




A new Wuttagoonaspid (Placodermi, Arthrodira) from the Lower Devonian of Yunnan (South China): origin, dispersal, and paleobiogeographic significance


Vincent Dupret


To cite this article: Vincent Dupret (2008) A new Wuttagoonaspid (Placodermi, Arthrodira) from the Lower Devonian of Yunnan (South China): origin, dispersal, and paleobiogeographic significance, *Journal of Vertebrate Paleontology*, 28:1, 12-20, DOI: [10.1671/0272-4634\(2008\)28\[12:ANWPAF\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2008)28[12:ANWPAF]2.0.CO;2)

To link to this article: [http://dx.doi.org/10.1671/0272-4634\(2008\)28\[12:ANWPAF\]2.0.CO;2](http://dx.doi.org/10.1671/0272-4634(2008)28[12:ANWPAF]2.0.CO;2)

 Published online: 02 Aug 2010.

 Submit your article to this journal [↗](#)

 Article views: 44

 View related articles [↗](#)

 Citing articles: 10 View citing articles [↗](#)

A NEW WUTTAGOONASPID (PLACODERMI, ARTHRODIRA) FROM THE LOWER DEVONIAN OF YUNNAN (SOUTH CHINA): ORIGIN, DISPERSAL, AND PALEOBIOGEOGRAPHIC SIGNIFICANCE

VINCENT DUPRET

Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, Xizhimenwai Dajie 142, 100044, Beijing, People's Republic of China, vincent@ivpp.ac.cn

ABSTRACT—Wuttagoonaspida is a very peculiar group of Arthrodira, hitherto known only in the Early-Middle Devonian deposits of Australia. The new genus and species *Yiminaspis shenme* described here is known from an incomplete skull roof from the Pragian of Zhaotong (Yunnan, South China). Despite sharing some features with the Petalichthyida (e.g. two pairs of posterior pitlines), it presents many features of the genus *Wuttagoonaspis* (e.g. long preorbital plates not separated by the pineal plate, pineal plate placed further anteriorly from the orbits). Some thoracic armor material, also from Zhaotong, is referred to this taxon on the basis of the ornamentation. The occurrence of such a basal arthrodira from the Lower Devonian of China, added to the ante-Emsian geographic isolation of the South China block (evidenced by its vertebrate endemism rate), suggests a Chinese origin for the Wuttagoonaspididae, and a migration episode into the northeastern margin of Gondwana dated at the end of the Pragian (E'Em bioevent).

INTRODUCTION

Placoderms (armored fishes) were the most diversified Devonian vertebrates, and represent the first major gnathostome (jawed vertebrates) radiation. Although their Silurian origin remains blurred, they showed a cosmopolitan distribution as soon as the Early Devonian. Among them, the Wuttagoonaspididae are a very peculiar group of Arthrodira, hitherto thought to be endemic to Australia (North eastern Gondwana).

Although initially confused with Upper Devonian phyllolepid remains because of the ridged ornamentation (e.g. Fletcher, 1964; Rade, 1964; see also Young, 2005c), some material from the Mulga Downs Group (western New South Wales, Australia) was described and attributed to a new arthrodiran suborder Wuttagoonaspida Ritchie, 1973, Family Wuttagoonaspididae Ritchie, 1973, genus *Wuttagoonaspis* Ritchie, 1973 and type-species *W. fletcheri* Ritchie, 1973. This author also noticed that “the range of variation in the genus is such that it is not yet clear whether we are dealing with an unusually variable species, several species, or sexual dimorphism”; Ritchie, 1973:60). From then and until now, the diagnoses for the type-species, genus, family and suborder (or infra-order, depending on the authors, e.g. Miles and Young, 1977; Denison, 1978; Long, 1984; Young and Goujet, 2003) have still stood. But the new form described here induces emended diagnoses for the Family Wuttagoonaspididae and the genus *Wuttagoonaspis* (see below).

Recently Young and Goujet described a second species of *Wuttagoonaspis*, *W. milligani* Young and Goujet, 2003, from the Georgina Basin (central Australia), which differs from the type species mainly in the antorbital and orbital regions of the skull roof.

The new form described here, though incomplete, sheds new light on the stratigraphic and paleogeographic origins of the Wuttagoonaspida.

GEOLOGICAL SETTING

The material described herein comes from an outcrop about 9 km from the town of Zhaotong (Eastern Yunnan, Fig.1A–C),

facing Qingmen reservoir. This outcrop is part of the Posonchong Formation of Zhaotong, eastern Yunnan, belongs to the *Sanchaspis-Asiaspis* assemblage (Macrovertebrate assemblage III of Zhu et al., 2000), and is dated as Pragian (early Devonian; Fig. 1B). The sandstone matrix presents a typical continental facies (Zhu et al., 2000). Associated macrovertebrates remains are the Galeaspida *Zhaotongaspis janvieri* Wang and Zhu, 1994, *Lungmenshanaspis yunnanensis* Wang et al., 1996, *Qingmenaspis microculus* Pan and Wang, 1981, *Sanqiaspis zhaotongensis* Liu, 1975, osteolepid indet. and onychodont indet. (Wang et al. 1996; Zhu and Janvier, 1994). No microvertebrate remain is encountered.

MATERIAL AND METHODS

The new form is known from one incomplete skull roof in dorsal view. Associated trunk armor plates are referred to this species on the basis of the ornamentation, despite a large size difference between the skull and some trunk plates. The material is housed in the Institute of Vertebrate Paleontology and Paleoanthropology collections (IVPP, Beijing, P.R. China).

Plate Nomenclature

For the rostral and orbital regions, the author follows the homologies of Ritchie (1973), not those of Miles and Young (1977) or Young (1980).

Abbreviations

Institutional—Repositories for the mentioned specimens are indicated by prefix as follows: **AMF**, Australian Museum, Sydney, New South Wales, Australia; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, P.R. China.

Anatomical—**AMV**, anterior median ventral plate; **AV**, anteroventral plate; **AVL**, anterior ventrolateral plate; **C**, central plate; **can**, canaliculi of the scapulocoracoid; **cc**, central sensory line groove; **CN**, centronuchal plate; **d.end.e**, external foramen for the endolymphatic duct; **gr**, groove on the ventral side of the anterior ventrolateral plate; **IL**, interolateral plate; **ins.AL**, in-

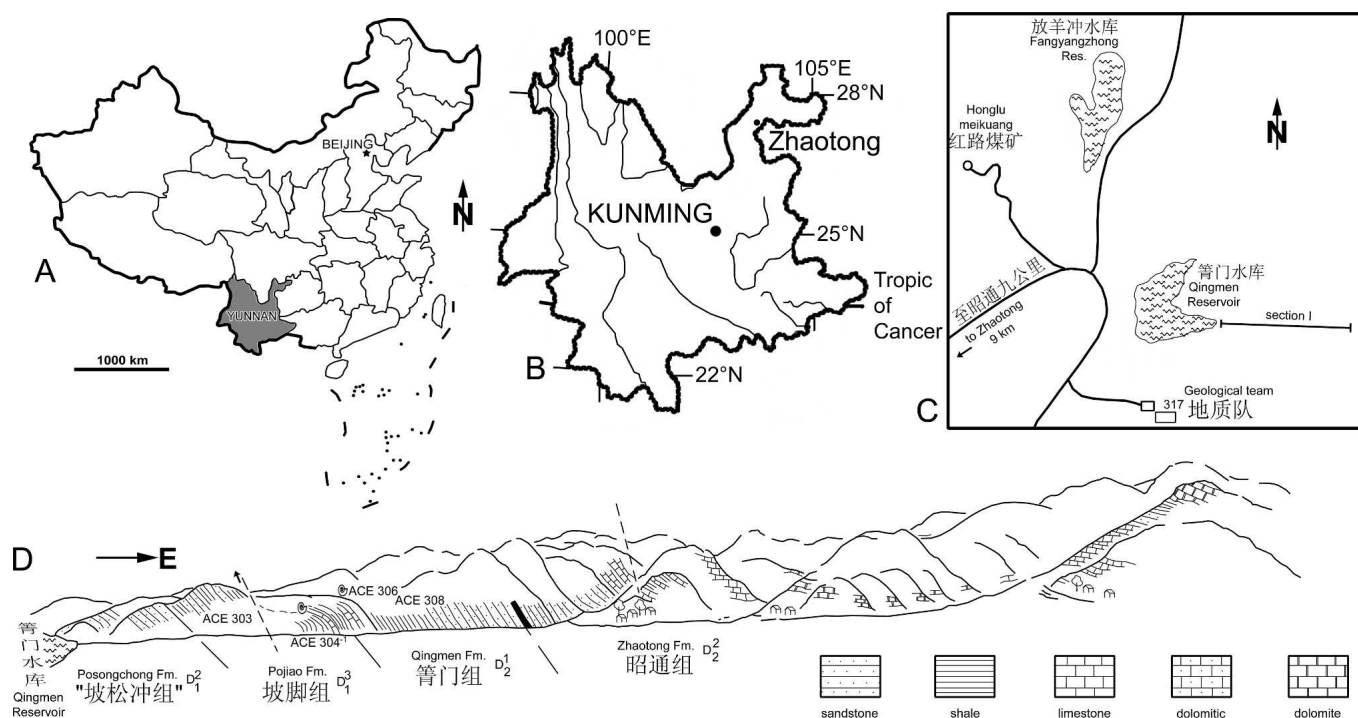


FIGURE 1. A–B, location of Zhaotong, Yunnan, South China. C, location of the fossil site and D, field section (C & D modified after Liao et al., 1979:fig. 6; without scale).

sertion groove for the anterolateral plate; **ioc**, infraorbital sensory line groove; **lc**, main cephalic lateral sensory line groove; **M**, marginal plate; **mpl**, median pitline; **N**, nuchal plate; **o.a.AMV**, overlap area for the anterior median ventral plate; **o.a.ESC**, overlap area for the extrascapular plate; **occ**, occipital cross commissure; **PaN**, paranuchal plate; **pect.n**, pectoral notch; **Pi**, pineal plate; **PM**, postmarginal plate; **pmc**, postmarginal sensory line groove; **PMV**, posterior median ventral plate; **ppl**, posterior pitline; **ppl1**, first posterior pitline; **ppl2**, second posterior pitline; **pr.d**, dorsal process of the interolateral plate; **PrO**, preorbital plate; **PSO**, postsuborbital plate; **PtN**, postnasal plate; **PtO**, postorbital plate; **PVL**, posterior ventrolateral plate; **r**, ridge on the dorsal side of the anterior ventrolateral plate; **R**, rostral plate; **r.comm**, rostral commissure; **rc**, rostral sensory line groove; **sav**, anteroventral sulcus; **SM**, submarginal plate; **SO**, suborbital plate; **soc**, supraorbital sensory line groove; **src**, supraoral sensory line groove; **sp**, sensory pit; **Sp**, spinal plate; **th.PaN**, thickening of the paranuchal plate.

SYSTEMATIC PALEONTOLOGY

Class PLACODERMI McCoy, 1848
 Order ARTHRODIRA Woodward, 1891
 Suborder ACTINOLEPIDOIDEI Miles, 1973
 Family WUTTAGOONASPIDIDAE Ritchie, 1973

Diagnosis—(modified from Ritchie, 1973) Actinolepidoidei with preorbital part of the skull roof very elongated; pineal plate placed further anteriorly from orbits; long paired pentagonal preorbital plates ($L/W \geq 1.5$) indented anteriorly by the pineal plate and posteriorly by the nuchal plate; postorbital plates small (about one half the size of the preorbital plates); central plates with radiation center mesially placed; nuchal plate strongly indented laterally by central plates; supraorbital canal extending onto the nuchal plate radiation center; central and nuchal plates might fuse into a centronuchal component; median and posterior

pitlines complete; spinal plates long, with strong free spine, tuberculated along lateral margin.

Type-genus *WUTTAGOONASPIS* Ritchie, 1973

Diagnosis—(modified from Ritchie, 1973) Wuttagoonaspidae with strongly convex skull roof; postnasal, suborbital, post-suborbital, rostral and pineal plates incorporated to the skull roof; postnasal and suborbital plates elongated; rostral and supraoral canals looping in the anterior part of the postnasal plate; postmarginal plate very narrow; posterolateral region with deep rounded ornamentation, occupied in life by a loosely articulated and sub-ovate submarginal plate; ornamentation variable: in juvenile tubercles arranged randomly in subconcentric rows; in adults strong subconcentric or subparallel ridges over much craniothoracic armor, tubercles persisting around rostral and lateral margins of head and over the orbits; median dorsal plate showing a *posterior sharp and rounded crest*.

Remarks—The original diagnoses of Ritchie (1973) for the Family Wuttagoonaspidae and the genus *Wuttagoonaspis* have been modified in order to fit with the erection of the new form *Yiminaspis shenme*. The following elements have been deleted from the original diagnosis of Ritchie (1973), because they refer to basal Arthrodira (i.e. Actinolepidoidei) symplesiomorphies: large and rounded paranuchal plates; sliding neck-joint craniothoracic articulation; median dorsal plate as wide as long, lacking internal keel. The lack of central plates is not assessed anymore in *W. fletcheri* (see Dupret, 2004:48), though possible in *W. milligani* (see Young and Goujet, 2003). The convergence of sensory grooves on one plate (i.e. centronuchal in Ritchie, 1973) is shared by many placoderms.

YIMINASPIS SHENME, gen. et sp. nov.
 (Figs. 2A–B, 3)

Etymology—Genus after Yi (Chinese), ethnic minority in Yunnan, *min* (Chinese) ‘people’, and *aspis* (Greek), ‘shield’.

Species after *shenme* (Chinese), meaning 'what' because of the puzzling homology of the first posterior pitline and the uncertain identification of the thoracic material.

Holotype—IVPP V 15097, incomplete skull roof, dorsal view.

Other Material—IVPP V 15088, incomplete median dorsal plate; IVPP V 15089, IVPP V 15090.1–2, IVPP V 15091-a-b, incomplete left ventral shields.

Locality—All the specimens were collected in Zhaotong, Yunnan, South China, at the Qingmen Reservoir locality (Fig. 1B, C).

Diagnosis—Wuttagoonaspididae in which the anterior median process of the nuchal plate indents the preorbital plates without separating them. External foramen for the endolymphatic duct in mesial position, close to the paranuchal-nuchal plate boundary. Two pairs of posterior pitlines, the first pair runs from the marginal plate to the nuchal plate radiation center, the second pair runs from paranuchal plate radiation center to that of the nuchal plate. The anterior ventrolateral plate shows a straight and oblique ridge in internal view. Tubercles of the spinal plate merge distally into ridges. Free mesial side of spinal plate bears at least three anteriorly directed spinelets.

Remark—The inclusion of the new form *Yiminaspis shenme* in the pre-existing genus *Wuttagoonaspis* is not supported by its stratigraphic and geographic distributions. Because the most anterior part of the skull roof of *Yiminaspis shenme* is unknown, the author took the liberty to use elements of the diagnosis of the genus *Wuttagoonaspis* for the reconstruction (Fig. 2B).

Description

Skull—The skull roof (Fig. 2A) is represented by a single specimen (IVPP V 15087) in dorsal view. Though incomplete, it displays the derived features of a wuttagoonaspid arthrodire (though the orbits seem proportionally larger than in the genus *Wuttagoonaspis*), except that it is not possible to affirm if the orbits were entirely enclosed in the skull roof or not. The greatest part of the posteriorly directed tubercles has been abraded, and there is no evidence for ridges. The skull roof is slightly convex dorsally, maybe because of the compaction, hence it is impossible to know whether it was as strongly convex as in the genus *Wuttagoonaspis* or not. The sutures between the different plates are indicated by shallow grooves, the less well defined ones (for slightly larger and shallower than the others) being the central, marginal and postmarginal plate boundaries.

Although the anterior part of the skull roof is not preserved (i.e. the rostral-pineal part), a tiny portion of the pineal plate (Pi, Fig. 2A, B) is preserved between the two preorbital plates, indicating that the rostral-pineal capsule was fused to the rest of the skull roof into a single dermal unit, as is the case in the Australian genus *Wuttagoonaspis* (Ritchie, 1973; Young and Goujet, 2003), in Antarctaspidae (White, 1968), in Petalichthyida (Denison, 1978), in some "Actinolepida" (e.g. *Lehmanosteus hyperboreus* Goujet, 1984), in some Phlyctaenii (e.g. *Arctolepis decipiens* Woodward, 1891) and in *Brindabellaspis* (Young, 1980). The pineal plate is placed further anteriorly from the orbits, which is a typical *Wuttagoonaspis* feature.

The preorbital plates (PrO, Fig. 2A, B) are very elongated anteroposteriorly and meet in the midline, thus resembling *W. fletcheri* (Ritchie, 1973) more closely than *W. milligani* (Young and Goujet, 2003). Their lateral edge forms the mesial border of the orbit. They are crossed anteroposteriorly by the supraorbital sensory line grooves (soc, Fig. 2A, B) that run posteriorly to the nuchal plate radiation center, where they merge into a short posteriorly directed groove (which may not be part of the sensory line system but rather a preservation artefact). A shallow groove (not associated to the sensory line system) runs anteromesially from the radiation center of the preorbital plates to the midline where it meets its antimeres; this could be interpreted as the internal extension of the nuchal plate. The poste-

rior edge of the preorbital plate is more transverse than the oblique orientation in *Wuttagoonaspis*.

The postorbital plate (PtO, Fig. 2A, B) forms the posterior edge of the orbit. It bears the infraorbital sensory line groove (ioc, Fig. 2A, B) and a barely distinguishable central sensory line groove (cc, Fig. 2A, B). The plate shape is very similar to that of *W. fletcheri* and its radiation center seems to be classically positioned at the junction between the infraorbital and central sensory line grooves. The postorbital plates meet the paranuchal plates posteriorly, separating the central and marginal plates. The anterolateral part of the infraorbital sensory line groove (surrounding the orbit posteriorly) is unclear.

The central plates (C, Fig. 2A, B) are present and classically cover the otic part of the head shield. They are separated by the nuchal plate. Because of the underlying saccula and semicircular canals, these are slightly raised relative to the other plates of the skull roof. They are about as long as one third of the nuchal plate. They are crossed by the oblique, shallow central sensory line groove (cc, Fig. 2A, B). The end of the middle pitline is clearly visible close to the mesial edge of the plate (mpl, Fig. 2A, B); the anterior end of the posterior pitline turns posteromesially and meets its antimeres in the midline (ppl2, Fig. 2A, B). A third groove extends laterally from the junction of the middle and posterior pitlines to meet the lateral line groove, further anteriorly from the radiation center of the paranuchal plate (ppl1, PaN, Fig. 2A, B). Homologies of these pitlines are discussed below.

It is noteworthy that the species *W. milligani*, though poorly preserved, does not provide evidence for separate central plates but rather for a centronuchal plate. In this respect, Young and Goujet (2003) consider that central plates are also absent in *W. fletcheri* (if boundaries are visible, they are interpreted as a raised central part of the nuchal plate, probably because of the underlying saccula, as in *Yiminaspis shenme*). Nevertheless, at least one specimen of *W. fletcheri* (AMF 54229) shows clear sutures between central and nuchal plates in internal view (Dupret, 2004:48; see also Young, 1980:text-fig. 23B).

The marginal plates (M, Fig. 2A–B) extend mesially to the infraorbital and cephalic main sensory line grooves and do not contact the central plates. The postmarginal sensory line groove runs parallel to the anterior edge and is anteriorly placed (pmc, Fig. 2A–B). The infraorbital and cephalic main sensory line grooves (lc, Fig. 2A–B) are very close to the mesial edge of the marginal plates. The outlines of the postmarginal plates (PM, Fig. 2A, B) are unclear.

The nuchal (N, Fig. 2A, B) plate shows a very peculiar oak-leaf shape. It indents the preorbital plates anteriorly with a rather elongated and slender process more similar to that of *W. milligani* (Fig. 2D) than that of *W. fletcheri* (Fig. 2C); it is widely laterally indented by the central plates (as in *W. fletcheri*; specimen AMF 54229). The most posterior part of the nuchal plate shows a median unornamented trapezoid zone (o.a.ESC, Fig. 2A, B) surrounded by a pair of anteromesially directed grooves; that may have been covered by an extrascapular element or by the anterior tip of the median dorsal plate. The radiation center of the nuchal plate is very posteriorly placed, close to its 5/6th length, and is crossed by the occipital cross commissure (occ, Fig. 2A, B).

The paranuchal plates (PaN, Fig. 2A, B) gently indent the nuchal plate posteromesially. The cephalic main sensory line groove bows around the radiation center of the plate. The occipital cross commissure is complete and has a transverse course. No trace of an external foramen for the endolymphatic duct is visible close to the paranuchal plate radiation center, but a pit (?d.end.e, Fig. 2A, B) is doubtfully referred to this foramen, because it is very mesially placed, close to the suture with the nuchal plate. The posteromesial edge of the paranuchal plates

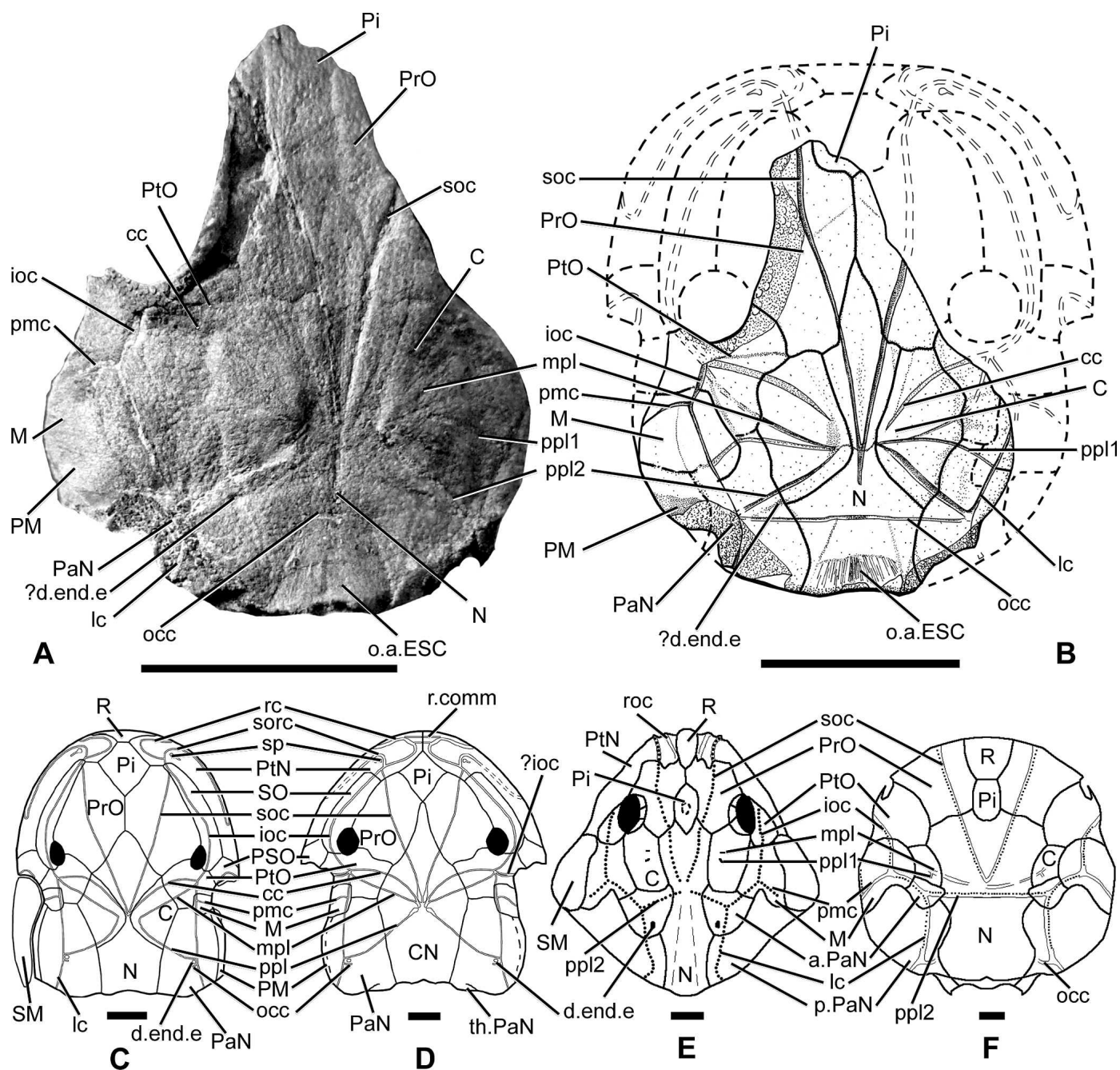


FIGURE 2. **A–B**, photograph (with matrix digitally removed) (**A**) and interpretation drawing (**B**) of the skull roof of *Yiminaspis shenme* gen. et sp. nov. (dorsal view, Holotype, IVPP V 15087). **C**, skull roof of *Wuttagoonaspis fletcheri* Ritchie, 1973 (dorsal view; modified after Ritchie, 1973:text-fig. 5A). **D**, skull roof of *Wuttagoonaspis milligani* Young and Goujet, 2003 (dorsal view, modified after Young and Goujet, 2003:figs. 4A–B, 5B, E; PM and M outlines after *W. fletcheri*). **E**, skull roof of *Lunaspis broilii* Gross, 1961 (modified after Gross, 1961). **F**, skull roof of *Eurycaraspis incilis* Liu, 1991 (modified after Liu, 1991). Scale bars equal 1 cm.

does not show any dermal thickening as occurs in *W. milligani* (th.PaN, Fig. 2D).

Remark—The following material is provisionally referred to *Yiminaspis shenme*, because of the similar ornamentation and the same beds in which they occur.

Thoracic Armor—The median dorsal plate (Fig. 3A) is presented by a single specimen (IVPP V 15088). Though incomplete, it shows the characteristic posteriorly pointing pentagonal ‘actinolepid’ shape, with a median radiation center. It is covered by anteroposteriorly elongated tubercles. There is no ventral keel.

The ventral armor is represented by four specimens, one of them displaying both internal and external surfaces. It is noteworthy that the angle between the interolateral and spinal plates is large (around 130°), thus resembling more the armor of *W. milligani* than that of *W. fletcheri* (for which the angle is about 110°).

The interolateral plate (IL, Figs. 3B–D, F, G) is slightly concave anteriorly. A short groove for the insertion of the postbranchial blade of the anterolateral plate is visible in the lateral part of the ascending lamina, continued on the mesial edge of the spinal plate (ins.AL, Fig. 3B). This groove is posteromesially

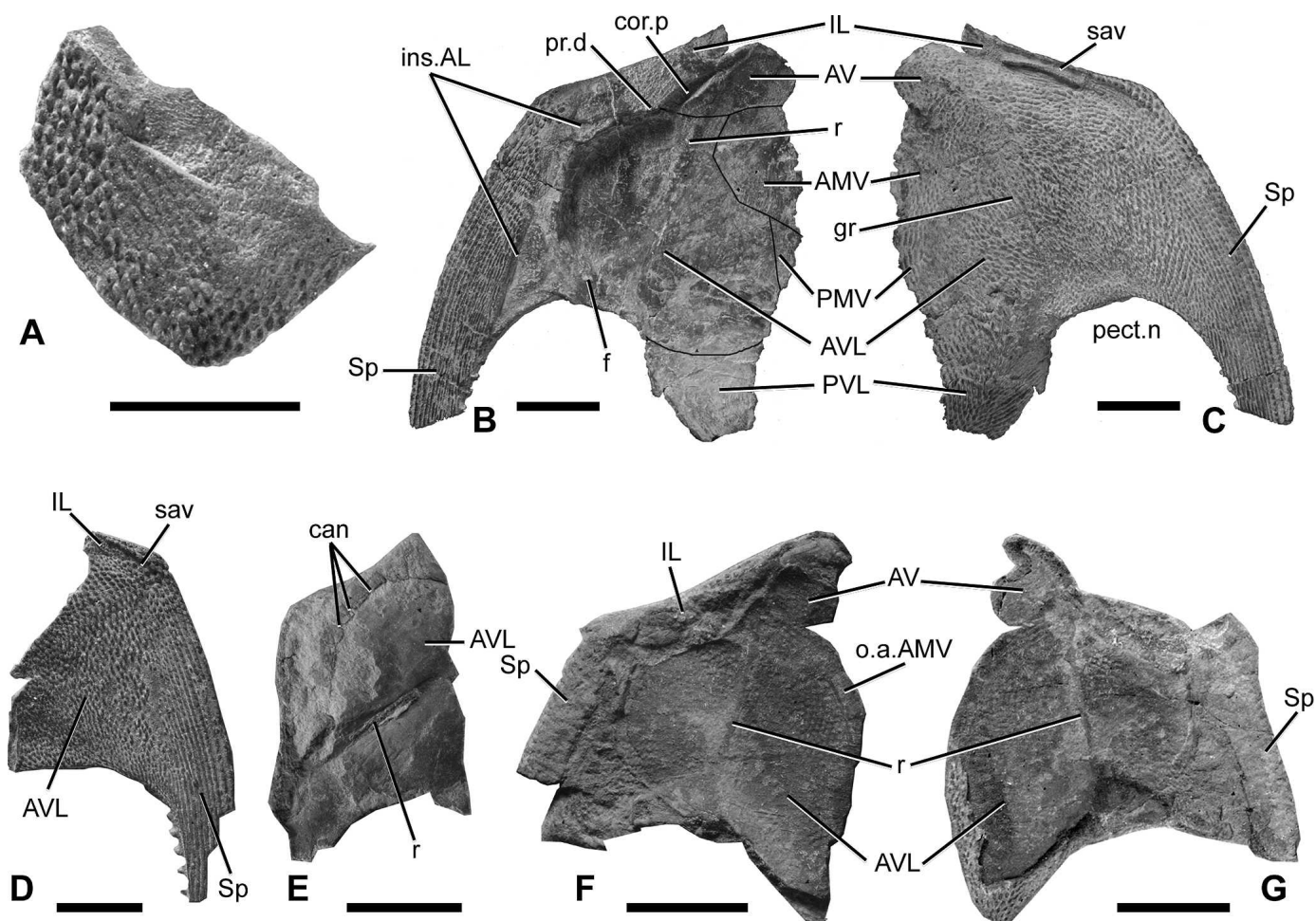


FIGURE 3. *Yiminaspis shenme* gen. et sp. nov. **A**, incomplete median dorsal plate (dorsal view, IVPP V 15088). **B–G**, incomplete left ventral shields. **B**, dorsal and **C**, ventral view of IVPP V 15089; **D**, ventral view of IVPP V 15090.1; **E**, dorsal internal view (IVPP V 15090.2); **F**, dorsal and **G**, ventral views of IVPP V 15091-a-b). **B** and **C** whitened with ammonium chloride sublimate. Scale bars equal 1 cm.

bordered by the posterodorsal process of the interolateral plate (pr.d, Fig. 3B); this process is laterally placed, as in most arthrodires and quasipetalichthyids (e.g. *Eurycaraspis incilis* Liu, 1991) but unlike *W. milligani* where it is mesially placed (see Young and Goujet, 2003:fig. 9). The anterior half of the ascending lamina is covered with fine rounded tubercles (as is the ventral lamina); the posterior half is smooth. The ventral lamina shows the anteroventral sulcus (sav, Figs. 3C, D), which is encountered in all Arthrodira and Quasipetalichthyida (e.g. *Eurycaraspis incilis* Liu, 1991).

The triangular anteroventral plate (AV, Figs. 3B, C, F, G) is wider than long. The internal face of the anterior ventrolateral plate (AVL, Figs. 3B–G) is crossed by a straight and oblique ridge (r, Figs. 3B, E–G) that runs from the suture between the interolateral, anteroventral and anterior ventrolateral plates to the posterior margin of the pectoral notch (pect.n, Fig. 3C); this ridge corresponds to a shallow groove on the external side of the plate (gr, Fig. 3C). The function of this ridge is still uncertain, but it could mark the mesial edge of the scapulocoracoid.

The anteromesial part of the coracoid process of the scapulocoracoid impression is very sharp, and underlines the suture between the interolateral and anteroventral plates with a groove. Some foramina are visible for the canaliculi (can, Fig. 3E) reaching the prepectoral process of the scapulocoracoid. A large foramen (f, Fig. 3B) is visible on the posterior wall of the coracoid

process, and seems to be connected to a tube that most likely led to the axillary area.

The anterior and posterior median ventral and the posterior ventrolateral plates are fragmentary (AMV, PMV, PVL, o.a.AMV, Figs. 3B, C, F).

The spinal plate (Sp, Fig. 3B–D, F, G) is long, and its posterior tip extended beyond the posterior edge of the anterior ventrolateral plate. The proximal part of the plate is covered by anteroposteriorly directed, pointed tubercles, distally merging into ridges, thus being very similar to that of *W. milligani* (Young and Goujet, 2003, fig. 8D). The mesial margin of the free portion of the spinal plate is covered by anteriorly pointing spinelets.

DISCUSSION

Relationships of *Yiminaspis shenme*: Wuttagoonaspidid Arthrodire or Petalichthyid?

The new form *Yiminaspis shenme* displays an interesting mosaic of characters reminding those of general Arthrodira, of Wuttagoonaspididae, or of Petalichthyida.

Yiminaspis shares with the Arthrodira the presence of a central sensory groove (compared with its absence in Petalichthyida and Ptyctodontida, even if the author concurs that this groove is represented in all other groups of placoderms), the nuchal plate

pointing anteriorly (except some Brachythoraci), the sliding neck-joint craniothoracic dermal articulation (with Actinolepidoidei only), a long and oblique endolymphatic duct, the possession of one single pair of paranuchal plates (though it is still unclear if this feature is derived when compared to the double pairs of the Petalichthyida), the median and posterior pitlines meeting on the central plates (or the centronuchal plate in the case of *W. milligani*). *Yiminaspis* shares with the Wuttagoonaspididae the contact between the nuchal and preorbital plates in the midline (also observed in the actinolepids *Aethaspis* and *Proaethaspis*, though the nuchal plate does not indent the preorbital plates anteriorly; see Denison, 1958, 1960, 1978), the anterior position of the pineal plate (compared with the position of the orbits or that of the preorbital plates), and the very elongated preorbital plates. *Yiminaspis* only shares with the Petalichthyida the presence of two pairs of posterior pitlines.

Homologies in *Wuttagoonaspis* and *Yiminaspis*

Skull Roof Plates—Ritchie named as the postnasal plate large element including the entire anterolateral border of the skull roof of *W. fletcheri* (see Ritchie, 1973:fig. 5A). Young (1980) rejected this hypothesis on the basis that this element would have covered the upper jaw (palatoquadrate), and hence assigned this element as a suborbital plate; consequently, he considered Ritchie's suborbital plate in *Wuttagoonaspis* as not homologous with any known placoderm plate, and named it the 'paraorbital' plate (see Young, 1980:fig. 23D). Young and Goujet (2003:16) noted in *W. milligani* that the internal side of this 'paraorbital' plate provides evidence that it is in fact composed by two elements, the former possibly being homologous with the arthrodire postnasal plate. The internal side of this 'paraorbital' plate also shows a ridge of equal length (according to their reconstructions; see Young and Goujet, 2003:figs. 4, 6A), which is interpreted as supporting the palatoquadrate. Nevertheless, comparing the photograph of the specimen with the reconstruction (ANU V2971, r.pq of Young and Goujet, 2003:figs.5E, 6A), this 'palatoquadrate ridge' is closer to the orbit than displayed in the reconstruction, and would be more likely an orbital vault or the internal impression of the infraorbital sensory line groove. Moreover, the postnasal plate (PN of Young and Goujet, 2003:fig. 6A) is located much further anteriorly to the anterior edge of their paraorbital plate (even if shown in dashed outline), within Ritchie's postnasal plate area. Besides, the specimen ANU V2971 is highly weathered and abraded, and the posterior edge of the so-called postnasal plate is more likely a crack in an altered area and the unlabelled ridge in the anterolateral edge of the suborbital is more likely the edge of the eroded border of the plate.

In internal view, the preorbital plates of *W. milligani* appear to meet in the midline (see holotype, Young and Goujet, 2003:fig. 5E).

The rostral plate is not shown in the reconstruction of *W. milligani*, but Young and Goujet (2003:figs. 4–6) think this dermal element was much reduced externally, invisible in internal view (cf. the 'suborbital' suture in the midplane).

Pitlines—In the Arthrodira (except *Yiminaspis shenme*), there is a single pair of posterior pitlines, associated with a single pair of paranuchal plates, on which they anchor posteriorly. In the basal Arthrodira (i.e. Wuttagoonaspididae and Antarctaspididae), the posterior pitline is anchored anteriorly on the central plate (*W. fletcheri*, see Young, 1980:fig. 23B) or to the nuchal-centronuchal plate (*W. milligani*, *Antarctaspis mcmurdoensis*, *Toombalepis tuberculata*, *Yujiangolepis liujingensis*; see Young and Goujet, 2003: figs. 4A, 16A; White, 1968:fig. 10; Wang et al., 1998:fig. 2, pl. 1 fig.1). In the Phyllolepididae, the posterior pitline anchors (when present) to the radiation center of the centronuchal plate (which could be an unpaired central plate without a nuchal element, according to Dupret and Zhu, 2007). As for the other

non-basal and non-phyllolepid Arthrodira, the posterior pitline anchors anteriorly on the central plate.

In the Petalichthyida, there are two pairs of posterior pitlines, associated with a skull roof composed by two pairs of paranuchal plates. The first posterior pitline is always anteriorly anchored on the central plate, and is never complete. It is nevertheless posteriorly directed onto the marginal plate in *Lunaspis broilii* (Gross, 1961) and to the anterior paranuchal plate in *Diandongpetalichthys liaojiaoshanensis*, *Eurycaraspis incilis* and in a Petalichthyida gen. et sp. nov. (Liu, 1991:fig. 1; Zhu, 1990:figs. 7, 43; see Zhu, 1991:fig. 1A, and Zhu, 2000:377 for Petalichthyida gen. et sp. nov.). The second posterior pitline is always anchored to both the nuchal and anterior paranuchal plate.

It is also noteworthy that in *D. liaojiaoshanensis* and in the Petalichthyida gen. et sp. nov., the external foramen for the endolymphatic duct is close to the suture between the anterior paranuchal and the nuchal plates, and according to the positions of both its external and internal foramina, the endolymphatic duct seems to be short and vertical.

In *Yiminaspis shenme*, the first posterior pitline is not anchored to any radiation center posteriorly. Nevertheless, it is possible that the bony rudiment on which this first posterior pitline was anchored has been incorporated to the marginal plate at an early stage of the ontogenesis. The skull roof of *Yujiangolepis liujingensis* shows a microplate in this area, which may be a remnant the petalichthyid anterior paranuchal plate (G. Young, J. Long, V. Dupret, pers. obs.; *Yujiangolepis* will be the topic of another article).

In *Yiminaspis shenme*, the external endolymphatic foramen is also close to the nuchal-paranuchal plate suture (if the structure is correctly interpreted); nevertheless, because of the raised position of the central plate (probably due to the underlying saccula and semicircular canals, and hence indicating these structures), and because of the distance between the presumed otic area of the neurocranium and the external foramen, the endolymphatic duct is more likely a long and oblique tube as in the Arthrodira (cf. Goujet and Young, 1995).

In conclusion, we can with certainty assert that 1) the first posterior pitline of *Yiminaspis* and that of the Petalichthyida are homologous with each other, but not with any homologous arthrodiran structure, and that 2) the second posterior pitlines of *Yiminaspis* and of the Petalichthyida are homologous with the single posterior pitline of the Arthrodira.

Yiminaspis nov. gen. and the Wuttagoonaspididae Phylogenetic Affinities

Yiminaspis and *Wuttagoonaspis* display characters of both the Petalichthyida (e.g. two pairs of posterior pitlines) and the Arthrodira (e.g. suture between the preorbital plates, long and oblique endolymphatic duct, one pair of paranuchal plates). Ritchie (1973) already noted this unusual skull roof pattern, and assigned *Wuttagoonaspis* to a basal position among the Arthrodira. Despite the ridged ornament, Ritchie (1973) and Dupret (2004) believed *Wuttagoonaspis* and the Phyllolepididae to be only distantly related, and recently Dupret did not consider the ornamentation between these two groups as homologous (Dupret, 2004; Dupret and Zhu, 2007): if both groups possess tubercles, ridges in *Wuttagoonaspis* clearly show low tubercles at their top (i.e., containing both bone and semidentine), whereas ridges of the Phyllolepididae are clearly osseous and lack dentinuous tissues. This view is not followed by Young (e.g., 1980, 2005c) who considered the wuttagoonaspid and the phyllolepid as close related taxa, because of the presence of a centronuchal plate and the ridged ornamentation, but not the convergence of the sensory line grooves on the centronuchal plate or at least in the median dermal element of the skull roof (this last feature being primitive; Young, 2005a:206; Young and Goujet, 2003:12–13). Ritchie

(1973) also noted that the skull roof of *Wuttagoonaspis fletcheri* presents intermediate structures between Arthrodira and Petalichthyida. Dupret (2003, 2004) and Dupret and colleagues (2007) confirmed the basal position of *Wuttagoonaspis* among Arthrodira, with Petalichthyida as outgroup.

Despite the incomplete skull roof of *Yiminaspis shenme*, we can identify it as a very basal member of Wuttagoonaspida, sharing some features with Petalichthyida (e.g. an external foramen of the endolymphatic duct close to the nuchal-paranuchal plate suture), and hence most probably the most basal Arthrodira known. An accurate phylogenetic analysis would require the study or revision of many basal arthrodira forms; that will be the subject of another article.

Paleobiogeographic Significance

The Devonian paleoglobe was divided into two major parts by the Rheic and Paleo-Tethys oceans, with a northern Laurussian and a southern Gondwanan landmass groups, except the main body of the China paleocontinent which belongs to the Pan-Cathaysian landmass group (Zhu and Zhao, 2006). Evidence for this is shown by the vertebrate faunas showing a high degree of endemism in South China during the Early Devonian. In Early Devonian global reconstructions (Scotese, 1997; Cocks and Torsvick, 2002; Torsvick and Cocks, 2004; Dupret and Zhu, 2006, 2007), Gondwana and Pan-Cathaysian landmass groups were situated much further apart.

Until now, the Wuttagoonaspida were only known from the Late Pragian-Early Emsian to the Eifelian of Australia (see Young, 2005b:fig.4). The Australian depositional environments are still unresolved (i.e. freshwater vs. shallow marine; see Young and Goujet, 2003:8–9). The discovery of *Yiminaspis shenme* gen. et sp. nov. implies a Chinese origin for the group and at least as old as the Lower Pragian. As Wuttagoonaspida were sub-benthic organisms (i.e., bottom feeders-like), the hypothesis of dispersion across a wide ocean between South China and the northern margin of Australia is unlikely.

The study of other early vertebrate groups (e.g. Sarcopterygii) reveals that a shallow marine connection between South China and north-eastern Gondwana may have occurred as late as the Pragian-Emsian boundary (E'-Em bioevent; Zhu, 2000). Indeed, before this bioevent, Placodermi and other early vertebrates (e.g., Galeaspida) showed a high level of endemism in South China. Most of these became extinct during and after this event, most probably because of the arrival of, and the consequent competition with, eastern Gondwanan forms (Zhu, 2000). This E'-Em bioevent is proposed to date the southward migration of the Wuttagoonaspida (together with that of the Phyllolepidia; Dupret and Zhu, 2006, 2007) into north-eastern Gondwanan margins (Fig 4). A vicariance scenario may be proposed as well, but the Chinese vertebrate endemism contradicts it at the present time; however, it is noteworthy that the age of the Australian *Wuttagoonaspis* assemblages are hard to establish (see Young and Goujet, 2003:9–11), and that assessed pre-Emsian forms are not encountered.

CONCLUSIONS AND PERSPECTIVES

Yiminaspis, the new taxon described here and assigned to the Wuttagoonaspida adds to the known diversity of basal arthrodira of China. *Yiminaspis*, from the Pragian of Yunnan, provides interesting anatomical characters intermediate between Chinese Petalichthyida and Arthrodira, leading to a better view of the common hypothetical ancestor for both groups. It shares the following petalichthyid features: two pairs of posterior pit-lines (the first one being homologous with that of Petalichthyida only, and the second one being homologous with that of Petalichthyida and the unique one of Arthrodira), an external for-

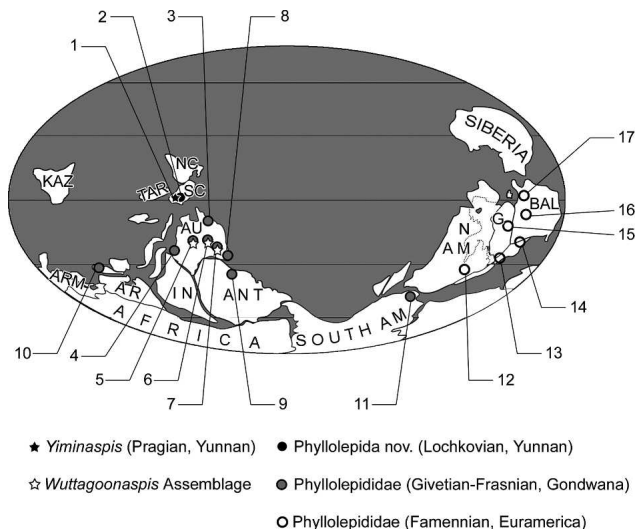


FIGURE 4. Global distribution pattern for Phyllolepidia and Wuttagoonaspida, plotted on a Devonian reconstruction (after Zhu and Zhao, 2006). **Chinese Lochkovian-Pragian localities:** 1. Zhaotong and 2. Qujing (Yunnan, South China; this paper and Dupret and Zhu, 2006, 2007); **Gondwanan Givetian-Frasnian localities:** 3. Townsville area (Queensland, Australia; Young, 2005b); 4. Carnarvon Basin (Western Australia; J. A. Long, unpublished data, in Young, 2005b); 5. Amadeus Basin and 6. Georgina Basin (central Australia; Young and Goujet, 2003; Young, 2005a, b); 7. West-central New South Wales (Australia; Hills, 1931, 1936; Ritchie, 1973; Young, 1993, 1999); 8. Braidwood-Pambula-Mount Howitt (south east Australia; Young, 1983; Long, 1984; Ritchie, 1984); 9. Transantarctic Mountains, southern Victoria land (Antarctica; Young and Long, 2005); 10. Antalya Nappe (Western Lycian Taurus, Turkey; Janvier, 1983; Dupret et al., 2005); 11. Sierra de Perihá (Venezuela; Young et al., 2000; Young and Moody, 2002); **Euramerican Famennian localities:** 12. Virginia-Pennsylvania (USA; Daeschler et al., 2003; Lane and Cuffey, 2005); 13. Scotland (United Kingdom; Agassiz, 1844; Woodward, 1915); 14. Wallonie (Belgium; Lohest, 1888; Leriche, 1931); 15. East Greenland (Heintz, 1930; Stensiö, 1934, 1939); 16. Baltic States (Vasiliaskas, 1963); 17. Timan (Russia; Esin et al., 2000).

men for the endolymphatic duct mesially placed and close to the suture between the paranuchal and nuchal plates. Nevertheless, some clear arthrodiran and wuttagoonaspid features support its systematic attribution (elongated preorbital plates and preorbital area, central plates indenting the nuchal plate mesially, elongated nuchal plate that does not separate the preorbital plates, endolymphatic duct most probably long and oblique, one pair of paranuchal plates).

The study of the vertebrate faunas from South China and Gondwana indicates that the dispersal of Wuttagoonaspida may have occurred at the Pragian-Emsian boundary, during the E'-Em bioevent of Zhu (2000), together with that of the Phyllolepidia (Dupret and Zhu, 2007).

As *Yiminaspis* represents the earliest Wuttagoonaspida and because Wuttagoonaspida are the most basal Arthrodira, it is likely that the Arthrodira may have originated in China. However, the presence of other Arthrodira in Lochkovian and Pragian localities in other parts of the world (e.g. *Eskimaspis* in the Lochkovian of the Canadian Arctic Archipelago; Dineley and Liu, 1984) suggest an earlier dispersal of the group (see also Zhu and Zhao, 2006, for the fossil Sarcopterygii record), that needs further investigation.

ACKNOWLEDGMENTS

The author thanks Dr. Zhu Min (IVPP), who provided the material. Dr. Gavin Young (Australian National University,

Canberra ACT) and Dr. John Long (Museum Victoria, Australia) also provided interesting discussions on early arthrodires. Dr. Zhao Wenjin helped in accessing and translating Chinese literature. Qiao Tuo, Lu Jing, Xiong Cui-hua and Jia Liantao (IVPP) collected the skull roof in February 2006. The material was prepared by Xiong Cui-hua; the photographs were taken by Jia Liantao. Gavin C. Young (ANU, Canberra, Australia) and an anonymous reviewer are thanked for their corrections and helpful comments. This work was supported by the Major Basic Research Projects (2006CB806400) of MST of China, the Chinese Foundation of Natural Sciences (40332017 and 0602005), and UNESCO-IGCP 491.

LITERATURE CITED

- Agassiz, L. 1844. Monographie des poissons fossiles du Vieux Grès Rouge ou système Dévonien (Old Red Sandstone) des Iles britanniques et de Russie, XXXVI. Jent and Gassmann, Neuchâtel, 171 pp.
- Cocks, L. R. M., and T. H. Torsvik. 2002. Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *Journal of the Geological Society, London* 159:631–644.
- Daeschler, E. B., A. C. Frumes, and C. F. Mullison. 2003. Groenlandaspidae Placoderm Fishes from the Late Devonian of North America. *Records of the Australian Museum* 55:45–60.
- Denison, R. H. 1958. Early Devonian Fishes from Utah—Part. III. *Arthrodira*. *Fieldiana: Geology* 11:461–551.
- Denison, R. H. 1960. Fishes of the Devonian Holland Quarry Shale of Ohio. *Fieldiana: Geology* 11:555–613.
- Denison, R. H. 1978. Placodermi. *Handbook of Paleichthyology*, Volume 2. H.-P. Schultz (ed.). Gustav Fischer Verlag, Stuttgart, New York, 128 pp.
- Dineley, D. L., and Y.-H. Liu. 1984. A new actinolepid arthrodire from the Lower Devonian of Arctic Canada. *Palaeontology* 27:875–888.
- Dupret, V. 2003. Etude anatomique des genres *Kujdanowiaspis* Stensjö 1942 et *Erikaspis* nov. gen. (Placodermi Arthrodira “Actinolepida”) du Dévonien inférieur de Podolie (Ukraine). Nouvelle proposition de la phylogénie des Arthrodira., Département Histoire de la Terre, Muséum national d’Histoire naturelle, Paris, 403 pp. [unpublished]
- Dupret, V. 2004. The phylogenetic relationships between actinolepides (Placodermi: Arthrodira) and other arthrodires (phlyctaeiid and brachythoracids); in G. C. Young (ed.), *Lower Vertebrates from the Palaeozoic*. First International Palaeontological Congress (IPC 2002), Sydney, Australia, July 2002. *Proceedings of Symposium 6 (Palaeozoic Vertebrates)*. *Fossils & Strata* 50:44–55.
- Dupret, V., and M. Zhu. 2006. A Chinese origin for Phyllolepidia (Placodermi, Arthrodira)?; pp. 329–330 in Q. Yang, Y.-D. Wang and E. A. Weldon (eds), *Ancient life and modern approaches—Abstracts of the second International Palaeontological Congress (IPC 2006)*, Beijing, China, June 2006.
- Dupret, V., D. Goujet, and E. Mark-Kurilke. 2007. A new genus of placoderm (Arthrodira: ‘Actinolepida’) from the Lower Devonian of Ukraine. *Journal of Vertebrate Paleontology* 27:266–284.
- Dupret, V., G. Clément, and P. Janvier. 2005. The Frasnian—Famennian interchange between Gondwanan and Euramerican vertebrate faunas. Which way? Middle East or South America? *Ichthyolith Issues Special Publication* 8:8–9.
- Dupret, V., and M. Zhu. 2007. The earliest phyllolepid (Placodermi, Arthrodira), *Gavinaspis convergens* from the late Lochkovian (Lower Devonian) of Yunnan (South China). *Geological Magazine* 145:1–22.
- Esin, D., M. Ginter, A. Ivanov, O. A. Lebedev, E. Luksevics, V. Avkhimovich, V. Golubtsov, and L. Petukhova. 2000. Vertebrate Correlation of the Upper Devonian on the East European Platform. *Courier Forschungsinstitut Senckenberg* 223:341–359.
- Fletcher, H. O. 1964. New linguloid shells from the Lower Ordovician and Middle Palaeozoic rocks of New South Wales. *Records of the Australian Museum* 26:283–294.
- Goujet, D. 1984. Les poissons placodermes du Spitsberg—Arthrodirés Dolichothoraci de la formation de Wood Bay (Devonien inférieur). *Cahiers de Paléontologie (section vertébrés)*. Editions du CNRS, Paris, 284 pp.
- Goujet, D., and G. C. Young. 1995. Interrelationships of placoderms revisited. *Geobios MS* 19:89–95.
- Gross, W. 1961. *Lunaspis broilii* und *Lunaspis heroldi* aus dem Hunsrückschiefer (Unterdevons, Rheinland). *Notizblatt Hessisches Landesamtes für Bodenforschung zu Wiesbaden* 89:17–43.
- Heintz, A. 1930. Oberdevonische Fischreste aus Öst-Grönlands. *Skrifter om Svalbard og Ishavet* 30:31–46.
- Hills, E. S. 1931. The Upper Devonian fishes of Victoria, Australia, and their bearing on the stratigraphy of the state. *Geological Magazine* 68:206–31.
- Hills, E. S. 1936. On certain endocranial structures in *Cocosteus*. *Geological Magazine* 73:213–225.
- Janvier, P. 1983. Les Vertébrés dévoniens de la Nappe Supérieure d’Antalya (Taurus Lycien occidental, Turquie). *Géologie Méditerranéenne* 10:1–13.
- Lane, J. A., and R. Cuffey. 2005. *Phyllolepis rossimontina* sp. nov. (Placodermi) from the Uppermost Devonian at Red Hill, North-Central Pennsylvania. *Revista Brasileira de Paleontologia* 8: 117–126.
- Leriche, M. 1931. Les poissons famenniens de la Belgique—Les faciès du Famennien dans la région gallo-belge—Les relations entre les formations marines et les formations continentales du Dévonien supérieur sur la bordure méridionale du Continent Nord-Atlantique. *Mémoire de la Classe des Sciences de l’Académie Royale de Belgique* 4:1–72.
- Liao, W.-H., H.-K. Xu, C.-Y. Wang, C.-Y. Cai, Y.-P. Ruan, D.-C. Mu, and L.-C. Lu. 1979. Description of several Devonian sections in South West China; pp. 221–249, in *Biostratigraphy of carbonates in South West China*. Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Science Press, Nanjing. [Chinese]
- Liu, Y.-H. 1975. Lower Devonian agnathans of Yunnan and Sichuan. *Vertebrata Palasiatica* 13:202–216. [Chinese, English summary]
- Liu, Y.-H. 1991. On a new petalichthyid, *Eurycaraspis incilis* gen. et sp. nov., from the middle Devonian of Zhanyi, Yunnan; pp. 139–177 in M.-M. Chang, Liu, Y.-H., and Z. Guo-rui (eds.), *Early Vertebrates and related Problems of Evolutionary Biology*, Beijing.
- Lohest, M. 1888. Recherche sur les poissons des terrains paléozoïques de Belgique. Poissons des Psammites du Condroz, Famennien supérieur. *Annales de la Société Géologique de Belgique Mémoire* 15:112–203.
- Long, J. A. 1984. New Phyllolepidia from the Victoria and the relationships of the Group. *Proceedings of the Linnean Society of New South Wales* 107:263–308.
- McCoy, F. 1848. On some new fossil fish of the Carboniferous period. *Annales and Magazine of Natural History* 2:1–10.
- Miles, R. S. 1973. An actinolepid arthrodire from the Lower Devonian Peel Sound Formation, Prince of Wales Island. *Palaeontographica* 143:109–118.
- Miles, R. S., and G. C. Young. 1977. Placoderm interrelationships reconsidered in the light of new ptyctodontids from Gogo, Western Australia. *Linnean Society Symposium Series* 4:123–198.
- Pan, J., and S.-T. Wang. 1981. New discoveries of polybranchiaspids from Yunnan Province. *Vertebrata Palasiatica* 19:113–211.
- Rade, J. 1964. Upper Devonian fish from the Mount Jack area, New South Wales, Australia. *Journal of Paleontology* 38:929–932.
- Ritchie, A. 1973. *Wuttagoonaspis* gen. nov., an unusual arthrodire from the Devonian of Western New South Wales, Australia. *Palaeontographica* 143:58–72.
- Ritchie, A. 1984. A new Placoderm, *Placolepis* gen. nov. (Phyllolepidae), from the Late Devonian of New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales* 107:321–353.
- Scotese, C. R. 1997. *Paleogeographic Atlas, PALEOMAP Progress Report 90–0497*. University of Texas Press, Arlington (Texas), 1–45 pp.
- Stensjö, E. 1934. On the Placodermi of the Upper Devonian of East Greenland. I. Phyllolepidia and Arthrodira. *Meddelelser om Grønland* 97:1–58.
- Stensjö, E. 1939. On the Placodermi of the Upper Devonian of East Greenland. Second supplement to Part I. *Meddelelser om Grønland* 97:1–33.
- Torsvik, T. H., and L. R. M. Cocks. 2004. Earth geography from 400 to 250 Ma: a palaeomagnetic, faunal and facies review. *Journal of the Geological Society, London* 161:555–572.
- Vasiliauskas, V. 1963. [*Phyllolepis tolli* sp. nov. and some questions of the stratigraphy of the Famennian deposits in the Baltic area]; pp. 407–429 in A. A. Grigialis and V. N. Karatajute-Talimaa (eds.), *Voprosy geologii Litvy. Geologijos ir geografijos institutas. Lietuvos TSR Mokslu akademija, Vilnius*. [Russian]

- Wang, J.-Q., and M. Zhu. 1994. *Zhaotongaspis janvieri* gen. et sp. nov., a galeaspid from Early Devonian of Zhaotong, Northeastern Yunnan. *Vertebrata Palasiatica* 32:231–243.
- Wang, J.-Q., N.-Z. Wang, and M. Zhu. 1996. The Middle Paleozoic early vertebrate fossils from Tarim Basin, China; pp. 8–16 in X.-G. Tong, D.-G. Liang, and C.-Z. Jia (eds.), *New advances of petroleum geology of Tarim*. Science Press, Beijing.
- Wang, S.-T., J. Pan, and J.-Q. Wang. 1998. Early Devonian fishes from central and southern Guangxi and correlation of the vertebrate biostratigraphy in south China. *Vertebrata Palasiatica* 36:58–69. [Chinese with English summary]
- White, E. I. 1968. Devonian Fishes of the Mawson-Mullock Area, Victoria land, Antarctica. *Trans-Antarctic Scientific Reports* 16:1–26.
- Woodward, A. S. 1891. Catalogue of the fossil fishes in the British Museum of Natural History. Part II. Containing the Elasmobranchii (Acanthodii), Holocephali, Ichthyodorulites, Ostracodermi, Dipnoi, and Teleostomi (Crossopterygii), and chondrosteian Actinopterygii, Volume II. British Museum of Natural History, London, 567 pp.
- Woodward, A. S. 1915. Preliminary report on the fossil fishes from Dura Den. *Reports of the British Association for Advance of Science, Australia* 84:122–123.
- Young, G. C. 1980. A new Early Devonian placoderm from New South Wales, Australia, with a discussion of placoderm phylogeny. *Palaeontographica (A)*:10–76.
- Young, G. C. 1983. A new asterolepidoid antiarch (Placodermi) from the Late Devonian of south-eastern Australia. *Bureau of Mineral Resources Journal of Australian Geology and Geophysics* 8:71–81.
- Young, G. C. 1993. Middle Palaeozoic macrovertebrate biostratigraphy of Eastern Gondwana; pp. 208–251 in J. A. Long (ed.), *Palaeozoic Vertebrate Biostratigraphy and Paleontology*. Belhaven Press, London.
- Young, G. C. 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 N° 57*:139–150.
- Young, G. C. 2005a. 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, G. C. 2005b. 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, G. C. 2005c. New phyllolepid (placoderm fishes) from the Middle-Late Devonian of Southeastern Australia. *Journal of Vertebrate Paleontology* 25:261–273.
- Young, G. C., and J. M. Moody. 2002. A Middle-Late Devonian fish fauna from the Sierra de Perijá. *Mitteilungen des Museums für Naturkunde Berlin. Geowissenschaftliche Reihe* 5:155–206.
- Young, G. C., and D. Goujet. 2003. Devonian fish remains from the Dulcie Sandstone and Craven Peak Beds, Georgina Basin, central Australia. *Records of the Western Australian Museum supplément n° 65*:1–85.
- Young, G. C., and J. A. Long. 2005. Phyllolepid placoderm fish remains from the Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Antarctic Science* 17:387–408.
- Young, G. C., J. M. Moody, and J. Casas. 2000. New discoveries of vertebrates from South America, and implications for Gondwana-Euramerica contact. *Comptes Rendus de l'Académie des Sciences de Paris* 331:755–761.
- Zhu, M. 1990. Phylogenetic studies of petalichthyids from Qujing, Yunnan. PhD thesis/dissertation, Academia Sinica, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China, 149 pp. [Chinese with English summary, unpublished]
- Zhu, M. 1991. New information on *Diandongpetalichthys* (Placodermi: Petalichthyida); pp. 179–192 in M.-M. Zhang (ed.), *Early vertebrates and related problems of evolutionary biology*. Science Press, Beijing.
- Zhu, M. 2000. Catalogue of Devonian vertebrates in China, with notes on bio-events; pp. 373–390 in A. Blicek and S. Turner (eds.), *Palaeozoic Vertebrate Biochronology and Global Marine/Non-Marine Correlation*. Final Report of IGCP 328 (1991–1996). Courier Forschungsinstitut Senckenberg, Frankfurt.
- Zhu, M., and P. Janvier. 1994. Un onychodontide (Vertebrata, Sarcopterygii) du Dévonien inférieur de Chine. *Comptes Rendus de l'Académie des Sciences, Séries II* 319:951–956.
- Zhu, M., and W. Zhao. 2006. Early diversification of sarcopterygians and trans-Panthalassic Ocean distribution; pp. 399–416; 885–887 [Chinese with English summary] in J.-Y. Rong (ed.), *Originations and Radiations—Evidences from the Chinese Fossil Record*. Science Press, Beijing.
- Zhu, M., N.-Z. Wang, and J.-Q. Wang. 2000. Devonian macro- and microvertebrate assemblages of China; pp. 361–372 in A. Blicek and S. Turner (eds.), *Palaeozoic Vertebrate Biochronology and Global Marine/Non-Marine Correlation*. Final Report of IGCP 328 (1991–1996). Courier Forschungsinstitut Senckenberg, Frankfurt.

Submitted December 13, 2006, accepted June 4, 2007.