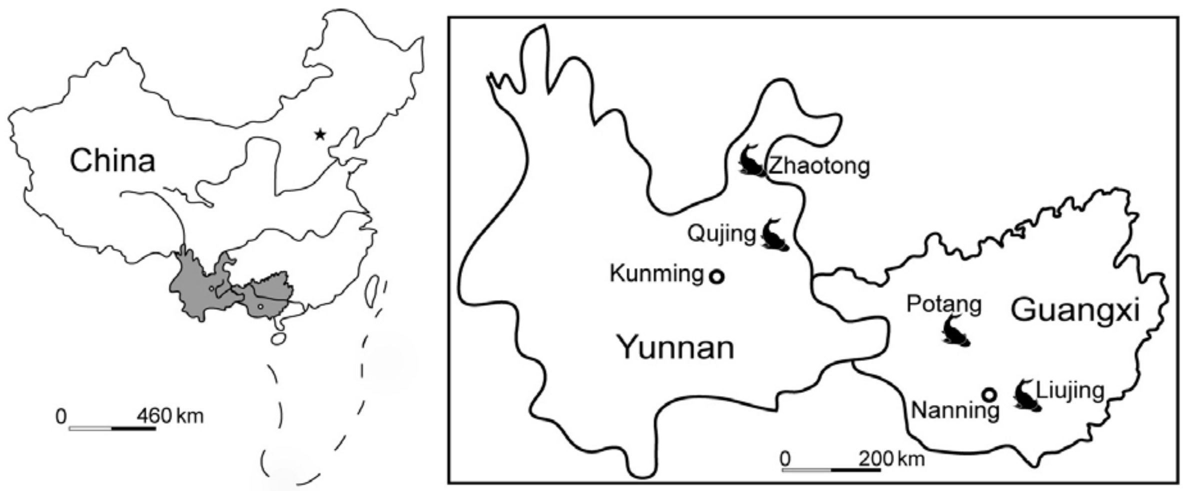

Fig. 1 Localities for the Devonian antarctaspid, wuttagoonaspid and phyllolepid arthrodires in South China
Potang, Pingguo County, Guangxi: *Potangaspis parvoculatus* gen. et sp. nov.; Liujing, Hengxian County, Guangxi: *Yujiangolepis liujingensis* Wang et al., 1998; Zhaotong, Yunnan: *Yiminaspis shenme* Dupret, 2008; Qujing, Yunnan: *Gavinaspis convergens* Dupret & Zhu, 2008

2 Systematic paleontology

Placodermi McCoy, 1848
Arthrodira Woodward, 1891
'Actinolepidoidei' Miles, 1973
Antarctaspidae White, 1968
***Potangaspis* gen. nov.**

Type species *Potangaspis parvoculatus* sp. nov.

Etymology The generic name derives from Potang village, the fossil locality.

Diagnosis A small antarctaspid arthrodire with small orbits enclosed by the skull roof. Rostral and pineal plates fused to form a rostropineal plate. Nuchal plate long and narrow on which the central and supraorbital sensory canals, middle and posterior pit-lines converge. Ornament of discrete tubercles with variable size.

Remarks The suborder 'Actinolepidoidei' including Antinolepidae, Antarctaspidae, Wuttagoonaspidae, Bulbocanthidae, Gavinaspidae and Phyllolepidae (Young and Goujet, 2003), represents a paraphyletic ensemble (Dupret and Zhu, 2008; Dupret et al., 2009), diagnosed mainly on plesiomorphic features of the Arthrodira (e. g. Denison, 1984; Johnson et al., 2000). The family Antarctaspidae includes *Antarctaspis* from Antarctica, *Toombalepis* from Australia, *Yujiangolepis* and the new genus from China. Previous phylogenetic analysis showed the Antarctaspidae as the most basal arthrodire group, however leaving the monophyly or paraphyly of the family unresolved (Dupret et al., 2009). For the time being, the family is only defined by a unique character combination, such as a nuchal plate on which the central and supraorbital sensory canals converge, the nuchal and pineal (or rostropineal) plates in contact, and the tubercular ornament. However, the converging sensory canals are also present in wuttagoonaspids and some phyllolepids; and the long and narrow nuchal plate in contact with the pineal plate is shared with petalichthyids. The tubercular ornament is evidently a primitive feature, considering its wide distribution in placoderms.

***Potangaspis parvoculatus* sp. nov.**
(Fig. 2A–D, 3A)

Diagnosis As for genus (monotypic genus).

Etymology The specific name derives from *parvus* (L.) small, *oculatus* (L.) ocular, an allusion to small orbits of the new form.

Holotype An incomplete skull-roof, IVPP V 15050.1.

Other material A bone fragment including part of central and marginal plates, IVPP V 15050.2.

Type locality and horizon Potang village, Tonglao, Pingguo County, Guangxi; Yukiang Formation, early Emsian, Early Devonian.

Remarks The new form is distinguishable from the other antarctaspids in its orbits enclosed by skull roof, and the presence of long middle pit-lines converging to the ossification center of the nuchal plate. The orbits enclosed by skull roof are also present in macropetalichthyid petalichthyids and antiarchs, evidently due to the parallelism. The petalichthyid *Eurycarapis* (Liu, 1991) and the Wuttagoonaspidae (Ritchie, 1973; Dupret and Zhu, 2008) exhibit the same developed middle pit-lines, suggesting an iterative evolution in placoderms. Among the Antarctaspidae, *Potangaspis* resembles *Antarctaspis* more than *Toombalepis* and *Yujiangolepis* in its fused rostropineal plate. Like *Antarctaspis* and *Yujiangolepis*, but unlike *Toombalepis*, the new form has no deep notch for the pineal (or rostropineal) plate along the anterior marginal of the nuchal plate.

Description The holotype is the external mould of an incomplete skull roof, which preserved anterior and posterior extremities but lost the majority of lateral margins. The skull roof has the midline length of about 37 mm, the smallest among the Antarctaspidae. The Australian species *Toombalepis tuberculata* attains to 190 mm in skull length (Young and Goujet, 2003), whereas *Yujiangolepis liujingensis* has a skull of about 45 mm (Wang et al., 1998), and *Antarctaspis mcmurdoensis* of about 47 mm (White, 1968). The preserved breadth is about 25 mm; when restored, the maximum breadth might reach 40 mm, roughly equaling the maximum length of skull roof.

Bone sutures on the anterior half of the skull roof are distinct, but those on the posterior half can only be discerned from the ornament pattern, and a slight thickening at the surface along the margins of the main head plates (e.g. nuchal, central plates), as in *Wuttagoonaspis milligani* (Young and Goujet, 2003).

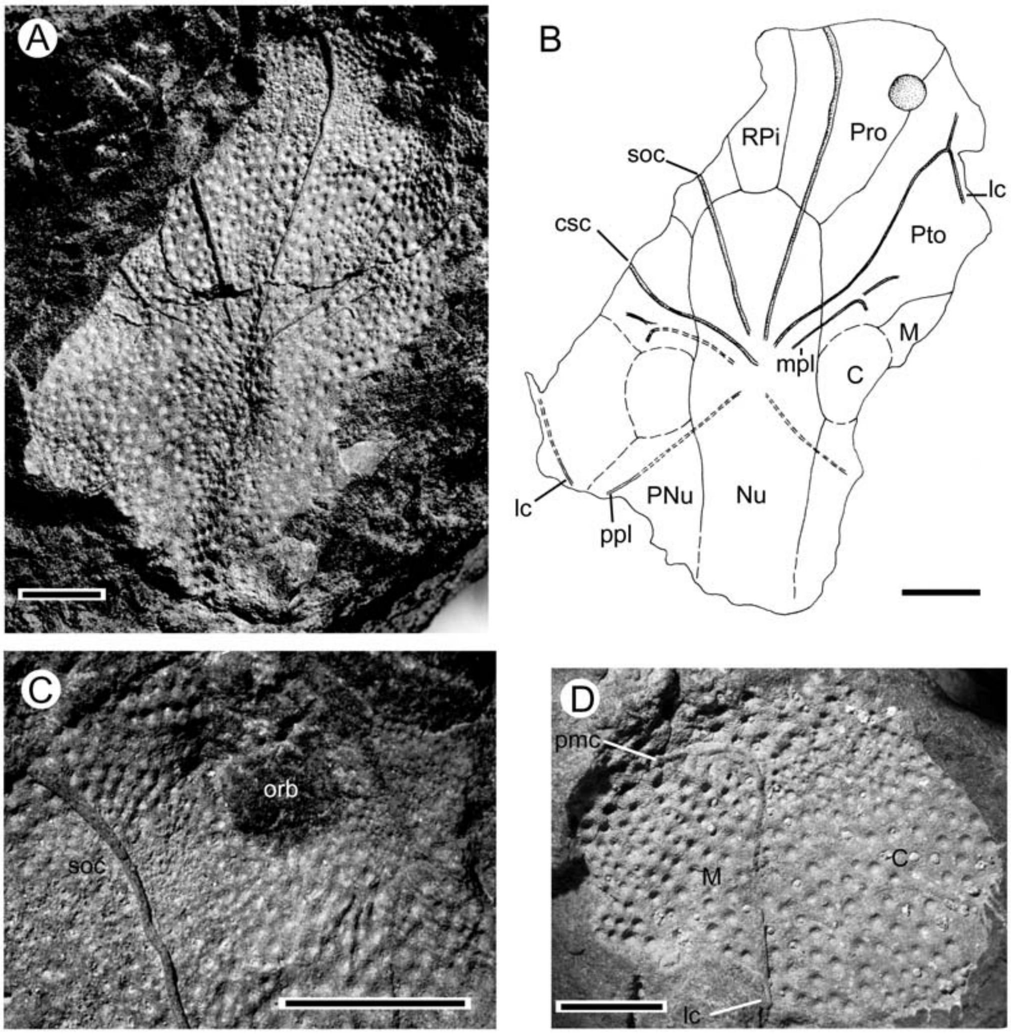

Fig. 2 *Potangaspis parvoculatus* gen. et sp. nov.

A–B. photo and illustrative drawing of the holotype, IVPP V 15050.1; C. close-up of the holotype to show the orbital opening enclosed by the skull roof; D. photo of right marginal and central plates, IVPP V 15050.2; all scales equal 5 mm

Abbreviations: C. central plate 中央片; csc. central sensory canal 中央感觉管; lc. main lateral line canal 主侧线管; M. marginal plate 缘片; mpl. middle pit-line 中凹线沟; Nu. nuchal plate 颈片; orb. orbital opening 眶孔; pmc. postmarginal sensory canal 后缘感觉管; PNu. paranuchal plate 副颈片; ppl. posterior pit-line 后凹线沟; Pro. preorbital plate 眶前片; Pto. postorbital plate 眶后片; RPi. rostropineal plate 吻-松果片; soc. supraorbital sensory canal 眶上感觉管

The rostral and pineal plates are fused to form a compound plate, the rostropineal plate (RPi, Fig. 2A, B, 3A), as in *Anatarctaspis* (White, 1968). The RPi plate is cup-shaped, with its length of about 10 mm and breadth of about 4 mm. Its anterior margin is straight, and forms part of the anterior extremity of the skull roof. The posterior margin is slightly convex, but does not form a deep notch on the anterior margin of the plate behind it.

The nuchal plate (Nu, Fig. 2A, B, 3A) is long and narrow, as in petalichthyids and other antarctaspids. It is in contact with the rostropineal plate in the front; together they form the midline series of skull roof bones and completely separate the paired bones. The Nu plate is about 27 mm in length, and attains to about 3/4 of the skull-roof length; its breadth is about 9 mm, 1/3 of its length. Four pairs of sensory grooves converge on the centrally placed ossification centre of the plate, inviting the comparison with *Wuttagoonaspis* (Fig. 3C), *Yiminaspis* (Fig. 3F), *Eurycaraspis* (Liu, 1991) and other antarctaspids (Fig. 3B, D, E). The lateral notches of the nuchal plate are clearly for the central plates as in *Toombalepis* (Young and Goujet, 2003). Its anterior margin has a median shallow notch which just holds the posterior process of the RPi plate, and the posterior margin is straight with a small embayment in the middle.

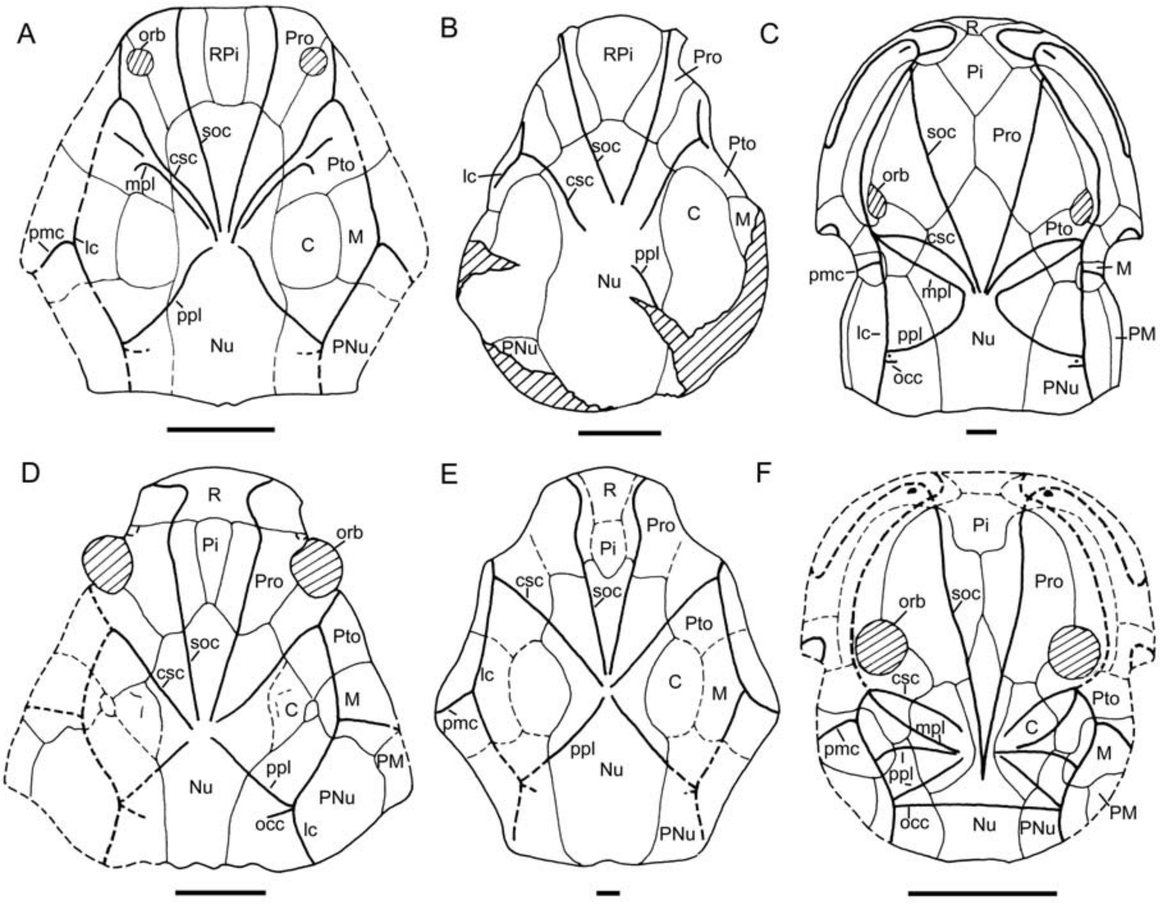

Fig. 3　Six representatives of the actinolepidoid families Antarctaspidae and Wuttagoonaspidae
A. *Potangaspis parvoculatus* gen. et sp. nov., attempted skull reconstruction after Fig. 2; B. attempted restoration of *Antarctaspis mcmurdoensis* White, 1968, based on White (1968) and Young and Goujet (2003, fig. 16B); C. *Wuttagoonaspis fletcheri*, after Ritchie (1973); D. *Yujiangolepis liujingensis*, after Dupret et al. (2009); E. *Toombalepis tuberculata*, after Young and Goujet (2003); F. *Yiminaspis shenme*, after Dupret (2008); all scales equal 1 cm
Abbreviations as in Fig. 2 plus: occ. occipital cross commissure 枕横联络支; Pi. pineal plate 松果片; PM. postmarginal plate 后缘片; R, rostral plate 吻片

The paired bones include the preorbital (Pro), postorbital (Pto), central (C), marginal (M), and paranuchal plates (PNu, Fig. 2A,B, 3A). Both the preorbital and postorbital plates are irregular quadrilateral in shape and have a similar size. It is noteworthy that they enclose the orbital opening (orb, Fig. 2C, 3A), which is about 2.5 mm in diameter. The skull roof bones enclosing the orbital openings were previously known only in macropetalichthyid petalichthyids and antiarchs among placoderms (Denison, 1978). *Wuttagoonaspis* (Fig. 3C) has similar small orbital openings, which are, however, enclosed laterally by the cheek plate.

The pentagon-shaped marginal plate is separated from the nuchal plate by the central plate. A disarticulated bone fragment (IVPP V 15050.2, Fig. 2D) preserved together with the holotype has the same tubercular ornament as the holotype. The trifurcating sensory canals, which are the postmarginal canal branching from the lateral line canal (pmc, lc, Fig. 2D), characterize it as part of the skull roof preserving the marginal and central plates. This complementary specimen helps to restore the skull roof (Fig. 3A). The paranuchal plate is also pentagonal in outline, with its length exceeding the width.

The sensory canal system of the new form is well observed in the holotype. The supraorbital and central sensory canals (soc, csc, Fig. 2A,B) converge towards the ossification center of the nuchal plate, as in some derived phyllolepids (Dupret and Zhu, 2008), wuttagoonaspids, and other antarctaspids. The junction of the central sensory canal with the main lateral line canal marks the ossification center of the preorbital plate. The supraorbital sensory canal bears an inflection at the level of orbital openings, which is evident in *Yujingolepis* and *Toombalepis*. The trajectory of the posterior pit-line (ppl, Fig. 2A,B), also converging towards the center of nuchal plate, can be inferred from the segments close to the main lateral line canal and the center of the nuchal plate on the right half. The occipital cross commissure is not preserved in the specimen. The sensory canal system of the new form is remarkable in its elongate middle pit-lines (mpl, Fig. 2A,B) converging on the ossification center of the nuchal plate, immediately behind the central sensory canal. The middle pit-line consists of two segments, the short anterior one straight, and the long posterior one inflected in the front. This elongate middle pit-line, which was found in the Wuttagoonaspidae (Dupret, 2008; Fig. 3C,F) and the quasipetalichthyid petalichthyid *Eurycarapis incilis* (Liu, 1991), is unique for antarctaspids.

The skull roof is covered with round tubercles, which have the changeable size throughout the surface. The tubercles in the posterior portion are obviously larger than those in the front, especially the areas around the orbital openings.

3 Discussion

3.1 Phylogenetic analysis

To determine the placement of *Potangaspis parvoculatus* in the Arthrodira, we constructed an extended character-taxon matrix including the new form, derived from that of Dupret et al. (2009), for the phylogenetic analysis. Several codings of Dupret et al. (2009) are corrected (in bold in Appendix 1). A new character (Character 66, long middle pit-line converging towards the ossification center of nuchal plate, absence 0, presence 1) was added. The phylogenetic analysis was conducted using PAUP 4.0b10, with the heuristic search option. The petalichthyids *Eurycarapis incilis* and *Lunaspis broilii* were assigned as the outgroup. All characters were set to equal weight and unordered. Phylogenetic analysis yields 342 equally most parsimonious (MP) trees, with a tree length = 167, consistency index = 0.4012, retention index = 0.7347. All 342 MP trees consistently places *Potangaspis parvoculatus* as the sister group of *Antarctaspis mcmurdoensis*, based on a single synapomorphy: the fused rostropineal plate. The 50% majority-rule consensus tree (Fig. 4) and the strict consensus tree are similar except that two nodes collapse in the latter (Nodes A and B, Fig. 4). Four genera referred to the Antarctaspida are placed at the base of the Arthrodira as in Dupret et al. (2009), however their interrelationship remains unresolved.

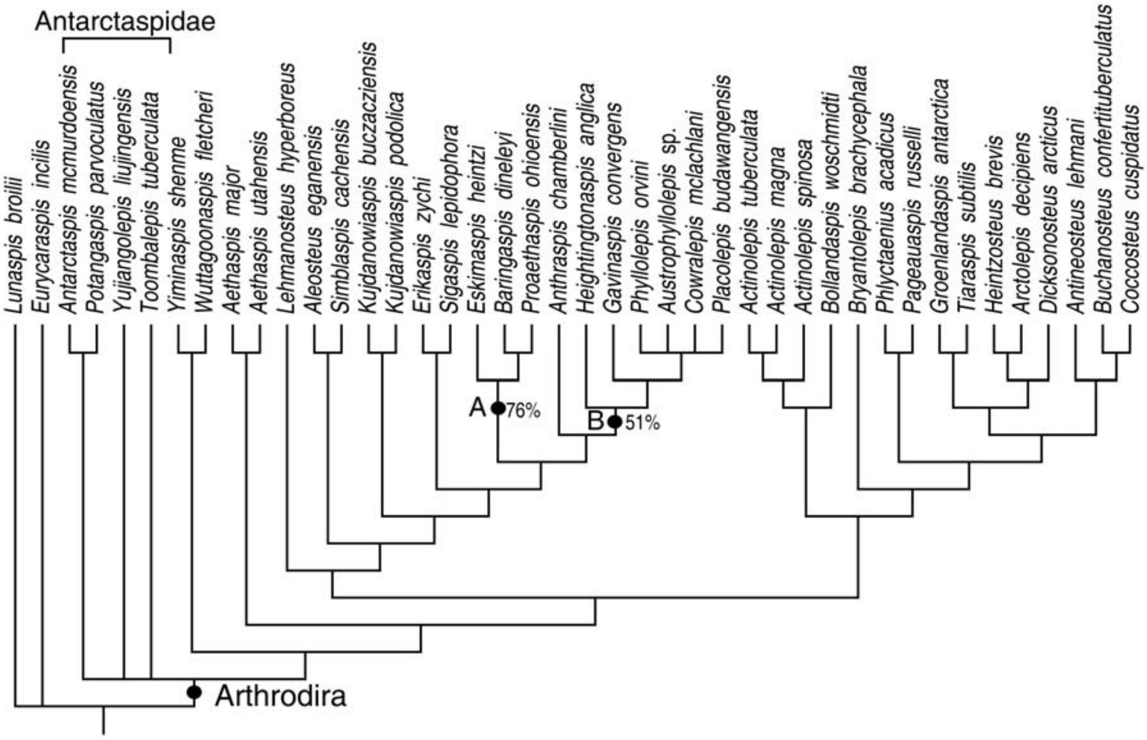

Fig. 4　50% majority-rule consensus tree of 342 most parsimonious trees based on an extended data matrix for basal arthrodires (Dupret et al., 2009), showing *Potangaspis parvoculatus* gen. et sp. nov. as the sister group of *Antarctaspis mcmurdoensis*

3.2　Biogeographic implications

The new genus of antarctaspids described here adds to the known diversity of the group in East Gondwana (Australia, New Zealand and Antarctica) and South China, and corroborates the biogeographic proximity between these two provinces during the early Emsian (E'Em bioevent, Walliser, 1995; Zhu, 2000). Based on the re-description of *Yujiangolepis liujingensis* Wang et al., 1998 and the phylogenetic analysis, Dupret et al. (2009) confirmed this Chinese species as the oldest member of antarctaspids (Young and Goujet, 2003), and proposed a South China origin for the family Antarctaspidae. However, although one of their phylogenetic analysis suggests the most basal position of *Yujiangolepis* in the family Antarctaspidae as well as in the Arthrodira (Dupret et al., 2009), other types of analyses indicated the uncertainty of this basal position. The dispersal of the Antarctaspidae from South China to East Gondwana was not supported, if *Antarctaspis* or *Antarctaspis* plus *Toombalepis* was placed at a position plesiomorphic to *Yujiangolepis* (Dupret et al., 2009, fig. 4).

With the inclusion of the new form, the interrelationship of the Antarctaspidae still remains unsettled. However, the sister pair between *Potangaspis* (Emsian of South China) and *Antarctaspis* (Middle Devonian of Antarctica) is consistently supported, thus rendering the compelling evidence for the dispersal of the Antarctaspidae from South China to East Gondwana. This migration route during the E'Em event conforms to the dispersals of primitive sarcopterygians (Zhu and Zhao, 2006) and other placoderm groups such as the Wuttagoonaspidae (Dupret, 2008) and the Phyllolepidae (Dupret et al., 2009). An earlier biogeographic proximity between these two vertebrate provinces (Young, 1981) is proposed based on possible sinacanthids and the ischanacanthid acanthodian *Radioporacanthodes* sp. cf. *R. qujingensis* from the Late Silurian Silverband Formation of Victoria, Australia (Burrow, 1997, 2003), compared to the coeval fish fauna in China. It is noteworthy that, although the Antarctaspidae and the Wuttagoonaspidae are placed at the base of the Arthrodira, as successive sister groups to all other arthrodires including phyllolepids, they are not the earliest members of the Arthrodira. The study of closely related petalichthyids (Liu, 1991; Zhu, 1991; Zhu and Wang, 1996) and earlier arthrodires such as *Szelepis* from the Lochkovian of South China (Liu, 1979) and *Eskimaspis* from the Lochkovian of the Canadian Arctic Archipelago (Dineley and Liu, 1984), will help to clarify the early radiation of the Arthrodira.

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Appendix 1　Character-taxon matrix for the phylogenetic analysis, derived from that of Dupret et al. (2009), with few corrections (in bold) and the addition of the new taxon (*Potangaspis parvoculatus* gen. et sp. nov.) and a new character (Character 66, long middle pit-line converging towards the ossification center of nuchal plate, absence 0, presence 1); for list of other characters see Appendix 2 of Dupret et al. (2009)

	000000000111111111122222222223333333333444444444455555555556666666
	123456789012345678901234567890123456789012345678901234567890123456
Lunaspis broilii	????11001100000010000011110-0100-11-0002-00-000110?111010011101000
Eurycaraspis incilis	????111011-10010100010111 00-0100-11100?2-01111110101100010111 01111
Actinolepis magna	1???1101110111101000001100111011000 10000-0???01001?110?00000101?10
Actinolepis spinosa	?????10111??110010000011 00?1111?000???00-??????001?11010??????1000
Actinolepis tuberculata	????11011101111010000011001110 1?0000??00-?11???101?110101?001?1000
Aethaspis major	1???11001101010010000001110011111-0010000-011?01101011?0101101011?0
Aethaspis utahensis	1???110?11?1010010000101100111 1?-0010000-??????101011001001???11?0
Aleosteus eganensis	?????10?10?1010010000??10001111?00010000-010?0100101100100001 01000
Anthraspis chamberlini	0???110000?101001000010100?11111000100?0-00-?01101011?0001101011?0
Antineosteus lehmani	????110011?1010011000011001111111 00?1111110-00?000???-000000101??0
Antarctaspis mcmurdoensis	????111111-101101000101110001?1?-10??0??????????????????101??????0
Arctolepis decipiens	1100111011-1010010100011000111110000101 1000-011110111110010111 1010
Austrophyllolepis sp.	????01----0101100--00100-0111010--0?01-0-00-000000?0100001-01-0100
Baringaspis dineleyi	0????10?00?10101100001011001 1111-0010000-011?0110101100000101 0?100
Bollandaspis woschmidti	????11011101110???000??1?0011?1??0??????-????????1?1100?0????????0
Bryantolepis brachycephala	????1100110101001000000110001111 1000100?0-00-?01101011000?000101100

Buchanosteus confertituberculatus	0101110111?10100110000110001111110001111111???11?00?110?00001?0?1?0
Coccosteus cuspidatus	1???11001101010011010011000111111001111110-01100001100000001001110
Cowralepis mclachlani	????01----0101000--00110-0111-10--0?01-0-00-000000?1100001-01-0100
Dicksonosteus arcticus	11001100111101001000000110000111100011011000-01111011111010110?010
Erikaspis zychi	00???10?00?10101100001010001111100010000-01110?001011?0100101001?0
Eskimaspis heintzi	?????10?00?1010110000101000 1111?00010000-011?01101011000001010010 0
Gavinaspis convergens	0????10?001101010-000100-0001110--010100-???????????????11-??????0
Groenlandaspis antarctica	????111011?10100101100110001111100011011000-00100001110000110001 10
Heightingtonaspis anglica	00???10?00?10101100001010001111100010000-??????001011??0011???01?0
Heintzosteus brevis	1100111011?1010010100011000111110001101100 0-0111101111100111111010
Kujdanowiaspis buczacziensis	00111100001101011000010100011111000100 00-010??1001011?110010111000
Kujdanowiaspis podolica	0011110000110101100001010001111100010000-010?1100101101100101110 00
Lehmanosteus hyperboreus	10111100110101011000010100011111000010000-??????????????001??????0
Pageauaspis russelli	0????10?10?10100100000110001111?000110110????0?00???????011??????0
Phlyctaenius acadicus	1???110011010100100000011000111110001101100 0-001000?110000111101000
Phyllolepis orvini	????01----0101000--00100-0111010--0101-0-00-010000?1000001-01-0100
Placolepis budawangensis	????01----0101000--00010-0111010--0?01-0-00-000000?0000001-01-0100
Proaethaspis ohioensis	0????10?00?10100100-110110001111-0010000-011???101011010?010??0000
Sigaspis lepidophora	?????1???????1?11000010100?1111100010000-01110100??11?01??10???100
Simblaspis cachensis	0????10?10?10100100001010001111100010000-011????????????0000?????0
Tiaraspis subtilis	????111011?1010010110011000111110001101100 0-001?00011110001 10??010
Toombalepis tuberculata	????111011?101101-0010111000?-10-1010000????????????????101??????0
Wuttagoonaspis fletcheri	????1010110101101-0-100110011011-0010000-011?0?10101???110101??0?1
Yiminaspis shenme	????100011?101101-00010110010011-0000000-0?????001?11?1?1010??1??1
Yujiangolepis liujingensis	????111011?101101-00101110001111-1110000????????????????101??????0
Potangaspis parvoculatus	????111111?001101-0010111000 1-1?-10100??????????????????101??????1