

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

Received 5 June 2008; accepted for publication 3 September 2008

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 arthrodirids *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.

© 2009 Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology. Journal compilation © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009.
doi: 10.1111/j.1096-3642.2009.00519.x

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 arthrodirids (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 Hengxi (Guangxi, south China; macrovertebrate assemblage MAV III of Zhu, Wang & Wang, 2000; Fig. 1). This formation also yielded the remains of the Galeaspid *Asiaspis expansa* Pan, Wang & Liu, 1975, *Antiquisagittaspis cornuta* Liu, 1985, the Arthrodira *Asiacanthus multituberculatus* Liu, 1982, and the

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

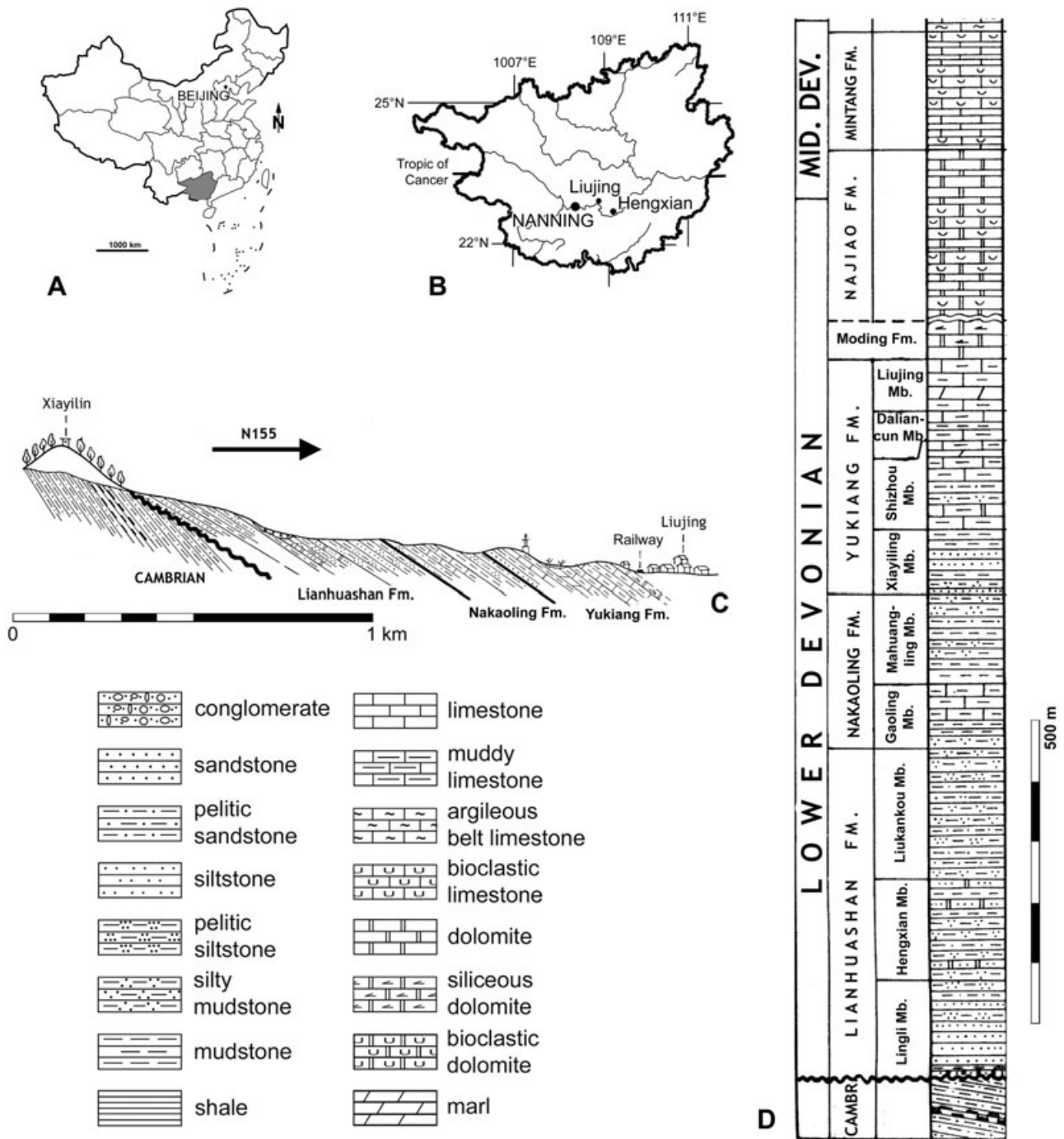


Figure 1. Guangxi province in China (A) and position of Liujing in Guangxi (B). Stratigraphical section (C) and column (D) in Liujing (slightly modified after Kuang *et al.*, 1989: figs 3–4).

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 PALAEOONTOLOGY

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 *Wuttageonaspis fletcheri* Ritchie, 1973 (pl. 5, figs 1–3; Fig. 2D), although the rest of the ornamentation is completely different from the latter genus (*Wuttageonaspis* 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 antimeres by the pineal plate. It constitutes the mesial part of the orbital margin. It is crossed longitudinally by the

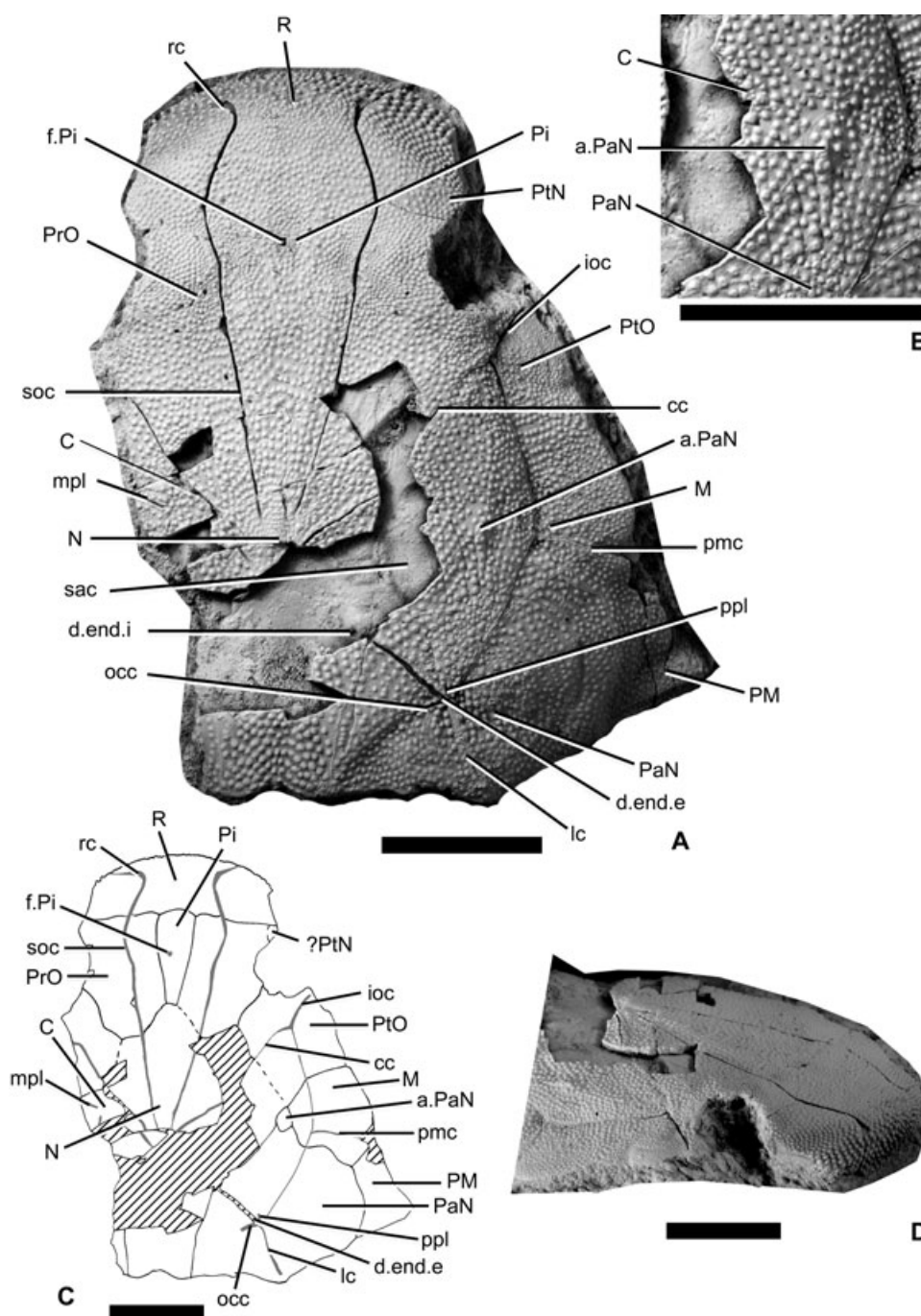


Figure 2. Subcomplete skull roof of *Yujiangolepis liujingensis* Wang *et al.*, 1998 (holotype IVPP V 1957). A, photograph of the skull roof in dorsal view; B, magnification around right central and anterior paranuchal plates; C, interpretative sketch of the skull roof after (A); D, right dorsolateral 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 Arthrodire 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 Arthrodire (Goujet, 1984).

RESULTS

PHYLOGENETIC ANALYSIS

In order to determine the systematic position of *Yujiangolepis liujingensis* within the Arthrodire, as well as enlighten the base of the Arthrodire, 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 Phyllolepidi (including the recently described *Gavinaspis convergens* Dupret & Zhu, 2008), and four species of basal Arthrodire ['Actinolepidoidei': the 'Antarctaspididae' *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 broillii* 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).

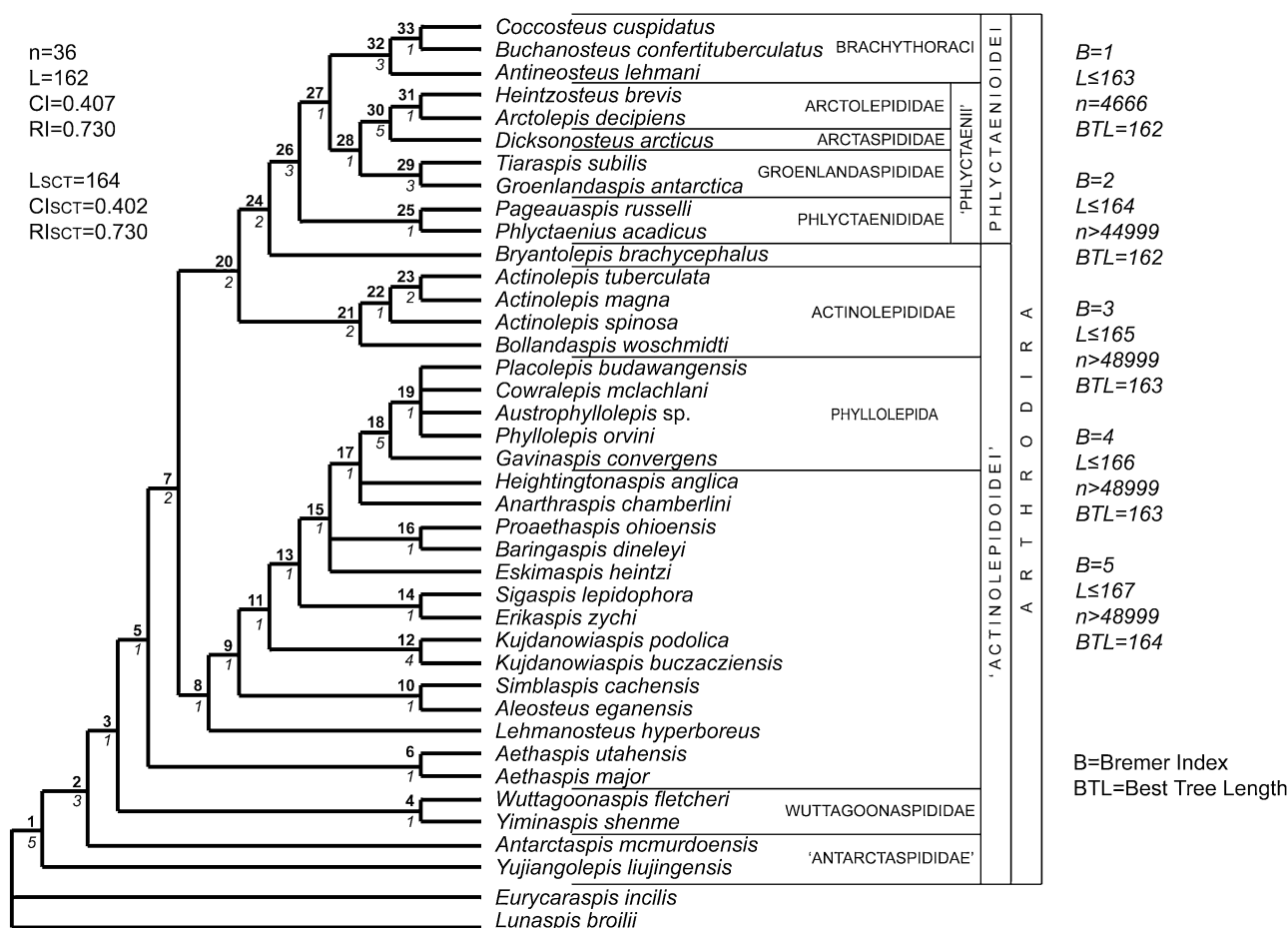


Figure 3. Phylogenetic relationships and classification amongst Arthrodira. Nodes are indicated with normal font; Bremer indices are given in italic below the corresponding branches, and characteristics for each Bremer research is given in the right column.

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 Wuttagoonaspididae 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 Wuttagoonaspididae (*Wuttagoonaspis* and *Yiminaspis*) appear monophyletic (node 4, Fig. 3).

Because of (1) the anatomical peculiarity of the most basal arthrodire (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

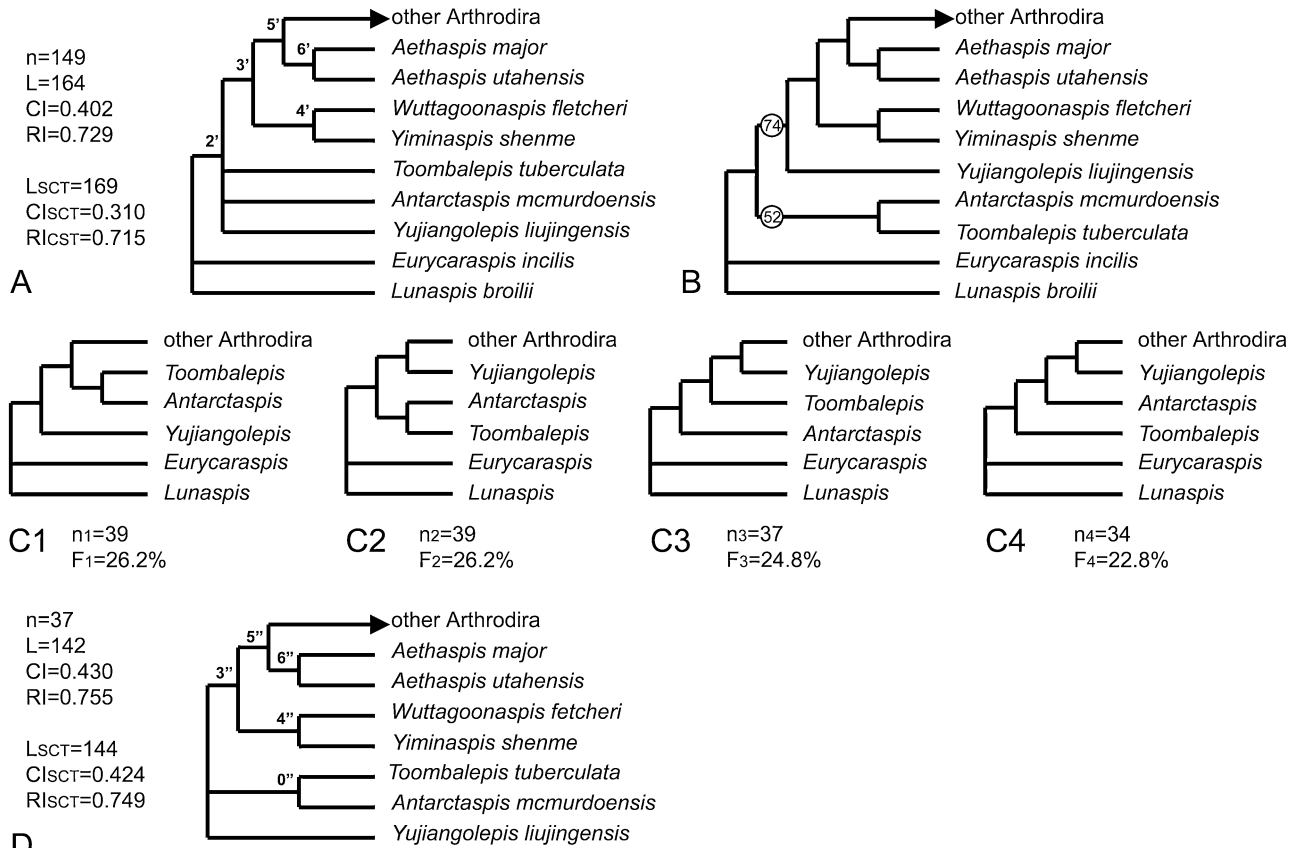


Figure 4. Phylogenetic relationships amongst Arthrodira after inclusion of the Australian *Toombalepis tuberculata* in the data matrix. A, strict consensus tree; B, majority rule consensus (indices given on the corresponding branches); C, the four possible topologies encountered (frequencies given); 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 (Wuttagoonaspididae + 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 Wuttagoonaspididae) 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 sympleisiomorphy.


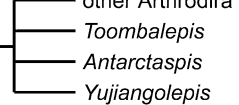
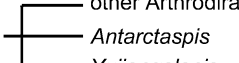
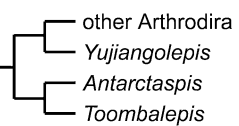
settings		without <i>Toombalepis</i>		with <i>Toombalepis</i>	
a.PaN coded <i>Yujiangolepis</i> #35=1	addsequ=simple	n=36 L=162 SC 50%		n=142 L=164 SC 50%	
	Hsearch start=stepwise add sequ=random nreps=1000	n=287 L=162 SC 50%		n=809 L=164 SC 50%	
a.PaN is not coded <i>Yujiangolepis</i> #35=0	addsequ=simple	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 ‘Antarctaspididae’ 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 ‘Antarctaspididae’ 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 arthrodire or sister group for non-antarctaspidid arthrodiros) is still unclear, it is nevertheless obvious that the family Antarcaspididae 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 arthrodiros, 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 surnumeral 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

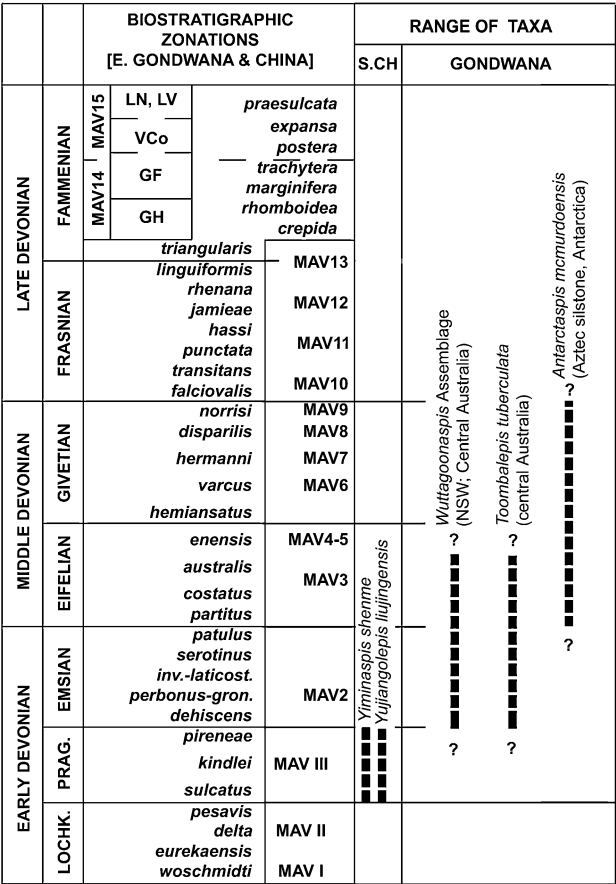


Figure 6. Summary of the stratigraphical ranges (Lochkovian–Famennian) for the Wuttagoonaspidae and the ‘Antarctaspididae’ (Arthrodira) of south China (S.CH) and Gondwana. Supposed stratigraphical ranges indicated by dashed lines with ‘?’. South Chinese taxa stratigraphical range after Dupret, 2008; 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

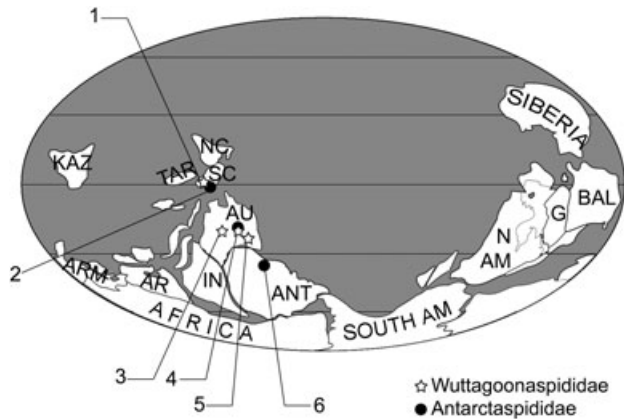


Figure 7. Global distribution pattern for Wuttagoonaspididae and 'Antarctaspididae', plotted on a Devonian reconstruction (after Zhao & Zhu, 2007). South Chinese Pragian localities: 1, Zhaotong (Yunnan; Dupret, 2008) and 2, Liujing (Guangxi; this paper); Gondwanan Givetian localities: 3, Amadeus Basin and 4, Georgina Basin (central Australia; Young, 2005a, b; Young & Goujet, 2003); 5, west-central New South Wales (Australia; Hills, 1931, 1936; Ritchie, 1973; Young, 1993, 1999); 6, Antarctic Aztec Siltstone, Victoria (White, 1968).

above. The 'Antarctaspididae' are most likely the most basal Arthrodira from a morphological (and subsequently systematic) point of view. Nevertheless, they are not the earliest Arthrodira. More derived groups appear before the most ancient stratigraphical occurrence of the 'Antarctaspididae'. As an example, one can refer to the Chinese sister-group of the Phyllolepididae, *Gavinaspis convergens*, from the Late Lochkovian of Qujing (Yunnan, south China; Dupret & Zhu, 2008). Comparatively, the most basal arthrodire is *Yujiangolepis liujingensis*, and is Pragian in age, i.e. occurring later than *Gavinaspis*. These considerations have three consequences.

First, if we consider the results of the previous phylogenetic analysis to be reliable, because the Antarctaspididae are considered as the most basal Arthrodira, yet not the most ancient Arthrodira, the origin of the 'Antarctaspididae' (and hence that of the Arthrodira) should be found in much more ancient strata than the Pragian, and even than the Lochkovian; that is within the Silurian.

Second, we can propose a south Chinese origin for the family 'Antarctaspididae'. Indeed, before the beginning of the Emsian, the south Chinese block shows an important rate of vertebrate endemism. During the Early Emsian (E'Em bioevent; Walliser, 1995), Gondwanan faunas invaded the south Chinese block, inducing competition and extinction for a large number of previously endemic vertebrate groups (e.g. Galeaspida; see Zhao & Zhu, 2007).

Third, because the 'Antarctaspididae' would then be encountered in Emsian–Givetian strata of Gondwana, it is most probable that during this E'Em bioevent, the 'Antarctaspididae' went into Gondwana, together with other groups like Phyllolepidida (Dupret & Zhu, 2008) or Wuttagoonaspididae (Dupret, 2008).

Furthermore, it is noteworthy that palaeobotanical data support this south China–north-eastern Gondwanan geographical proximity. Indeed, the floristic composition from the late Pragian Posongchong and from the late Pragian to early Emsian Xujiachong floras of eastern Yunnan (south China) are similar to those from the upper *Baragwanathia* flora (late Pragian) of Australia, and are supposed to belong to the same north-eastern Gondwanan palaeophytogeographical unit (possibly together with the Shan Thai palaeoblock). This single unit is divided into two subunits (because of the presence of dominant or endemic taxa): the *Eophyllophyton* subunit in south China, and the *Hedeia* subunit in Australia (Hao & Gensel, 1998; Wang, Hao & Liu, 2002). The fact that the palaeobotanical evidence occurs slightly earlier than the vertebrate data may not only be a result of a passive eolian dispersal (rather than the active swimming dispersal process of fishes), but also the fossil record biases. More investigation is therefore required in this south Chinese–north-eastern Gondwanan unit.

CONCLUSION

The revision of the holotype of the 'Antarctaspididae' *Yujiangolepis liujingensis* Wang *et al.*, 1998 has revealed the presence on the skull roof of an anterior paranuchal plate (probably vestigial because it is small and lacks a sensory line system) as it occurs in the Petalichthyida. A computerized phylogenetic analysis revealed that the family 'Antarctaspididae' is paraphyletic and most basal amongst all Arthrodira. Nevertheless, the position of *Yujiangolepis* as the most basal 'Antarctaspididae' is not assessed. Being the most ancient 'Antarctaspididae', but not the most ancient Arthrodira, a Chinese origin of both groups requires more research, most probably in the Silurian of south China.

ACKNOWLEDGEMENTS

John Long (Museum Victoria, Australia) and Gavin Young (ANU, Canberra ACT, Australia) pointed out some major features on the holotype, thus initiating the present article. Photographs of Figure 2 were taken by Jia Liantao (IVPP). This work is part of the UNESCO IGCP 491 Project (Middle Palaeozoic Vertebrate Biogeography, Palaeogeography, and Climate). This work was funded by grants from the

Natural Science Foundation of China (40332017 and 40602005) and the Major State Basic Research Projects (2006CB806400) of MST of China. The authors thank the two anonymous reviewers for their constructive remarks.

REFERENCES

- Denison RH. 1978.** *Placodermi*. Stuttgart; New York: Gustav Fischer Verlag.
- Dupret V. 2004.** The phylogenetic relationships between actinolepids (Placodermi: Arthrodira) and other arthrodires (phlyctaeniids and brachythoracids). *Fossils and Strata* **50**: 40–55.
- Dupret V. 2008.** First wuttagoonaspids (Placodermi, Arthrodira) from the Lower Devonian of Yunnan, South China. Origin, dispersal and palaeobiogeographic significance. *Journal of Vertebrate Paleontology* **28**: 12–20.
- Dupret V, Goujet D, Mark-Kurik E. 2007.** A new genus of placoderm (Arthrodira: 'Actinolepida') from the Lower Devonian of Podolia (Ukraine). *Journal of Vertebrate Paleontology* **27**: 266–284.
- Dupret V, Zhu M. 2008.** The earliest phyllolepid (Placodermi, Arthrodira), *Gavinaspis convergens*, from the late Lochkovian (Lower Devonian) of Yunnan (South China). *Geological Magazine* **145**: 257–278.
- Fowler HW. 1947.** New taxonomic names of fish-like vertebrates. *Notulae naturae of the Academy of Natural Sciences of Philadelphia* **187**: 1–16.
- Gao L-D. 1978.** The spores and *Acritarcha* from Early Devonian of Liujing, Guangxi. *Symposium on the Devonian System of China*. Beijing: Geological Press, 346–358.
- Goujet D. 1984.** *Les poissons placodermes du Spitzberg – Arthrodires Dolichothoraci de la formation de Wood Bay (Devonien inferieur)*. Paris: Editions du CNRS.
- Goujet D, Young GC. 1995.** Interrelationships of placoderms revisited. *Geobios* **MS 19**: 89–95.
- Gross W. 1932.** Die Arthrodire Wildungen. *Geologische und Palaeontologische Abhandlungen* **19**: 1–61.
- Gross W. 1937.** Die Wirbeltiere des rheinischen Devons. Teil II. *Abhandlungen der Preussischen Geologischen Landesanstalt* **176**: 1–83.
- Gross W. 1958.** Über die älteste Arthrodiren-Gattung. *Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden* **86**: 7–30.
- Halstead L. 1985.** The vertebrate invasion of fresh water. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **309**: 243–258.
- Halstead LB, Liu Y-H, P'an K. 1979.** Agnathans from the Devonian of China. *Nature* **282**: 831–833.
- Hao S-G, Gensel P. 1998.** Some new plant finds from the Posongchong Formation of Yunnan, and consideration of a phytogeographic similarity between South China and Australia during the Early Devonian. *Science in China (series D)* **41**: 1–13.
- Hills ES. 1931.** The Upper Devonian fishes of Victoria, Australia, and their bearing on the stratigraphy of the state. *Geological Magazine* **68**: 206–231.
- Hills ES. 1936.** On certain endocranial structures in *Cocco-steus*. *Geological Magazine* **73**: 213–225.
- Jaekel O, ed. 1911.** *Die Wirbeltiere. Eine Übersicht über die fossilen und lebenden Formen*. Berlin.
- Janvier P. 1996.** *Early vertebrates*. Oxford: Oxford Science Publications.
- Johnson HG, Elliot DK, Wittke JH. 2000.** A new Actinolepid arthrodire (Class Placodermi) from the Lower Devonian Sevy Dolomite, East-Central Nevada. *Zoological Journal of the Linnean Society* **129**: 241–266.
- Kuang G-D, Zhao M-T, Tao Y-B, Su Y-B, Huang Y-Q, Wang S-T, eds. 1989.** *Liujing section of Guangxi*. Guilin: China University of Sciences Press.
- Liu S-F. 1982.** Preliminary note on the Arthrodire from Guangxi, China. *Vertebrata Palasiatica* **20**: 106–114.
- Liu Y-H. 1985.** A galeaspid (Agnatha) *Antiquisagittaspis cornuta* gen. et sp. nov., from the Lower Devonian of Guangxi, China. *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: Chang M-M, Liu Y-H, Zhang G-R, eds. *Early vertebrates and related problems of evolutionary biology*. Beijing: Science Press, 139–177.
- McCoy F. 1848.** On some new fossil fish of the Carboniferous period. *Annals and Magazine of Natural History* **2**: 1–10.
- Miles RS. 1973.** An actinolepid arthrodire from the Lower Devonian Peel Sound Formation, Prince of Wales Island. *Palaeontographica* **143**: 109–118.
- P'an K, Wang S-T. 1978.** *Devonian agnatha and Pisces of South China symposium on the Devonian system of China*. Beijing: Geological Press, 298–333.
- P'an K, Wang S-T, Liu YP. 1975.** The Lower Devonian Agnatha and Pisces from South China. *Professional Paper in Stratigraphy and Palaeontology* **1**: 135–169.
- Page RDM. 2001.** *Nexus data editor for windows*. 0.5.0 edn. Available at <http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde.html>
- Ritchie A. 1973.** *Wuttagoonaspis* gen. nov., an unusual arthrodire from the Devonian of Western New South Wales, Australia. *Palaeontographica* **143**: 58–72.
- Stensiö E. 1944.** Contributions to the knowledge of the vertebrate fauna of the Silurian and Devonian of Podolia II – Note on two Arthrodires from the Downtonian of Podolia. *Arkiv för Zoologi* **35**: 1–83.
- Swofford DL 1989–1997.** *PAUP – Phylogenetic analysis using parsimony*. 4.0.b10 edn. Sunderland, Massachusetts: Swofford, D. L.
- Talent JA, Mawson R, Aitchison JC, Becker RT, Bell KN, Bradshaw MA, Burrow CJ, Cook AG, Dargan GM, Douglas JG, Edgecombe GD, Feist M, Jones PJ, Long JA, Phillips-Ross JR, Pickett JW, Playford G, Rickards RB, Webby BD, Winchester-Seeto T, Wright AJ, Young GC, Zhen Y-Y. 2000.** Devonian palaeobiogeography of Australia and adjoining regions. In: Wright AJ, Young GC, Talent JA, eds. *Palaeobiogeography of Australasian faunas and floras*. Association of Australasian Palaeontologists, 167–257.

- Walliser OH. 1995.** Global events in the Devonian and Carboniferous. In: Walliser OH, ed. *Global events and event stratigraphy in the Phanerozoic*. Berlin; Heidelberg; New York: Springer, 225–250.
- Wang D-M, Hao S-G, Liu Z-F. 2002.** Researches on Plants from the Lower Devonian Xujiachong Formation in the Qujing District, Eastern Yunnan. *Acta Geologica Sinica* **76**: 393–407.
- Wang S-T, Pan J, Wang J-Q. 1998.** Early Devonian fishes from central and southern Guangxi and correlation of the vertebrate biostratigraphy in south China. *Vertebrata Palasiatica* **36**: 58–69.
- White EI. 1968.** Devonian Fishes of the Mawson-Mullock Area, Victoria land, Antarctica. *Trans-Antarctic Scientific Reports* **16**: 1–26.
- Woodward AS. 1891.** *Catalogue of the fossil fishes in the British Museum of Natural History. Part II. Containing the Elasmobranchii (Acanthodii), Holocephali, Ichthyodolulites, Ostracodermi, Dipnoi, and Teleostomi (Crossopterygii), and chondrosteian Actinopterygii*. London: British Museum of Natural History.
- Young GC. 1980.** A new Early Devonian placoderm from New South Wales, Australia, with a discussion of placoderm phylogeny. *Palaeontographica (A)* 10–76.
- Young GC. 1993.** Middle Palaeozoic macrovertebrate biostratigraphy of Eastern Gondwana. In: Long JA, ed. *Palaeozoic Vertebrate Biostratigraphy and Paleontology*. London: Belhaven Press, 208–251.
- Young GC. 1996.** Devonian (Chart 4). In: Young GC, Laurie JR, eds. *An Australian Phanerozoic timescale*. Melbourne: Oxford University Press, 96–109.
- Young GC. 1999.** Preliminary report on the biostratigraphy of new placoderm discoveries in the Hervey group (Upper Devonian) of central New South Wales. *Records of the Western Australian Museum Supplement* **57**: 139–150.
- Young GC. 2005a.** An articulated phyllolepid fish (Placodermi) from the Devonian of central Australia: implications for non-marine connections with the Old Red Sandstone continent. *Geological Magazine* **142**: 173–186.
- Young GC. 2005b.** A new phyllolepid placoderm occurrence (Devonian fish) from the Dulcie Sandstone, Georgina Basin, central Australia. *Proceedings of the Linnean Society of New South Wales* **126**: 203–214.
- Young GC, Goujet D. 2003.** Devonian fish remains from the Dulcie Sandstone and Craven Peak Beds, Georgina Basin, central Australia. *Records of the Western Australian Museum Supplement* **65**: 1–85.
- Young GC, Long JA. 2005.** Phyllolepid placoderm fish remains from the Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Antarctic Science* **17**: 387–408.
- Young GC, Turner S. 2000.** Devonian microvertebrates and marine-nonmarine correlation in East Gondwana. In: Blicek A, Turner S, eds. *CFS 223. Palaeozoic Vertebrate Biochronology and Global Marine/Non-Marine Correlation. Final Report of IGCP 328 (1991–1996)*. Frankfurt a. M.: Courier Forschungsinstitut Senckenberg, 453–470.
- Zhao W, Zhu M. 2007.** Diversification and faunal shift of Siluro-Devonian vertebrates of China. *Geological Journal* **42**: 351–369.
- Zhong K, Wu Y, Yin B-N. 1992.** *The Devonian system of Guangxi, China*. Wuhan: Geological University Publishing House.
- Zhu M. 1990.** Phylogenetic studies of petalichthyids from Qujing, Yunnan. PhD thesis, Chinese Academy of Science, Beijing.
- Zhu M, Wang N-Z, Wang J-Q. 2000.** Devonian macro- and microvertebrate assemblages of China. In: Blicek A, Turner S, eds. *Palaeozoic vertebrate biochronology and global marine/non-marine correlation. Final report of IGCP 328 (1991–1996)*. Frankfurt: Courier Forschungsinstitut Senckenberg, 361–372.

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.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

APPENDIX 1

Data matrix Taxa*Characters

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Lunaspis broilii</i> (OG)	?	?	?	?	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0
<i>Eurycaraspis incilis</i> (OG)	?	?	?	?	1	1	1	0	1	1	-	1	0	0	1	0	1	0	0	0
<i>Antineosteus lehmani</i>	?	?	?	?	1	1	0	0	1	1	?	1	0	1	0	0	1	1	0	0
<i>Actinolepis magna</i>	1	?	?	?	1	1	0	1	1	1	0	1	1	1	1	0	1	0	0	0
<i>Actinolepis spinosa</i>	?	?	?	?	?	1	0	1	1	1	?	?	1	1	0	0	1	0	0	0
<i>Actinolepis tuberculata</i>	?	?	?	?	1	1	0	1	1	1	0	1	1	1	1	0	1	0	0	0
<i>Aethaspis major</i>	1	?	?	?	1	1	0	0	1	1	0	1	0	1	0	0	1	0	0	0
<i>Aethaspis utahensis</i>	1	?	?	?	1	1	0	?	1	1	?	1	0	1	0	0	1	0	0	0
<i>Aleosteus eganensis</i>	?	?	?	?	?	1	0	?	1	0	?	1	0	1	0	0	1	0	0	0
<i>Anarthraspis</i> sp.	0	?	?	?	1	1	0	0	0	0	?	1	0	1	0	0	1	0	0	0
<i>Antarctaspis mcmurdoensis</i>	?	?	?	?	1	1	1	1	1	1	-	1	0	1	1	0	1	0	0	0
<i>Arctolepis decipiens</i>	1	1	0	0	1	1	1	0	1	1	-	1	0	1	0	0	1	0	1	0
<i>Austrophyllolepis</i> sp.	?	?	?	?	0	1	-	-	-	-	0	1	0	1	1	0	0	-	-	0
<i>Baringaspis dineleyi</i>	0	?	?	?	?	1	0	?	0	0	?	1	0	1	0	1	1	0	0	0
<i>Bollandaspis woschmidtii</i>	?	?	?	?	1	1	0	1	1	1	0	1	1	1	0	?	?	?	0	0
<i>Bryantolepis brachycephala</i>	?	?	?	?	1	1	0	0	1	1	0	1	0	1	0	0	1	0	0	0
<i>Buchanosteus confertituberculatus</i>	0	1	0	1	1	1	0	1	1	1	?	1	0	1	0	0	1	1	0	0
<i>Cocosteus cuspidatus</i>	1	?	?	?	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	1
<i>Cowralepis mclachlani</i>	?	?	?	?	0	1	-	-	-	-	0	1	0	1	0	0	0	-	-	0
<i>Dicksonosteus arcticus</i>	1	1	0	0	1	1	0	0	1	1	1	1	0	1	0	0	1	0	0	0
<i>Erikaspis zychi</i>	0	0	?	?	?	1	0	?	0	0	?	1	0	1	0	1	1	0	0	0
<i>Eskimaspis heintzi</i>	?	?	?	?	?	1	0	?	0	0	?	1	0	1	0	1	1	0	0	0
<i>Gavinaspis convergens</i>	0	?	?	?	?	1	0	?	0	0	1	1	0	1	0	1	0	-	0	0
<i>Groenlandaspis antarcticus</i>	?	?	?	?	1	1	1	0	1	1	?	1	0	1	0	0	1	0	1	1
<i>Heightingtonaspis anglica</i>	0	0	?	?	?	1	0	?	0	0	?	1	0	1	0	1	1	0	0	0
<i>Heintzosteus brevis</i>	1	1	0	0	1	1	1	0	1	1	?	1	0	1	0	0	1	0	1	0
<i>Kujdanowiaspis buczacziensis</i>	0	0	1	1	1	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0
<i>Kujdanowiaspis podolica</i>	0	0	1	1	1	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0
<i>Lehmanosteus hyperboreus</i>	1	0	1	1	1	1	0	0	1	1	0	1	0	1	0	1	1	0	0	0
<i>Pageauaspis russelli</i>	0	?	?	?	?	1	0	?	1	0	?	1	0	1	0	0	1	0	0	0
<i>Phlyctaenius acadicus</i>	1	?	?	?	1	1	0	0	1	1	0	1	0	1	0	0	1	0	0	0
<i>Phyllolepis orvini</i>	?	?	?	?	0	1	-	-	-	-	0	1	0	1	0	0	0	-	-	0
<i>Placolepis budawangensis</i>	?	?	?	?	0	1	-	-	-	-	0	1	0	1	0	0	0	-	-	0
<i>Proaethaspis ohioensis</i>	0	?	?	?	?	1	0	?	0	0	?	1	0	1	0	0	1	0	0	-
<i>Sigaspis lepidophora</i>	?	?	?	?	?	1	?	?	?	?	?	?	?	1	?	1	1	0	0	0
<i>Simblaspis cachensis</i>	0	?	?	?	?	1	0	?	1	0	?	1	0	1	0	0	1	0	0	0
<i>Tiaraspis subtilis</i>	?	?	?	?	1	1	1	0	1	1	?	1	0	1	0	0	1	0	1	1
<i>Toombalepis tuberculata</i>	?	?	?	?	1	?	1	0	1	1	?	1	0	1	1	0	1	-	0	0
<i>Wuttagoonaspis fletcheri</i>	?	?	?	?	1	0	1	0	1	1	0	1	0	1	1	0	1	-	0	-
<i>Yiminaspis shenme</i>	?	?	?	?	1	0	0	0	1	1	?	1	0	1	1	0	1	-	0	0
<i>Yujiangolepis liujingensis</i>	?	?	?	?	1	1	1	0	1	1	?	1	0	1	1	0	1	-	0	0

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
<i>Lunaspis broilii</i> (OG)	0	0	1	1	1	1	0	-	0	1	0	0	-	1	1	-	0	0	0	2
<i>Eurycaraspis incilis</i> (OG)	1	0	1	1	1	0	0	-	0	1	0	0	-	1	1	1	0	0	?	2
<i>Antineosteus lehmani</i>	0	0	1	1	0	0	1	1	1	1	1	1	1	0	0	?	1	1	1	1
<i>Actinolepis magna</i>	0	0	1	1	0	0	1	1	1	0	1	1	0	0	0	1	0	0	0	0
<i>Actinolepis spinosa</i>	0	0	1	1	0	0	?	1	1	1	1	?	0	0	0	?	?	?	0	0
<i>Actinolepis tuberculata</i>	0	0	1	1	0	0	1	1	1	0	1	?	0	0	0	0	?	?	0	0
<i>Aethaspis major</i>	0	0	1	1	1	0	0	1	1	1	1	1	-	0	0	1	0	0	0	0
<i>Aethaspis utahensis</i>	0	1	0	1	1	0	0	1	1	1	1	?	-	0	0	1	0	0	0	0
<i>Aleosteus eganensis</i>	0	?	?	1	0	0	0	1	1	1	1	?	0	0	0	1	0	0	0	0
<i>Anarthraspis</i> sp.	0	1	0	1	0	0	?	1	1	1	1	1	0	0	0	1	0	0	?	0
<i>Antarctaspis mcmurdoensis</i>	1	0	1	1	1	0	0	0	1	?	1	?	-	1	0	?	?	0	?	?
<i>Arctolepis decipiens</i>	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1
<i>Austrophyllolepis</i> sp.	0	1	0	0	-	0	1	1	1	0	1	0	-	-	0	?	0	1	-	0
<i>Baringaspis dineleyi</i>	0	1	0	1	1	0	0	1	1	1	1	1	-	0	0	1	0	0	0	0
<i>Bollandaspis woschmidtii</i>	0	?	?	1	?	0	0	1	1	?	1	?	?	0	?	?	?	?	?	?
<i>Bryantolepis brachycephala</i>	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	?	0
<i>Buchanosteus confertituberculatus</i>	0	0	1	1	0	0	0	1	1	1	1	1	1	0	0	0	1	1	1	1
<i>Coccosteus cuspidatus</i>	0	0	1	1	0	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1
<i>Cowralepis mclachlani</i>	0	1	1	0	-	0	1	1	1	-	1	0	-	-	0	?	0	1	-	0
<i>Dicksonosteus arcticus</i>	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	1	1	0	1	1
<i>Erikaspis zychi</i>	0	1	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0
<i>Eskimaspis heintzi</i>	0	1	0	1	0	0	0	1	1	1	1	?	0	0	0	1	0	0	0	0
<i>Gavinaspis convergens</i>	0	1	0	0	-	0	0	0	1	1	1	0	-	-	0	1	0	1	0	0
<i>Groenlandaspis antarcticus</i>	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0	1	1	0	1	1
<i>Heightingtonaspis anglica</i>	0	1	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0
<i>Heintzosteus brevis</i>	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0	1	1	0	1	1
<i>Kujdanowiaspis buczacziensis</i>	0	1	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0
<i>Kujdanowiaspis podolica</i>	0	1	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0
<i>Lehmanosteus hyperboreus</i>	0	1	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0
<i>Pageauaspis russelli</i>	0	0	1	1	0	0	0	1	1	1	1	?	0	0	0	1	1	0	1	1
<i>Phlyctaenius acadicus</i>	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0	1	1	0	1	1
<i>Phyllolepis orvini</i>	0	1	0	0	-	0	1	1	1	0	1	0	-	-	0	1	0	1	-	0
<i>Placolepis budawangensis</i>	0	0	1	0	-	0	1	1	1	0	1	0	-	-	0	?	0	1	-	0
<i>Proaethaspis ohioensis</i>	1	1	0	1	1	0	0	0	1	1	1	1	-	0	0	1	0	0	0	0
<i>Sigaspis lepidophora</i>	0	1	0	1	0	0	?	1	1	1	1	1	0	0	0	1	0	0	0	0
<i>Simblaspis cachensis</i>	0	1	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0
<i>Tiaraspis subtilis</i>	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0	1	1	0	1	1
<i>Toombalepis tuberculata</i>	1	0	1	1	1	0	0	0	?	-	1	0	-	1	0	1	0	0	0	0
<i>Wuttagoonaspis fletcheri</i>	1	0	0	1	1	0	0	1	1	0	1	1	-	0	0	1	0	0	0	0
<i>Yiminaspis shenme</i>	0	1	0	1	1	0	0	1	0	0	1	1	-	0	0	0	0	0	0	0
<i>Yujiangolepis liujingensis</i>	0	0	1	1	1	0	0	1	1	1	1	1	-	1	1	1	0	0	0	0

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>Lunaspis broilii</i> (OG)	-	0	0	-	0	0	0	1	1	0	?	1	1	1	0	1	0	0	1	1
<i>Eurycaraspis incilis</i> (OG)	-	0	1	1	1	1	1	1	0	1	0	1	1	0	0	0	1	0	1	1
<i>Antineosteus lehmani</i>	1	1	0	-	0	0	?	0	0	0	?	?	?	-	0	0	0	0	0	0
<i>Actinolepis magna</i>	-	0	?	?	?	0	1	0	0	1	?	1	1	0	?	0	0	0	0	0
<i>Actinolepis spinosa</i>	-	?	?	?	?	?	?	0	0	1	?	1	1	0	1	0	?	?	?	?
<i>Actinolepis tuberculata</i>	-	?	1	1	?	?	?	1	0	1	?	1	1	0	1	0	1	?	0	0
<i>Aethaspis major</i>	-	0	1	1	?	0	1	1	0	1	0	1	1	?	0	1	0	1	1	0
<i>Aethaspis utahensis</i>	-	?	?	?	?	?	?	1	0	1	0	1	1	0	0	1	0	0	1	?
<i>Aleosteus eganensis</i>	-	0	1	0	?	0	1	0	0	1	0	1	1	0	0	1	0	0	0	0
<i>Anarthraspis</i> sp.	-	0	0	-	?	0	1	1	0	1	0	1	1	?	0	0	0	1	1	0
<i>Antarctaspis mcmurdoensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?
<i>Arctolepis decipiens</i>	0	0	0	-	0	1	1	1	1	0	1	1	1	1	1	0	0	1	0	1
<i>Austrophyllolepis</i> sp.	-	0	0	-	0	0	0	0	0	0	?	0	1	0	0	0	0	1	-	0
<i>Baringaspis dineleyi</i>	-	0	1	1	?	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0
<i>Bollandaspis woschmidtii</i>	-	?	?	?	?	?	?	?	?	1	?	1	1	0	0	?	0	?	?	?
<i>Bryantolepis brachycephala</i>	-	0	0	-	?	0	1	1	0	1	0	1	1	0	0	0	?	0	0	0
<i>Buchanosteus confertituberculatus</i>	1	1	?	?	?	1	1	?	0	0	?	1	1	0	?	0	0	0	0	1
<i>Cocosteus cuspidatus</i>	1	1	0	-	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1
<i>Cowralepis mclachlani</i>	-	0	0	-	0	0	0	0	0	0	?	1	1	0	0	0	0	1	-	0
<i>Dicksonosteus arcticus</i>	0	0	0	-	0	1	1	1	1	0	1	1	1	1	1	1	0	1	0	1
<i>Erikaspis zychi</i>	-	0	1	1	1	0	?	0	0	1	0	1	1	?	0	1	0	0	1	0
<i>Eskimaspis heintzi</i>	-	0	1	1	?	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0
<i>Gavinaspis convergens</i>	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	-	?
<i>Groenlandaspis antarcticus</i>	0	0	0	-	0	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1
<i>Heightingtonaspis anglica</i>	-	?	?	?	?	?	?	0	0	1	0	1	1	?	?	0	0	1	1	?
<i>Heintzosteus brevis</i>	0	0	0	-	0	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1
<i>Kujdanowiaspis buczacziensis</i>	-	0	1	0	?	?	1	0	0	1	0	1	1	?	1	1	0	0	1	0
<i>Kujdanowiaspis podolica</i>	-	0	1	0	?	1	1	0	0	1	0	1	1	0	1	1	0	0	1	0
<i>Lehmanosteus hyperboreus</i>	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	?
<i>Pageauaspis russelli</i>	0	?	?	?	?	0	?	0	0	?	?	?	?	?	?	?	0	1	1	?
<i>Phlyctaenius acadicus</i>	0	0	0	-	0	0	1	0	0	0	?	1	1	0	0	0	0	1	1	1
<i>Phyllolepis orvini</i>	-	0	0	-	0	1	0	0	0	0	?	1	0	0	0	0	0	1	-	0
<i>Placolepis budawangensis</i>	-	0	0	-	0	0	0	0	0	0	?	0	0	0	0	0	0	1	-	0
<i>Proaethaspis ohioensis</i>	-	0	1	1	?	?	?	1	0	1	0	1	1	0	1	0	?	0	1	0
<i>Sigaspis lepidophora</i>	-	0	1	1	1	0	1	0	0	?	?	1	1	?	0	1	?	?	1	0
<i>Simblaspis cachensis</i>	-	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0
<i>Tiaraspis subtilis</i>	0	0	0	-	0	0	1	?	0	0	0	1	1	1	1	0	0	0	1	1
<i>Toombalepis tuberculata</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	?
<i>Wuttagoonaspis fletcheri</i>	-	0	1	1	?	0	?	1	0	1	0	1	?	?	?	1	1	0	1	0
<i>Yiminaspis shenme</i>	-	0	?	?	?	?	?	0	0	1	?	1	1	?	1	?	1	0	1	0
<i>Yujiangolepis liujingensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?

	61	62	63	64	65
<i>Lunaspis broilii</i> (OG)	1	0	1	0	0
<i>Eurycaraspis incilis</i> (OG)	1	0	1	1	1
<i>Antineosteus lehmani</i>	1	0	1	?	?
<i>Actinolepis magna</i>	1	0	1	?	1
<i>Actinolepis spinosa</i>	?	?	1	0	0
<i>Actinolepis tuberculata</i>	1	?	1	0	0
<i>Aethaspis major</i>	1	0	1	1	?
<i>Aethaspis utahensis</i>	?	?	1	1	?
<i>Aleosteus eganensis</i>	1	0	1	0	0
<i>Anarthraspis</i> sp.	1	0	1	1	?
<i>Antarctaspis mcmurdoensis</i>	?	?	?	?	?
<i>Arctolepis decipiens</i>	1	1	1	0	1
<i>Austrophyllolepis</i> sp.	1	-	0	1	0
<i>Baringaspis dineleyi</i>	1	0	?	1	0
<i>Bollandaspis woschmidtii</i>	?	?	?	?	?
<i>Bryantolepis brachycephala</i>	1	0	1	1	0
<i>Buchanosteus confertituberculatus</i>	?	0	?	1	?
<i>Coccosteus cuspidatus</i>	0	0	1	1	1
<i>Cowralepis mclachlani</i>	1	-	0	1	0
<i>Dicksonosteus arcticus</i>	1	0	?	0	1
<i>Erikaspis zychi</i>	1	0	0	1	?
<i>Eskimaspis heintzi</i>	1	0	0	1	0
<i>Gavinaspis convergens</i>	?	?	?	?	?
<i>Groenlandaspis antarcticus</i>	0	0	0	1	1
<i>Heightingtonaspis anglica</i>	?	?	0	1	?
<i>Heintzosteus brevis</i>	1	1	1	0	1
<i>Kujdanowiaspis buczacziensis</i>	1	1	1	0	0
<i>Kujdanowiaspis podolica</i>	1	1	1	0	0
<i>Lehmanosteus hyperboreus</i>	?	?	?	?	?
<i>Pageauaspis russelli</i>	?	?	?	?	?
<i>Phlyctaenius acadicus</i>	1	0	1	0	0
<i>Phyllolepis orvini</i>	1	-	0	1	0
<i>Placolepis budawangensis</i>	1	-	0	1	0
<i>Proaethaspis ohioensis</i>	?	?	0	0	0
<i>Sigaspis lepidophora</i>	?	?	?	1	0
<i>Simblaspis cachensis</i>	?	?	?	?	?
<i>Tiaraspis subtilis</i>	0	?	?	0	1
<i>Toombalepis tuberculata</i>	?	?	?	?	?
<i>Wuttagoonaspis fletcheri</i>	1	?	?	0	?
<i>Yiminaspis shenme</i>	?	?	1	?	?
<i>Yujiangolepis liujingensis</i>	?	?	?	?	?

APPENDIX 2

List of the characters

1. Link between the two neurocranium components (ethmoid and postethmoid parts):
 0. no link ("loose nose" fishes)
 1. fusion (by osseous trabeculae or complete fusion)
2. Position of the foramen for the hyomandibular branch of the facial nerve (fVIIHm) in relation to the anterior postorbital process:
 0. foramen in the distal part of the anterior postorbital process
 1. foramen in a proximal and posterior position
3. Neurocranial supraorbital process:
 0. absent
 1. present
4. Neurocranial basal process:
 0. absent
 1. present
5. Rostral, pineal or rostropineal plates:
 0. absent
 1. present

6. Position of the pineal plate:
- 0. further anteriorly from orbits
 - 1. same level as orbits
7. Pineal or rostrompineal plate separates the preorbital plates:
- 0. no
 - 1. yes
8. Rostral and pineal plates fused into a single rostrompineal component:
- 0. no
 - 1. yes
9. Preorbital plates show an embayment for the insertion of the pineal or the rostrompineal plate:
- 0. no, or very shallow
 - 1. yes, very deep
10. Pineal or rostrompineal plate fused to the skull roof:
- 0. no fusion
 - 1. fusion
11. Postnasal plates fused to the preorbital plates:
- 0. yes
 - 1. no

12. Position of the orbits in the skull roof:
- 0. dorsal
 - 1. lateral
13. Preorbital plates:
- 0. separate
 - 1. fused
14. External morphology of the sensory line system:
- 0. canals with external pores
 - 1. grooves
15. Supraorbital sensory lines:
- 0. separate
 - 1. meet posteriorly
16. Infraorbital and cephalic main sensory line grooves run along the mesial margin of the marginal plate:
- 0. no
 - 1. yes
17. Central plates :
- 0. fused into a centronuchal plate
 - 1. individualized paired elements

18. Suture between the central plates contact:
- 0. straight
 - 1. sinuous
19. Pineal (or rostrompineal) plate contacts the central plates:
- 0. no
 - 1. yes
20. Posterior edge of the preorbital plate indents the anterior edge of the central plate:
- 0. no
 - 1. yes
21. Contact between central and preorbital plates:
- 0. yes
 - 1. no
22. Contact between the central and marginal plates:
- 0. yes
 - 1. no
23. Contact between the postorbital and paranuchal plates:
- 0. yes
 - 1. no

24. Nuchal plate:
- 0. absent
 - 1. present
25. Nuchal plate separates the central plates:
- 0. no
 - 1. yes
26. Contact between orbits and central plates:
- 0. no
 - 1. yes
27. Preorbital plates contribute to the orbital margin:
- 0. yes
 - 1. no
28. Central sensory line groove leaves the postorbital plate until the radiation centre of the central plates :
- 0. no
 - 1. yes
29. Number of posterior pit-lines:
- 0. two pairs
 - 1. one pair

30. **Posterior pit-line present on both central and paranuchal plates:**
- 0. anterior and posterior ends clearly connected
 - 1. anterior and posterior ends not connected, implying a superficial course
31. **Central sensory lines:**
- 0. absent
 - 1. present
32. **Postmarginal plate:**
- 0. absent
 - 1. present
33. **Morphology of the anterior external nuchal - central plates contact suture :**
- 0. nuchal plate indents the central plates
 - 1. straight contact
34. **Contact between the pineal and nuchal plates:**
- 0. no
 - 1. yes
35. **Number of paranuchal plates:**
- 0. one pair
 - 1. two pairs

36. Occipital cross commissure:
- 0. on both nuchal and paranuchal plates
 - 1. only on paranuchal plates
37. Posterolateral edge of the paranuchal plates:
- 0. convex
 - 1. concave
38. Posterior process of the paranuchal plate behind the nuchal plate (external side):
- 0. absent
 - 1. present
39. Position of the external foramen for the endolymphatic duct:
- 0. well anteriorly to the paranuchal plate, or on the anterior paranuchal plate for Petalichthyida
 - 1. near to the posterior edge of the paranuchal plate
40. Type of exoskeletal dermal craniothoracic articulation:
- 0. actinolepid "sliding neck joint"
 - 1. ginglymoid phlyctaenoid type
 - 2. "spoon-like" petalichthyid type
41. Articular dermal condyle of anterior dorsolateral plates:

- 0. close together
 - 1. further apart
42. Ventral keel on the internal side of the median dorsal plate:
- 0. absent
 - 1. present
43. Unornamented (overlapped) area on the anterior margin of the median dorsal plate:
- 0. absent
 - 1. present
44. Type of the unornamented zone on the anterior margin of the median dorsal plate:
- 0. simple
 - 1. double
45. Extrascapular plate:
- 0. absent
 - 1. present
46. Dorsolateral groove (for an accessory sensory line) on the anterior dorsolateral plate:
- 0. absent
 - 1. present

47. Posterolateral plate:

- 0. absent
- 1. present

48. Pectoral notch of the anterior ventrolateral plate:

- 0. shallow
- 1. deep

49. Prepectoral process of the anterior ventrolateral plate:

- 0. short
- 1. long

50. Anteroventral plates:

- 0. absent
- 1. present

51. Anterolateral and anterior ventrolateral plates connect behind the pectoral fenestra:

- 0. no
- 1. yes

52. Anterior median ventral plate:

- 0. absent
- 1. present

53. Posterior median ventral plate:

- 0. absent
- 1. present

54. Mutual overlap of the posterior ventrolateral plates:

- 0. simple overlapping
- 1. sinusoidal / double overlapping

55. Spinelets on the mesial side of spinal plate:

- 0. absent
- 1. present

56. Postmedian dorsal plates:

- 0. absent
- 1. present

57. (Width/length) of the preorbital plates:

- 0. $(W/L) > 0.5$
- 1. $(W/L) \leq 0.5$

58. Central plates length ratio to the skull roof length (from the anterior edge of preorbital plates to posteriormost edge of the skull roof):

- 0. $(LC/LSR) < 45\%$
- 1. $(LC/LSR) \geq 45\%$

59. (Length/width) ratio of the nuchal plate:

0. $(L/W) \leq 1.5$

1. $(L/W) > 1.5$

60. (Length/width) ratio of the median dorsal plate:

0. $(L/W) < 1.5$

1. $(L/W) \geq 1.5$

61. (Length/height) ratio of the anterior dorsolateral plate:

0. $(L/H) < 1$

1. $(L/H) \geq 1$

62. (Length/height) ratio of the posterior dorsolateral plate:

0. $(L/H) < 2$

1. $(L/H) \geq 2$

63. Angle between interolateral and spinal plates:

0. angle $< 110^\circ$

1. angle $\geq 110^\circ$

64. (LSp beard by AVL / LSp) ratio = RSp:

0. RSp $< 60\%$

1. RSp $\geq 60\%$

65. (Length / width) ratio of posterior ventrolateral plates:

0. $(L/W) < 1.5$

1. $(L/W) \geq 1.5$