An articulated phyllolepid fish (Placodermi) from the Devonian of central Australia: implications for non-marine connections with the Old Red Sandstone continent

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Abstract – A second species of the placoderm genus *Placolepis* (*Pl. harajica* sp. nov.), based on a single articulated specimen from Givetian–Frasnian strata in the MacDonnell Ranges, demonstrates the occurrence of this taxon across the Australian craton. *Placolepis* (order Phyllolepida) is endemic to east Gondwana, and other phyllolepids are widespread in the Givetian and younger of Gondwana (Australia, Antarctica, Turkey, Venezuela), but do not occur until Late Devonian (Famennian) time in the Northern Hemisphere (Europe, Russia, Greenland, North America). The disjunct space–time distribution of the Phyllolepida is inconsistent with palaeomagnetic evidence indicating a wide equatorial ocean between Gondwana and Laurussia in Late Devonian time. This new species provides additional evidence supporting a Gondwana origin for the group, and later access to northern landmasses resulting from closure of the ocean between Gondwana and Laurussia and continental connection at or near the Frasnian–Famennian boundary.

Keywords: Devonian, central Australia, placoderm fish, phyllolepid, biostratigraphy, palaeogeography.

1. Introduction

Placoderms (armoured fishes) represent the first major radiation of the jawed vertebrates, and were the most diverse Devonian fish group, with a cosmopolitan distribution established by Early Devonian time. Their remains are diverse and often abundant in Middle and Upper Devonian strata (both marine and non-marine). They disappeared from the fossil record at or near the Devonian–Carboniferous boundary. Their heavily ossified skeleton had good preservation potential, and with some 300 placoderm genera they represent the most complex global biogeographic database for investigating palaeogeographic patterns during the Devonian Period. Amongst the eight orders, the stratigraphic record of the order Phyllolepida is unique, restricted only to the last stage of the Devonian (Famennian) in the Northern Hemisphere, where they are the only major group with no known Early or Middle Devonian representatives. However, the earlier occurrence of phyllolepids in the Gondwana continents is now well established.

The genus *Phyllolepis* was erected by Agassiz (1844) for an isolated bone with highly distinctive sinuous ridged ornament from Upper Devonian strata of Clashbennie, Scotland. In the following century, phyllolepids were shown to be widely distributed in Upper Devonian 'Old Red Sandstone', being recorded from Russia, Greenland, North America and Belgium

(Lohest, 1888; Fritsch, 1889; Newberry, 1889; Rohon, 1900; Heintz, 1930; Leriche, 1931). The first Southern Hemisphere record was by Hills (1931), but since the description of two new phyllolepid genera from southeastern Australia (Ritchie, 1984; Long, 1984), it has been unclear whether the early fragmentary remains actually belonged to the genus *Phyllolepis*. Since then, phyllolepids have been recorded by incomplete remains from most of the southern continents: Antarctica (Young, 1989*a*, fig. 4A), Turkey (Janvier, 1983, fig. 3), Venezuela (Young, Moody & Casas, 2000; Young & Moody, 2002, figs 12, 13), and from many new localities in Australia. In central Australia, Hills (1959) first illustrated phyllolepid material from the Dulcie Sandstone in the Georgina Basin, and Young (1985) demonstrated their occurrence in the Amadeus Basin (Fig. 1). Young (1988*a*) described isolated phyllolepid plates from three localities in the Amadeus and Georgina Basins, including one incomplete specimen provisionally referred to *Placolepis* Ritchie, 1984, previously known from a single locality in the Lachlan Fold Belt of southeastern Australia. The new articulated phyllolepid described here now confirms that this taxon also occurs in Devonian rocks of the Australian craton. This represents only the fourth locality in 160 years of scientific documentation to produce an articulated specimen. Most phyllolepid occurrences are isolated bones or fragments, but these are readily recognized by the distinctive ridged ornament, and the dermal skeleton of a single fish could have produced some 25 identifiable ornamented bones.
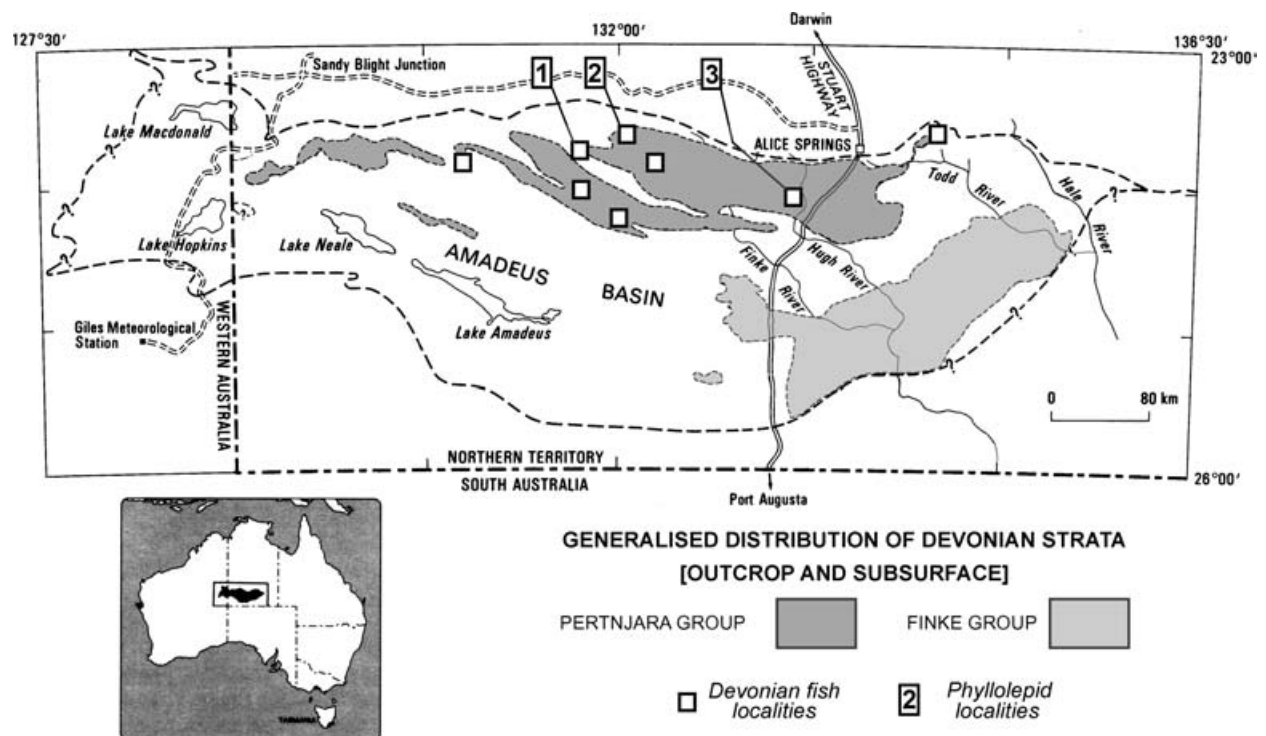
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Figure 1. The Amadeus Basin in central Australia (for location see small map), showing generalized Devonian geology and fossil fish localities (updated from Young, 1985, 1988*a*). Phyllolepid placoderms are known from three localities (1–3), and ANU V3059 described in this paper comes from locality 2.

The first articulated specimen ever found (from Dura Den, Scotland; Fig. 2a) convinced A. S. Woodward (1915, 1920) that *Phyllolepis* was a jawless heterostracan 'most nearly allied to the Drepanaspidae or Psammosteidae'. Its affinities remained uncertain, until description of extensive material from East Greenland by Stensiö (1934, 1936, 1939) proved beyond doubt that *Phyllolepis* was a highly aberrant placoderm. The sudden appearance of phyllolepids in Upper Devonian strata of the 'Old Red Sandstone continent', and their documented earlier Devonian history in Gondwana, is a stratigraphic anomaly requiring explanation in terms of palaeogeographic reconstructions for the Devonian Period (see Discussion). Of added interest is the fact that in four widely separated sequences (Aina Dal Formation, East Greenland; Duncannon Member, Pennsylvania; Evieux Formation, Belgium; Cloghnan Shale, Jemalong, Australia), phyllolepids occur in the same formation as Late Devonian tetrapods (Clack & Neininger, 2000; Daeschler *et al*. 1994; Clément *et al*. 2004; Campbell & Bell, 1977).

2. Material and methods

The described specimen (ANU V3059) is part of a large collection made in the MacDonnell Ranges in 1990. It was uncovered in a large sandstone slab containing numerous articulated impressions of the antiarch placoderm *Bothriolepis* (e.g. Young, 1985, fig. 7B–D). The bone is gone, and the material is studied by latex rubber casts whitened with ammonium chloride. Homologies of phyllolepid skull bones to those of other placoderms have been differently interpreted, and terminology here follows Long (1984) rather than Ritchie (1984). The homology of the element named the 'postnasal (PN)' plate remains uncertain. Repositories for specimens mentioned in the text are indicated by prefix as follows: ANU V, Dept Earth & Marine Sciences, Australian National University, Canberra; AMF, Australian Museum, Sydney; NMV, National Museum of Victoria. Bone proportions are given as a ratio of breadth to length expressed as a percentage (the B/L index). Standard abbreviations for placoderm dermal bones and other structures as used in the text and figures are listed in Table 1.

3. Locality and age

The specimen comes from the Pertnjara Group of the Amadeus Basin, central Australia, near Stokes Pass in the MacDonnell Ranges about 190 km west of Alice Springs (Fig. 1). Phyllolepid remains were first documented from this locality by Young (1985, fig. 8C–E). The locality is within the Parke Siltstone of the Pertnjara Group (Wells *et al*. 1970), adjacent to the type section of the Harajica Sandstone Member as defined by Jones (1972). The fossiliferous horizon is some 75–90 m above the base of this member, with remains of the antiarch placoderm *Bothriolepis* the most abundant fossils. The assemblage is considered
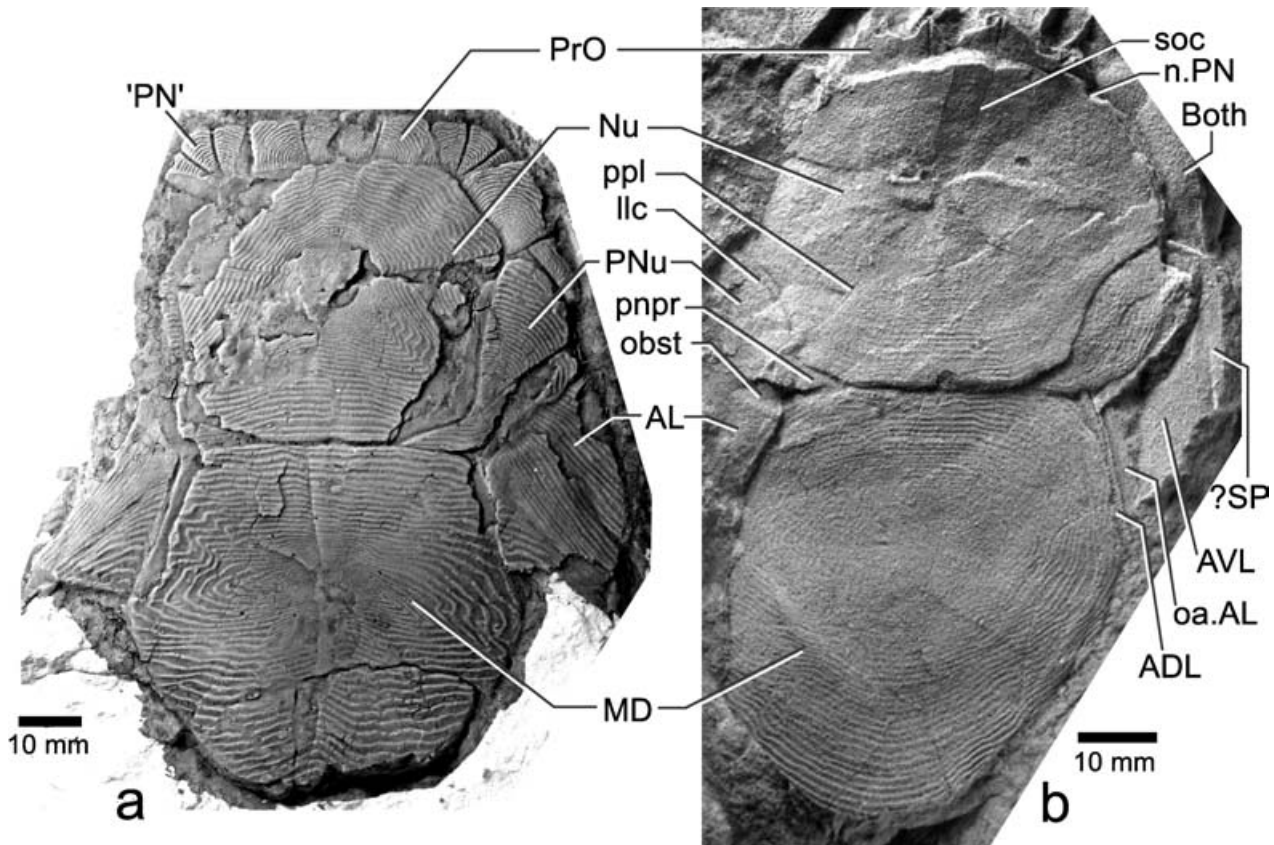
Figure 2. (a) Holotype and only known specimen of *Phyllolepis woodwardi* Stensiö, 1939 from Dura Den, Scotland, the first discovered articulated phyllolepid placoderm (photograph of plaster copy of dorsal surface, ANU V3054, × 0.8). Published illustrations of the original specimen include Woodward (1915, fig. 4) and Stensiö (1934, fig. 2; 1936, figs 3, 5; 1939, fig. 2). (b) Holotype (ANU V3059) of *Placolepis harajica* sp. nov., an articulated dermal armour in dorsal view (latex cast whitened with ammonium chloride; natural size).

Table 1. Abbreviations used in text and figures

Abbreviation	Structure
ADL	anterior dorsolateral plate
AL	anterior lateral plate
AVL	anterior ventrolateral plate
Both	remains of *Bothriolepis* sp.
csc	central sensory canal groove
llc	main lateral line sensory canal groove
M	marginal plate
MD	median dorsal plate
n.PN	notch for 'postnasal' plate
Nu	nuchal plate
oa.AL	area overlapped by AL plate
obst	obstantic process of AL
'PN'	skull bone possibly homologous with postnasal plate
pnpr	postnuchal process on paranuchal plate
PNu	paranuchal plate
ppl	posterior pitline
PrO	preorbital plate
PtO	postorbital plate
SO	suborbital plate
soc	supraorbital sensory canal groove
SP	spinal plate

to be Givetian in age (Young & Turner, 2000, fig. 4, column C), aligned with macrovertebrate zone 6d or younger in the scheme for East Gondwana of Young (1996).

4. Systematic palaeontology

Order PHYLLOLEPIDA Stensiö, 1934

Diagnosis. Placoderms in which the nuchal plate is much enlarged, as broad or broader than long, and surrounded by five smaller paired bones including paranuchal, marginal, postorbital and preorbital plates. Rostral, pineal, and central plates absent from skull roof, and posterior lateral plate absent from trunk armour. Median dorsal plate lacks an inner keel, and anterior dorsolateral plate has a narrow elongate exposed area. Posterior ventrolateral plate of sub-triangular shape, lacking a lateral lamina. Dermal ornament mainly of smooth concentric ridges, with some tubercles and tubercle rows.

Remarks. The above is modified from Denison (1978, p. 41) and Ritchie (1984), to incorporate new data on Australian phyllolepids. Denison included two phyllolepid suborders, 'Antarctaspina' and 'Phyllolepina', the latter distinguished by loss of rostral and pineal plates. *Antarctaspis* is now considered to be closely related to *Yujiangolepis* from China and *Toombalepis* from Australia, placed in the actinolepidoid family Antarctaspidae, which has no close relationship to the

Phyllolepida (Young & Goujet, 2003). Some of the above characters were included in the diagnoses for 'Phyllolepina' (suborder) of Denison (1978), 'Phyllo-lepidi' (infraorder) of Long (1984), and 'Phyllolepidae' (family) of Ritchie (1984).

Genus *Placolepis* Ritchie, 1984

Diagnosis. Phyllolepids in which the nuchal plate has a rounded anterior margin, with lateral corners posteriorly placed, and posterolateral margins relatively short, concave and anterolaterally directed. Paranuchal plate relatively small, less than half the length of the nuchal, and not in contact with postorbital plate. Main lateral line sensory groove traverses paranuchal, marginal and postorbital plates in close proximity to lateral margin of nuchal plate. External surface of marginal plate broader than long, and subdivided by postmarginal sensory canal into areas of similar size. Trunk armour lacking anterior and posterior median ventral plates.

Type species. *Placolepis budawangensis* Ritchie, 1984

Remarks. Ritchie's (1984) diagnosis has been modified, with some characters (e.g. median dorsal shape and ossification centre position) omitted because they are not clearly different from *Phyllolepis*. The shape of the rounded Nu and small PNu plates in the skull roof of *Placolepis* are its most distinctive features. In both *Phyllolepis* and *Austrophyllolepis* the Nu is distinctly six-sided, with a transverse anterior margin, and anterolateral, lateral and posterolateral corners. In addition, the PNu is longer, makes extensive contact with the PtO plate, and has a large external surface between the sensory canal and the nuchal margin. The presence of a PMV plate in the trunk armour distinguishes *Austrophyllolepis* from *Placolepis*, and probably from *Phyllolepis*. *Placolepis* is also distinguished from the other two genera in the shape and form of the M plate, with the symmetrical position of the sensory canal junction giving a distinctive 'T' shape (Ritchie, 1984, fig. 7K, M).

Placolepis harajica sp. nov.
Figures 2b, 3d

1993. 'phyllolepid'; Young, pp. 228, 248.
2000. 'complete phyllolepid'; Young & Turner, p. 464

Holotype. ANU V3059, an articulated fish preserved as an impression in dorsal view.

Etymology. From Harajica bore, an artesian water supply near the type locality.

Diagnosis. A *Placolepis* in which the nuchal plate of the skull has a more transverse anterior margin, and the paranuchal plate is elongate, with a breadth/length index of about 57. The ridges and grooves of the dermal ornament are of similar width, are less concentric on

the paranuchal plate, and there are about 10 ridges per centimetre behind the ossification centre of the median dorsal plate.

Remarks. *Placolepis harajica* sp. nov. is very similar to the type species *Placolepis budawangensis* Ritchie, 1984 as far as preserved, with the shape of the anterior margin of the Nu plate, and the ornament pattern and narrower PNu being the main differences to the described type material. The ornament as generally developed was probably coarser than in the type species, but since it is only well preserved on the MD plate this difference is specified in the diagnosis.

Description. The holotype was evidently a complete armour when preserved (Fig. 2b). Skull and trunk armour plates are close to original position, but the smaller head plates and lateral plates of the trunk armour are displaced or missing. The specimen was buried on top of abundant remains of the antiarch *Bothriolepis* (both, Fig. 2b), and was compressed over these remains during compaction. There is a slight oblique distortion, which may have made bone proportions slightly more elongate than in the original. The measured dorsal midline length of the preserved armour (including PrO plates) is 103 mm, of which slightly more than half (about 52 %) comprises the MD plate of the trunk armour, the same proportion as reconstructed for the type species (Ritchie, 1984, fig. 2C). The overall size is also close to the 'approximate natural size' of Ritchie's reconstruction of *Placolepis budawangensis* (Fig. 3c), although most of the figured material of the type species comes from considerably larger individuals (up to 50 % larger).

Skull. The Nu plate is well displayed except for the left anterolateral margin (Fig. 2b), and shows the characteristic shape for the genus, with prominent lateral corners giving maximum breadth in the middle of the length of the plate, at about the level of the ossification centre, and with a rounded to subcircular anterior margin (Fig. 3c, d). In *Phyllolepis* and *Austrophyllolepis* the Nu has a different shape, being broadest in its anterior half, with both lateral and anterolateral angles giving a more hexagonal shape (Fig. 3a, b). The ridged ornament of ANU V3059 is weathered over much of the external surface of the Nu, and is only visible in the posterior central part of the plate. In *Placolepis budawangensis* the concentric ridges are more or less continuous around the margins of the Nu. Much of the central area may be smooth, but a triangular posterior part seems to consistently show ornament. In four illustrated Nu plates of the type species (Ritchie, 1984, figs 4, 6A) this triangular area has 30–40 ornamental ridges from the posterior margin to the smooth unornamented central area. In *Phyllolepis woodwardi* there are about 31 ridges on this part of the Nu (Fig. 2a). By comparison, ANU V3059 has about 20 ridges. On the ossification centre
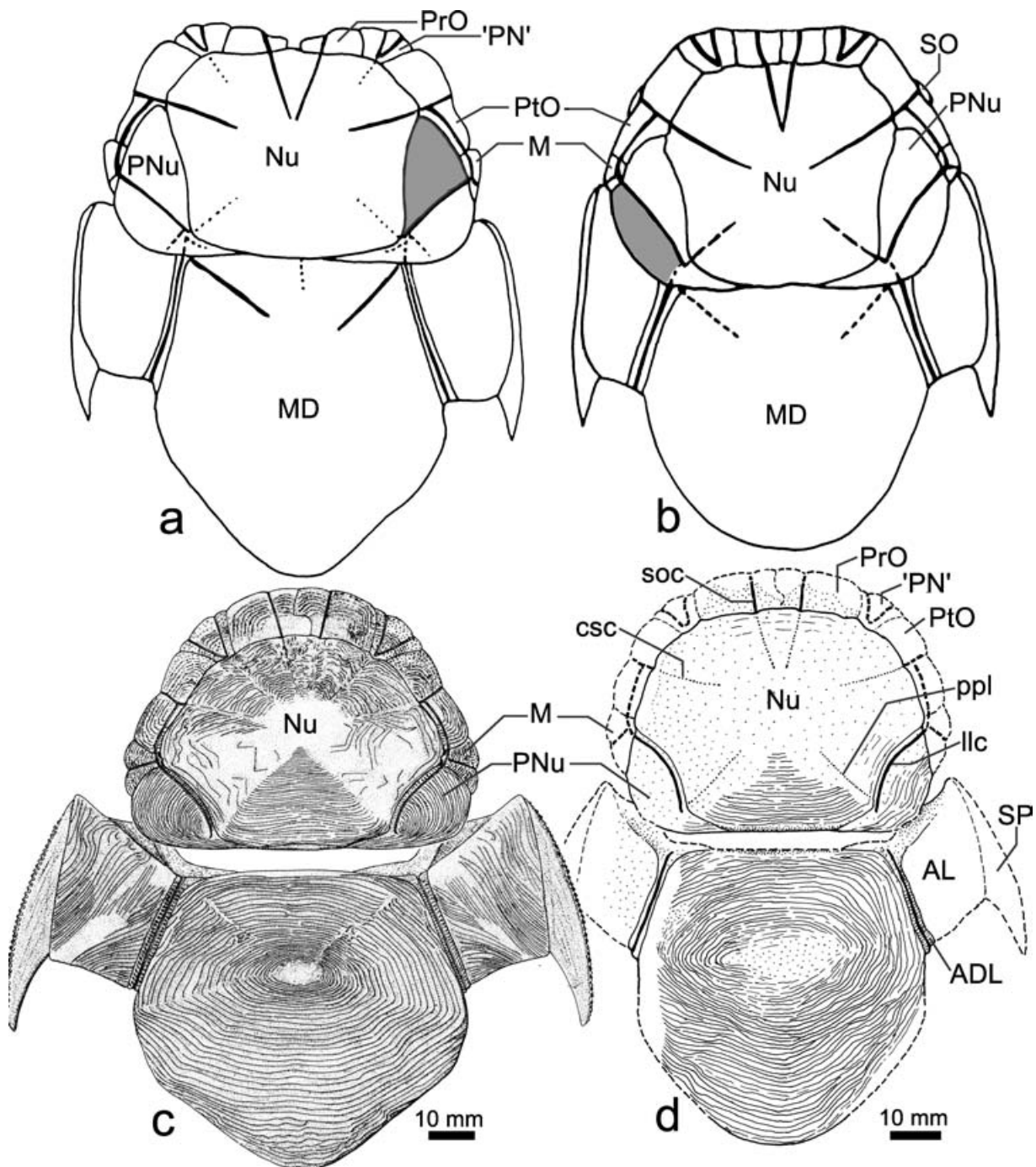
Figure 3. Dorsal armour patterns compared in three phyllolepid genera. (a) *Phyllolepis orvini*, after Stensiö (1936, fig. 2); (b) *Austrophyllolepis youngi*, after Long (1984, fig. 13A); (c) *Placolepis budawangensis*, after Ritchie (1984, fig. 8A); (d) *Placolepis harajica* sp. nov. (missing bones restored after c). Shaded area of the PNu plate (a, b) illustrates a main generic difference (larger area in front of sensory groove in *Phyllolepis*, and behind in *Austrophyllolepis*). (a, b not to scale.)

itself the surface is normally smooth, or the ridges are too fine to be discerned.

Four pairs of sensory grooves have been reconstructed on the Nu of *Placolepis budawangensis* (Ritchie, 1984, fig. 2C). These may be obscure on the external surface (Fig. 3c). In *Pl. Harajica* sp. nov. the posterior pitline and central sensory groove are faintly discerned on both sides (ppl, csc, Fig. 2b), and the

right supraorbital sensory groove can be seen, partly obscured by a crack (soc). Both supraorbital grooves are clearly preserved on the PrO plates, opposite which the anterior nuchal margin shows two slight notches. The intervening area projects anteriorly probably slightly more than in the Nu plate illustrated by Ritchie (1984, fig. 6A), which has similar notches for the supraorbital grooves. To the right, the Nu margin in ANU V3059 is

slightly sinuous as far as a rounded process immediately lateral to the preserved edge of the right PrO plate (Fig. 2b). The corresponding process on the left side is more angular. These mark the lateral extent of the PrO plates (Fig. 3d). Further laterally is a shallow notch (n.PN, Fig. 2b), corresponding to that for the 'PN' plate in *Placolepis budawangensis* (Fig. 3c). Another slight notch marks the position of the central sensory groove or pitline (csl, largely obscured by a crack on the left side). Based on the reconstruction, the new species has a less rounded anterior margin than in *Placolepis budawangensis* (Fig. 3c, d). Maximum breadth is just behind the middle of the plate ($\sim$49 % of total length from the posterior margin). In figured Nu plates of *Placolepis budawangensis* this varies between about 46 and 51 % (Ritchie, 1984, figs 4, 6A).

Both PNu plates are preserved in ANU V3059, the right one slightly displaced beneath the Nu, obscuring the sensory groove (Fig. 2b). On both sides the postnuchal process is well displayed (pnpr). The left plate is slightly displaced away from the Nu, and shows the sensory groove (llc) running close to the mesial margin in the typical position for *Placolepis*, by which this genus is readily distinguished from both *Phyllolepis* and *Austrophyllolepis* (see Long, 1984, fig. 2A). As noted in Ritchie's (1984) generic diagnosis, the fact that the PNu plate only forms anterior contact with one bone (M plate, Fig. 3c, d), compared with two in *Austrophyllolepis* and *Phyllolepis* (PtO and M, Fig. 3a, b) is a significant difference between *Placolepis* and the other genera. In ANU V3059 the external surface is poorly preserved on both plates. The right plate shows faint concentric ornament, and two slight angles on the lateral margin are reflected in the ornamental ridges. These subdivide the margin into three segments, overlapping the M plate anteriorly, loosely overlapping the obstantic margin (obst) of the anterior lateral (AL) plate in the middle segment, and forming the rear edge of the skull posteriorly. The same angles can be seen in illustrated PNu plates of *Placolepis budawangensis* (Ritchie, 1984, fig. 6B–D), but these are clearly shorter and broader bones, with a more rounded external margin, and the ornament is concentric. In contrast, the right PNu of *Pl. harajica* sp. nov. shows ornament (faintly preserved) that is laterally inflected, and truncated by the lateral margin. Shape variation in the PNu plate is slight in the three illustrated examples for the type species (external B/L index 76–79; length measured normal to posterior margin, and breadth the maximum at 90° to this, excluding the postnuchal process). The corresponding value for *Pl. harajica* sp. nov. is 57.

Of the smaller bones of the skull, only the two PrO plates of *Pl. harajica* sp. nov. are incompletely preserved. They lie partly obscured beneath the anterior edge of the Nu plate (PrO, Fig. 2b). The supraorbital

sensory grooves are deeply incised (soc, Fig. 3), and otherwise these bones are assumed to be developed as in *Placolepis budawangensis*, with midline contact (Fig. 3c, d). Stronger development of the supraorbital sensory groove on the PrO compared to the Nu plate is a feature both of *Placolepis budawangensis*, and also some *Phyllolepis* species (e.g. *Ph. woodwardi*, Fig. 2a). The left skull margin in ANU V3059 is not preserved, and the 'PN', PtO, and M plates have been lost from the right side where the skull was compacted over the underlying *Bothriolepis* armour. These bones can be restored after the type species (Fig. 3c, d), based on the similar notches in the margin of the Nu plate described above.

Trunk armour. The preserved dorsal armour has the large MD plate sufficiently complete for a reliable estimate of proportions (Fig. 2b), but adjacent bones are incomplete, or missing. The right AL plate has gone, exposing its overlap area on the ADL (oa.AL, Fig. 2b). On the left side a poorly preserved impression of the displaced AL shows the anterior obstantic process (obst), and suggests the short high shape illustrated for *Placolepis budawangensis* (Ritchie, 1984, fig. 10D–I). The right ADL plate shows the narrow exposed area, with lateral line groove and short vertical ridges of ornament typical of phyllolepids. As far as preserved it is the same as in *Placolepis budawangensis* (Ritchie, 1984, fig. 10A–C). The inner surface of the presumed right AVL and SP plates project out from beneath the armour on the right side, but show no diagnostic features (these could also be indeterminate *Bothriolepis* plates).

The MD plate is incomplete on the left margin, but proportions estimated from the preserved midline (breadth 60 mm, length 55 mm) give a B/L index of 109, at the lower end of the range for *Placolepis budawangensis* (100–125). In *Austrophyllolepis* the MD has a B/L index of 122–145 in *A. ritchiei*, but is more elongate (96–108) in *A. youngi* (Long, 1984). The position of the ossification centre in *Pl. harajica* sp. nov., estimated from the preserved outer concentric ornament, is about 36 % of total length from the anterior margin, and a little in front of the level of the lateral corners. Again, this is as in *Placolepis budawangensis*. Ritchie (1984) suggested the more rounded shape of the MD plate, and the anterior rather than central position of its ossification centre, as generic differences to the MD of *Phyllolepis*. In *Placolepis* the ossification and ornament centre of the MD was described as in the anterior half slightly in front of the lateral corners, but in *Ph. orvini* (based on the four specimens summarized by Stensiö, 1936, fig. 17) the ossification centre is also in the anterior half of the plate. However, it is about 43–45 % of total length from the anterior margin, compared to about 35 % in *Placolepis* (see above). The B/L index

(93–108) indicates a more elongate bone in *Ph. orvini*, but with some overlapping of the range for *Placolepis budawangensis* in the smaller MD plates, which tend to be broader (Stensiö, 1936).

There is no clear indication of a sensory groove on the MD in ANU V3059 (but there is a crack in about the right position passing back from the left anterolateral corner). Ritchie (1984) noted that this sensory canal is not always observed in *Placolepis budawangensis*. The entry of the dorsal pitline at the anterolateral corner of the MD, rather than part-way along the anterolateral margin as in *Phyllolepis*, was suggested by Ritchie (1984) as a generic difference to *Placolepis*. *Austrophyllolepis* is similar to *Placolepis* in this feature (Long, 1984), but the presence of two separate pitlines on material from Antarctica (e.g. Young, 1989*a*, fig. 4A) might indicate that homologies have been incorrectly assessed (Young & Long, in press).

Dermal ornament. On the MD of ANU V3059 about 33 ornamental ridges can be counted from the posterior margin into the central smooth zone, with a density of about 10 ridges per centimetre. Ridges and grooves are of similar width. This is the best-preserved part of the ornament on the holotype. Direct comparison with both larger (AMF 61772) and smaller (AMF 61769) MD plates of *Placolepis budawangensis* (casts in the Museum für Naturkunde, Berlin) indicate that the ornament ridges were more closely spaced in *Pl. harajica* sp. nov. On the examples illustrated by Ritchie (1984, fig. 9A, B, D), ridge density is about 7 ridges per centimetre, and they are more widely spaced, with grooves about twice the width of ridges. These assumed specific differences in ornament may also apply to the Nu plate (see above), but its ornament is less well preserved. The preserved part of the right ADL, showing vertical ridges, is closely similar to the corresponding area on the type species (Ritchie, 1984, fig. 10A–C).

Restoration. A scanned image of ANU V3059 was digitally corrected for the slight oblique distortion to prepare a restoration in dorsal view (Fig. 3d), using the restoration of the type species (Fig. 3c) for missing or incomplete bones. The midline axis of ANU V3059 is defined by the position of the supraorbital sensory grooves on the PrO plates, and the ossification centres of Nu and MD plates, and a transverse axis is given by joining the posterolateral corners of the Nu plate. These intersect at an angle of 84°, digitally restored to 90° to remove the oblique distortion. As restored the length of the Nu plate is about 76 % of the MD, and proportionately longer than in the reconstruction of *Placolepis budawangensis* (71 %; Fig. 3c). However, associated Nu and MD plates on the holotype (Ritchie, 1984, fig. 3) have similar relative lengths to *Pl. harajica* sp. nov.

5. Discussion

5.a. Phyllolepid relationships

Goujet & Young (1995, fig. 1), presented a relationships scheme for placoderms in which *Wuttagoonaspis*, phyllolepids, and the three major arthrodiran subgroups (brachythoracids, phlyctaeniids, actinolepids) were represented as a polytomy, thus including the hypothesis that phyllolepids could be a subgroup of the Arthrodira, as earlier suggested by Long (1984). Denison (1978) considered the poorly known *Antarctaspis* to be closest to Phyllolepida, but new evidence has overturned this view (Young & Goujet, 2003). Denison (1978) noted that the skull roof in both *Wuttagoonaspis* and phyllolepids lacked a central plate, but considered this convergent, although the similar ridged ornament (resulting in earlier confusion of remains of these taxa; Ritchie, 1973) is another possible shared derived character. A close relationship between wuttagoonaspids and phyllolepids has been supported by various authors (e.g. Miles, 1971; Long, 1984; Young & Goujet, 2003), and the anterior supragnathal toothplate is a shared derived character of phyllolepids and arthrodires (Goujet & Young, 2004).

However, a recent phylogenetic analysis by Dupret (2004) has produced a different result, with Phyllolepida placed in a sister group relationship to the phlyctaenioid arthrodires, but he did not code for the ridged ornament, considering it non-homologous between wuttagoonaspids and phyllolepids. It was argued that 'phyllolepid ornamentation consists of thin and concentric bony ridges, whereas *Wuttagoonaspis* shows both tubercles . . . and ridges' (Dupret, 2004, p. 5), but this is negated by the tuberculate ornament in parts of the dermal armour of *Austrophyllolepis*, which was well documented by Long (1984). The sister group relationship between Phyllolepida and phlyctaenioid arthrodires was supported by four characters at node 20 in the strict consensus tree (Dupret, 2004, fig. 6). One of these (position of endolymphatic foramen) is coded as 'non-applicable' for phyllolepids, another (anterior unornamented zone on MD plate) is coded as absent for phyllolepids but is present (e.g. *Placolepis budawangensis*; Ritchie, 1984, fig. 9), and a third (absence of anterior ventral plates) is negated by the recent description of these plates in the new Australian groenlandaspid *Mulgaspis* Ritchie, 2004. The fourth character (postnuchal process in the skull roof) is the only one requiring discussion. The skull roof in both brachythoracid arthrodires and phyllolepids shows lateral expansion of the Nu over the PNu plates, but the completely different shape of the Nu plate clearly indicates that this development evolved in parallel. However, in both groups the PNu produces a mesial process behind the Nu, a surprising similarity until its function is considered. This part of the skull roof supports the dermal neck-joint between the head and

the trunk armour. In phyllolepids this is a less complex sliding joint compared to the ball and socket joint of brachythoracids. However, the corresponding articular flange on the phyllolepid ADL plate (e.g. Stensiö, 1936, pl. 14, fig. 2) extends mesially to articulate beneath the PNu, and could not function if obliterated by the expanded Nu. Thus, I consider the postnuchal process also to be a parallel development in the two groups.

The suggested relationship of the three phyllolepid genera in Dupret's strict consensis tree, [*Placolepis* [*Austrophyllolepis* [*Phyllolepis*]]], is the same as suggested by Long (1984, fig. 27) and Young (1987, fig. 5), although the characters supporting nodes 21, 22 (Dupret, 2004, fig. 6) are not specified. This question remains unresolved; the fact that in the skull of most actinolepid arthrodires the PNu plate is in anterior contact with both PtO and M plates (e.g. Denison, 1978, fig. 31) would indicate that *Placolepis* may be derived compared to *Phyllolepis* by outgroup comparison.

5.b. Phyllolepid distributions in time and space

Although mainly represented by fragmentary remains, the distinctive ridged ornament of phyllolepids led to their discovery in widely separated localities, and they became accepted as an index fossil for uppermost (Famennian) strata of the Old Red Sandstone (e.g. Westoll, 1979). Their initial interpretation as heterostracan agnathans (see Section 1) gave a neat picture of faunal succession in adaptively similar benthic agnathans, from the Early Devonian *Drepanaspis*, to Middle–Late Devonian psammosteid heterostracans (extinct at the end of the Frasnian), and finally Famennian phyllolepids. Correctly interpreted as placoderms, phyllolepids were still seen as replacing the adaptively similar psammosteid heterostracans that flourished during the Givetian–Frasnian in the Baltic Province (e.g. Miles, 1968).

The precise timing of their first appearance in the Famennian of Euramerican sequences is improved by new data permitting approximate alignment with conodont or palynomorph zones (Fig. 4). In Belgium (Lohest, 1888; Leriche, 1931), close to the presumed southern margin of the 'Old Red Sandstone Continent', two *Phyllolepis* species (*Ph. konincki, Ph. undulata*) are known from four localities (Chèvremont, Evieux, Modave, Strud), the last of which has recently produced tetrapod remains (Clément *et al*. 2004). These localities are assigned a middle Famennian (*marginifera* conodont zone) age (H. Lelièvre, pers. comm). In the 'main Devonian field' of Russia *Phyllolepis* sp. is first recorded from the Kursa, and *Phyllolepis tolli* from the overlying Akmene regional stage of the East European Platform (*rhomboidea–marginifera* zones; Esin *et al*. 2000, figs 2, 3). The last psammosteid heterostracan (*Psammosteus tenuis*) occurs in the youngest (Amula) stage of the Frasnian. In the Timan region the last psammosteid (*Psammosteus* sp.) occurs in the latest
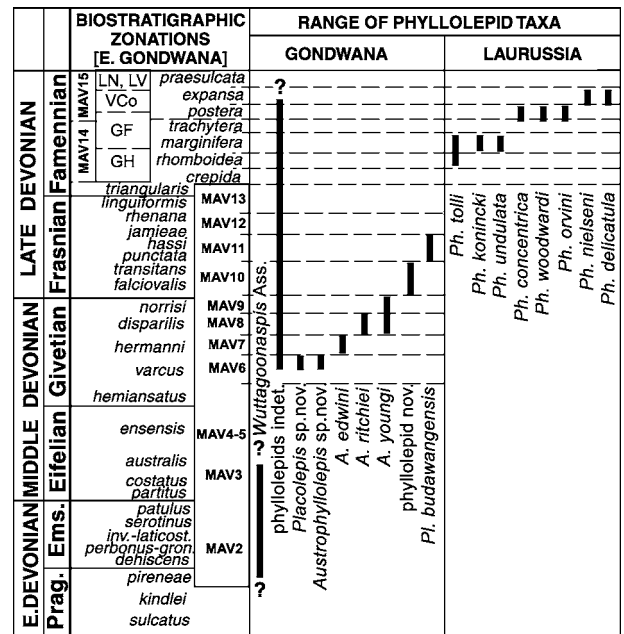

Figure 4. Summary of known stratigraphic ranges (?Pragian–Famennian) for wuttagoonaspids–phyllolepids in East Gondwana (Australia, Antarctica), and the genus *Phyllolepis* in Laurussia. Australian data updated from Young (1993, fig. 9.3) and Young (1999, fig. 5). Conodont zonation from Talent *et al*. (2000). Alignment of macrovertebrate (MAV), miospore (GH, GF, VCo, LN, LV), and conodont zones is approximate (modified from Young, 1996 and Young & Turner, 2000).

Frasnian Ukhta stage, with *Phyllolepis* sp. appearing in the Famennian Pokayama regional stage of north Timan (Esin *et al*. 2000, figs 4, 5). *Phyllolepis* '*delicatula*' in the Catskill Formation, eastern USA (Duncannon Member, material under study; Daeschler, Frumes & Mullison, 2003), could be slightly younger (equivalent to the upper VCo miospore zone; Traverse, 2003). A similar age based on spores is indicated for the East Greenland succession, where GF zone spores (approximating to the upper *marginifera* zone) occur in the upper part of the Elsa Dal Formation (Marshall, Astin & Clack, 1999). In the overlying '*Phyllolepis* and *Remigolepis* Series' (Jarvik, 1961, 1996), *Ph. orvini* occurs in the Aina Dal, and *Ph. nielseni* in the younger Britta Dal formations (updated stratigraphy from Clack & Neininger, 2000). The Famennian age of these fish-tetrapod faunas is well established (e.g. Bendix-Almgreen, 1976; Stemmerik & Bendix-Almgreen, 1998). The Upper Devonian *Phyllolepis* horizons in Scotland (Rosebrae Beds in the Moray Firth area, approximately equivalent faunas at Dura Den and Clashbennie in the Midland Valley, and Sundhope Burn in south Scotland) were correlated by Miles (1968, table 2) with the upper part of the East Greenland '*Phyllolepis* Series'. These ranges are summarized in Figure 4.

In Gondwana, phyllolepids when first discovered were assumed to have the same Famennian age

as in the Northern Hemisphere. Thus Hills (1931) assigned the Cerberean Volcanics of eastern Victoria to the Upper Devonian, and concluded the same for occurrences in New South Wales (Hills, 1932, 1936), as did Rade (1964). This not unreasonable assumption led to associated isotopic dates in Victoria being applied to the question of the numerical age of the Devonian–Carboniferous boundary (Evernden & Richards, 1962; McDougall, Compston & Bofinger, 1966). The first indication that Australian phyllolepids could be pre-Famennian was the documentation in southeastern Australia of phyllolepid remains beneath marine strata that contained invertebrates indicating a late Frasnian age (Young, 1974, 1979), and now assessed as representing the global transgression at the Frasnian–Famennian boundary (e.g. Mawson & Talent, 2000). It is also noteworthy that the antiarch *Remigolepis* (e.g. Johanson, 1997) in Australia is associated with phyllolepids, whereas in the type area of East Greenland the '*Remigolepis* Series' overlies the '*Phyllolepis* Series'.

The age of the Victorian fish faunas has been assessed as close to the Givetian–Frasnian boundary (Young, 1993, 1996). A late Middle Devonian age was recently suggested (Long, 1999), and a re-evaluation of isotopic data at 374 ± 1.4 Ma (Compston, 2004) is close to the 375 Ma alignment for oldest phyllolepids in the revised macrovertebrate zonation for East Gondwana of Young & Turner (2000, fig. 2). Precise correlations are still unresolved between these Victorian fish assemblages, and those in southeastern New South Wales, which contain different phyllolepid genera (Ritchie, 1984; Young, in press). However, their approximate age equivalence is indicated by genera in common amongst several other groups (e.g. Young, 1989*b*; Long, 1989, 1999; Johanson & Young, 1999), and the NSW localities underlie strata attributed to the late Frasnian marine transgression. In the slightly older Aztec sequence of southern Victoria Land, Antarctica, phyllolepids appear towards the top of the sequence (Young, 1988*b*). In the Cook Mountains (Long & Young, 1995, fig. 2), J. A. Long discovered phyllolepid remains two zones lower than in the initial assessment of Young (1988*b*, fig. 5), but still above the level of turiniid thelodonts, which are abundant in the lower part of the Aztec Siltstone (Turner & Young, 1992). As currently understood, phyllolepids occur first in zone 6d (*karawaka* zone of the Aztec sequence), and in all higher macrovertebrate zones in the system worked out by Young (1993, fig. 9.3), now including MAV15 (*Grenfellaspis* assemblage; Ritchie *et al.* 1992), where rare phyllolepids are associated with sinolepid antiarchs (Young, unpub. data). Known occurrences are summarized in Figure 4.

A similar age to these oldest phyllolepids of east Gondwana is assigned to the recently documented phyllolepid occurrence in Venezuela (Young & Moody, 2002). This is associated with miospores ranging from middle Givetian to middle Frasnian in the schemes for the ORS of Richardson & McGregor (1986) and Streel *et al.* (1987). The age of the phyllolepid occurrence in the Antalya Nappe of Turkey (Janvier, 1983), first assessed as Famennian, was reconsidered by Lelièvre, Janvier & Blieck (1993, p. 157), who suggested a probably older (Givetian–Frasnian) age based on other faunal elements (*Holonema*, primitive megalichthyid) indicating Gondwana affinities. This would be consistent with its assumed palaeogeographic position on the northern Gondwana margin (locality 8, Fig. 5). Note that phyllolepids are not known from southern Africa, contrary to a report by Anderson, Hiller & Gess (1994), which proved to be an incorrect determination (Long *et al.* 1997).

5.c. Biogeography

The systematic revisions of all Northern Hemisphere phyllolepid material by Stensiö (1934, 1936, 1939), together with subsequent work (Vasiliauskas, 1963), has documented eight separate species of the genus *Phyllolepis*. In the Southern Hemisphere, there are many indeterminate occurrences in Australia and elsewhere (e.g. Janvier, 1983; Turner, Basden & Burrow, 2000, fig. 10E). Of named taxa, we now have two described species each in the Gondwanan genera *Austrophyllolepis* and *Placolepis* from Australia, new species of both genera in Antarctica (Young & Long, in press), plus at least two new phyllolepid genera in southeastern Australia (Young, 1999, in press). The wuttagoonaspid placoderms, considered here to be the closest relatives to phyllolepids, plus related poorly known groups with similar ridged ornament, are widely distributed in older (Lower–Middle Devonian) strata in Australia. On present evidence these are endemic to East Gondwana; in terms of dispersal capabilities, they can be assigned to category 'd' in the scheme of biogeographic utility discussed by McKerrow *et al.* (2000), with a strong provincial distribution suggesting restriction by marine barriers (Young, 2003). Recent systematic documentation of the *Wuttagoonaspis* assemblage, the first vertebrate fauna to occupy the rivers and lakes of the Australian landmass (Young & Goujet, 2003), has revealed a fauna containing at least 20 genera (including agnathans of the endemic class Pituriaspida described by Young, 1991). This assemblage is known from localities extending over some one million square kilometres of the Australian craton. It is predicted that taxon diversity of wuttagoonaspids–phyllolepids in East Gondwana will continue to increase as research progresses on the many new fossil localities.

Summarizing known data on a palaeogeographic reconstruction (Fig. 5) clearly illustrates a well-documented disjunct distribution in both time and space for wuttagoonaspids–phyllolepids. Wuttagoonaspids (open triangles) are known only from the Early–Middle
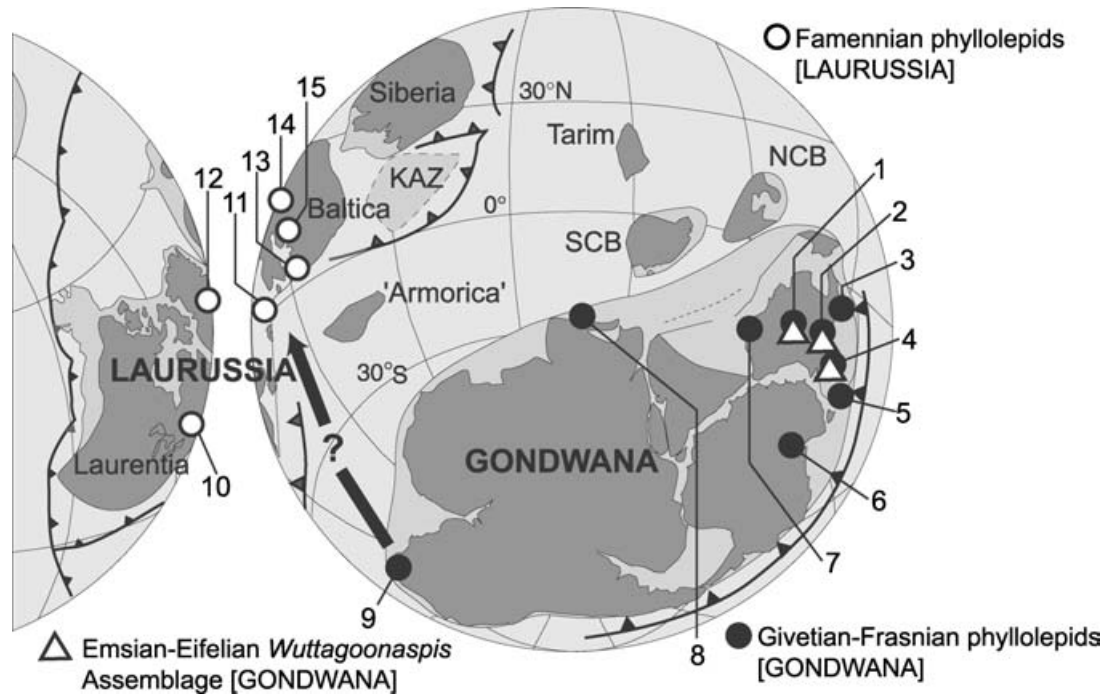
Figure 5. Global distribution patterns for some key placoderm fish groups, plotted on the Late Devonian reconstruction of Li &
Powell (2001, fig. 13). The *Wuttagoonaspis* assemblage (Early–Middle Devonian Gondwanan endemics) is indicated by open triangles
(for more locality detail see Young & Turner, 2000, fig. 1.). Phyllolepid placoderms (Middle–Late Devonian) are shown as two
biostratigraphically and geographically disjunct groups: Gondwanan (Givetian or younger, closed circles) and Laurussian (mid–
late Famennian, open circles). Postulated Late Devonian continental dispersal for non-marine vertebrates between Gondwana and
Laurussia indicated by an arrow. Numbered Gondwanan localities are: 1 – Amadeus Basin and 2 – Georgina Basin (central Australia);
3 – Townsville area, Queensland; 4 – west-central NSW (numerous localities; Hills, 1931, 1936; Ritchie, 1973; Young, 1993, 1999);
5 – Braidwood–Pambula–Mt Howitt, SE Australia (Long, 1984; Ritchie, 1984; Young, 1983); 6 – Transantarctic Mountains, southern
Victoria Land, Antarctica; 7 – Carnarvon Basin, WA (J. A. Long, unpub. data); 8 – Antalya Nappe, Turkey; 9 – Sierra de Periha,
Venezuela. Numbered Laurussian localities (mid–late Famennian) are: 10 – Virginia–Pennsylvania, USA; 11 – Scotland, UK; 12 – east
Greenland; 13 – Belgium; 14 – Timan, Russia; 15 – Baltic States.

Devonian of East Gondwana. Givetian–Frasnian phyl-
lolepids occur only in Gondwana (closed circles,
Fig. 5), and phyllolepids in Laurussia (Laurentia +
Baltica) are restricted to the Famennian, the last stage
of the Late Devonian (open circles, Fig. 5).

5.d. Palaeogeographic implications

The first evidence of this major disjunction suggested
a non-marine dispersal episode across the northern
Gondwana margin during the Late Devonian (Young,
1981, 1990), implying continental connection at or
near the Frasnian–Famennian boundary to permit
the phyllolepids to gain access to Laurussia. Two
predictions by Young (1989*a*, p. 58) regarding future
phyllolepid discoveries have been supported by new
data. No representatives of this group have yet been
found in Asia (e.g. Zhu, 2000), but the discovery of
phyllolepids in Venezuela (Young, Moody & Casas,
2000; Young & Moody, 2002) has extended the range
of the group right across to the northwestern Gondwana
margin.

This evidence directly contradicts a long-standing
palaeogeographic hypothesis for a wide equatorial

ocean separating Gondwana from Laurussia during the
Late Devonian (Fig. 5), based on an interpretation of
apparent polar wander paths for the Middle Palaeozoic
accepted by many palaeomagnetists (e.g. Van Der Voo,
1988, 1993; Li, Powell & Trench, 1993; Tait *et al*. 2000;
Li & Powell, 2001). As an alternative to closing this
ocean to explain vertebrate distributions, Li, Powell &
Trench (1993) suggested a 'stepping stone' migration
route via the South or North China blocks, and Tarim,
Kazakhstan or Siberia. However, this is completely
unsupported by current evidence; although Devonian
fish assemblages have been extensively documented
in these regions, distinctive and readily recognized
phyllolepid remains have never been identified. Other
Devonian faunal and floral data also require at least
continental shelf proximity between Gondwana and
Laurussia by Middle or Late Devonian time, consistent
with some alternative palaeogeographic reconstruc-
tions (e.g. Carls, 2001; Feist, 2001; Meyer-Berthaud,
Wendt & Galtier, 1997; Meyer-Berthaud *et al*. 2003).
A complicating factor (Young, 1986, 1995*a,b*), was the
proposal, also based on palaeomagnetic evidence, that
a mid-oceanic terrane, representing the 'Armorican'
part of Europe, had fragmented from Gondwana

to traverse this equatorial ocean and collide with Laurussia during Late Devonian–Early Carboniferous times (Fig. 5). There may be five or more terranes in this 'Armorican Terrane Assemblage' (Franke, 2000), each of which would require separate biogeographic analysis (Young, 2003). Nevertheless, faunal data for a range of fossil groups accumulated over many years consistently indicate that 'Armorica' probably represents the northern Gondwana margin (e.g. Young, 1987; Robardet, Paris & Racheboeuf, 1990; Robardet, 2003).

6. Conclusion and summary

The new species *Placolepis harajica* described here adds specific taxonomic data derived from complex vertebrate morphology to the question of fish distributions during the Devonian Period. This was a crucial time in earth history, when the first forests were established, and the first complex terrestrial ecosystems evolved. Compared to other well-documented placoderm groups, the distribution of the order Phyllolepida is highly unusual, and the major disjunction within the group in both time and space gives a clear indication that the phyllolepids were largely confined by marine barriers, and could only have gained access to landmasses in the Northern Hemisphere by continental proximity or connection between Gondwana and Laurussia during Late Devonian time.

References

AGASSIZ, L. 1844. *Monographie des poissons fossiles du vieux grès rouge du système Dévonien (Old Red Sandstone) des Îles Britanniques et de Russie*. Neuchâtel: Jent & Gassmann, 171 pp.

ANDERSON, M. E., HILLER, N. & GESS, R. W. 1994. The first *Bothriolepis*-associated Devonian fish fauna from Africa. *South African Journal of Science* **90**, 397–403.

BENDIX-ALMGREEN, S. E. 1976. Palaeovertebrate faunas of Greenland. In *Geology of Greenland* (ed. A. Escher and W. S. Watt), pp. 536–73. Copenhagen: Geological Survey of Greenland.

CAMPBELL, K. S. W. & BELL, M. W. 1977. A primitive amphibian from the Late Devonian of New South Wales. *Alcheringa* **1**, 369–81.

CARLS. P. 2001. Kritik der Plattenkinematik um das Rhenohercynicum bis zum fruhen Devon. *Braunschweiger geowissenschaftliche Arbeiten* **24**, 27–108.

CLACK, J. A. & NEININGER, L. 2000. Fossils from the Celsius Bjerg Group, Late Devonian sequences, East Greenland; significance and sedimentological distribution. In *New Perspectives on the Old Red Sandstone* (eds P. F. Friend and B. P. J. Williams), pp. 557–66. Geological Society of London, Special Publication no. 180.

CLÉMENT, G., AHLBERG, P. E., BLIECK, A., BLOM, H., CLACK, J. A., POTY, E. THOREZ, J. & JANVIER, P. 2004. Devonian tetrapod from western Europe. *Nature* **427**, 412–13.

COMPSTON, W. 2004. SIMS U–Pb zircon ages for the Upper Devonian Snobs Creek and Cerberean Volcanics from Victoria, with age uncertainty based on UO_2/UO v. UO/U precision. *Journal of the Geological Society, London* **161**, 223–8.

DAESCHLER, E. B., FRUMES, A. C. & MULLISON, C. F. 2003. Groenlandaspid placoderm fishes from the Devonian of North America. *Records of the Australian Museum* **55**, 25–60.

DAESCHLER, E. B., SHUBIN, N. H., THOMSON, K. S. & AMARAL, W. W. 1994. A Devonian tetrapod from North America. *Science* **265**, 639–42.

DENISON, R. H. 1978. Placodermi. In *Handbook of Paleoichthyology, volume 2* (ed. H.-P. Schultze). Stuttgart: Gustav Fischer Verlag, 128 pp.

DUPRET, V. 2004. The phylogenetic relationships between actinolepids (Placodermi: Arthrodira) and other arthrodires (phlyctaeniids and brachythoracids). In *Lower vertebrates from the Palaeozoic* (ed. G. C. Young), pp. 44–55. First International Palaeontological Congress (IPC 2002), Sydney, Australia, July 2002. Proceedings of Symposium 6 (Palaeozoic Vertebrates). *Fossils & Strata* **50**.

ESIN, D., GINTER, M., IVANOV, A., LEBEDEV, O., LUKSEVICS, E., AVKHIMOVICH, V., GOLUBTSOV, V. & PETUKHOVA, L. 2000. Vertebrate correlation of the Upper Devonian on the East European Platform. *Courier Forschungsinstitut Senckenberg* **223**, 341–59.

EVERNDEN, J. F. & RICHARDS, J. R. 1962. Potassium–argon ages in eastern Australia. *Journal of the Geological Society of Australia* **9**, 1–49.

FEIST, R. 2001. North Gondwana/Laurussia interaction: testing geodynamic models with trilobites. *15th International Senckenberg Conference, Frankfurt am Main, 2001, Abstract volume*, p. 36. Frankfurt am Main: Senckenberg Museum.

FRANKE, W. 2000. The mid-European segment of the Variscides: tectonostratigraphic units, terrane boundaries and plate tectonic evolution. In *Orogenic processes: quantification and modelling in the Variscan belt* (eds W. Franke, V. Haak, O. Oncken and D. Tanner), pp. 35–61. *Geological Society of London, Special Publication* no. 179.

FRITSCH, A. J. 1889. *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens*. Prague, vol. 2, 114 pp.

GOUJET, D. & YOUNG, G. C. 1995. Interrelationships of placoderms revisited. *Geobios, Memoire special* **19**, 89–96.

GOUJET, D. & YOUNG, G. C. 2004. Placoderm anatomy and phylogeny: new insights. In *Recent Advances in the Origin and Early Radiation of Vertebrates* (eds G. Arratia, M. V. H. Wilson and R. Cloutier), pp. 109–26. München: Verlag Dr Friedrich Pfeil.

HEINTZ, A. 1930. Oberdevonische Fischereste aus Ost-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. 1932. Upper Devonian fishes from New South Wales. *Quarterly Journal of the Geological Society of London* **88**, 850–8.

HILLS, E. S. 1936. Records and descriptions of some Australian Devonian fishes. *Proceedings of the Royal Society of Victoria* **48**, 161–71.

HILLS, E. S. 1959. Record of *Bothriolepis* and *Phyllolepis* (Upper Devonian) from the Northern Territory of Australia. *Journal and Proceedings of the Royal Society of New South Wales* **92**, 174–5.

JANVIER, P. 1983. Les vertébrés dévoniens de la Nappe Supérieure d'Antalya (Taurus lycien occidental, Turquie). *Géologie Méditerranéenne* **10**, 1–13.

JARVIK, E. 1961. Devonian vertebrates. In *Geology of the Arctic* (ed. G. O. Raasch), pp. 197–204. Toronto: Toronto Press.

JARVIK, E. 1996. The Devonian tetrapod *Ichthyostega*. *Fossils and Strata* **40**, 1–213.

JOHANSON, Z. 1997. New *Remigolepis* (Placodermi; Antiarchi) from Canowindra, New South Wales, Australia. *Geological Magazine* **134**, 813–46.

JOHANSON, Z. & YOUNG, G. C. 1999. New *Bothriolepis* (Antiarchi: Placodermi) from the Braidwood region, New South Wales, Australia (Frasnian). *Records of the Western Australian Museum Supplement* **57**, 55–75.

JONES, B. G. 1972. Upper Devonian to Lower Carboniferous stratigraphy of the Pertnjara Group, Amadeus Basin, central Australia. *Journal of the Geological Society of Australia* **19**, 229–49.

LELIÈVRE, H., JANVIER, P. & BLIECK, A. 1993. Siluro–Devonian vertebrate biostratigraphy of western Gondwana and related terranes (South America, Africa, Armorica–Bohemia, Middle East). In *Palaeozoic Vertebrate Biostratigraphy and Biogeography* (ed. J. A. Long), pp. 139–73. London: Belhaven Press.

LERICHE, M. 1931. Les poissons famenniens de la Belgique. *Academie Royal de Belgique, Memoire* (Ser. 2) **10**, 1–72.

LI, Z. X. & POWELL, C. MCA. 2001. An outline of the palaeogeographical evolution of the Australasian region since the beginning of the Neoproterozoic. *Earth Science Reviews* **53**, 237–77.

LI, Z. X., POWELL, C. MCA. & TRENCH, A. 1993. Palaeozoic global reconstructions. In *Palaeozoic Vertebrate Biostratigraphy and Biogeography* (ed. J. A. Long), pp. 25–53. London: Belhaven Press.

LOHEST, M. 1888. Recherches sur les poissons des terrains paléozoïques de Belgique. Poissons des Psammites du Condroz, Famennien supérieur. *Annals de la Societé Geologique de Belgique* **15**, 112–203.

LONG, J. A. 1984. New phyllolepids from the Victoria, and the relationships of the group. *Proceedings of the Linnean Society of New South Wales* **107**, 263–308.

LONG, J. A. 1989. Phyllolepid placoderms from the Late Devonian of eastern Victoria. In *Pathways in Geology: Essays in Honour of Edwin Sherbon Hills* (ed. R. W. Le Maitre), pp. 52–8. Melbourne: Blackwells Scientific Publications, 463 pp.

LONG, J. A. 1999. A new genus of fossil coelacanth (Osteichthyes: Coelacanthiformes) from the Middle Devonian of southeastern Australia. *Records of the Western Australian Museum, Supplement* **57**, 37–53.

LONG, J. A., ANDERSON, M. E., GESS, R. W. & HILLER, N. 1997. New placoderm fishes from the Late Devonian of South Africa. *Journal of Vertebrate Paleontology* **17**, 253–68.

LONG, J. A. & YOUNG, G. C. 1995. Sharks from the Middle–Late Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Records of the Western Australian Museum* **17**, 287–308.

MARSHALL, J. E. A., ASTIN, T. R. & CLACK, J. A. 1999. East Greenland tetrapods are Devonian in age. *Geology* **27**, 637–40.

MAWSON, R. & TALENT, J. A. 2000. The Devonian of eastern Australia: stratigraphic alignments, stage and series boundaries, and the transgression–regression pattern reconsidered. *Courier Forschungsinstitut Senckenberg* **225**, 243–70.

MCDOUGALL, I., COMPSTON, W. & BOFINGER, V. M. 1966. Isotopic age determinations on Upper Devonian rocks from Victoria, Australia; a revised estimate of the age of the Devonian – Carboniferous boundary. *Bulletin of the Geological Society of America* **77**, 1075–8.

MCKERROW, W. S., MAC NIOCAILL, C., AHLBERG, P. E., CLAYTON, G., CLEAL, C. J. & EAGAR, R. M. C. 2000. In *Orogenic processes: quantification and modelling in the Variscan belt* (eds W. Franke, V. Haak, O. Oncken and D. Tanner), pp. 9–20. Geological Society of London, Special Publication no. 179.

MEYER-BERTHAUD, B., FAIRON-DEMARET, M., STEEMANS, P., TALENT, J. & GERRIENNE, P. 2003. The plant *Leclercqia* (Lycopsida) in Gondwana: implications for reconstructing Middle Devonian palaeogeography. *Geological Magazine* **140**, 119–30.

MEYER-BERTHAUD, B., WENDT, J. & GALTIER, J. 1997. First record of a large *Callixylon* trunk from the late Devonian of Gondwana. *Geological Magazine* **134**, 847–53.

MILES, R. S. 1968. The Old Red Sandstone antiarchs of Scotland: family Bothriolepididae. *Palaeontographical Society Monographs (London)* **122**, 1–130.

MILES, R. S. 1971. The Holonematidae (placoderm fishes), a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Philosophical Transactions of the Royal Society of London B. Biological Sciences* **263**, 101–234.

NEWBERRY, J. S. 1889. The Paleozoic fishes of North America. *United States Geological Survey Monograph* **16**, 1–340.

RADE, J. 1964. Upper Devonian fish from the Mount Jack area, New South Wales, Australia. *Journal of Paleontology* **38**, 929–32.

RICHARDSON, J. B. & MCGREGOR, D. C. 1986. Silurian and Devonian spore zones of the Old Red Sandstone Continent and adjacent regions. *Geological Survey of Canada, Bulletin* **364**, 1–79.

RITCHIE, A. 1973. *Wuttagoonaspis* gen. nov., an unusual arthrodire from the Devonian of Western New South Wales, Australia. *Palaeontographica* **143A**, 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**, 321–53.

RITCHIE, A. 2004. A new genus and two new species of groenlandaspidid arthrodire (Pisces: Placodermi) from the Early–Middle Devonian Mulga Downs Group of western New South Wales, Australia. In *Lower vertebrates from the Palaeozoic* (ed. G. C. Young), pp. 56–81. First International Palaeontological Congress (IPC 2002), Sydney, Australia, July 2002. Proceedings of Symposium 6 (Palaeozoic Vertebrates). *Fossils & Strata* **50**.

RITCHIE, A., WANG, S. T., YOUNG, G. C. & ZHANG, G. R. 1992. The Sinolepidae, a family of antiarchs (placoderm fishes) from the Devonian of South China and eastern Australia. *Records of the Australian Museum* **44**, 319–70.

ROBARDET, M., 2003. The Armorica 'microplate': fact or fiction? Critical review of the concept and contradictory palaeobiogeographical data. *Palaeogeography, Palaeoclimatology, Palaeoecology* **195**, 125–48.

ROBARDET, M., PARIS, F. & RACHEBOEUF, P. R. 1990. Palaeogeographic evolution of southwestern Europe during Early Palaeozoic times. In *Palaeozoic biogeography and palaeogeography* (eds W. S. McKerrow and C. R. Scotese), pp. 411–19. Geological Society of London, Memoir no. 12.

ROHON, J. V. 1900. Die devonischen Fische von Timan in Russland. *Sitzungsberichte der Königlichen Kgl. Böhmischen Gesellschaft der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse* (1899) **41**, 1–77.

STEMMERICK, L. & BENDIX-ALMGREEN, S. 1998. Carboniferous age for the East Greenland "Devonian" basin: paleomagnetic and isotopic constraints on age, stratigraphy, and plate reconstructions: comment. *Geology* **26**, 284–5.

STENSIÖ, E. A. 1934. On the Placodermi of the Upper Devonian of East Greenland. I. Phyllolepida and Arthrodira. *Meddelelser om Grønland* **97**(1), 1–58, 25 pl.

STENSIÖ, E. A. 1936. On the Placodermi of the Upper Devonian of East Greenland. Supplement to Part I. *Meddelelser om Grønland* **97**(2), 1–52, 30 pl.

STENSIÖ, E. A. 1939. On the Placodermi of the Upper Devonian of East Greenland. Second supplement to Part I. *Meddelelser om Grønland* **97**(3), 1–33, 6 pl.

STREEL, M., HIGGS, K., LOBOZIAK, S., RIEGEL, W. & STEEMANS, P. 1987. Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenne-Rhenish regions. *Review of Palaeobotany and Palynology* **50**, 211–29.

TAIT, J., SCHATZ, M., BACHTADSE, V. & SOFFEL, H. 2000. Palaeomagnetism and Palaeozoic palaeogeography of Gondwana and European terranes. *Geological Society of London, Special Publication* **179**, 21–34.

TALENT, J. A., MAWSON, R., AITCHISON, J. C., BECKER, R. T., BELL, K. N., BRADSHAW, M. A., BURROW, C. J., COOK, A. G., DARGAN, G. M., DOUGLAS, J. G., EDGECOMBE, G. D., FEIST, M., JONES, P. J., LONG, J. A., PHILLIPS-ROSS, J. R. PICKETT, J. W., PLAYFORD, G., RICKARDS, R. B., WEBBY, B. D., WINCHESTER-SEETO, T., WRIGHT, A. J., YOUNG, G. C. & ZHEN, Y.-Y. 2000. Devonian palaeobiogeography of Australia and adjoining regions. In *Palaeobiogeography of Australasian Faunas and Floras* (eds A. J. Wright, G. C. Young and J. A. Talent), pp. 167–257. Association of Australasian Palaeontologists, Memoir no. 23.

TRAVERSE, A. 2003. Dating the earliest tetrapods: a Catskill palynological problem in Pennsylvania. In *Studies on fossil and extant plants and floras. Dedicated to Friedemann Schaarschmidt on the occasion of his 65th birthday* (ed. V. Wilde), pp. 19–49. *Courier Forschungsinstitut Senckenberg* **241**.

TURNER, S., BASDEN, A. & BURROW, C. J. 2000. Devonian vertebrates of Queensland. In *IGCP 328, Final Report* (eds A. Blieck and S. Turner), pp. 487–521. *Courier Forschungsinstitut Senckenberg* **223**.

TURNER, S. & YOUNG, G. C. 1992. Thelodont scales from the Middle–Late Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Antarctic Science* **4**, 89–105.

VAN DER VOO, R. 1988. Paleozoic paleogeography of North America, Gondwana, and displaced terranes: comparisons of paleomagnetism with paleoclimatology and biogeographical patterns. *Geological Society of America Bulletin* **100**, 311–24.

VAN DER VOO, R. 1993. *Paleomagnetism of the Atlantic, Tethys and Iapetus oceans*. Cambridge: Cambridge University Press, 41 pp.

VASILIAUSKAS, V. M. 1963. *Phyllolepis tolli* sp. nov. and some problems concerning the stratigraphy of the Famennian deposits in the Baltic states. In *Geology of the Lithuania* (eds A. Grigelis and V. Karatajute-Talimaa), pp. 407–29. Vilnius (in Russian).

WELLS, A. T., FORMAN, D. J., RANFORD, L. C. & COOK, P. J. 1970. Geology of the Amadeus Basin, central Australia. *Bureau of Mineral Resources, Australia, Bulletin* **100**, 222 pp.

WESTOLL, T. S. 1979. Devonian fish biostratigraphy. *Special Papers in Palaeontology* **23**, 341–53.

WOODWARD, A. S. 1915. Preliminary report on the fishes from Dura Den. *Reports of the British Association for the Advancement of Science* (1914) **84**, 122–3.

WOODWARD, A. S. 1920. Presidential address. *Proceedings of the Linnean Society of London* **1920**, 25–34.

YOUNG, G. C. 1974. Stratigraphic occurrrence of some placoderm fishes in the Middle and Late Devonian. *Newsletters on Stratigraphy* **3**, 243–61.

YOUNG, G. C. 1979. Appendix: vertebrate palaeontology. *Journal of the Geological Society of Australia* **26**, 102–3.

YOUNG, G. C. 1981. Biogeography of Devonian vertebrates. *Alcheringa* **5**, 225–43.

YOUNG, G. C. 1983. A new asterolepidoid antiarch (Placodermi) from the Late Devonian of south-eastern Australia. *BMR Journal of Australian Geology & Geophysics* **8**, 71–81.

YOUNG, G. C. 1985. New discoveries of Devonian vertebrates from the Amadeus Basin, central Australia. *BMR Journal of Australian Geology & Geophysics* **9**, 239–54.

YOUNG, G. C. 1986. Cladistic methods in Paleozoic continental reconstruction. *Journal of Geology* **94**, 523–37.

YOUNG, G. C. 1987. Devonian palaeontological data and the Armorica problem. *Palaeogeography, Palaeoclimatology, Palaeoecology* **60**, 283–304.

YOUNG, G. C. 1988*a*. New occurrences of phyllolepid placoderms from the Devonian of central Australia. *BMR Journal of Australian Geology & Geophysics* **10**, 363–76.

YOUNG, G. C. 1988*b*. Antiarchs (placoderm fishes) from the Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Palaeontographica* **202A**, 1–125.

YOUNG, G. C. 1989*a*. The Aztec fish fauna of southern Victoria Land – evolutionary and biogeographic significance. In *Origins and Evolution of the Antarctic Biota* (ed. J. A. Crame), pp. 43–62. Geological Society of London, Special Publication no. 47.

YOUNG, G. C. 1989*b*. New occurrences of culmacanthid acanthodians (Pisces, Devonian) from Antarctica and southeastern Australia. *Proceedings of the Linnean Society of New South Wales* **111**, 12–25.

YOUNG, G. C. 1990. Devonian vertebrate distribution patterns, and cladistic analysis of palaeogeographic hypotheses. In *Palaeozoic biogeography and palaeogeography* (eds W. S. McKerrow and C. R. Scotese), pp. 243–55. Geological Society of London, Memoir no. 12.

YOUNG, G. C. 1991. The first armoured agnathan vertebrates from the Devonian of Australia. In *Early Vertebrates and Related Problems of Evolutionary Biology* (eds M. M. Chang, Y. H. Liu and G. R. Zhang), pp. 67–85. Beijing: Science Press, 514 pp.

YOUNG, G. C. 1993. Middle Palaeozoic macrovertebrate biostratigraphy of eastern Gondwana. In *Palaeozoic Vertebrate Biostratigraphy and Biogeography* (ed. J. A. Long), pp. 208–51. London: Belhaven Press.

YOUNG, G. C. 1995*a*. Application of cladistics to terrane history – parsimony analysis of qualitative geological data. *Journal of Southeast Asian Earth Sciences* **11**, 167–76.

YOUNG, G. C. 1995*b*. Early vertebrates and palaeogeographic models. *Geobios, Memoire special* **19**, 129–34.

YOUNG, G. C. 1996. Devonian (chart 4). In *An Australian Phanerozoic Timescale* (eds G. C. Young and J. R. Laurie), pp. 96–109. Melbourne: Oxford University Press.

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* **57**, 139–50.

YOUNG, G. C. 2003. North Gondwanan mid-Palaeozoic connections with Euramerica and Asia; Devonian vertebrate evidence. *Courier Forschungsinstitut Senckenberg* **242**, 169–85.

YOUNG, G. C. In press. New phyllolepids (placoderm fishes) from the Middle-Late Devonian of southeastern Australia. *Journal of Vertebrate Paleontology.*

YOUNG, G. C. & GOUJET, D. 2003. Devonian fish remains from the Dulcie Sandstone and Cravens Peak Beds. Georgina Basin, central Australia. *Records of the Western Australian Museum, Supplement* **65**, 85 pp., 42 figures.

YOUNG, G. C. & LONG, J. A. In press. Phyllolepid placoderm fish remains from the Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Antarctic Science.*

YOUNG, G. C. & MOODY J. M. 2002. A Middle–Late Devonian fish fauna from the Sierra de Perijá, western Venezuela, South America. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe* **5**, 153–204.

YOUNG, G. C., MOODY, J. & CASAS, J. 2000. New discoveries of Devonian vertebrates from South America, and implications for Gondwana-Euramerica contact. *Comptes Rendus de l'Academie des Sciences, Paris* **331**, 755–61.

YOUNG, G. C. & TURNER, S. 2000. Devonian microvertebrates and marine-nonmarine correlation in East Gondwana: Overview. *Courier Forschungsinstitut Senckenberg* **223**, 453–70.

ZHU, M. 2000. Catalogue of Devonian vertebrates in China, with notes on bio-events. *Courier Forschungsinstitut Senckenberg* **223**, 373–90.