

The morphology of *Yujiangolepis liujingensis* (Placodermi, Arthrodira) from the Pragian of Guangxi (south China) and its phylogenetic significance

VINCENT DUPRET*, MIN ZHU and JUN-QING WANG

Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Xizhimenwai Dajie, 142, Beijing 100044, China

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The morphology of the arthrodire placoderm *Yujiangolepis liujingensis* Wang, Pan & Wang, 1998, from the Lower Devonian of Guangxi is redescribed, and compared to that of the basal arthrodirans *Antarctaspis* White, 1968 from Antarctica, *Toombalepis* Young & Goujet, 2003 and *Wuttagoonaspis* Ritchie, 1973 from Australia, and *Yiminaspis* Dupret, 2008 from south China. A very small plate of the skull roof at the junction of the nuchal, marginal, postorbital, and paranuchal plates is considered as the vestigial homologue of the anterior paranuchal plate in the Petalichthyida and Acanthothoraci. *Yujiangolepis* is attributed to the family ‘Antarctaspididae’ White, 1968, together with the genera *Antarctaspis* and *Toombalepis*. A computerized phylogenetic analysis resolved *Yujiangolepis* as the most basal arthrodire, and the family ‘Antarctaspididae’ appears paraphyletic, *Yujiangolepis* being possibly the most basal. The family Wuttagoonaspididae contains the genera *Wuttagoonaspis* and *Yiminaspis*, and remains monophyletic. A Chinese origin of the ‘Antarctaspididae’ is proposed, together with a southward dispersal into Gondwana during the Early Emsian.

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ADDITIONAL KEYWORDS: Actinolepidoidei – Early Devonian – palaeobiogeography – phylogeny.

INTRODUCTION

The Placodermi McCoy, 1848, also known as ‘armoured fishes’, were the most successful group of vertebrates during the Devonian period. They most probably appeared during the Early Silurian and disappeared without leaving any descendants at the end of the Famennian. Amongst the Placodermi, the Arthrodira Woodward, 1891 were the most diversified. Nevertheless, their origins remain blurred (Janvier, 1996). Recent phylogenetic analyses have proposed that the Antarctaspididae White, 1968 and the Wuttagoonaspididae Ritchie, 1973 are the most basal arthrodirans (Dupret, 2004; Dupret, Goujet &

Mark-Kurik, 2007; Dupret & Zhu, 2008). The family Antarctaspididae is composed of three genera: *Antarctaspis* White, 1968 from Antarctica, *Toombalepis* Young & Goujet, 2003 from Australia, and *Yujiangolepis* Wang, Pan & Wang, 1998 from south China. In the present article, we propose a revision of this latter taxon.

Yujiangolepis liujingensis Wang *et al.*, 1998, is known by a single subcomplete skull roof, from the Pragian Nakaoling (Nagaoling) Formation of Hengxian (Guangxi, south China; macrovertebrate assemblage MAV III of Zhu, Wang & Wang, 2000; Fig. 1). This formation also yielded the remains of the Galeaspida *Asiaspis expansa* P’an, Wang & Liu, 1975, *Antiquisagittaspis cornuta* Liu, 1985, the Arthrodira *Asiacanthus multituberculatus* Liu, 1982, and the

*Corresponding author. E-mail: vincent@ivpp.ac.cn

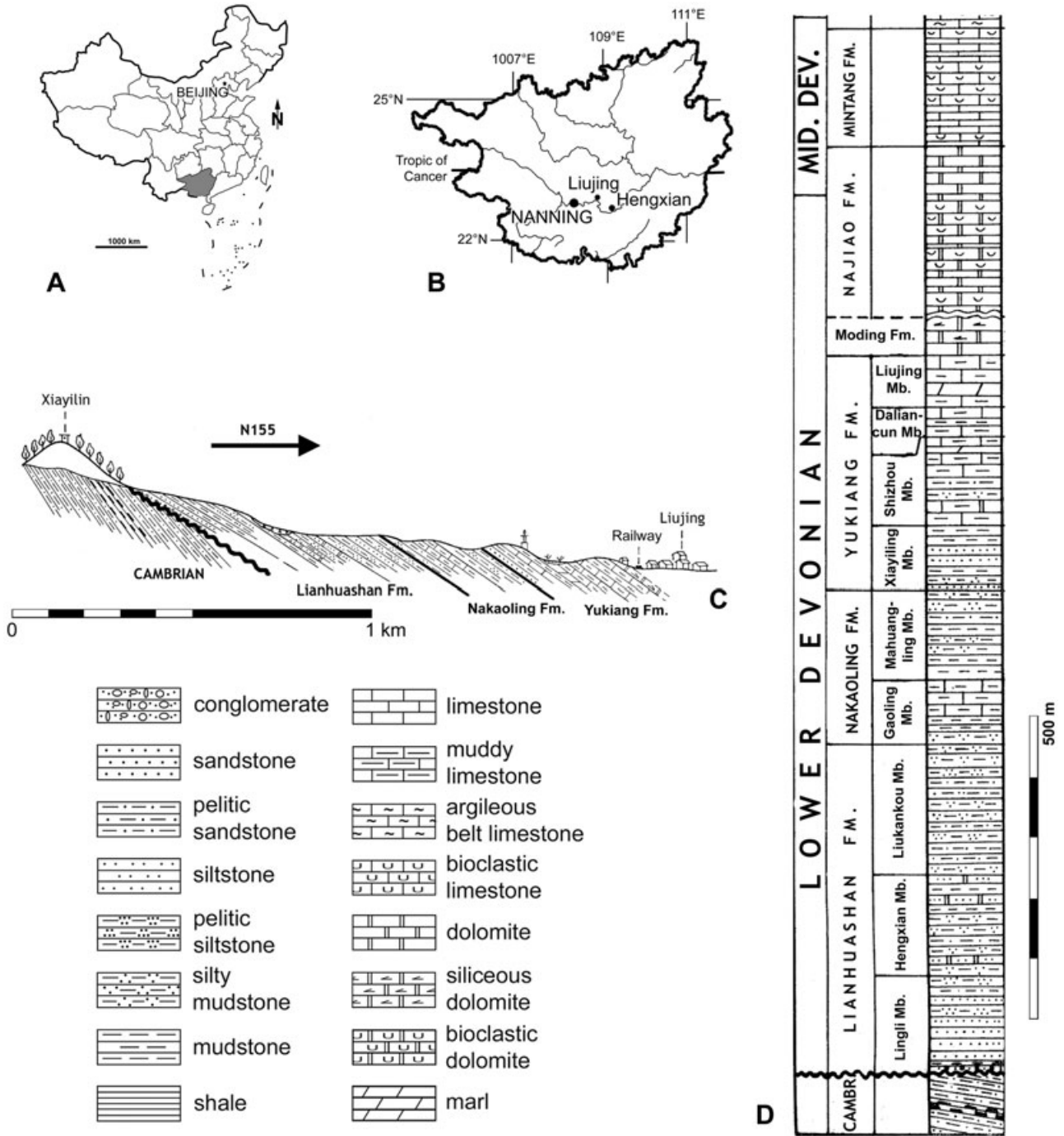


Figure 1. Guangxi province in China (A) and position of Liujing in Guangxi (B). Stratigraphical section (C) and column (D) in Liujing (slightly modified after Kuang *et al.*, 1989: figs 3–4).

Antiarchi *Nakaolinaspis devonica* P'an & Wang, 1978 of debatable affinity (Halstead, Liu & P'an, 1979; Halstead, 1985). The vertebrates are associated with corals, chitinozoans, brachiopods, conodonts (Zhong, Wu & Yin, 1992), plus spores and acritarchs (Gao,

1978), indicating a neritic facies of deposition (see also Zhu *et al.*, 2000). Liujing belongs to the Cathaysian terranes, and is close to the southern boundary of the South China Block (see Zhao & Zhu, 2007: fig. 1).

Yujiangolepis liujingensis was first classified within the Phlyctaeniidae Fowler, 1947, because of the supposed fusion between the rostral and the postnasal plates and the deep orbital notches, as is the case in *Arctolepis decipiens* Woodward, 1891. Nevertheless, the posterolateral corner of the skull roof is more developed, and the radiation centre of the paranuchal plate is anteriorly positioned, thus this pattern more resembles that of the 'Actinolepidoidei' Miles, 1973. Later, Young & Goujet (2003) compared *Yujiangolepis* with the Australian *Toombalepis tuberculata* Young & Goujet, 2003, and with the Antarctic *Antarctaspis mcmurdoensis* White, 1968, and assigned all of them within the basal actinolepidoid family 'Antarctaspididae' White, 1968. Our redescription and phylogenetic analyses generally support Young & Goujet's (2003) assumptions (see below).

MATERIAL AND METHODS

ABBREVIATIONS

Institutional abbreviations

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, People's Republic of China.

Anatomical abbreviations

a.PaN, anterior paranuchal plate; C, central plate; cc, central sensory groove; d.end.e, external foramen of the endolymphatic duct; d.end.i, internal foramen of the endolymphatic duct; f.Pi, pineal foramen; ioc, infraorbital sensory groove; lc, main lateral sensory groove; M, marginal plate; mpl, middle pit-line; N, nuchal plate; occ, occipital cross commissure; PaN, paranuchal plate; Pi, pineal plate; PM, postmarginal plate; pmc, postmarginal sensory groove; ppl, posterior pit-line; PrO, preorbital plate; PtN, postnasal plate; PtO, postorbital plate; R, rostral plate; rc, rostral sensory groove; sac, saccula of the inner ear; soc, supraorbital sensory groove.

Phylogenetic analysis abbreviations

50%, 50% majority rule consensus tree; B, Bremer index; BTL, best tree length; CI, consistency index; CISCT, consistency index of the strict consensus tree; L, length of trees (in evolutionary steps); LSCT, length of the strict consensus tree; n, number of trees; RI, retention index; RISCT, retention index of the strict consensus tree; SC, strict consensus tree.

SYSTEMATIC PALAEOLOGY
 CLASS PLACODERMI MCCOY, 1848
 ORDER ARTHRODIRA WOODWARD, 1891
 SUBORDER 'ACTINOLEPIDOIDEI' MILES, 1973
 FAMILY 'ANTARCTASPIDIDAE' WHITE, 1968
 GENUS *YUJIANGOLEPIS* WANG *ET AL.*, 1998
 SPECIES *YUJIANGOLEPIS LIUJINGENSIS*
 WANG *ET AL.*, 1998

Holotype IVPP V 1957

Wang *et al.*, 1998: fig. 2; pl I, fig. 1

Young & Goujet, 2003, fig. 16C

DESCRIPTION

The only material available for *Yujiangolepis liujingensis* is a 3D-preserved subcomplete head showing a small part of the underlying neurocranium (Fig. 2A). Neither diagenesis nor compaction seems to have altered the specimen. Radiation centres are easily recognizable because of the numerous minute tubercles around; the plate boundaries are indicated with low and very thin ridges. The ethmoid components (R, Pi, PtN, Fig. 2A, C) are fused to the rest of the skull roof, although the boundaries of the postnasal plates are not distinguishable. From what can be seen, only a small mesial part of the postnasal plate can be detected just anterior to the right orbit. The anterior face of the rostral plate bears large and pointed tubercles, reminiscent of the snout of *Wuttagoonaspis fletcheri* Ritchie, 1973 (pl. 5, figs 1–3; Fig. 2D), although the rest of the ornamentation is completely different from the latter genus (*Wuttagoonaspis* also exposes ridges). The rostral sensory groove (rc, Fig. 2A, C) shows a mesial loop, as is visible in *W. fletcheri* (see Ritchie, 1973: text. fig. 5A), and to a lesser extent in *Toombalepis tuberculata* (Young & Goujet, 2003: fig. 16). Owing to its anteromesial position, the groove is referred to the rostral groove rather than the 'supramaxillary groove' in *W. fletcheri*. A shallow depression extends posterolaterally from the loop, as in *T. tuberculata*. *Antarctaspis mcmurdoensis* does not show any loop, but this absence might be explained because of the incompleteness of the most anterior part of the snout (see White, 1968: pl. II figs 1–2). In *Yujiangolepis*, the rostral groove then extends ventrally. The pineal plate is elongate and very narrow. A small crack is situated at the level of the pineal foramen/eminence; hence it is impossible to say if this was a closed (eminence) or an open (foramen) structure.

The preorbital plate (PrO, Fig. 2A, C) is a large element entirely separated from its antimer by the pineal plate. It constitutes the mesial part of the orbital margin. It is crossed longitudinally by the

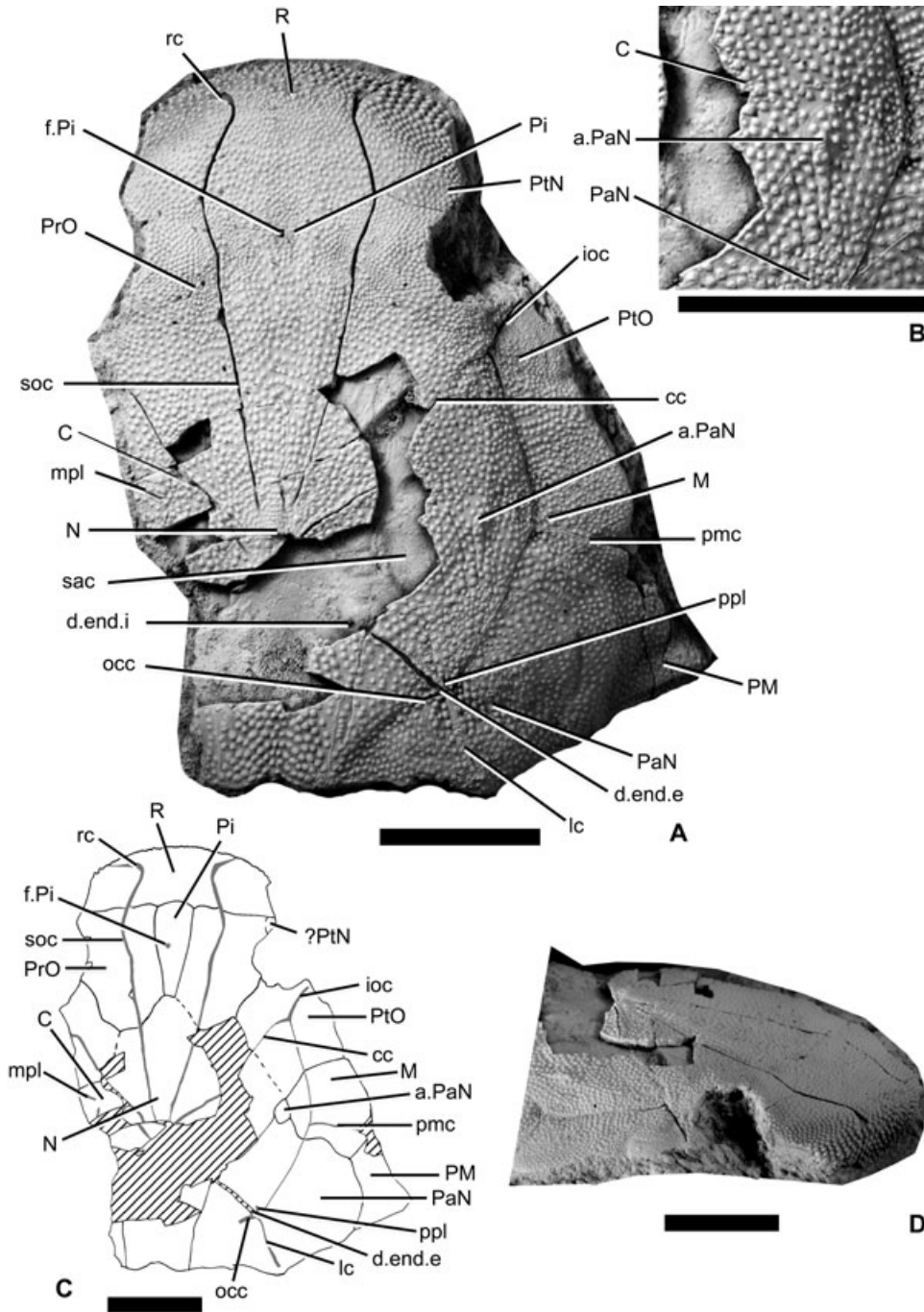


Figure 2. Subcomplete skull roof of *Yujiangolepis liujingensis* Wang *et al.*, 1998 (holotype IVPP V 1957). A, photograph of the skull roof in dorsal view; B, magnification around right central and anterior paranuchal plates; C, interpretative sketch of the skull roof after (A); D, right dorsolateral view of the skull roof. Abbreviations: a.PaN, anterior paranuchal plate; C, central plate; cc, central sensory groove; d.end.e, external foramen of the endolymphatic duct; d.end.i, internal foramen of the endolymphatic duct; f.Pi, pineal foramen; ioc, infraorbital sensory groove; lc, main lateral sensory groove; M, marginal plate; mpl, middle pit-line; N, nuchal plate; occ, occipital cross commissure; PaN, paranuchal plate; Pi, pineal plate; PM, postmarginal plate; pmc, postmarginal sensory groove; ppl, posterior pit-line; PrO, preorbital plate; PtN, postnasal plate; PtO, postorbital plate; R, rostral plate; rc, rostral sensory groove; sac, saccula of the inner ear; soc, supraorbital sensory groove. Scale bars = 1 cm.

supraorbital groove (soc, Fig. 2A, C), which is the posterior extension of the rostral groove.

The postorbital plate constitutes the posterior edge of the orbit. Its radiation centre classically corresponds to the junction between the infraorbital and central sensory grooves (ioc, cc, Fig. 2A, C). The boundary with the central plate is unclear.

The case of the central plates is more problematic, because the area where they should be visible, assuming a 'classic' arthrodire pattern, is not preserved. We can only assess the presence of these plates owing to a slight difference in the tubercle distribution: very tiny tubercles are visible at the level of the crack (right half of the specimen; C, Fig. 2A–C) just posteriorly to the central sensory groove (cc, Fig. 2A, C), and most probably indicate the position of the radiation centre of the plate. Unfortunately, it is impossible to determine either the mesial extension of the central plates or their size.

The nuchal plate (N, Fig. 2A, C), although unknown in its middle part, extends further anteriorly, and contacts the preorbital and most probably postorbital plates. The supraorbital and central sensory grooves clearly converge toward the radiation centre of the nuchal plate; there is no evidence that the posterior pit-lines also converge onto this point (as the corresponding parts of the skull roof are not preserved, and as only the dorsal side of the neurocranium is exposed). The boundary between the paranuchal and nuchal plates is outlined by a low and thin ridge (see Fig. 2A).

The marginal plate (M, Fig. 2A, C) is present mesially to the infraorbital and main lateral sensory grooves; in other words, it separates the postorbital and the paranuchal plates. Its radiation centre is located at the level of the junction between the infraorbital, main lateral, and postmarginal sensory grooves. The postmarginal plate (PM, Fig. 2A, C) constitutes a pointed posterolateral edge of the skull roof, slightly more anterior than in other species of 'Actinolepidoidei' (in which it is almost at the level of the posterior margin of the paranuchal plates).

The paranuchal ensemble is very interesting in its composition of two plates. The biggest and main paranuchal plate (PaN, Fig. 2A–C) bears the main lateral sensory line groove, the occipital cross commissure, the posterior pit line, and the external foramen for the endolymphatic duct. It would be homologous with the posterior paranuchal plate of the Petalichthyida Jaekel, 1911 and of the Acanthothoraci Stensiö, 1944. Anteriorly to this plate, the smaller one is considered here as a possible vestigial anterior paranuchal plate similar to that of the Petalichthyida and of the Acanthothoraci (a.PaN, Fig. 2A–C), because it is visible at the junction with the central and the marginal plates ('topographic' hypothesis for homology; see discussion

below). This anterior paranuchal plate is outlined by low and smooth ridges. Contrary to what can be observed in the Petalichthyida (a group of Placodermi that is closely related to the Arthrodira and possessing two pairs of posterior pit-lines and of paranuchal plates), the anterior paranuchal plate of *Yujiangolepis* is not crossed by any sensory groove and is much smaller, suggesting it as a vestigial element.

Obviously, the dermal craniothoracic joint is of the 'sliding' type, as in all 'Actinolepidoidei'.

The visible part of the dorsal side of the neurocranium exposes the saccula of the inner ear (sac, Fig. 2A), and the internal foramen for the endolymphatic duct on a bump (d.end.i, Fig. 2A) of the neurocranium, mesially to the nuchal–paranuchal plate boundary. The respective positions of the external (d.end.e, Fig. 2A, C) and internal foramina for the endolymphatic duct imply the possession of a long and oblique endolymphatic tube within the dermal bone that is characteristic of the Arthrodira (Goujet, 1984).

RESULTS

PHYLOGENETIC ANALYSIS

In order to determine the systematic position of *Yujiangolepis liujingensis* within the Arthrodira, as well as enlighten the base of the Arthrodira, a computerized phylogenetic analysis using the parsimony approach was performed. The ingroup is initially composed of 38 taxa, containing 19 species of the 'Actinolepida', seven species of the Phlyctaenii, three species of the Brachythoraci, five species of the Phyllolepida (including the recently described *Gavinaspis convergens* Dupret & Zhu, 2008), and four species of basal Arthrodira ['Actinolepidoidei': the 'Antarctaspidae' *Yujiangolepis liujingensis* and *A. mcmurdoensis* and the Wuttagoonaspidae *W. fletcheri*, and the recently described *Yiminaspis shenme* Dupret, 2008 (see White, 1968; Ritchie, 1973; Wang *et al.*, 1998; Young & Goujet, 2003; Dupret, 2008; Dupret & Zhu, 2008)]. The outgroup is composed of the Petalichthyida *Lunaspis broilii* Gross, 1937 and *Eurycaraspis incilis* Liu, 1991. The data matrix is given in Supporting Information Appendix S1; the list of the 65 characters involved in the analysis is given in Supporting Information Appendix S2.

Remark: Several types of analyses were performed, as explained in the text below; nevertheless, in Figure 5, we present a recapitulation of the indices and topologies for each research performed.

The data matrix was treated with Nexus Data Editor 0.5.0 (Page, 2001), and the analysis was performed with PAUP 4.0.b10 (Swofford, 1989–1997).

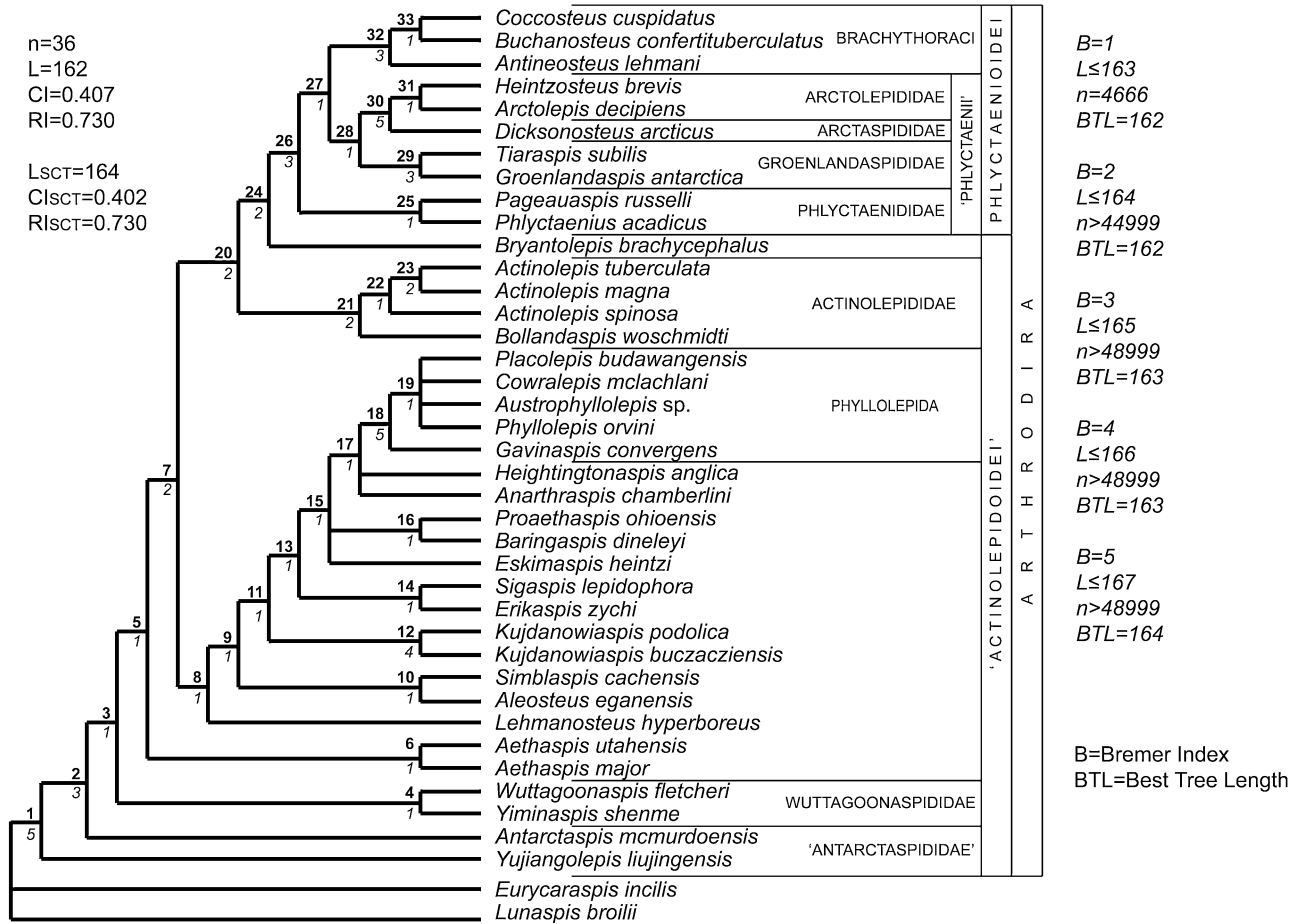


Figure 3. Phylogenetic relationships and classification amongst Arthrodira. Nodes are indicated with normal font; Bremer indices are given in italic below the corresponding branches, and characteristics for each Bremer research is given in the right column.

The heuristic search logarithm was used because of the large number of taxa. All characters were unordered a priori, and the trees were rooted with the two outgroup taxa (Petalichthyida). Wagner optimization was used because it accepts both reversions and convergences. The optimization of the missing data was carried out using ACCTRAN (reversions favoured).

The search led to 36 equiparsimonious trees, of 162 steps each (CI = 0.407; RI = 0.730). The strict consensus tree obtained (Fig. 3) is 164 steps long (CI_{SCT} = 0.402; RI_{SCT} = 0.730). The Bremer indices were calculated by permitting one more step in each search; they are indicated below the branches, as well as the maximum of trees retained by the computer before saturation.

In the strict consensus tree, the Arthrodira are monophyletic (node 1, Fig. 3), and *Yujiangolepis* is the most basal member amongst them. The Brachythoraci are monophyletic (node 32, Fig. 3), and belong to the clade Phlyctaenioidei (node 26) together with the

paraphyletic 'Phlyctaenii' (nodes 25 and 28, Fig. 3); the 'Actinolepidoidei' appear paraphyletic (nodes 1 to 24, Fig. 3), and the Phyllolepidia is a derived group amongst them (node 18, Fig. 3; see also Dupret, 2004; Dupret *et al.*, 2007; Dupret & Zhu, 2008). The 'Antarctaspididae' and the Wuttagoonaspidae are still the successive most inclusive arthrodire taxa, although in this new consensus tree the 'Antarctaspididae' appear paraphyletic (*Yujiangolepis* being more basal than *Antarctaspis*; nodes 1 to 2, Fig. 3), whereas the Wuttagoonaspidae (*Wuttagoonaspis* and *Yiminaspidis*) appear monophyletic (node 4, Fig. 3).

Because of (1) the anatomical peculiarity of the most basal arthrodires (i.e. shared states of characters with the Petalichthyida); (2) the Petalichthyida constituting the outgroups and being as such used for the polarization of the character states (i.e. shared states of characters between the Petalichthyida and the basal Arthrodira are regarded as symplesiomorphies); and (3) the subsequent paraphyletic sequence

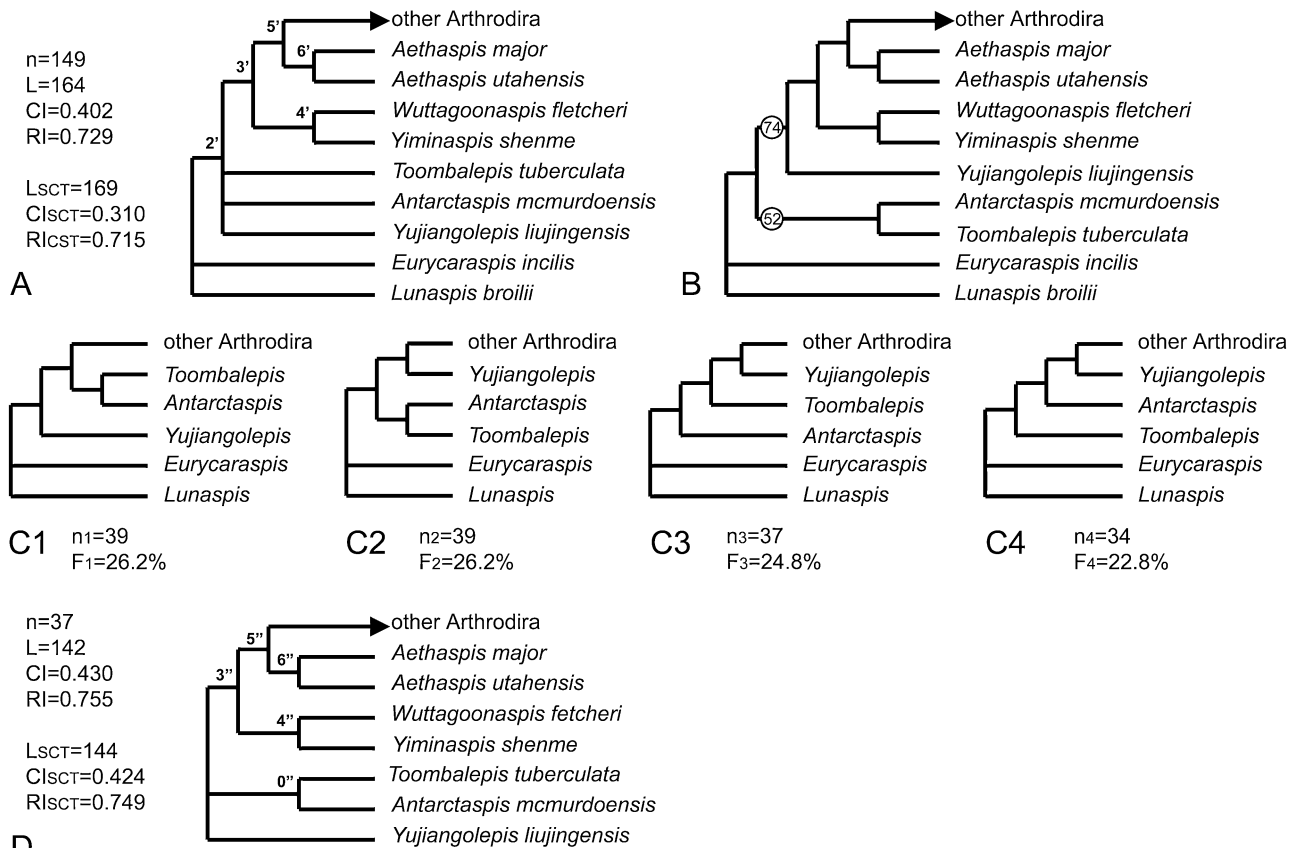


Figure 4. Phylogenetic relationships amongst Arthrodira after inclusion of the Australian *Toombalepis tuberculata* in the data matrix. A, strict consensus tree; B, majority rule consensus (indices given on the corresponding branches); C, the four possible topologies encountered (frequencies given); D, strict consensus tree obtained after deletion of *Lunaspis* and *Eurycaraspis* and inclusion of *Antarctaspis mcmurdoensis*, *T. tuberculata*, and *Yujiangolepis liujingensis* in the outgroup.

at the base of the Arthrodira, a precise definition of the Arthrodira based on one single node cannot be provided. In other words, the synapomorphies that defined the Arthrodira on one single node in previous phylogenies are now positioned on several nodes. Nevertheless, the states of characters from node 1 to node 5 are relevant enough, and described below.

The very base of the Arthrodira (node 1: *Yujiangolepis liujingensis* and other Arthrodira) is defined by the presence of sensory grooves (as opposed to sensory canals with pores in the Petalichthyida), of one pair of posterior pit-lines, of a central sensory groove, of a postmarginal plate, and of a 'sliding' dermal craniothoracic articulation (characters 14, 29, 31, 32, and 40; $CI_{14} = 1$, $CI_{29} = 0.5$, $CI_{31} = 1$, $CI_{32} = 0.5$, $CI_{40} = 1$). One more character has to be added to the previous ones, that is the possession of a long and oblique endolymphatic duct, as opposed to the straight vertical one observed in the Petalichthyida and the Acanthothoraci (see Goujet & Young, 1995).

Node 2 (*Antarctaspis mcmurdoensis* and other crownward Arthrodira) is defined by the possession of

a single pair of paranuchal plates (character 35; $CI_{35} = 1$). This explains the paraphyletic status of the family 'Antarctaspididae', because *Yujiangolepis* shares the possession of two paranuchal plates with the Petalichthyida (despite the fact that this anterior paranuchal plate would actually be a vestigial element).

Node 3 (Wuttagoonaspidae + other crownward Arthrodira) is supported by a lack of contact between the pineal and nuchal plate, and a length : width ratio of the median dorsal plate lower than 1.5 (characters 34, 60; $CI_{34} = 1$, $CI_{60} = 0.333$).

Node 4 (family Wuttagoonaspidae) is supported by a very anterior position of the pineal plate relative to that of the orbits, no contact between the postorbital and paranuchal plates, and connected anterior and posterior ends of the posterior pit-lines (characters 6, 23, 30; $CI_6 = 1$, $CI_{23} = 0.2$, $CI_{30} = 0.333$). It is noteworthy that the presence of two pairs of posterior pit-lines in *Yiminaspis shenme* is considered as a reversal or a convergence with the Petalichthyida, rather than a symplesiomorphy.

settings		without <i>Toombalepis</i>		with <i>Toombalepis</i>	
a.PaN coded <i>Yujiangolepis</i> #35=1	addsequ=simple	n=36 L=162 SC 50%		n=142 L=164 SC 50%	
	Hsearch start=stepwise add sequ=random nreps=1000	n=287 L=162 SC 50%		n=809 L=164 SC 50%	
a.PaN is not coded <i>Yujiangolepis</i> #35=0	addsequ=simple	n=115 L=162 SC 50%		n=117 L=163 SC 50%	
	Hsearch start=stepwise add sequ=random nreps=1000	n=705 L=162 SC 50%		n=707 L=163 SC 50%	

Figure 5. Recapitulative table of the different phylogenetic analyses performed. Key: 50%, 50% majority rule consensus tree; a.PaN, anterior paranuchal plate; addsequ, addition sequence; CS, strict consensus tree; L, length of each equiparsimonious tree; n, number of equiparsimonious trees; nreps, number of replications.

Node 5 (genus *Aethaspis* and other crownward Arthrodira) is supported by preorbital plates not separated by the pineal plate, separate supraorbital sensory grooves, and the width : length ratio of the preorbital plates greater than 0.5 (characters 7, 15, 57; $CI_7 = 0.2$, $CI_{15} = 0.25$; $CI_{57} = 0.25$).

Node 7 is supported by central plates not separated by the nuchal plate, and a shallow pectoral notch of the anterior ventrolateral plate (characters 25, 48; $CI_{25} = 0.5$, $CI_{48} = 0.125$). From this node, it can be considered that the ‘regular’ pattern of the Arthrodira is acquired, and is subject to only minor changes in some groups (e.g. the Phyllolepidia, the Groenlandaspidae).

The inclusion of the Australian *Toombalepis tuberculata* in the research (the ingroup is then composed of 39 taxa) led to 149 equiparsimonious trees of 164 steps each. The corresponding strict consensus tree shows a polytomy at the base of the Arthrodira between the three ‘Antarctaspidae’ and the other Arthrodira (node 2’, Fig. 4A), whereas the 50% majority rule consensus tree displays the clade (*Antarctaspis*, *Toombalepis*) as sister group to *Yujiangolepis* and other Arthrodira (Fig. 4B). The clade (*Antarctaspis*, *Toombalepis*) appears in 78 out of the 149 trees ($F = 52%$; Fig. 4B, C1-2), and the clade (*Yujiangolepis*, other Arthrodira) appears in 110 trees out of 149 ($F = 74%$, Fig. 4B, C2-4). Surprisingly, *Yujiangolepis* as the most basal arthrodire is only retained in only 39 trees out of 149 ($F = 26%$; Fig. 4C1). It is also noteworthy that the deletion of the two Petalichthyida, together with the transposition of the three ‘Antarctaspidae’ within the outgroup, led to 37 equiparsimonious trees of 142 steps each, and *Antarctas-*

pis and *Toombalepis* appear to be monophyletic (Fig. 4D). In all cases, the rest of the strict consensus tree topology is unchanged with regard to the one illustrated in Figure 3.

Some other series of analyses were performed (Fig. 5), changing the coding of character 35 (number of paranuchal plates; from state ‘1’ to state ‘0’) in *Yujiangolepis*: this time, the surnumeral element is not considered as homologous with the petalichthyid anterior paranuchal plate, but rather as a novelty, and therefore as an autapomorphy of *Yujiangolepis*. Without *Toombalepis*, the analysis led to 115 equiparsimonious trees of 162 steps each. Both strict consensus and 50% majority rule consensus trees show a polytomy at the base of the tree amongst *Antarctaspis*, *Yujiangolepis*, and the other Arthrodira. The inclusion of *Toombalepis* in the analysis led to 117 equiparsimonious trees of 163 steps each, and the strict consensus and 50% majority rule consensus trees are identical: *Yujiangolepis* is the sister-group of the other Arthrodira, and a clade formed by *Antarctaspis* and *Toombalepis* is sister-group of the previous ensemble.

A last sequence of analyses was performed, changing the options in PAUP (i.e. addsequ = random; nreps = 1000). The consensus tree topologies are not very different from those displayed in the previous analyses. Without *Toombalepis*, and with *Yujiangolepis* possessing an anterior paranuchal plate (#35:1), the research led to 287 equiparsimonious trees of 162 steps each; both the strict consensus and the 50% majority rule consensus show (*Yujiangolepis* (*Antarctaspis*, other Arthrodira)). The addition of *Toombalepis* led to 809 equiparsimonious trees of 164 steps

each. The strict consensus tree shows a polytomy between the three antarctaspidids and the other Arthrodira. The 50% majority rule consensus tree shows a sister group relationship between *Antarctaspis* and *Toombalepis*, this clade being sister-group of the clade *Yujiangolepis* + other Arthrodira.

The modification of character 35 from state '1' to '0' for *Yujiangolepis*, together with the deletion of *Toombalepis*, led to 705 equiparsimonious trees of 162 steps. The strict consensus tree shows a polytomy amongst *Antarctaspis*, *Yujiangolepis*, and the other Arthrodira. The 50% majority rule consensus tree shows (*Yujiangolepis* (*Antarctaspis*, other Arthrodira)). The inclusion of *Toombalepis* in the analysis led to 707 equiparsimonious trees of 163 steps each; both the strict consensus and the 50% majority rule consensus show the same topology: ((*Antarctaspis*, *Toombalepis*)(*Yujiangolepis*, other Arthrodira)).

In conclusion, even though the accurate phylogenetic position of *Yujiangolepis* (most basal arthrodirid or sister group for non-antarctaspidid arthrodirids) is still unclear, it is nevertheless obvious that the family Antarctaspididae is not monophyletic given the characters at hand.

DISCUSSION

HOMOLOGIES OF THE PARANUCHAL PLATES AND THE POSTERIOR PIT-LINES IN THE PETALICHTHYIDA AND THE ARTHRODIRA

In the Arthrodira, a single paranuchal plate classically bears the posterior pit-line, the occipital cross commissure, and the external foramen for the endolymphatic duct (except in the Phyllolepidia). In the Petalichthyida, the anterior paranuchal plate bears the second posterior pit-line and the external foramen for the endolymphatic duct, whereas the posterior paranuchal plate bears the occipital cross commissure.

Until recently, two pairs of paranuchal plates were only encountered in the Petalichthyida, the Acanthothoraci Stensiö, 1944, and *Brindabellaspis* Young, 1980, whereas two pairs of posterior pit-lines were only found in the Petalichthyida and the Acanthothoraci (Denison, 1978; Young, 1980; Goujet & Young, 1995). In the Petalichthyida, the first posterior pit-line is never complete (implying a superficial run), and it connects the radiation centres of the central and of the nuchal plates; the second posterior pit-line is complete and connects the radiation centres of the anterior paranuchal and nuchal plates.

Recent discoveries in the Early Devonian south Chinese material have revealed the presence of such 'petalichthyid' features in basal arthrodirids, yet until now the two characters have not been known to

co-occur. *Yujiangolepis liujingensis* possesses two pairs of paranuchal plates, associated with one pair of posterior pit-lines. *Yiminaspis shenme* possesses one pair of paranuchal plates, associated with two complete pairs of posterior pit-lines (the first pair connects the radiation centres of the nuchal and the marginal plates, whereas the second pair connects those of the nuchal and paranuchal plates; Dupret, 2008).

Dupret (2008) suggested that the second pair of posterior pit-lines of the Petalichthyida and of *Yiminaspis* was homologous with that of the Arthrodira, because of the branching onto the central or nuchal plate and on the paranuchal plate (independently of whether it is the anterior or posterior one).

The homologies of the paranuchal plates can rely on three scenarios. The single paranuchal plate of the Arthrodira may be homologous to (1) the anterior and posterior paranuchal plates of the Petalichthyida (fusion of both plates involved); (2) the anterior paranuchal plate of the Petalichthyida (loss of the posterior one involved); (3) the posterior paranuchal of the Petalichthyida (loss of the anterior one involved).

As the Arthrodira *Yujiangolepis* displays both anterior and posterior paranuchal plates – the anterior one seeming vestigial –, and because the single posterior pit-line anchors on the posterior paranuchal plate (together with the external foramen for the endolymphatic duct and the occipital cross commissure), it would be legitimate to consider that the posterior paranuchal plate of *Yujiangolepis* is homologous with the paranuchal of the other Arthrodira. The problem is that the second posterior pit-line does not anchor posteriorly on the posterior paranuchal plate in the Petalichthyida (although it is possible in some Acanthothoraci; see *Radotina prima* Gross, 1958).

It is also possible that the element labelled 'anterior paranuchal plate' in *Yujiangolepis* may not be homologous with that of the Petalichthyida, but rather a surnumerical element; in such a case, the result is not so different as this plate is coded as autapomorphic for *Yujiangolepis* only, hence the presence of one pair of paranuchal plates would appear at the first node of the Arthrodira. Anyhow, it is noteworthy that the material of the south China basal Arthrodira is extremely rare (one skull roof for *Yujiangolepis* and *Yiminaspis*). Hence, it should be noted that it is presently impossible to figure out whether these features (e.g. second posterior pit-line in *Yiminaspis shenme* and presence of an anterior paranuchal plate in *Yujiangolepis liujingensis*) are encountered widely and consistently within the species (i.e. complete populations) or not, leading to an accurate diagnosis (definition) of these taxa, or, in the other case, leading to polymorphism or an unstable (or not established yet) arthrodiran pattern.

For the present time, we consider that the posterior pit-line of the Arthrodira is homologous with the second posterior pit-line of the Petalichthyida and of *Yiminaspis*, and that the paranuchal plate of the Arthrodira is homologous with the posterior one of *Yujiangolepis*.

SYSTEMATIC CONSIDERATIONS

The only phylogenetic analysis taking into account all of the major placoderm taxa was performed by Goujet & Young (1995). *Inter alia*, the authors concluded there was a sister-group relationship between the ensemble Petalichthyida + Ptyctodontida Gross, 1932, and the Arthrodira, the latter being unresolved. Nevertheless, by that time, the gap between these two clades was very large. More recent analyses of some Arthrodira (e.g. Johnson, Elliot & Wittke, 2000; Dupret, 2004; Dupret *et al.*, 2007) attempted to resolve the internal relationships of the Arthrodira and/or the ‘Actinolepidoidei’.

The sharing of some anatomical features in the basal Arthrodira and Petalichthyida (i.e. two pairs of posterior pit-lines or of paranuchal plates) induces a possible ancestor within a Chinese quasipetalichthyid pool (also because the Quasipetalichthyida share with the ‘Actinolepidoidei’ the possession of anteroventral plates and of an anteroventral sulcus on the belly armour), or that the Petalichthyida and the Arthrodira share the same common ancestor (see also Goujet & Young, 1995). Zhu (1990: figs 56–58) also proposed that Petalichthyida are a subgroup of ‘Actinolepidoidei’ Arthrodira.

The Chinese forms described recently (i.e. *Yujiangolepis* and *Yiminaspis*) fill in the gap between the Petalichthyida and the Arthrodira, but at the same time reduce the numbers of characters diagnosing the very base of the Arthrodira (see above), and at the same time the robustness of the branches. In addition, the convergence of the sensory lines in the medial element of the skull roof (i.e. on the nuchal or centronuchal plate) is considered as a primitive feature amongst the Arthrodira (and even Placodermi; Young, 2005b: 206), as well as the possession of an elongated nuchal plate separating the central plates. With the Petalichthyida *Lunaspis* and *Eurycaraspis* in the outgroup, it is obvious that the ‘Antarctaspididae’ share with them these plesiomorphic states of characters, thus explaining their basal position amongst the Arthrodira.

THE FAMILY ‘ANTARCTASPIDIDAE’: ORIGINS AND DISPERSAL

The family ‘Antarctaspididae’ is composed of three genera: *Antarctaspis* from the Givetian Antarctic

		BIOSTRATIGRAPHIC ZONATIONS [E. GONDWANA & CHINA]		RANGE OF TAXA	
				S.CH	GONDWANA
LATE DEVONIAN	FAMMENIAN	MAV15 LN, LV VCo GF MAV14 GH	<i>praesulcata</i> <i>expansa</i> <i>postera</i> <i>trachytera</i> <i>marginifera</i> <i>rhomboidea</i> <i>crepida</i>		
	FRASNIAN		<i>triangularis</i> <i>linguiformis</i> <i>rhenana</i> <i>jamieae</i> <i>hassi</i> <i>punctata</i> <i>transitans</i> <i>falciovalis</i>	MAV13 MAV12 MAV11 MAV10	
MIDDLE DEVONIAN	GIVETIAN		<i>norrisi</i> <i>disparilis</i> <i>hermanni</i> <i>varcus</i> <i>hemiansatus</i>	MAV9 MAV8 MAV7 MAV6	
	EIFELIAN		<i>ensis</i> <i>australis</i> <i>costatus</i> <i>partitus</i> <i>patulus</i> <i>serotinus</i> <i>inv.-laticost.</i> <i>perbonus-gron.</i> <i>dehiscens</i>	MAV4-5 MAV3	
EARLY DEVONIAN	EMSIAN		<i>pireneae</i> <i>kindlei</i> <i>sulcatus</i>	MAV III	
	PRAG.		<i>pesavis</i> <i>delta</i> <i>eurekaensis</i> <i>woschmidti</i>	MAV II MAV I	
	LOCHK.		<i>Yiminaspis shenme</i> <i>Yujiangolepis lujiingensis</i>		

Figure 6. Summary of the stratigraphical ranges (Lochkovian–Famennian) for the Wuttagoonaspidae and the ‘Antarctaspididae’ (Arthrodira) of south China (S.CH) and Gondwana. Supposed stratigraphical ranges indicated by dashed lines with ‘?’. South Chinese taxa stratigraphical range after Dupret, 2008; Wang *et al.*, 1998. Gondwanan taxa stratigraphical range after Ritchie, 1973; White, 1968; Young & Goujet, 2003. Conodont zonation from Zhu *et al.*, 2000 (Lochkovian) and Talent *et al.*, 2000 (Pragian–Famennian). Lochkovian macrovertebrate assemblages (MAV I–III, left side of the column) after Zhu *et al.*, 2000; Pragian–Famennian macrovertebrate assemblages (MAV2–15, right side of the column), miospore (GH, GF, VCo, LN, LV) and conodont zone is approximate (modified after Young, 1996, 2005a, b; Young & Turner, 2000; Young & Long, 2005).

Aztec Siltstone, *Yujiangolepis* from the Nakaoling (Nagaoling) Formation of Guangxi, south China, and *Toombalepis* from the Dulcie Sandstone and Craven Peak Beds of Australia (plus an undescribed new genus from Australia; G. C. Young, pers. comm.) (Figs 6–7). Until now, as far as we know, no synapomorphic character for the family ‘Antarctaspididae’ has been found. This is why this family appears to be paraphyletic in the phylogenetic hypothesis described

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Data matrix taxa*characters.

Appendix S2. List of the characters.

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