Phyllolepid placoderm fish remains from the Devonian Aztec Siltstone, southern Victoria Land, Antarctica

GAVIN C. YOUNG[1]* and JOHN A. LONG[2]

[1]*Department of Earth and Marine Sciences, Australian National University, Canberra, ACT 0200, Australia*
[2]*Museum Victoria, PO Box 666E, Melbourne, VIC 3001, Australia*
gyoung@ems.anu.edu.au

Abstract: Phyllolepid placoderm remains from the Aztec Siltstone fish fauna are described as *Austrophyllolepis quiltyi* sp. nov., *Austrophyllolepis* cf. *A. youngi*, *Placolepis tingeyi* sp. nov., and phyllolepid indet. The new Antarctic species of two genera previously only known from Australia reinforce evidence from other fish taxa of close biogeographic affinity, as part of the eastern margin of Palaeozoic Gondwana. At least three genera and four species gives the Aztec Siltstone fish fauna the most diverse phyllolepid assemblage known, and probably the oldest documented so far (?late Middle Devonian). Specimens of *Austrophyllolepis* from the type locality at Mount Howitt, Victoria, are refigured for comparison with the Antarctic species. The order Phyllolepida is a key group for understanding Devonian vertebrate biogeography and palaeogeography, with a unique disjunct distribution in both time and space between the Southern and Northern hemispheres. Phyllolepids document one of the major dispersal events in early vertebrate history, which approximately coincided with the Frasnian–Famennian boundary mass extinction during the Late Devonian.

Introduction

Devonian fish remains found in glacial moraine by T. Griffith Taylor's northern party during the British Antarctic '*Terra Nova*' expedition of 1910–13 were the first Devonian fossils, and the first fossil vertebrates, to be discovered on the Antarctic continent. The Aztec fish fauna of southern Victoria Land, now known to contain some 45 taxa, is the most diverse Antarctic fossil assemblage of Palaeozoic age. Nearly half of the fauna belongs to the class Placodermi (armoured fishes), the most diverse Devonian fish group, representing the first major radiation of the jawed vertebrates. Placoderms were rare in the Silurian, but by the early stages of the Devonian Period had established a cosmopolitan distribution. They are widespread and diverse in Middle–Upper Devonian strata, but disappeared at the end of the Devonian Period.

The placoderm genus *Phyllolepis* Agassiz, 1844 has an interesting taxonomic history and enigmatic distribution pattern. The type was an isolated bone with highly distinctive sinuous ridged ornament from the Upper Devonian of Clashbennie, Scotland, and *Phyllolepis* remains were later found at many localities in the Upper Devonian of the Old Red Sandstone, including Russia, Latvia, Greenland, North America, and Belgium (Lohest 1888, Newberry 1889, Rohon 1900, Heintz 1930, Leriche 1931, Vasiliauskas 1963). The first Southern Hemisphere record was by Hills (1931) in south-eastern Australia, and they were later found across the Australian continent (Hills

1959, Young 1985, 1988a). All such remains were initially assigned to various species of *Phyllolepis*, but 140 years after the genus was erected two new phyllolepid genera were documented from south-eastern Australia: *Austrophyllolepis* Long, 1984 and *Placolepis* Ritchie, 1984. Recent research has demonstrated greater taxonomic diversity in Australian phyllolepids than previously thought (Long 1989, Young 2005a, 2005b), and phyllolepid occurrences have been documented in other 'Gondwana' areas, including Turkey (Janvier 1983), and Venezuela (Young *et al*. 2000, Young & Moody 2002).

Phyllolepid remains were first recorded from Antarctica by Ritchie (1972), and some examples were illustrated by Young (1989a, 1991). Here we provide the first systematic account, based on a study of all the known phyllolepid material in the various Antarctic collections of the Aztec Siltstone fish assemblage. Detailed analysis demonstrates that both of the Australian genera also occur in Aztec Siltstone Devonian fish fauna, and that phyllolepids are much more diverse than first thought.

Geological setting

The original Aztec Siltstone fossil fish material came from glacial moraine at Mount Suess, near the mouth of the Mackay Glacier at Granite Harbour (locality 2, Fig. 1a), and was correctly assumed by Debenham (1921) to derive from the thick sequence of sedimentary rocks called the 'Beacon
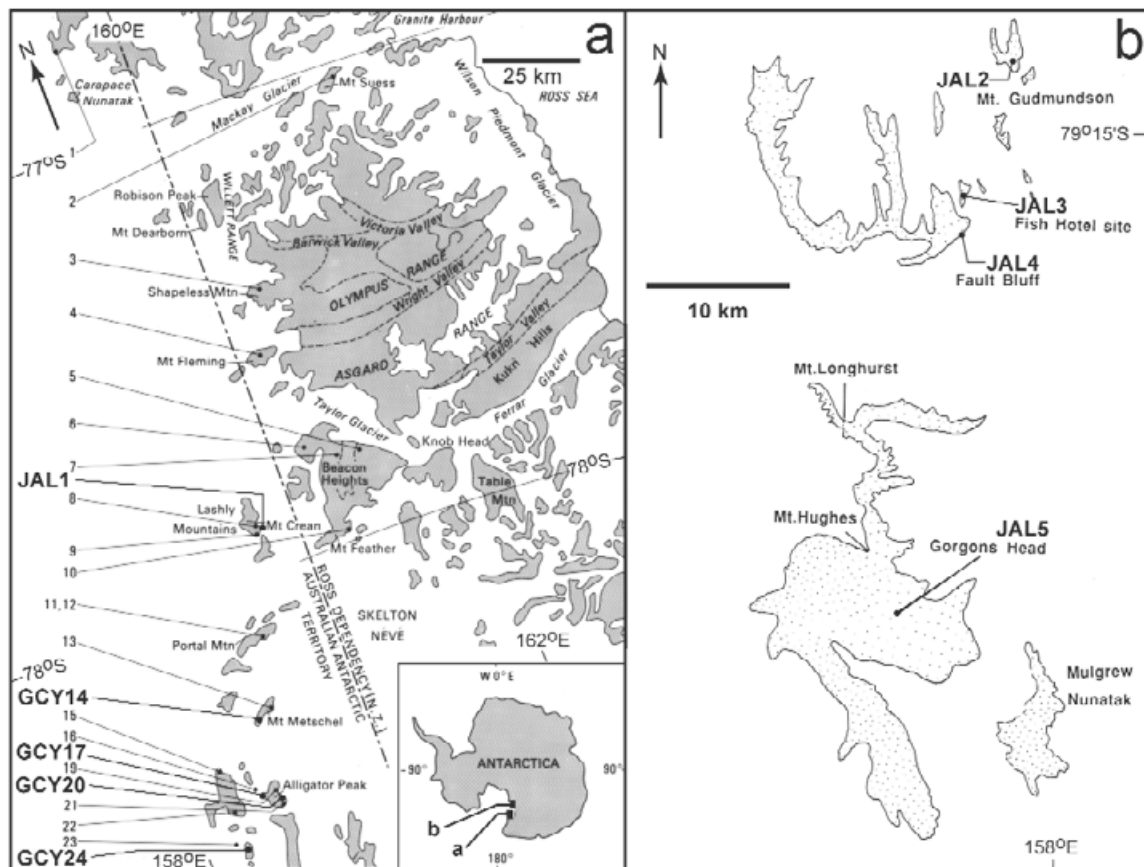
Fig. 1. Localities for the Devonian Aztec Siltstone fish fauna of southern Victoria Land. **a**. 24 localities from 1970–71 and earlier discoveries (modified from Young 1988b, fig. 3), **b**. new localities in the Cook Mountains discovered in 1988–89 and collected 1991–92 summer field seasons (modified from Long & Young 1995, fig. 1). The prefix GCY or JAL indicates that phyllolepid placoderm material was collected from that locality (see text for details).

Sandstone'. Woodward (1921) identified eight Devonian fish taxa, and pronounced the age as 'Upper Devonian'. The first *in situ* material, described by White (1968), was collected in the Skelton Névé region during the Trans-Antarctic Expedition of 1955–58 (Gunn & Warren 1962). However, phyllolepid placoderm remains were not recognized until new fossil localities to the south were discovered during the 1968–69 summer field season of the New Zealand Antarctic Research Program (NZARP). A large collection from these localities was made by a Victoria University of Wellington Antarctic Expedition (VUWAE 15) in the 1970–71 field season. Later expeditions (1976–77, 1988–89, 1991–92) found new fossil localities in the Cook Mountains (Woolfe *et al.* 1990, Long & Young 1995), 100 km to the south of previously known sites (M.A. Bradshaw, NZARP, event 33; J.A. Long, NZARP–ANARE expedition; see Long 2000, 2001 for detailed field account). The remains of phyllolepid placoderms from all these collections are described in this paper.

Almost all the fish material comes from the Aztec Siltstone, the uppermost formation of the Taylor Group, Beacon Supergroup (McKelvey *et al.* 1972, McPherson

1978). A few fish remains have been found in the upper beds of the underlying Beacon Heights Orthoquartzite. The Aztec Siltstone is a redbed sequence reaching a maximum thickness of some 220 m in the southern Boomerang Range. It includes point bar, back swamp and lacustrine lithologies, with plant remains at various levels, and is interpreted as deposited by meandering streams in an alluvial plain environment (McPherson 1978, McLoughlin & Long 1994). Associated conchostracans, trace fossils, and carbonaceous root structures are consistent with a non-marine depositional environment (Bradshaw & Webers 1989). The large size of some of the fishes indicates substantial water bodies (Young 1989a), but there are also numerous soil and caliche horizons in the lower part of the formation indicating subaerial exposure (McPherson 1979). The fossil fish fauna as currently documented (Table I) is one of the most diverse known fossil fish assemblages of Middle–Late Devonian age, including representatives of most of the major vertebrate groups: thelodont agnathans (Turner & Young 1992), chondrichthyans (Young 1982, Long & Young 1995, Hampe & Long 1999), other placoderms (Ritchie 1975, Young 1988b, Long 1995),

Table I. Current faunal list for the Aztec Siltstone fish fauna, including new taxa described in this paper.

AGNATHA	*Turinia antarctica* Turner & Young 1992
OSTEICHTHYES	
Dipnoi:	?*Eoctenodus* sp.
	Howidipterus sp.
	?ctenodontid indet.
Rhipidistia:	*Gyroptychius? antarcticus* (Woodward)
	Koharalepis jarviki Young, Long & Ritchie 1992
	Mahalalepis resima Young, Long & Ritchie 1992
	Platyethmoidia antarctica Young, Long & Ritchie 1992
	Vorobjevaia dolonodon Young, Long & Ritchie 1992
	Notorhizodon mackelveyi Young, Long & Ritchie 1992
	Aztecia mahalae Johanson & Ahlberg 2001
	porolepiform indet.
Actinopterygii:	palaeoniscoid gen. nov.
	?palaeoniscoid indet.
CHONDRICHTHYES	
	Mcmurdodus featherensis White 1968
	Antarctilamna prisca Young 1982
	Anareodus statei Long & Young 1995
	Aztecodus harmsenae Long & Young 1995
	Portalodus bradshawae Long & Young 1995
ACANTHODII	*Gyracanthides warreni* White 1968
	Antarctonchus glacialis White 1968
	Byssacanthoides debenhami Woodward 1921
	Culmacanthus antarctica Young 1989b
	Milesacanthus antarctica Young & Burrow 2004
	ischnacanthid indet. Long & Young 1995
PLACODERMI	
Antiarchi:	*Bothriolepis antarctica* Woodward 1921
	Bothriolepis alexi Young 1988b
	Bothriolepis askinae Young 1988b
	Bothriolepis barretti Young 1988b
	Bothriolepis karawaka Young 1988b
	Bothriolepis kohni Young 1988b
	Bothriolepis macphersoni Young 1988b
	Bothriolepis mawsoni Young 1988b
	Bothriolepis portalensis Young 1988b
	Bothriolepis vuwae Young 1988b
	Bothriolepis sp. indet. 1–13
	Venezuelepis antarctica Young & Moody 2002
Arthrodira	*Antarctolepis gunni* White 1968
	Groenlandaspis antarcticus Ritchie 1975
	Groenlandaspis spp.
	Boomeraspis goujeti Long 1995
	phlyctaeniid sp. nov.
Phyllolepida:	*Austrophyllolepis quiltyi* sp. nov.
	Placolepis tingeyi sp. nov.
	phyllolepid indet.
incertae sedis:	*Antarctaspis mcmurdoensis* White 1968

sarcopterygians (Young *et al.* 1992), and acanthodians, actinopterygians, and dipnoans (Young 1989a, 1989b, 1991, Campbell & Barwick 1987, Young & Burrow 2004). Six 'biozones' have been recognized within the Aztec Siltstone fauna, but only the lower ones are preserved to the north. This has been attributed to stripping of the upper strata by ice sheet erosion during the late Palaeozoic (McPherson 1978). In sections measured on the southern side of the Darwin Glacier (Askin *et al.* 1971a) the Aztec Siltstone is completely absent, whereas in the Cook Mountains on the northern side it is over 90 m thick, with fish remains throughout. The upper biozones characterized by the phyllolepids described below are relatively well represented in these southern localities, whereas the lower biozones characterized by thelodont agnathans have not been found anywhere in the region. This is the case even for fish remains documented from just a few metres above the Beacon Heights Orthoquartzite (e.g. Mount Gudmundson section; Long & Young 1995, fig. 2), and it indicates that the entire Aztec Siltstone is diachronous, becoming younger to the south.

Materials and methods

Fossil material is mainly preserved as white bone in a sandstone/siltstone matrix. Mechanical preparation was used to exposed bone margins, or poorly preserved bone was removed and the impressions studied using latex rubber casts whitened with ammonium chloride. This included direct comparison of dermal ornament and bone shape with similar cast material from phyllolepid type localities in southeastern Australia (Mount Howitt, Victoria; Nettletons Creek, New South Wales). Homologies of phyllolepid skull bones have been differently interpreted, and terminology here follows Long (1984) rather than Ritchie (1984). The homology of the element named here the 'postnasal' (PN) plate remains uncertain. Repositories for specimens mentioned in the text are indicated by prefix as follows: ANU V = Department of Earth & Marine Sciences, Australian National University, Canberra, AMF = Australian Museum, Sydney, NMV P = Museum Victoria, Melbourne, WAM = Western Australian Museum, Perth. The fossil locality prefix MS refers to the Antarctic catalogue of the New Zealand Geological Survey. Bone proportions are given as a ratio of breadth to length expressed as a percentage (the B/L index). Abbreviations for placoderm dermal bones and other structures used in the text and figures are as follows: **ADL** = anterior dorsolateral plate, **AL** = anterior lateral plate, **alc** = anterolateral corner, **AMV** = anterior median ventral plate, **arth** = arthrodire bone, **AVL** = anterior ventrolateral plate, **csl** = central sensory canal, **dep** = depression, **dlg1,2** = anterior and posterior dorsal pitline grooves, **dup** = duplicated section of ornament ridges, **lc** = lateral corner, **llc** = main lateral line sensory canal, **MD** = median dorsal plate, **Mg** = marginal plate, **Nu** = nuchal plate, **oa.AL** = area overlapped by AL plate, **oa.AVL** = area overlapped by AVL plate, **oa.MD** = area overlapped by MD plate, **oa.Nu** = area overlapped by Nu plate, **oa.PrO** = area overlapped by PrO plate, **oa.PtO** = area overlapped by PtO plate, **oss.c** = ossification centre for dermal bone, **pa** = posterior angle, **pect** = pectoral embayment (margin) of AVL plate, **pl** = pitline, **plc** = posterolateral corner, **pmc** = posteromesial corner, **PMV** = posterior median ventral plate, '**PN**' = skull bone possibly homologous with the postnasal plate, **PNu** = paranuchal

plate, **ppec** = prepectoral corner, **PrO** = preorbital plate, **PtO** = postorbital plate, **ptpec** = postpectoral corner, **PVL** = posterior ventrolateral plate, **SM** = submarginal plate, **SO** = suborbital plate, **soc** = supraorbital sensory groove, **unorn** = smooth zones on the posterior skull margin and anterior trunk armour margin, **vpl** = ventral pitline.

The distinctive phyllolepid ridged ornament is unlikely to be confused with that of other taxa in the Aztec Siltstone fauna, but one fragment from Portal Mountain, originally collected as a phyllolepid, now seems to belong to the very common antiarch *Bothriolepis*. Ridged ornament is unusual in this taxon, but an exception is in small areas of the skull of *B. portalensis* (see Young 1988b, pl. 7, fig. 8). However the ridges are normally nodose, as in the fragment just mentioned.

Differences in the phyllolepid ornament of smooth ridges varies from fine to coarse, and this is specified in terms of the number of ridges that are included in one cm counting from the first ridge at right angles to the ridges (ridges per cm). The ridges may be widely spaced, or close together, with intervening grooves of similar or greater width. We express this as a 'groove/ridge index' (e.g. 1 when ridges and grooves are of similar width; 2 when ridges are more widely spaced and grooves are twice ridge width). Again this is measured at right angles to the ridges.

Localities

The distinctive phyllolepid ridged ornament was first identified by Ritchie (1972) in fragmentary material from two localities in the Boomerang Range, on the south-western side of the Skelton Névé (MS236, 238). Additional samples were obtained from MS236 during the main 1970/71 collecting expedition (A. Ritchie and G.C. Young). New localities in the Cook Mountains (Woolfe *et al.* 1990) were collected in the 1991/92 field season by J.A. Long, who also revisited some of the previous Skelton Névé localities, and found phyllolepid remains at three additional sites. The nine known phyllolepid localities are summarized below (north to south) as numbered in Fig. 1 (prefix GCY for locality numbers of Young 1988b; prefix JAL for additional 1991/92 localities):

GCY14 (Fig. 1a). 50 m of the upper Aztec Siltstone was measured at the south-western end of Mount Metschel in section M2 of Askin *et al.* (1971b). Remains of the antiarch *Bothriolepis* and the sarcopterygian *Notorhizodon* were described from here by Young (1988b) and Young *et al.* (1992; see Johanson & Ahlberg 2001 for a revision of *Notorhizodon*). Two phyllolepid specimens (WAM 95.2.127, 00.6.13) were collected from 7 m below the top of the Aztec Siltstone at this locality in 1991/92 (JAL).

GCY17 (Fig. 1a). This is the 'Alligator Ridge Pavement' locality (MS236), from which Ritchie (1972) first identified phyllolepid remains, corresponding to Unit 32 in Section A1 of Askin *et al.* (1971b; 8 m below the top of the Aztec

Siltstone). This is the most abundant phyllolepid locality (AMF 55439, 482, 493, 520, 534; ANU V3060–63).

GCY20 (Fig. 1a). Ritchie (1972, p. 352) noted a fragment with 'ornament reminiscent of *Phyllolepis*' from this locality (MS238), apparently from about 70 m above the base of the Aztec Siltstone in section 4 of Barrett & Webb (1973), but the specimen has not been re-located (cited as AMF 54417 in Young 1988b, p. 14). The horizon is doubtfully correlated (Young 1988b, p. 9) with the upper fossiliferous horizon (MS2) from which White (1968) described *Bothriolepis*, sarcopterygian scales, and two acanthodian taxa (*Antarctonchus* and *Gyracanthides*). Spines of the latter acanthodian also occur at the 'Alligator Ridge Pavement' locality (McKelvey *et al.* 1972, fig. 3), so MS238 probably represents a similar level near the top of the Aztec Siltstone sequence.

GCY24 (Fig. 1a). Two fragments with ridged ornament (AMF 117074, WAM 00.6.12) were collected from scree at Mount Ritchie (WAM specimen in top 20 m, field locality 'T'). These presumably derive from the upper horizons at 187 and 212 m above the base of the Aztec Siltstone, which are abundantly fossiliferous (units 54, 62, section A4 of Askin *et al.* 1971b). Phyllolepid scrap material was noted in 1991/92 at a lower level (locality 'M'; JAL field note book), supposedly *in situ*, but no sample was collected, so this cannot be verified.

JAL1 (Fig. 1a). This additional Lashly Range locality, first collected in 1991/92, is in the third Aztec Siltstone outcrop to the south-east of the main Mount Crean locality, where Gunn & Warren (1962; locality 8 of Young 1988b) first documented fish remains. One phyllolepid plate (WAM 00.6.148) comes from the 38 m level (LA-1) in the section, and may be one of the lowest levels in the Aztec Siltstone sequence from which phyllolepid remains can be confirmed. Associated fauna (see Long & Young 1995, p. 291) contains the shark *Portalodus*, which ranges right through the higher Aztec Siltstone sequence, but there are no thelodont scales, even though there is apparently basal contact between the Aztec Siltstone and Beacon Heights Orthoquartzite in this section. Because it is an isolated exposure, correlation with adjacent sections is uncertain, but. Long & Young (1995, p. 299) considered the associated chondrichthyan *Aztecodus* to occur in the *karawaka* Zone, possibly ranging down into the upper *portalensis* Zone (upper macrovertebrate zone 6c of Young 1993).

JAL2 (Fig. 1b; 'Mount Gudmundson'). This is the northernmost Cook Mountains locality, producing one phyllolepid specimen (WAM 00.6.11) from horizon 4 (21 m above the base of the Aztec Siltstone. Long & Young (1995, fig. 3) referred this to the '*portalensis*' biozone (macrovertebrate zone 6c). Associated fauna in lower horizons of this 93 metre section of Aztec Siltstone include *Groenlandaspis* and *Bothriolepis* plates, but no thelodonts.

JAL3 (Fig. 1b; 'Fish Hotel'). This site has produced material from two horizons. One phyllolepid specimen

(WAM 00.6.5) comes from the lowest fossiliferous horizon A in the Fault Bluff section (within 30 m of base of outcrop). The highest Z horizon, at the top of the Fault Bluff section, produced the lycopod and psilophyte plant remains described by McLoughlin & Long (1994). Four phyllolepid samples (WAM 00.6.3, 00.6.4, 00.6.7, 00.6.10) occur in the associated fish fauna, which includes *Notorhizodon*, *Bothriolepis*, *Portalodus*, and a large, coarsely tuberculated, new arthrodire with an elongated MD plate.

JAL4 (Fig. 1b; 'Fault Bluff'). This is adjacent to the previous locality, with four phyllolepid samples (WAM 00.6.6, 00.6.8, 00.6.9, 00.6.16) coming from the upper horizon A (25 m from the top) in the 'Fault Bluff' section (site 1), including holotypes of both *Austrophyllolepis quiltyi* sp. nov. and *Placolepis tingeyi* sp. nov. described below. The lower horizon B has produced remains of the same coarsely tuberculated new arthrodire as at the 'Fish Hotel' site (Z horizon), a large brachythoracid MD plate, and *Gyracanthides* spines, but no phyllolepids.

JAL5 (Fig. 1b; 'Gorgon's Head'). One fragment of a phyllolepid plate (WAM 90.2.40) was the basis of the determination first recorded by Woolfe *et al*. (1990).

Biostratigraphy and age

Woodward's (1921) initial age assessment of 'Upper Devonian' was queried by White (1968), and the Aztec Siltstone fish fauna is now considered to be somewhat older, and referred to the late Middle Devonian (Givetian; see Young 1993, 1996). Turner (1997) considered the thelodont *Turinia antarctica* to be of early Givetian age; this taxon identifies the lowest two zones in the biostratigraphic scheme for the Aztec Siltstone sequence proposed by Young (1988b). Young (1993, p. 228) combined the upper two '*Pambulaspis*' and overlying 'phyllolepid' zones, partly on the evidence that the antiarch *Pambulaspis* co-occurs with phyllolepids in south-eastern Australia (Young 1983). The Antarctic '*Pambulaspis*' is now assigned to the genus *Venezuelepis* Young & Moody, 2002, but the same argument applies, because this taxon is associated with phyllolepid remains in the Venezuelan fish fauna (Young *et al*. 2000, Young & Moody 2002, fig. 13), and fragmentary phyllolepids occur with an unnamed species of *Venezuelepis* at the Victorian Tatong locality (Long 1989, p. 57).

Had phyllolepids been present in the original Antarctic material, Woodward's (1921) 'Upper Devonian' age assessment would have been greatly strengthened, because *Phyllolepis* was long considered to be a reliable index fossil for uppermost (Famennian) strata of the Old Red Sandstone (e.g. Westoll 1979). When first discovered in the Southern Hemisphere the same Famennian age was assumed, on which basis Hills (1931) assigned the Cerberean Volcanics of eastern Victoria to the Upper Devonian. Much later it was shown that phyllolepids in south-eastern Australia occurred 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). A gap of at least four conodont zones across this boundary may separate the pre-Famennian ranges of the Gondwanan phyllolepids *Placolepis* and *Austrophyllolepis* from Laurussian occurrences of *Phyllolepis* (Young 2005a). A lower limit to Gondwanan phyllolepid occurrences is more difficult to ascertain, but the Aztec Siltstone faunal sequence is the only one known to include turiniid thelodonts in lower, and phyllolepids in higher strata within the same succession. Previously, the oldest known phyllolepid remains were referred to Zone 6d (*karawaka* zone) of the Aztec Siltstone sequence (Young 1993, fig. 9.3). The new evidence presented here revises this downwards, at least to Zone 6c, supporting the view that the Aztec Siltstone phyllolepid occurrences are the oldest documented so far for the group, and possibly extend down into the early part of the Givetian stage (late Middle Devonian; see Fig. 12). The lowermost Zones 6a–b of the Aztec Siltstone sequence are defined by the unique co-occurrence of the turiniid thelodont *Turinia antarctica* with the first *Bothriolepis* species (*B. askinae*, *B. kohni*). Although phyllolepid remains occur close to the base of the Aztec Siltstone at several localities (see above), they have not so far been found in association with turiniid thelodonts.

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 subtriangular in shape, and lacks a lateral lamina. Dermal ornament mainly of smooth concentric ridges, with some tubercles and tubercle rows.

Remarks. The above has been modified from Denison (1978, p. 41) and Ritchie (1984), to incorporate new data on Antarctic phyllolepids. Denison included two phyllolepid suborders ('Antarctaspina' and 'Phyllolepina'). The arthrodire *Antarctaspis*, described by White (1968) from the Aztec Siltstone fauna, is now considered to be closely related to the Chinese genus *Yujiangolepis*, and *Toombalepis* from central Australia. All three genera are now placed in the actinolepidoid family Antarctaspidae, which has no close relationship to phyllolepids (Young & Goujet 2003). Thus the above diagnosis combines characters from the subordinal diagnosis for 'Phyllolepina'
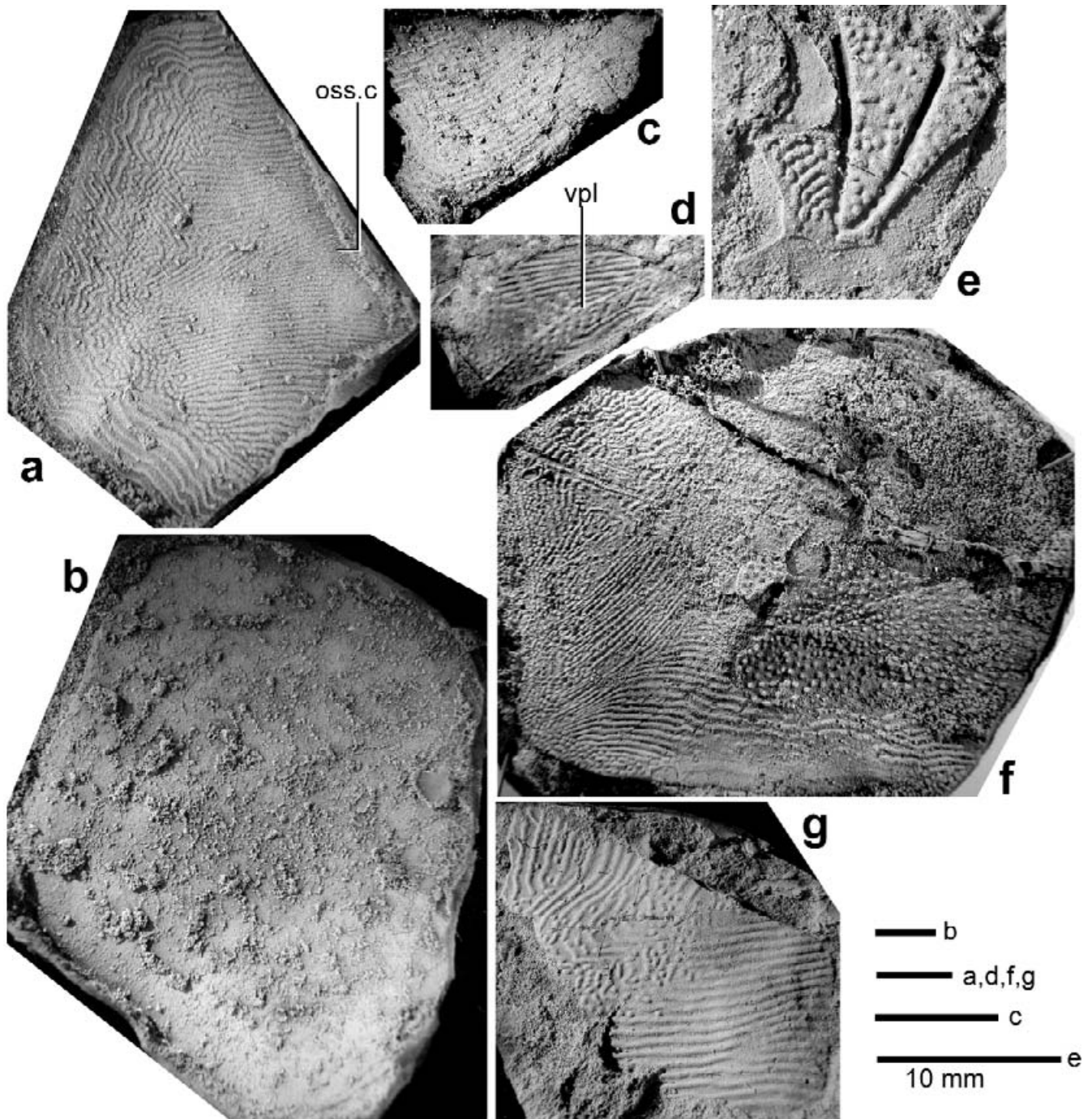
Fig. 2. *Austrophyllolepis quiltyi* sp. nov. **a & b.** holotype MD plate (WAM 00.6.8) in external and internal views respectively; **c.** indeterminate fragment (WAM 00.6.7) from the type locality; **d.** incomplete AVL plate (AMF 55482); **e**, incomplete 'PN' plate (AMF 55493); **f.** incomplete Nu plate (WAM 00.6.3); **g.** incomplete MD plate (AMF 55534). All specimens latex casts whitened with ammonium chloride, in external view except b (internal view).

of Denison (1978) and the family diagnosis of Ritchie (1984).

Genus *Austrophyllolepis* Long, 1984

Diagnosis. Phyllolepids in which the sensory groove passes off the paranuchal plate in the anterior third of plate length, and the external surface of the marginal plate is similar in breadth and length, with the postmarginal sensory canal junction in about the middle of plate length. A small suborbital plate is articulated to an ossified process below the postorbital plate, and the submarginal plate may be

ossified. The trunk armour has a posterior median ventral plate that forms a distinct notch in the mesial margins of anterior and posterior ventrolateral plates. The ridged ornament includes extensive areas of tuberculation, and some ridge duplication.

Type species. Austrophyllolepis ritchiei Long, 1984

Remarks. The original diagnosis (Long 1984, p. 266) has been modified to omit some characters that are general for larger groups (e.g. the placoderm AMV, when present, is always overlapped by AVL and PVL plates). The original diagnosis stated: 'Marginal plate broad with an external B/L index close to 36', but that was an error. The comparative figure in Long (1984, fig. 2b) shows the B/L index of the Mg plate at about 51 for *Austrophyllolepis ritchiei*, compared to 37 for *Ph. orvini* (measured on the external surface), so this bone is more elongate in *Phyllolepis*. In addition, the sensory canal junction on the Mg plate of *Ph. orvini* is about one third of plate length from the posterior margin (this bone is not known in *Ph. woodwardi*), but in both *Placolepis* and *Austrophyllolepis* the sensory canal junction is about midway along the length of a shorter, broader plate. *Placolepis* is further distinguished in the symmetrical 'T' shape of the sensory canal junction. The level where the main lateral line sensory groove crosses the PNu/Mg suture was given in the original diagnosis as '68–72% of the total length of the paranuchal plate', with the length of the PNu measured perpendicular to the posterior skull margin (Long 1984, fig. 2). This character is clarified and re-expressed in the diagnosis. The small SO and SM plates are features only observable in good articulated material, but it seems that they were absent in the genus *Phyllolepis*, based on articulated *Ph. woodwardi* and *Ph. orvini* (Stensiö 1936, fig. 3, pl. 25). For the present this is retained as a generic character for *Austrophyllolepis*, although the condition in *Placolepis* is uncertain.

All trunk armour bones of *Placolepis* from the type locality (Nettletons Creek; Ritchie 1984, figs 9–12) show only meandering ridged ornament, but areas of tuberculation are always present in *Austrophyllolepis*, including juvenile forms (e.g. Long 1984, figs 4 & 9). Available evidence, based on sample size of the type material (over 60 specimens from Mount Howitt, including the 32 articulated fish cited in the published description; numerous disarticulated plates from Nettletons Creek) indicates that this is a reliable generic character to separate the Australian genera. Tubercles in *Placolepis* seem to be restricted to the smaller bones forming the skull margin (Ritchie 1984, fig. 7). In *Phyllolepis* the ornament is almost entirely of smooth concentric ridges, and amongst the extensive Greenland material illustrated by Stensiö (1934, 1936, 1939), there is only a single PVL plate that shows a marginal zone of tuberculation (Stensiö 1934, pl. 16, fig. 2). A clear notch for the PMV plate is always seen on the AVL of *Austrophyllolepis* from Victoria, but there is no notch in *Placolepis* (Ritchie 1984, fig. 11). This is another character to separate the Australian genera, but may not consistently distinguish *Austrophyllolepis* from *Phyllolepis*, since a possible sliver-like PMV has been illustrated for *Ph. woodwardi* (Stensiö 1939, fig. 2). In addition, in the neotype of *Ph. concentrica* the posteromesial angle of the AVL could be interpreted as a margin for the PMV, rather than being incomplete, as was assumed by Stensiö (1939, p. 5).

Previously the validity of the genus *Austrophyllolepis* has been questioned (e.g. Johanson & Young 1999, p. 72). Our restudy of the Victorian material supports the presence of two species at the type locality, although the distinctions based on plate proportions used by Long (1984, fig. 8) may have been accentuated by tectonic distortion in the material (A. Ritchie, personal communication 2000). The new characters just discussed confirm that *Austrophyllolepis* is generically distinct from *Phyllolepis*, and there are two additional potentially useful characters, not preserved in the new Antarctic material. The sensory canal junction on the PtO plate is closer to the lateral margin in *Austrophyllolepis*, and closer to the mesial margin in *Phyllolepis* (Long 1984, p. 269), and the lack of contact between the PtO and the PNu is a feature distinguishing *Placolepis* from both *Phyllolepis* and *Austrophyllolepis*. In basal arthrodires contact between the PNu and PtO plates of the skull roof is a more general condition (Denison 1978, fig. 31), so both *Phyllolepis* and *Austrophyllolepis* might be primitive in this respect, and *Placolepis* advanced.

*Austrophyllolepis quiltyi* sp. nov.
Figs 2, 6a, 8a, 11b

1972   'armour … similar to that found in *Phyllolepis*'; Ritchie, p. 352
1980   '*Phyllolepis*'; Chaloner *et al.*, p. 153
1988   '*Phyllolepsis*' (sic); Bradshaw & Webers, p. 787
1988b 'phyllolepid'; Young, pp. 13, 16, fig. 5
1989a 'median dorsal plate of a phyllolepid'; Young, fig. 4A
1991   'median dorsal plate of a phyllolepid'; Young, fig. 15.8A
1992   'phyllolepid placoderm'; Young *et al.*, p. 8
1993   '*Austrophyllolepis*'; Young, p. 229
1994   'phyllolepid placoderms'; McLoughlin & Long, p. 86
1995   'phyllolepids, ?*Austrophyllolepis* sp.'; Long & Young, p. 86, table 1
1999   '*Austrophyllolepis*'; Johanson & Young, p. 72
2003   '*Austrophyllolepis* … from … Antarctica'; Long, p. 190

Etymology. For Dr Pat Quilty, former Chief Scientist of the Australian Antarctic Division.

Holotype. WAM 00.6.8, an incomplete MD plate in part and counterpart.

Other material. WAM 00.6.3 (incomplete Nu), WAM
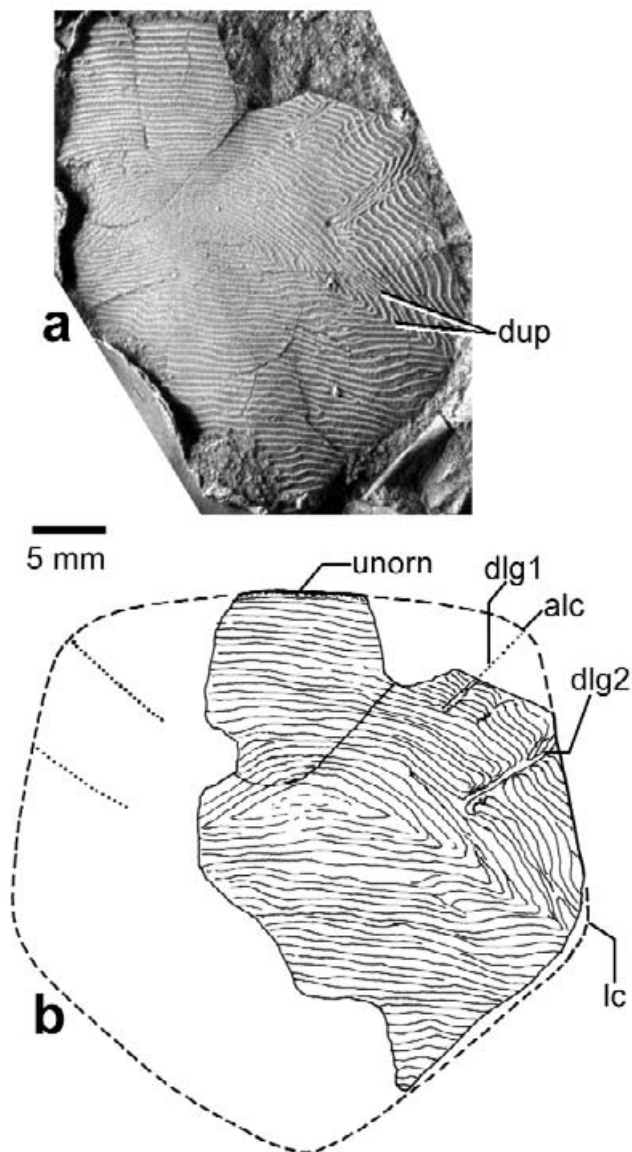
Fig. 3. *Austrophyllolepis* cf. *A. youngi* Long, 1984. ANU V3060 (incomplete MD plate) in **a.** external view, and **b.** reconstruction. (**a.** latex cast whitened with ammonium chloride.)

00.6.7 (indeterminate fragment), AMF 55534 (incomplete MD), AMF 55493 (incomplete 'PN'), AMF 55482, ANU V3062 (incomplete AVL plates).

Localities. JAL4 ('Fault Bluff', holotype); JAL3 ('Fish Hotel', other WAM material), GCY17 ('Alligator Ridge Pavement', AMF, ANU material).

Horizons. Horizon A (site 1), 25 m from top of sequence (holotype); Z horizon (other WAM material); 8 m from top of Aztec Siltstone (AMF, ANU material).

Diagnosis. Austrophyllolepis in which ornament on the Nu comprises an outer zone of tubercle rows and short ridges around the lateral margin, and an inner zone with fine ridges

radiating towards the posterolateral corner. MD plate shows a distinctive outer zone about 7 mm wide around the plate margins with ornament broken up into short meandering ridges with scattered tubercles, particularly along the anterolateral margin. The ridges on the inner ornamented area are mainly transverse, moderately coarse (11 ridges cm^{-1}), and closely spaced (groove/ridge index of 0.5).

Remarks. This poorly known new species is represented by only a few isolated plates. The holotype is a distinctively ornamented MD plate, and the referred Nu plate came from an individual of similar size at an adjacent locality and the same horizon, and displays similar ornament. We are confident these belong to one species. Direct comparison with type material of the Victorian species of *Austrophyllolepis* shows that these few specimens are readily distinguished on ornament, but a larger sample is required to establish variability in this character for the Antarctic species. Another phyllolepid fragment from the type locality, and several samples from the Alligator Ridge Pavement with the same distinctive ornament, are provisionally referred to the species, although incomplete preservation means we cannot demonstrate that any of these bones compares closely in shape and proportions with the type material. Ornament details are likely to be specific characters, but those included in the diagnosis are provisional until a larger sample is available to assess variability in this character.

Description. The holotype (WAM 00.6.8) is a MD plate about 81 mm long, showing the ornament of most of the left half (Fig. 2a). The impression of the inner surface (Fig. 2b) includes the entire left lateral margin, the posterior corner, and left side of the anterior margin, which allows a restoration of the whole bone (Fig. 8a). The B/L index is 108, at the broadest end of the range for the MD of *Austrophyllolepis youngi* from Victoria (B/L 96–108; Long 1984). In *A. ritchiei* the MD was described as considerably broader (B/L 122–145), but these proportional differences may have been accentuated by distortion in the Victorian material (see above). There is no evidence of distortion in the Antarctic material.

The inner surface of the holotype is smooth (Fig. 2b), without clear overlaps for adjacent plates, and lacking the median groove and associated ridges seen in *Ph. orvini* from Greenland (Stensiö 1934, fig. 15, pl. 10). The well-preserved ornament on the counterpart (Fig. 2a), includes the narrow concentric pattern around the ossification centre (oss.c), about 33% of total length from the anterior margin. In the central posterior part of the preserved ornament the ridges are mainly transverse, and moderately coarse (11 ridges per cm), with a groove/ridge index of 0.5. A distinctive outer zone about 7 mm wide around the plate margins shows the ornament broken up into short meandering ridges with scattered tubercles, particularly along the anterolateral margin. In European species of
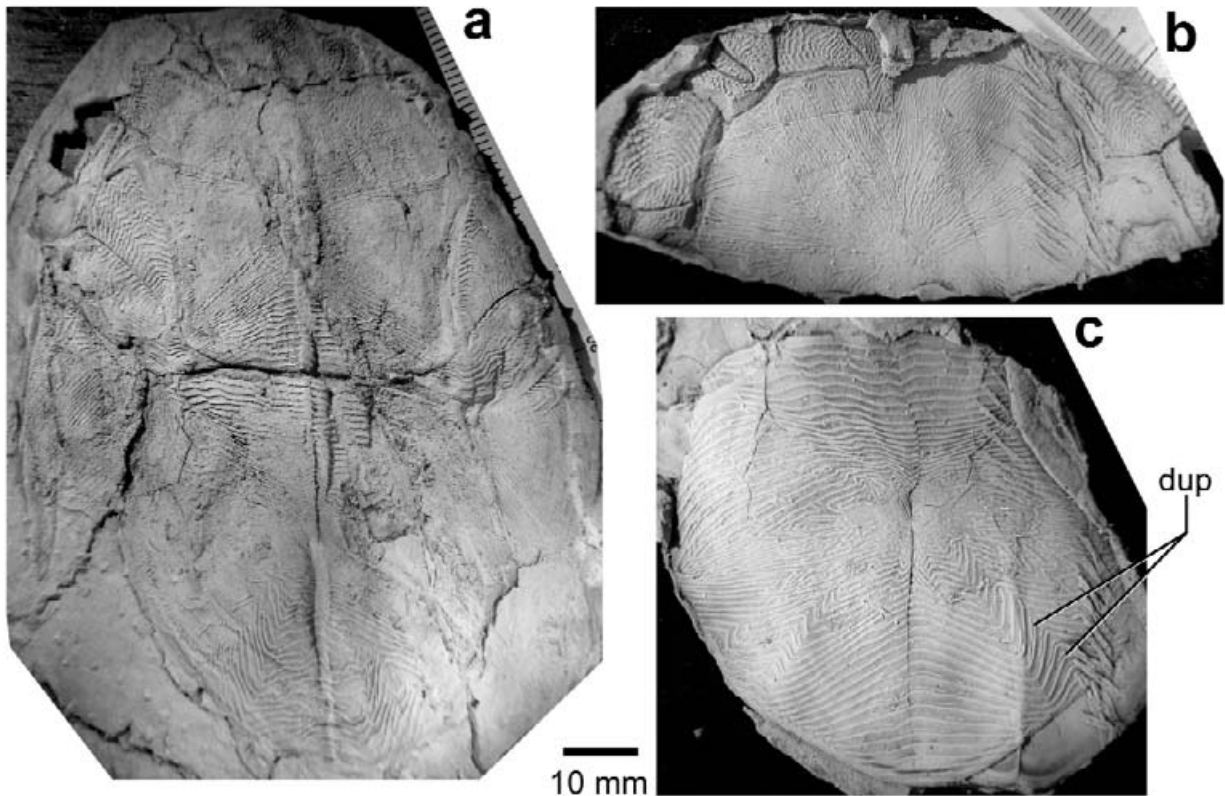
Fig. 4. *Austrophyllolepis youngi* Long, 1984, from Mount Howitt, eastern Victoria. **a.** Holotype (NMV P160718), complete armour in dorsal view, **b.** incomplete skull roof (NMV P160747), **c.** MD plate from the same individual (NMV P160747). All specimens latex casts whitened with ammonium chloride in external view.

Phyllolepis tuberculation is never seen on the MD, which consistently shows only sinuous concentric ridges (e.g. Stensiö 1939, fig. 5). The style of ornament in WAM 00.6.8A is reminiscent of that on an AVL from Freestone Creek, Victoria, provisionally referred to *Austrophyllolepis youngi* by Long (1989, fig. 5A), although this needs reconsideration in the light of the new Antarctic material. Another MD plate from the same locality (Long 1989, fig. 5B) has more regular ridged ornament, and this is the case with both Victorian species from the type locality for the genus, where MD plates are consistently ornamented with sinuous ridges (Long 1984, figs 3, 9A, 10, 12A), although with some differences discussed below. Examples of these plates are refigured for comparison here (Figs 4a & c, 5c & d). On this evidence the differences in ornament are proposed as a specific character for *Austrophyllolepis quiltyi* sp. nov.

A Nu plate from the top of the nearby Fault Bluff section (WAM 00.6.3; Fig. 2f) matches the holotype MD in both size and ornament. It has most of the posterior and left lateral margins preserved, and the approximate right angle between these margins indicates that this Nu belongs to *Austrophyllolepis* rather than *Placolepis*, in which the Nu expands in width towards the lateral corners (see below). An arthrodire bone obscures much of the central part of WAM

00.6.3, but the posterior margin is well exposed, showing a median slightly bilobed smooth zone (arth, unorn, Fig. 6a). Around the lateral margin the ornament is again broken up into an outer zone of tubercle rows and short ridges, and an inner zone with fine ridges radiating towards the posterolateral corner. Similar ornament with the outer tuberculate zonation is seen on the Nu of Victorian species (e.g. Fig. 5b & d). The lateral corner of WAM 00.6.3 is not quite preserved, and the central sensory canal extends inwards about 20 mm from this corner. The anterolateral corner is missing, but the configuration of the anterior parts of the plate is indicated by the ornament orientation, permitting a reconstruction (Fig. 6a). The supraorbital sensory groove (soc) is very indistinct.

One other phyllolepid from the type locality is an indeterminate ridged fragment (WAM 00.6.7; Fig. 2c), which is very provisionally referred to *Austrophyllolepis quiltyi* sp. nov. because it comes from the same locality, and has apparently similar ornament (but very poorly preserved).

Some incomplete bones from the Alligator Ridge Pavement may be clearly referred to *Austrophyllolepis*, and are provisionally included in the new species. AMF 55534 (Fig. 2g) is a diagonal fragment some 50 mm across with mainly broken margins, from a larger bone than the material

described above, but again showing the acute angulation of ridges indicating either a Nu or MD plate. The transverse posterior ridges are 8–9 cm^{-1}, but there is no indication that the posterior preserved edge is a natural margin. However a short anterolateral segment may be natural, suggesting that this came from a MD rather than a Nu plate. The ornament differs from the holotype MD only in being coarser, so AMF 55534 is provisionally interpreted as a larger example of the same species. The short meandering ridges may break up into rows of tubercles. Just inside the anterolateral margin are short rows of tubercles developed between the subparallel ridges, and this distinctive feature is also seen on the holotype (Fig. 2a). AMF 55493 is a small bone from the Alligator Ridge Pavement with a sensory loop combined with three overlap-areas characteristic of the PN plate (Fig. 2e). The broader ornamented area on the left side shows that this is a right PN, in contrast to *Placolepis*, where the sensory loop is symmetrically arranged on the bone, one of the characters originally used by Long (1984, fig. 2C) to distinguish *Austrophyllolepis*, *Placolepis*, and *Phyllolepis*. In *Phyllolepis* the outer margin of this bone typically shows a corner between the two sides of the sensory loop, marking the boundary between anterolateral and anterior margins of the skull. This is well marked in both *Phyllolepis woodwardi* and *Ph. orvini* (Stensiö 1934, pl. 8, fig. 2; 1936, fig. 3). For *Ph. orvini* the PN reconstruction previously shown by Ritchie (1984, fig. 8F, 'PrO') was based on an incomplete example (Stensiö 1934, pl. 13, fig. 1), and the reconstruction by Stensiö (1936, fig. 2) using the complete bone includes this external angle. In AMF 55493 the outer margin is mainly broken, but a restoration based on the short complete section suggests that the angle was absent (Fig. 11b). In *Placolepis* this bone has a rounded or scalloped outer margin, also lacking a distinct angle (Ritchie 1984, fig. 7C, E, F). In the holotype of *Austrophyllolepis ritchiei* the outer angle is present, but it is indistinct in NMV P160723 (Fig. 5b). The outer margin of the PtO is poorly preserved in *A. youngi* (Fig. 4a). Long (1984, p. 275) characterized *A. youngi* as having a posterior margin (of the ornamented area) more than half (50–57%) the length of the outer margin, whereas in *A. ritchiei* the posterior margin was narrower (~44%). In AMF 55493 as reconstructed (Fig. 11b) it seems even more narrow (≤ 35%). In both Victorian species the ornamented area mesial to the sensory loop is about twice that lateral to the loop, as in *Phyllolepis*. In AMF 55493 it is less than twice the area lateral to the loop, so this is inferred to be a specific difference. The almost completely tuberculate ornament in the three species of *Austrophyllolepis* is a difference to both *Placolepis* (tubercles only on the outer margin) and *Phyllolepis* (ridged ornament on the PN). The overlap for the PtO in AMF 55493 terminates before the outer margin, and this was probably the case also for the PrO overlap, which is very narrow at its broken outer preserved edge. In *Ph. orvini* these overlap areas extend right along these

margins (Stensiö 1934, pl. 8, fig. 2).

Two other very incomplete specimens from the Alligator Ridge Pavement are provisionally included on ornament. A small portion from a right AVL plate (AMF 55482; Fig. 2d) shows the ventral sensory pitline groove (vpl) crossing inside the posterior margin. A short section of the pectoral margin is also preserved, indicating a relatively obtuse postpectoral angle of about 90°, as in *A. ritchiei* (cf. Long 1984, fig. 5), whereas it is more acute in both *A. youngi* and in *Placolepis*, where the pectoral margin is more strongly embayed. Again the ridged ornament breaks up towards the pectoral margin into short segments and tubercle rows, exactly as in the holotype of *A. ritchiei*, and also seen in *A. youngi* (Long 1984, figs 4A, 20). In *Placolepis budawangensis* this part of the AVL typically shows clear ridges, with no tubercles (Ritchie 1984, figs 10K, 11F–G), as is also the case with Northern Hemisphere *Phyllolepis* (e.g. Stensiö 1936, pls. 20, 21, 22). ANU V3062 is a piece of ridged bone 26 x 25 mm in size, with a shallow groove 7 mm inside a straight margin, suggesting it may also be part of an AVL. Again the ornament is similar to AMF 55482 and 55534, with coarse ridges giving way to tubercles near the margin. These similarities in ornament with the MD from the same locality (Fig. 2g), and with the holotype MD from Fault Bluff (Fig. 2a), suggest that this material is conspecific.

Austrophyllolepis sp. cf. *A. youngi* Long, 1984
Fig. 3

1988b 'phyllolepid'; Young, p. 13, fig. 5
1989a 'median dorsal plate of a phyllolepid'; Young, fig. 4A
1991   'median dorsal plate of a phyllolepid'; Young, fig. 15.8A
1992   'phyllolepid placoderm'; Young *et al*., p. 8
1995   '?*Austrophyllolepis* sp.'; Long & Young, table 1

*Material.* ANU V3060, an incomplete MD plate preserved as in external impression.

Locality. Locality GCY17 (Fig. 1a), the 'pavement' locality at MS 236 figured by McKelvey *et al*. (1972, fig. 3).

Horizon. 8 m beneath the top of the Aztec Siltstone, unit 32, section A1 of Askin *et al*. (1971b).

Remarks. This specimen has distinctive ornament, with features otherwise seen only in material of *Austrophyllolepis youngi* Long, 1984 from Victoria. However it differs somewhat from that material, so for the present is left in open nomenclature.

Description. ANU V3060 has the distinctive concentric ornament ridges with angular inflections directed posterolaterally from both sides of the ossification centre (Fig. 3a), a feature of both of the large unpaired bones in the phyllolepid dermal armour (Nu and MD plates). This
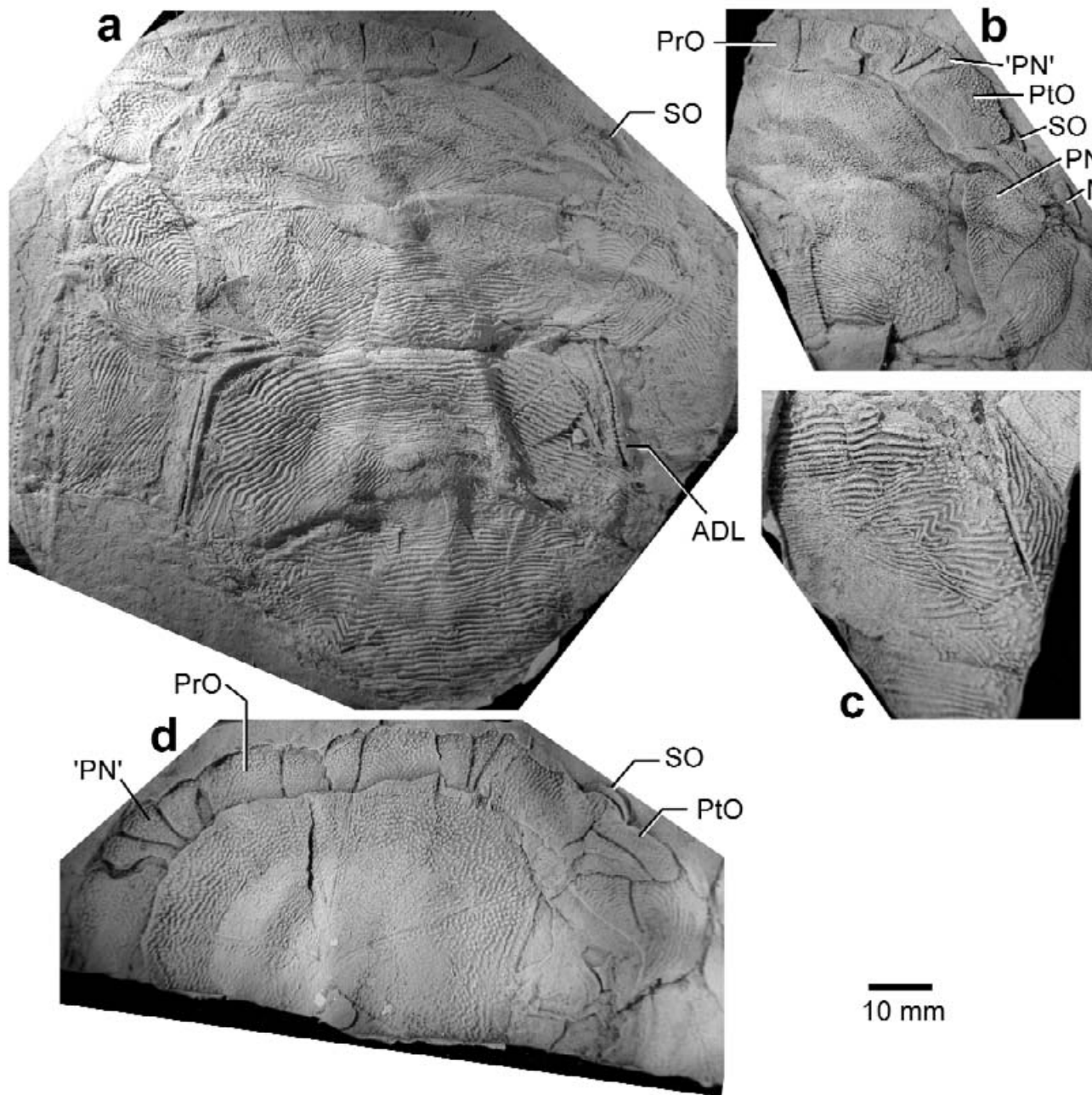
Fig. 5. *Austrophyllolepis ritchiei* Long, 1984, from Mount Howitt, eastern Victoria. **a.** Holotype (NMV P160721), complete armour in dorsal view, **b.** incomplete skull roof (NMV P160723), **c.** MD plate from the same individual (NMV P160723), **d.** incomplete skull roof (NMV P160722). All specimens latex casts whitened with ammonium chloride in external view.

specimen is shown to be a MD plate because the inflection is directed towards a point just behind the lateral corner, as on the MD plate in *Phyllolepis* (e.g. *Ph. woodwardi*, *Ph. orvini*; Stensiö 1936, fig. 3, pl. 10–13; *Ph. undulata, Ph. delicatula, Ph. nielseni*; Stensiö 1939, figs 5, 7, pl. 2). The similar inflection on the phyllolepid Nu plate (including *Placolepis*) has a more posterior direction, towards the posterolateral corner of the bone. The posterolateral rather than transverse orientation of the posterior preserved margin in ANU V3060 confirms that this specimen must be

a MD plate, even though it carries at least two sensory canals, a condition not seen in any other phyllolepid (see below).

This MD is considerably smaller than the holotype of *A. quiltyi* described above (maximum preserved L, B: 44, 39 mm). It is clear that the ornament inside the anterolateral margin is very differently developed (Fig. 3a), and completely lacks the marginal zone of short ridge segments and tubercle rows of that species (cf. Fig. 2a). However one distinctive feature, apparently not developed in *Placolepis*,
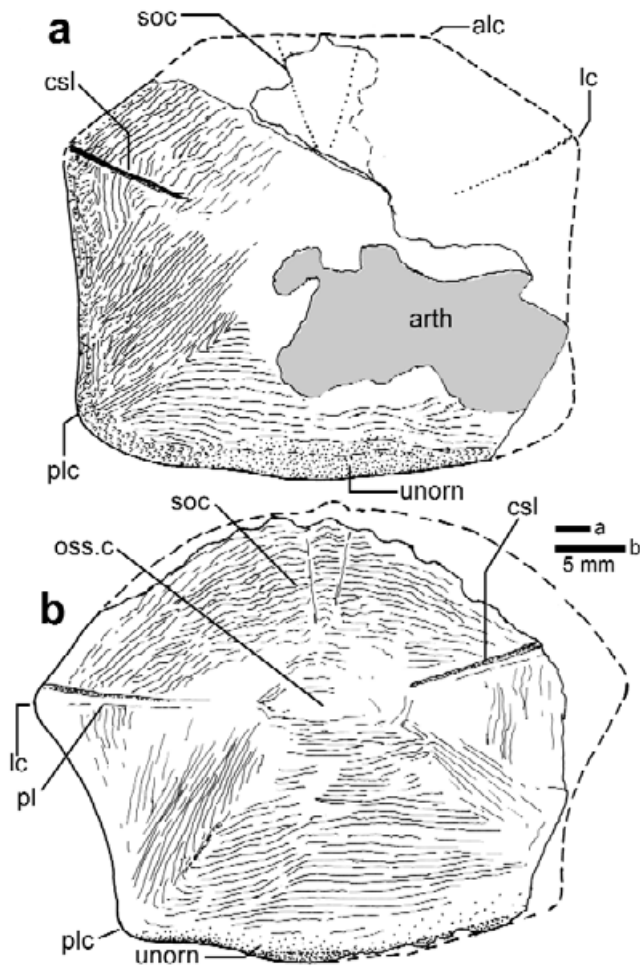
Fig. 6. Phyllolepid Nu plates from Antarctica, partly restored. **a.** *Austrophyllolepis quiltyi* sp. nov. (WAM 00.6.3; cf. Fig. 2f), **b.** *Placolepis tingeyi* sp. nov. (holotype, WAM 00.6.6; cf. Fig. 7a).

is the splitting of some ornament ridges into double ridges (dup). This ridge duplication is otherwise recorded only on the MD plate of Victorian material referred to *A. youngi* by Long (1984), where it is more strongly developed (Fig. 5c). This similarity is the main reason for assigning ANU V3060 to the genus *Austrophyllolepis*.

ANU V3060 has about 35 concentric ridges from the front margin back to the smooth area on the ossification centre, and about 45 ridges backwards to the posterior preserved edge. NMV P160747 (Fig. 4c) differs in the more widely spaced ridges (no more than 20 in front of the ossification centre, about 27 behind). The external surface in ANU V3060 is flat to slightly convex anteriorly, but more arched towards the back, where it subtended an angle of about 140–160° at the midline of the most posterior preserved part. Thus the body form of this phyllolepid was clearly not as depressed as in Stensiö's (1936, fig. 12) reconstruction of *Ph. orvini*. The width across the lateral corners can be estimated, even though the extremity on the

preserved right side is missing. The short preserved section of the anterior margin is definitely original, with a narrow bevelled edge, and the posterior part of the anterolateral margin is also complete. The ornament ridges run into the edge of the posterolateral margin at a high angle, so this may be broken, with a small part of the lateral corner missing (lc, Fig. 3b). In *Placolepis* the ornament on the posterolateral margin of both the Nu and the MD tends to be subparallel to the margin (Ritchie 1984, fig. 8). However, in some *Phyllolepis* species ornament on the MD may vary from subparallel to oblique to the posterolateral margin (e.g. Stensiö 1936, pl. 12, 13), and it is oblique in *A. youngi* (Fig. 5c).

ANU V3060 shows sections of two sensory grooves directed towards the ossification centre from the missing anterolateral portion (dlg1, 2, Fig. 3b). An intervening interruption to the ornament may be a third sensory line, but is much less distinct. The presence of sensory grooves on the phyllolepid MD is well established, one groove being rarely present in *Ph. orvini* (Stensiö 1936, pl. 10), evidently in a similar position to the posterior canal in ANU V3060, and reaching the lateral margin somewhat behind the anterolateral corner. Ritchie (1984, p. 340) found what was assumed to be the same groove on the MD of *Placolepis*, but noted that it was directed towards the anterolateral corner, as in *Austrophyllolepis* (Long 1984). This is the first time two sensory grooves have been clearly documented on the MD plate of phyllolepids, but we note the occasional presence of two distinct interruptions to the ornament in some other species (e.g. *Ph. orvini*; Stensiö 1936, pl. 12). It is possible therefore that the canal identified by Ritchie (1984) and Long (1984) in *Placolepis* and *Austrophyllolepis* is the homologue of the anterior rather than the posterior canal. Since two pairs of sensory grooves occur on the anterior median dorsal plate in antiarchs, this may be a retained primitive condition.

The restored plate (Fig. 3b) has breadth equal to length, with the lateral corners in the posterior half of the plate, and the ossification centre about 36% of restored total length from the anterior margin, a comparable distance to *Placolepis* as described by Ritchie (1984). For *Austrophyllolepis ritchiei* from Victoria the MD is considerably broader than long (B/L 122–145). The Antarctic specimen is slightly larger (restored L ~68 mm) than NMV P160747 (L 57 mm), which is estimated at slightly broader than long (lateral corners are missing), with the ossification centre about 42% of total length from the front margin. The range of the B/L index in *A. youngi* is 96–108 (Long 1984).

The unusual ornament on ANU V3060 comprises short additional branches off the main ridges, and bifurcations to form short or longer segments of double ridges. The short double sections are conspicuous around the lateral inflections, and there are at least five double ridges in the transverse ornament behind the ossification centre, each

separated by a variable number of single ridges (6, 5, 1, 4, 5 from anterior to posterior). The ornament pattern on NMV P160747 differs in the wider ridge spacing (see above), but again has both short duplicated ridge segments around the lateral inflection, plus at least four transverse double ridges behind the ossification centre, interspersed with single ridges. It differs from ANU V3060 in that the double ridges are less continuous, often forming short interrupted segments. The ridge pattern is also much more complex, with many inflections close to the ossification centre. The holotype of *A. youngi* has the ornament behind the ossification centre of the MD also very irregular, but again with several double ridges (Fig. 4a). As noted above, the ornament pattern on the MD of *A. ritchiei* is rather different, and ridge duplication has not been observed so far on any MD plates of *Placolepis budawangensis*. We also note that the strong radiating arrangement of ridges on the Nu plate of the skull roof (Fig. 4a & b) may be another specific difference in ornament to *A. ritchiei*, where it tends to form concentric tuberculate ridges and tubercle rows (Fig. 5a–c).

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 oriented anterolaterally. 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. 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 differences from *Phyllolepis* are not clear. Ritchie (1984, p. 346) included the following statement about the Nu plate: 'rounded anteriorly, widest opposite, or slightly posterior to, centre of ossification'. The small PNu plate, and the rounded Nu (Fig. 6b) are the most distinctive features in the skull of *Placolepis*. In contrast, the Nu plate in both *Phyllolepis* and *Austrophyllolepis* is distinctly six-sided, with a transverse anterior margin, and anterolateral, lateral and posterolateral corners (Fig. 6a). 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 distinguishes *Austrophyllolepis* from *Placolepis*, and probably from *Phyllolepis*. Previously the same diagnosis was used for the genus *Placolepis* and the type species *Placolepis budawangensis*, the only species known at the time. The above revision takes account of a new species from central Australia (Young 2005a).

Placolepis tingeyi sp. nov.
Figs 6b, 7, 8b, 9

1972   'armour … similar to that found in *Phyllolepis*'; Ritchie, p. 352
1980   '*Phyllolepis*'; Chaloner *et al.*, p. 153
1988   '*Phyllolepsis*' (sic); Bradshaw & Webers, p. 787
1988b   'phyllolepid'; Young, pp. 13, 16, fig. 5
1992   'phyllolepid placoderm'; Young *et al.*, p. 8
1994   'phyllolepid placoderms'; McLoughlin & Long, p. 86
1995   'phyllolepid indet.'; Long & Young, p. 86, table 1

Etymology. For R.J. (Bob) Tingey, to acknowledge his significant contribution to understanding the geology of Antarctica.

Diagnosis. A species of *Placolepis* in which the Nu plate has relatively long lateral margins, with lateral corners situated about 40% the length of the plate from the anterior margin, and the ossification centre is just behind this level. The lateral corners are angular, and the posterior Nu margin is relatively broad, at about 90% of total breadth. The AVL has a slightly bevelled pectoral margin, and a posteromesial angle of about 130°. The ornament is relatively fine, with a distinct angulation on the Nu plate directed towards the posterolateral corner.

Holotype. WAM 00.6.6, an almost complete Nu plate in part and counterpart.

Other material. WAM 00.6.11 (MD plate), WAM 00.6.4, 00.6.14, AMF 55520 (AVL plates), WAM 00.6.9 (PVL plate), WAM 90.2.40 (indeterminate fragment).

Localities. JAL4 (type locality, 'Fault Bluff', WAM 00.6.6, 00.6.9); JAL1 ('Lashly Range'; WAM 00.6.14); JAL2 ('Mount. Gudmundson', WAM 00.6.11); JAL3 ('Fish Hotel'; WAM 00.6.4), GCY17 ('Alligator Ridge Pavement', AMF 55520), JAL5 ('Gorgons Head'; WAM 90.2.40).

Horizons. Horizon A (site 1), 25 m from top of sequence (JAL4, type locality); 38 m above the base of section LA-1 (JAL1); Z horizon, top of section (JAL3); within 25 m of eroded top of Aztec Siltstone (JAL5); 8 m from top of Aztec Siltstone (GCY17).

Remarks. The presence of *Placolepis* Ritchie, 1984 in the Aztec Siltstone fish assemblage is demonstrated by the distinctive rounded Nu plate, which has quite a different shape to the Nu of *Austrophyllolepis* just described. The referred specimens are provisionally included on less definitive characters (e.g. ornament), and suggest that both genera co-occur in the Aztec Siltstone sequence, in contrast to southeastern Australia, where *Austrophyllolepis* and *Placolepis* are known so far only from separate localities.

Description. The holotype Nu plate (WAM 00.6.6; Figs 6b & 7a) gives a good indication of the typical *Placolepis* shape, although part of the anterior and most of the right
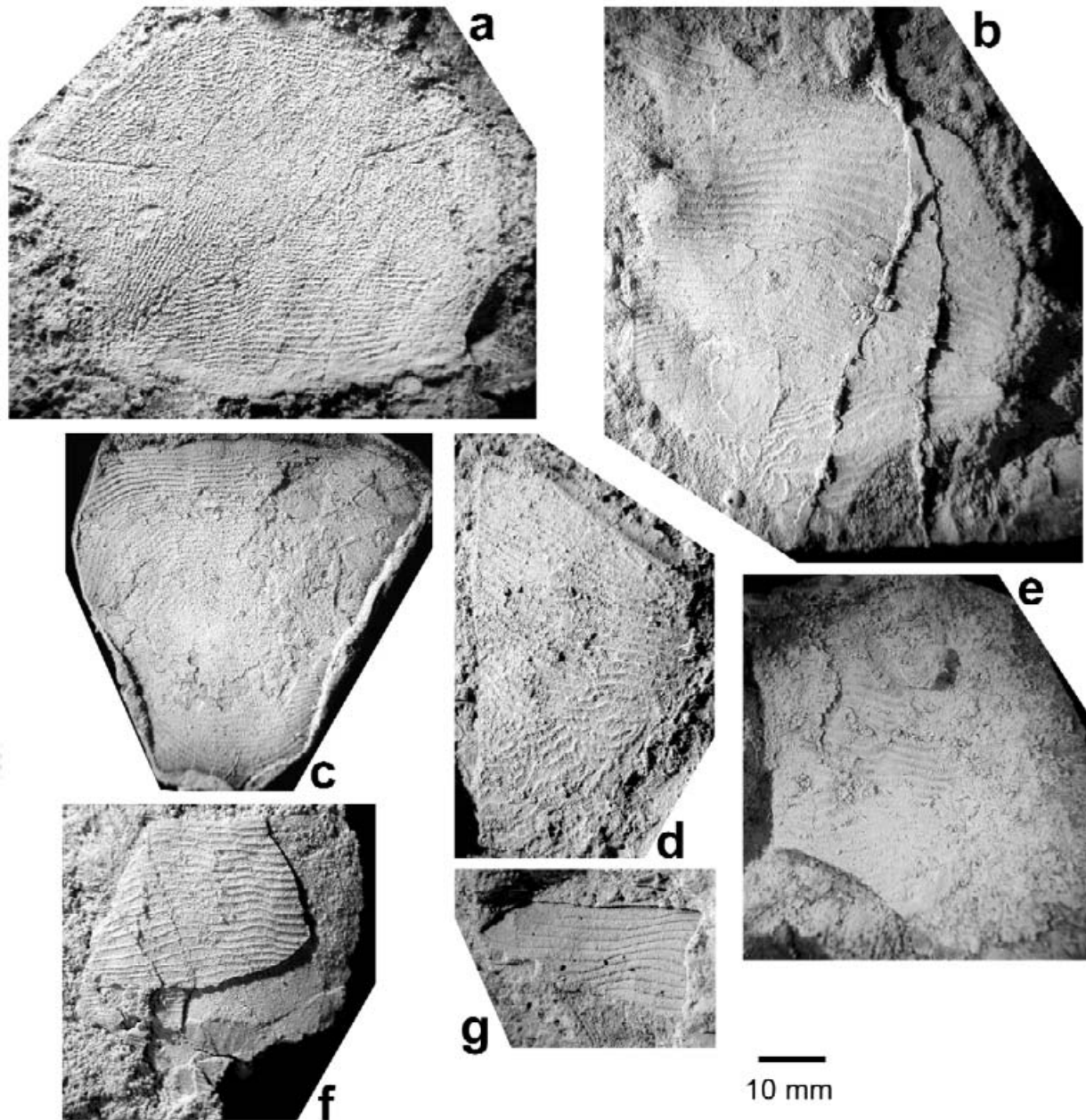
Fig. 7. *Placolepis tingeyi* sp. nov. **a.** holotype, a nearly complete Nu plate (WAM 00.6.6), **b.** left AVL plate (AMF 55520), **c.** incomplete MD plate (WAM 00.6.11), **d.** PVL plate (WAM 00.6.9), **e.** incomplete AVL plate (WAM 00.6.4), **f.** incomplete right AVL plate (WAM 00.6.14), **g.** possible AVL fragment (WAM 90.2.40). All specimens in external view, whitened with ammonium chloride, and latex casts except f, g (bone and impressions in the rock).

margins are missing. The anterior margin from the latex cast can be restored using the bone edge still preserved in the rock, which suggests a slight anterior process projecting forward between the supraorbital sensory grooves, as occurs in some examples of *Phyllolepis* (e.g. Stensiö 1936, fig. 16). The restoration shows a similar shape but different proportions to *Placolepis budawangensis*, both plates differing from *Phyllolepis* and *Austrophyllolepis* in the absence of anterolateral corners (alc, Fig. 6a). For *Placolepis budawangensis*, Ritchie (1984, p. 330) described

the Nu as showing considerable variation in proportions (B/L index 115–164), but some of this is evidently due to distortion. WAM 00.6.6 is near the elongate end of that range (B/L index about 119). In *Placolepis budawangensis* the lateral corners are more rounded, with the broadest part of the plate sometimes just anterior to this level (Ritchie 1984, figs 4 & 6A). The rounded anterior division of the bone always makes up more than 50% of total Nu length. In *Pl. antarctica* the lateral corners are more angular, and situated only about 40% of total length from the anterior

margin. The central sensory grooves (csl) pass off the plate just in front of the lateral corners, whereas in *Placolepis budawangensis* they have a more anterior position, about halfway along the anterolateral margin. On both sides a fine pitline can be seen just behind the main groove (pl). The supraorbital sensory grooves are much less distinct (soc). The posterior margin of the Nu is relatively broad, about 90% of total breadth, whereas in *Placolepis budawangensis* it is about 60%. The ornament in WAM 00.6.6 appears finer than in the type species, with a more distinct angulation directed towards the posterolateral corner, somewhat as in *Phyllolepis* (e.g. Stensiö 1936, pl. 2 fig. 1).

WAM 00.6.11 is an incomplete MD plate of which only the anterior margin is well preserved (Fig. 7c). It has similar ornament to the holotype (Fig. 7a), and lacks the tubercles and tuberculate ridges described above in the MD of *A. quiltyi* sp. nov. The right anterolateral corner shows a short section of the dorsal pitline, but all other margins are missing. The standard ornament pattern for the MD is concentric around the ossification centre, which is smooth and situated in the middle of the preserved area, about 17 mm from the anterior margin. The anterior margin is about 34 mm wide as restored (Fig. 8b), with a central narrow smooth zone that is slightly convex anteriorly. The dorsal pitline occupies the same position as previously described for both *Placolepis* and *Austrophyllolepis*. As noted above, the pitline in *Phyllolepis* that enters the MD partway along the anterolateral margin may not be homologous. Behind the ossification centre in WAM 00.6.11 is a central area of transverse ridges, intersected laterally by a marginal zone of posterolaterally oriented ridges subparallel to the posterolateral margin. This pattern is seen in many examples of the MD of *Placolepis budawangensis*, including the holotype (Ritchie 1984, fig. 3), but is not developed in *Phyllolepis*, and is thus another character supporting the assignment of WAM 00.6.11 to *Placolepis tingeyi* sp. nov. In *Austrophyllolepis* the corresponding area is occupied by a zone of tuberculate rows (Long 1984, fig. 10). An approximation of the original MD shape of WAM 00.6.11 based on ornament orientation (Fig. 8b) suggests a B/L index of about 115, within the range of *Placolepis budawangensis* (100–125).

AMF 55520 (Fig. 7b) is a left AVL missing part of the mesial and posterior margins, and the prepectoral corner. There is no notch for the PMV plate, so this plate cannot be referred to *Austrophyllolepis*. A short section of the ventral pitline runs through a sharp inflection in the ornament ridges. These are generally widely spaced (~12 ridges per cm in the central anterior part), and concentrically arranged around the pectoral margin, all features very reminiscent of the type species *Placolepis budawangensis* (Ritchie 1984, fig. 11). In *Austrophyllolepis* the region inside the pectoral margin is often strongly tuberculate (Long 1984, fig. 5), and in various northern hemisphere *Phyllolepis* species the ridges often meet the pectoral margin at a high angle (e.g.
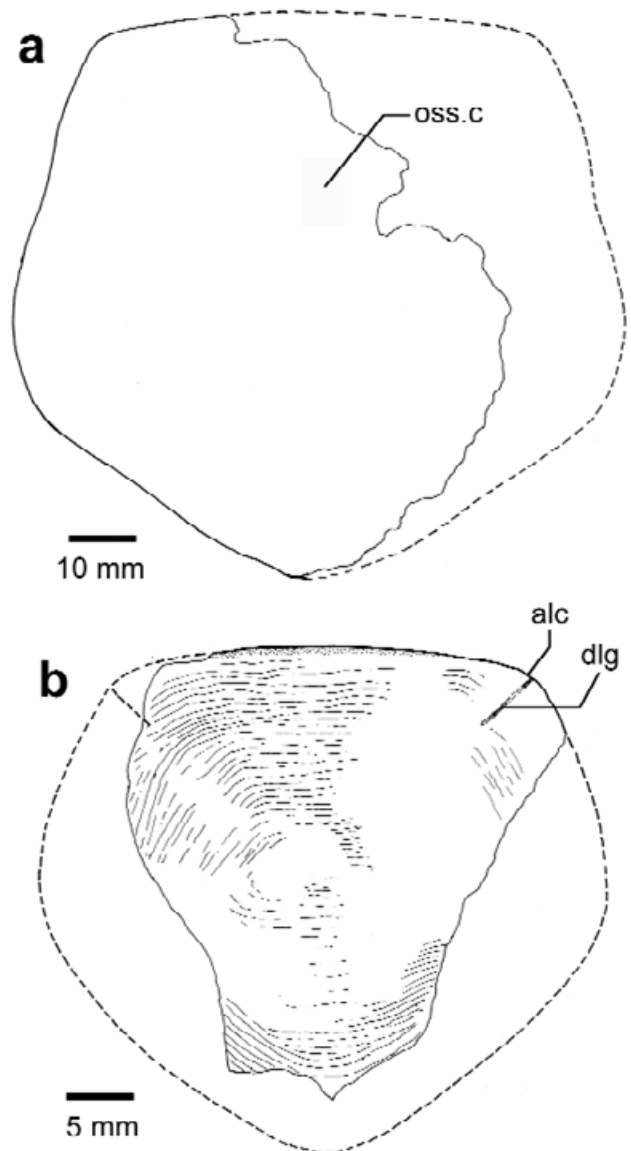
Fig. 8. Phyllolepid MD plates from Antarctica. **a.** *Austrophyllolepis quiltyi* sp. nov. (holotype, WAM 00.6.8, restored from the internal impression; cf. Fig. 2b), **b.** *Placolepis tingeyi* sp. nov. (WAM 00.6.11; cf. Fig. 7c).

Ph. woodwardi, *Ph. orvini*; Stensiö 1939, fig. 5, pl. 22). The pectoral margin in AMF 55520 is slightly bevelled, and the posteromesial angle of the AVL is about 130°, compared to 120° in *Pl. budawangensis* (Ritchie 1984, fig. 11).

Very similar widely spaced ornament is seen on a small left PVL also referred to this taxon (WAM 00.6.9; Fig. 7d). Its anterior margin, showing the normal overlap area for the AVL (oa.AVL, Fig. 9c), is oriented at about 125° to the straight mesial margin (L 24 mm). This approximates the corresponding shape of the AVL just described. The missing lateral corner is readily restored from the orientation of adjacent margins (Fig. 9c). PVL proportions (B/L 65, level of lateral corner 65%), are similar to the PVL of the type
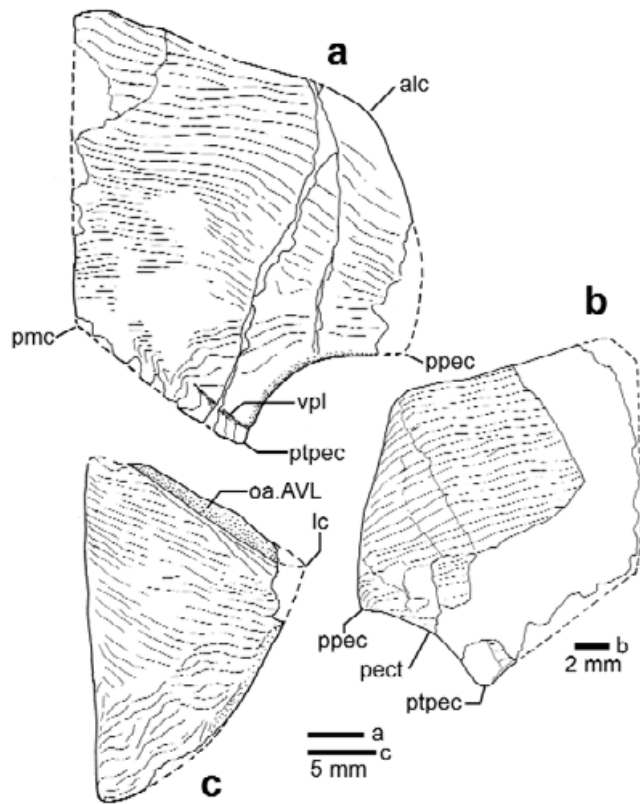
Fig. 9. *Placolepis tingeyi* sp. nov., AVL and PVL plates in external
view, partly restored. **a.** Left AVL (AMF 55520; cf. Fig. 7b),
b. right AVL (WAM 00.6.14; cf. Fig. 7f), **c.** left PVL (WAM
00.6.9; cf. Fig. 7d).

species (Ritchie 1984, fig. 13). Features noted on the
ornamented surface area are a smooth zone in the middle
part of the posterolateral margin, and a thickened rim at the
posterior edge of the overlap for the AVL, where two
posterolaterally directed ornament ridges run off the broken
corner of the plate.

WAM 00.6.14 (Fig. 7f) is a very incomplete right AVL
plate, much smaller than AMF 55520, but with similar fine,
widely spaced ornament ridges. The lateral margin is
complete (length 13 mm) and the pectoral margin is
preserved partly as an impression of the inner surface,
including the postpectoral corner. Posterior and mesial
margins are missing. The restored plate (Fig. 9b) shows a
less convex spinal margin, and a less concave pectoral
margin, than in AMF 55520 (Fig. 9a). These could be
ontogenetic variations, given the difference in size, but the
specimens are from different localities, in horizons for
which no reliable correlation exists, so the two AVL's are
only provisionally included here in one species. WAM
00.6.4 (Fig. 7e) is a much less complete presumed left AVL
preserved as an impression. The straight mesial margin is
partly preserved, and the posteromesial corner shows no
notch for the PMV, on which basis this specimen is also
referred to *Placolepis*. It shows the mesial section of the
posterior margin, if complete, to be gently concave rather

than straight, a condition occasionally seen in other
phyllolepids (e.g. *Ph. nielseni*; Stensiö 1936, fig. 10).
Finally WAM 90.2.40 (Fig. 7g) is a small fragment,
possibly from another AVL, with the same fine widely
spaced ornament as seen in WAM 00.6.14, on which basis it
is also provisionally included in *Placolepis tingeyi* sp. nov.

<div align="center">

phyllolepid gen. et sp. indet.
Figs 10, 11a & c

</div>

1972   'anterior dorso-lateral plate … characteristic of
            Phyllolepis'; Ritchie, p. 352
1990   'phyllolepid gen. indet.'; Woolfe *et al.*, table 1
1994   'phyllolepid placoderms'; McLoughlin & Long, p. 86
1995   'phyllolepid indet.'; Long & Young, p. 86, table 1

Remarks. Included here are various specimens that clearly
belonged to phyllolepids, but cannot be referred with any
confidence to the two taxa just described. They suggest that
several other phyllolepid taxa were present in the Aztec
Siltstone fauna. However the material is so limited that they
are grouped together here for convenience.

Material. AMF 55439 (ADL plate), AMF 117074 (?MD
plate fragment), WAM 00.6.13, 00.6.16 (AVL plates), WAM
00.6.5, 95.2.127 (?PNu plates), WAM 00.6.12 (possible
fragment of left AL plate).

Localities. GCY14 ('Mount Metschel'; WAM 95.2.127,
00.6.13); GCY17 ('Alligator Ridge Pavement'; AMF
55439), GCY24 ('Mount Ritchie'; AMF 117074, WAM
00.6.12), JAL4 ('Fault Bluff'; WAM, 00.6.5, 00.6.16).

Horizons. 7 m below top of Aztec Siltstone (GCY14); 8 m
from top of Aztec Siltstone (GCY17); collected in scree,
presumably from upper 25 m of Aztec Siltstone (GCY24);
horizon A (site 1), 25 m from top of sequence (JAL4).

Description. AMF 55439 (Fig. 10a) is a highly distinctive
ADL plate, associated with other ridged phyllolepid
remains on the Alligator Ridge Pavement, but entirely
devoid of ornament, even though it shows the narrow
external surface typical of a phyllolepid ADL. In the
Greenland *Phyllolepis* material, the dorsal process of the
ADL, which extends in front of the MD, projects forward
more than the ventral process (e.g. Stensiö 1934, fig. 22).
Thus the incomplete larger process in AMF 55439
(Fig. 11c) is probably the dorsal process of a right plate. For
Placolepis, the ADL was interpreted by Ritchie (1984,
p. 340) as 'narrow in front of the MD but wider under in
front of the AL where it forms part of an articular condyle'.
However it seems likely that at least one of the figured
ADLs (Ritchie 1984, fig. 10B) may be from the left side.

AMF 55439 is 22 mm long at the level of the sensory
groove, and is proportionately much shorter than in
Phyllolepis, *Austrophyllolepis* or *Placolepis*. All margins of
the plate are preserved except the extremity of the
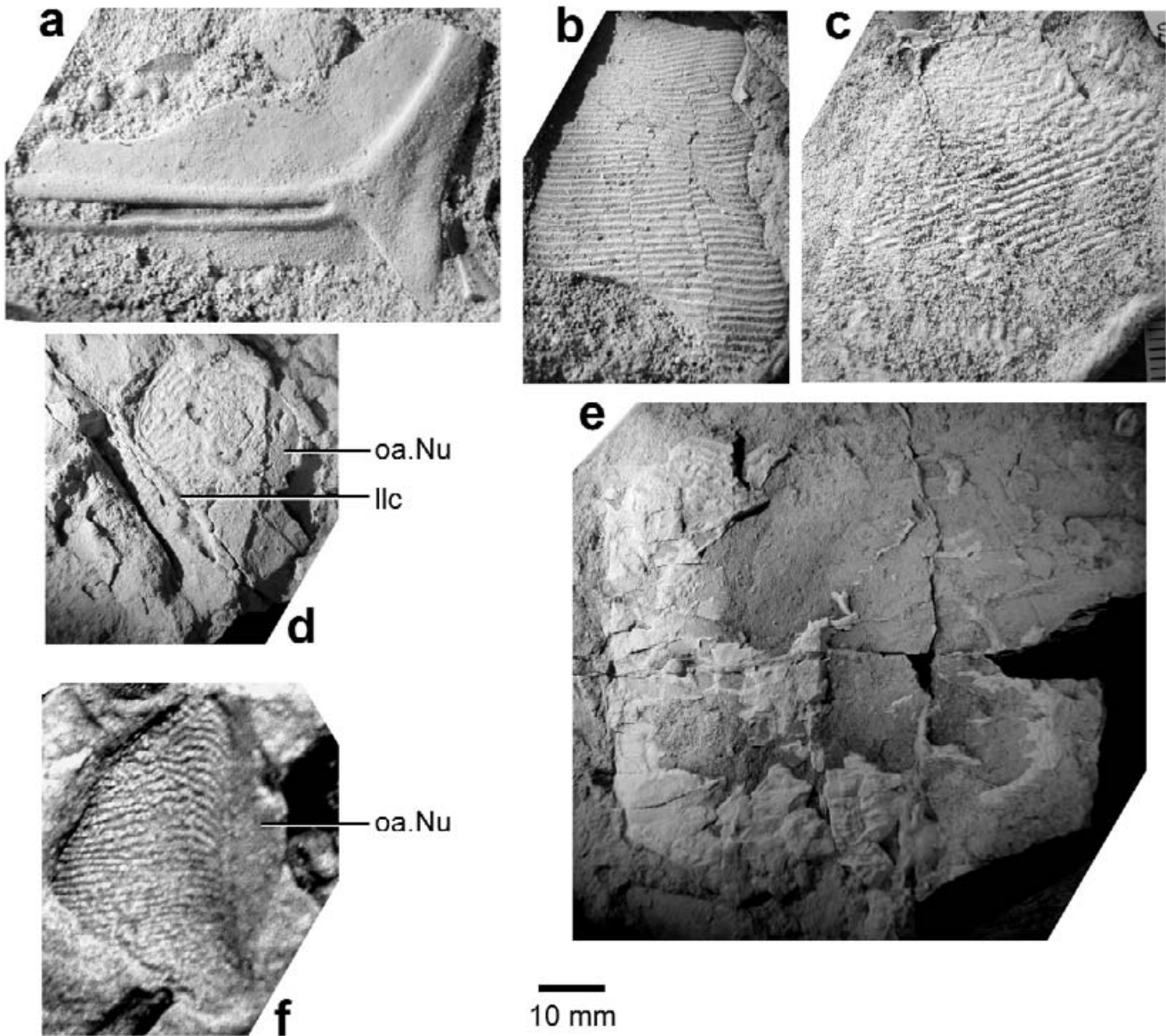
Fig. 10. Indeterminate phyllolepid placoderm bones from Antarctica. **a.** Right ADL plate (AMF 55439), **b.** probable incomplete AVL plate (WAM 00.6.16), **c.** probable incomplete MD plate (AMF 117074), **d & f.** probable PNu plates (WAM 95.2.127, 00.6.5), **e.** left AVL plate (WAM 00.6.13). a–c are latex casts, and d–f are bone remains and impressions in the rock, all in external view, and whitened with ammonium chloride.

anterodorsal process, and the posterior part of the ventral overlap. It is completely smooth, whereas the ADL in *Phyllolepis* is strongly ornamented with vertical ridges (e.g. Stensiö 1934, pl. 8, fig. 3; pl. 17, fig. 1). This is also the condition in *Placolepis* (Ritchie 1984, fig. 10A–C, Young 2005a), and in *Austrophyllolepis* (e.g. Fig. 5a). The only other described phyllolepid with externally smooth dermal bones is a new taxon from south-eastern Australia (Young 2005b), represented by a few incomplete plates including the ADL, which was evidently considerably more elongate than this Antarctic specimen (probably a specific difference). The deep sensory groove in AMF 55439 (llc, Fig. 11c) separates the dorsal part of the external bone

surface, forming a smooth rounded ridge, from the thinner, smooth ventral ridge below the groove. The overlap area for the MD (oa.MD) is broader than that for the AL (oa.AL), and suggests a rounded anterolateral corner on the MD plate. The anterior flange for the sliding neck-joint is broader than reconstructed for *Phyllolepis* (Stensiö 1934, fig. 22). The shallow rounded 'condyle' of Stensiö is not present, but there is a slight lunate depression in this position (dep, Fig. 11c). The ADL plate of *Austrophyllolepis*, well displayed on the left side in the holotype of *A. ritchiei* (Fig. 5a), measures 20 mm from the front of the sensory groove to the posterior angle, with the anterodorsal process 13 mm long. The exposed surface (in
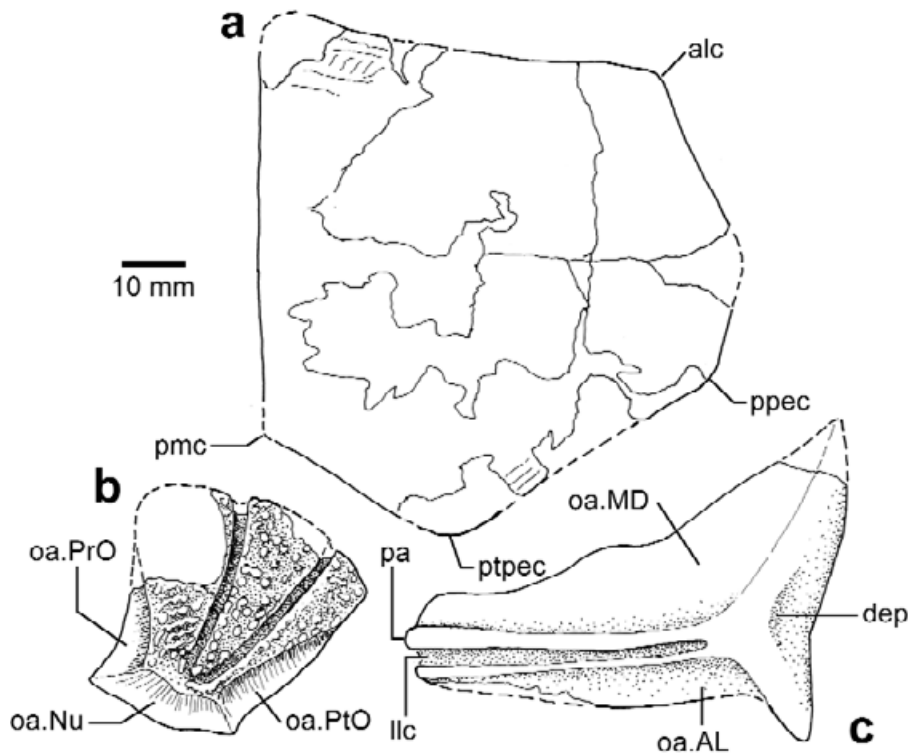
Fig. 11. a. Phyllolepid indet., left AVL plate, partly restored (WAM 00.6.13; cf. Fig. 10e), **b.** *Austrophyllolepis quiltyi* sp. nov., right PN plate, partly restored (AMF 55493; cf. Fig. 2e), **c.** phyllolepid indet., right ADL plate, partly restored (AMF 55439; cf. Fig. 10a).

this case ornamented) is 2 mm wide at the anterior end of the sensory groove, and is twice the width above the groove as below it, as in AMF 55439. As in *Phyllolepis* (e.g. Stensiö 1934, fig. 22), there is a posterior angle projecting back above the sensory groove (pa, Fig. 11c). The distinct ventral edge to the exposed surface of the ADL of *Austrophyllolepis* (Fig. 5a), manifested in *Placolepis* as the sharp dorsal margin of the AL plate (see Ritchie 1984, fig. 10D–I), contrasts with the rounded edges to the exposed surface in AMF 55439 (Fig. 10a). In summary, this highly unusual ADL plate is quite different from the ADL in both *Placolepis* and *Austrophyllolepis* from Australia, suggesting that it probably represents a third phyllolepid taxon in the Aztec Siltstone fauna. It seems closely related to the new taxon *Yurammia browri* Young, 2005b from south-eastern Australia, but differs from that species in its much shorter proportions.

Several other fragmentary specimens with ridged ornament from the Alligator Ridge Pavement are briefly listed, but are too incomplete to be reliably determined. ANU V3061 is the impression of a fragment 15 x 25 mm in size with one straight margin, showing inflections in the ornament suggesting that it may have broken from a much larger MD plate. ANU V3062 includes a small (5 x 3 mm) fragment with fine ridged ornament similar to that on the AVL plate from the Lashly Range referred above to *Placolepis tingeyi* sp. nov. ANU V3063 is a 23 x 12 mm fragment showing meandering coarse ornament, evidently from a much larger plate, but too incomplete to determine.

From Mount Metschel come two phyllolepid specimens

exhibiting similar ridged ornament, which is coarser than in any of the specimens from the other localities. We therefore assume they belong to the same taxon. WAM 95.2.127 is interpreted as a left PNu plate (Fig. 10d), with a broad overlap for the Nu (oa.Nu), and a poorly preserved sensory groove (llc). The lateral margin and postnuchal process are missing. The ornament orientation is consistent with its interpretation as a PNu (cf. Stensiö 1936, pl. 4). The position of the sensory groove shows that it cannot belong to *Placolepis*, whereas the associated AVL plate (WAM 00.6.13; Fig. 10e) lacks a notch for the PMV, so this cannot be referred to *Austrophyllolepis*. The AVL, preserved mainly as an impression of the inner surface, comes from a large individual (length of mesial margin 55 mm). Some bone is retained in the mesial half of the plate, mainly abraded, but with the ornament preserved near the anteromesial margin, and on a piece of bone near the pectoral margin, with the rounded postpectoral corner preserved as an impression (Fig. 11a). The spinal margin is missing its middle part, but orientation of preserved margins indicates some convexity, as in the AVL of *Phyllolepis concentrica* (Stensiö 1939, fig. 1). However that AVL differs in having a longer posterior margin. The pectoral margin in WAM 00.6.13 is relatively long (~38 mm) and straight, a point of difference to both *Ph. concentrica* and *Ph. woodwardi* (Stensiö 1939, fig. 2). An AVL from Freestone Creek, Victoria, referred to *Austrophyllolepis youngi* by Long (1989, fig. 7) also has a convex spinal margin, but is a more elongate plate, again with a strongly concave pectoral margin, and a notch for the PMV.
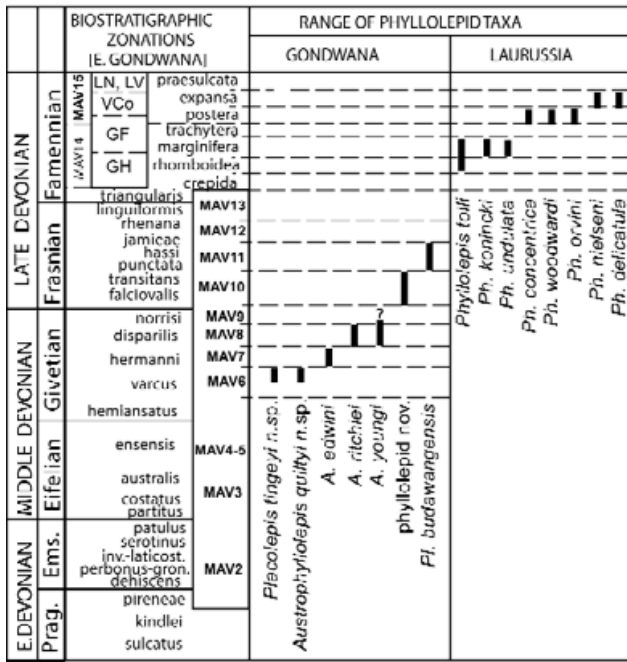
Fig. 12. Summary of known stratigraphic ranges (Givetian–Famennian) for named phyllolepid placoderm taxa in East Gondwana (Australia, Antarctica), and Laurussia. Australian data updated from Young (1993, fig. 9.3), Young (1999, fig. 5), and Long (2003, fig. 6.30). For conodont zonation see Mawson & Talent (2000). Alignment of macrovertebrate (MAV), miospore (GH, GF, VCo, LN, LV), and conodont zones is approximate (modified from Young 1996, Young & Turner 2000).

Assuming that the similar coarse ornament indicates that this AVL belongs to the same taxon as the WAM 95.2.127 from the same locality and horizon, their combined characteristics preclude them being referred to either *Austrophyllolepis* or *Placolepis*. They are unlikely to belong with the smooth ADL plate just described, and may therefore represent a fourth phyllolepid taxon.

WAM 00.6.16 (Fig. 10b) is a very incomplete presumed left AVL preserved as an impression showing a strongly concave pectoral margin, but with all other margins broken. The complete plate would have been similar in size to AMF 55520, but the ornament is completely different, with ridges and grooves of similar width, and closely spaced (16 ridges per cm), whereas in AMF 55520 the ridges are widely spaced (Fig. 7b). Another very incomplete impression from the scree at Mount Ritchie (AMF 117074; Fig. 10c) shows angulation in the ornament which seems too obtuse to be from a Nu plate, and is therefore assumed to be part of a MD plate, where this angle can be much wider (e.g. Ritchie 1984, fig. 9A, B, D). Ornament is somewhat similar to the previous specimen, with coarse ridges and grooves of similar width, and as far as preserved it shows little similarity to the other MD plates described above (Figs 2a & g, 7c). However we cannot exclude the possibility that

these two specimens are ornament variations of one of the taxa described above.

Finally, WAM 00.6.5 from Fault Bluff (Fig. 10f) is a ridged triangular impression with one overlap area that is difficult to interpret. The triangular shape suggests a PVL plate, but the broad overlap for the opposite PVL is anomalous for a phyllolepid, although known in other placoderms. If it is a PVL, then the truncated anteromesial corner might suggest a notch for a PMV plate. Alternatively, it could be interpreted as part of a left PNu plate, showing the overlap for the Nu, but broken along the sensory groove such that the lateral part of the plate is completely missing. The preserved mesial part is similar to isolated incomplete PNu plates in the Greenland *Phyllolepis* material (e.g. Stensiö 1934, pl. 18, fig. 1). Under this interpretation, the lateral position of the sensory groove would indicate affinity with *Phyllolepis* rather than *Austrophyllolepis* or *Placolepis*, where the groove has a more mesial position. However the PNu in *Phyllolepis* is rather flat, whereas WAM 00.6.5 shows a slight but distinct transverse convexity. Therefore we remain uncertain about the position of this bone in the dermal armour.

Discussion

The above descriptions indicate possibly three genera and four species of phyllolepid in the Aztec Siltstone fish fauna, which would make it the most diverse association of phyllolepid taxa so far known from one assemblage. Other new genera and species have recently added to known phyllolepid diversity from Australia (Young 2005a, 2005b). The two named Antarctic species are referred with confidence to the Australian genera *Austrophyllolepis* and *Placolepis*, but clearly lie outside the range of variation seen in the type localities for these genera. In contrast, the diversity of the group in the Northern Hemisphere has remained at only eight species within the genus *Phyllolepis* (Stensiö 1939, Vasiliauskas 1963). These are confined to the last stage of the Devonian (Famennian), and Carr (1995) previously noted that phyllolepids were the only placoderm group to show a diversity increase across the Frasnian–Famennian boundary, the time of a major Palaeozoic extinction event. As discussed elsewhere (Young 2003, p. 179), there is little evidence relating extinction amongst placoderms and other Devonian fish groups to this boundary, and the systematic descriptions presented above, and recently documented new phyllolepid taxa from Australia, actually reverse the previously noted diversity trend across the extinction boundary. The new Gondwanan taxa are of Givetian–Frasnian age, and hence older than all phyllolepid occurrences in the Northern Hemisphere (Fig. 12). For the Victorian *Austrophyllolepis* type locality (Mount Howitt), Long (1999) has proposed a revised late Middle Devonian age. This is consistent with a re-evaluation of isotopic data from interbedded volcanic rocks

at 374 ± 1.4 Ma (Compston 2004), which agrees with the 375 Ma alignment for oldest phyllolepids in the revised macrovertebrate zonation for East Gondwana of Young & Turner (2000, fig. 2).

Rather than providing evidence for extinction, the phyllolepid placoderms demonstrate a unique disjunct distribution in both time and space between the Southern and Northern hemispheres (Fig. 12). It has been proposed that this evidence documents a major vertebrate dispersal event, which approximately coincided with the Frasnian–Famennian boundary mass extinction of various invertebrate groups during the Late Devonian (Young 1990, 2003, 2005a, Young *et al*. 2000). Regarding the unusually early phyllolepid occurrences in the Antarctic Aztec Siltstone fauna, Young (1989a, p. 58) made two predictions for future discoveries of the group, both of which have been confirmed by subsequent research. No phyllolepids have yet been found in Asia (e.g. Zhu 2000), and their predicted discovery in South America (Venezuela; Young & Moody 2002) has extended their range across to the north-western Gondwana margin, an expected distribution pattern if they underwent non-marine dispersal between the two major Late Devonian continental areas (Gondwana, Laurussia).

For the eastern Gondwana margin, the new species *Austrophyllolepis quiltyi* and *Placolepis tingeyi* described above add to evidence from other Devonian fish taxa of close biogeographic affinity between southern Victoria Land and eastern Australia, for example the acanthodian *Culmacanthus* (Long 1983, Young 1989b), the lungfish *Howidipterus* (Long 1992, 2003) and the antiarch *Venezuelepis antarctica* (the latter first referred to the genus *Pambulaspis* from south-eastern Australia by Young 1988b). *Culmacanthus* is not known from elsewhere, whereas *Venezuelepis* is represented by one species in South America (Young & Moody 2002), and another from Tatong in Victoria (J.A. Long, unpublished data). In a global analysis of Givetian–Frasnian fish faunas from 40 localities involving 67 genera, Schultze & Cloutier (1996) also found a close grouping between Australia and Antarctica based primarily on the genera *Austrophyllolepis* and *Groenlandaspis*. As with phyllolepids just discussed, *Groenlandaspis* is also known from many Famennian localities in the Northern Hemisphere, but occurs in the Givetian–Frasnian only in Australia and Antarctica (Ritchie 1975).

Acknowledgements

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.

ASKIN, R.A., BARRETT, P.J., CURREEN, S. & YOUNG, G.C. 1971a. Stratigraphic sections of the Beacon Supergroup (Devonian and older (?) to Jurassic) in the Darwin Mountains, Antarctica. *Publication of the Geology Department, Victoria University of Wellington, Antarctic Data Series,* **1**, 1–32.

ASKIN, R.A., BARRETT, P.J., KOHN, B.P. & MCPHERSON, J.G. 1971b. Stratigraphic sections of the Beacon Supergroup (Devonian and older (?) to Jurassic) in South Victoria Land. *Publication of the Geology Department, Victoria University of Wellington, Antarctic Data Series,* **2**, 1–88.

BARRETT, P.J. & WEBB, P.N., *eds*. 1973. Stratigraphic sections of the Beacon Supergroup (Devonian and older (?) to Jurassic) in South Victoria Land. *Publication of the Geology Department, Victoria University of Wellington, Antarctic Data Series,* **3**, 1–165.

BRADSHAW, M.A. & WEBERS, G.F. 1988. The Devonian rocks of Antarctica. *In* MCMILLAN, N.J., EMBRY, A.F. & GLASS, D.J., *eds. Devonian of the World, Volume 1*. Calgary: Canadian Society of Petroleum Geologists Memoir, **14**, 783–795.

CAMPBELL, K.S.W. & BARWICK, R.E. 1987. Paleozoic lungfishes - a review. *Journal of Morphology, Supplement,* **1** (1986), 93–131.

CARR, R.K. 1995. Placoderm diversity and evolution. *Bulletin du Muséum national d'Histoire naturelle, Paris, Section C,* **17**, 85–125.

CHALONER, W.G., FOREY, P.L., GARDINER, B.G., HILL, A.J. & YOUNG, V.T. 1980. Devonian fish and plants from the Bokkeveld Series of South Africa. *Annals of the South African Museum,* **81**, 127–157.

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**, 223–228.

DEBENHAM, F. 1921. The sandstone, etc., of the McMurdo Sound, Terra Nova Bay, and Beardmore Glacier regions. *British Antarctic (Terra Nova) Expedition, 1910. Natural History Report (Geology),* **1**, 101–119.

DENISON, R.H. 1978. Placodermi. *In* SCHULTZE, H.-P., *ed. Handbook of Paleoichthyology,* vol. 2. Stuttgart: Gustav Fischer, 128 pp.

Gunn, B.M. & Warren, G. 1962. Geology of Victoria Land between the Mawson and Mulock glaciers, Antarctica. *Trans-Antarctic Expedition 1955–1958. Scientific Reports, Geology,* **11**, 1–157.

Hampe, O. & Long, J.A. 1999. The histology of Middle Devonian chondrichthyan teeth from southern Victoria Land, Antarctica. *Records of the Western Australian Museum Supplement,* **57**, 23–36.

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**, 206–231.

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**, 174–175.

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

Johanson, Z. & Ahlberg, P.E. 2001. Devonian rhizodontids and tristichopterids (Sarcopterygii; Tetrapodomorpha) from East Gondwana. *Transactions of the Royal Society of Edinburgh: Earth Sciences,* **92**, 43–74.

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.

Leriche, M. 1931. Les poissons Famenniens de la Belgique. *Acadamie Royal de Belgique, Memoire* (Series 2), **10**, 1–72.

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

Long, J.A. 1983. A new diplacanthoid acanthodian from the Late Devonian of Victoria. *Memoir of the Association of Australasian Palaeontologists,* **1**, 51–65.

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* Le Maitre, R.W., *ed. Pathways in geology: essays in honour of Edwin Sherbon Hills*. Melbourne: Blackwell Scientific, 52–58.

Long, J.A. 1992. Cranial anatomy of two new Late Devonian lungfishes (Pisces: Dipnoi) from Mount Howitt, Victoria. *Records of the Australian Museum,* **44**, 299–318.

Long, J.A. 1995. A new groenlandaspidid arthrodire (Pisces: Placodermi) from the Middle Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Records of the Western Australian Museum,* **17**, 35–41.

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. 2000. *Mountains of madness - a journey through Antarctica*. Sydney: Allen & Unwin, 236 pp.

Long, J.A. 2003. Palaeontology (Middle Devonian to Carboniferous). *In* Birch, W.D., *ed. Geology of Victoria*. Geological Society of Australia, Special Publication No. 23, 190–192.

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.

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**, 243–270.

McKelvey, B.C., Webb, P.N., Gorton, M.P. & Kohn, B.P. 1972. Stratigraphy of the Beacon Supergroup between the Olympus and Boomerang Ranges, Victoria Land. *In* Adie, R.J., *ed. Antarctic geology and geophysics*. Oslo: Universitetsforlaget, 345–352.

McLoughlin, S. & Long, J.A. 1994. New records of Devonian plants from southern Victoria Land, Antarctica. *Geological Magazine,* **131**, 81–90.

McPherson, J.G. 1978. Stratigraphy and sedimentology of the Upper Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *New Zealand Journal of Geology & Geophysics,* **21**, 667–683.

McPherson, J.G. 1979. Calcrete (caliche) palaeosols in fluvial redbeds of the Aztec Siltstone (Upper Devonian), southern Victoria Land, Antarctica. *Sedimentary Geology,* **22**, 267–285.

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

Ritchie, A. 1972. Appendix. Devonian fish. *In* Adie, R.J., *ed. Antarctic geology and geophysics.* Oslo: Universitetsforlaget, 351–352.

Ritchie, A. 1975. *Groenlandaspis* in Antarctica, Australia and Europe. *Nature,* **254**, 569–73.

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.

Rohon, J.V. 1900. Die devonischen Fische von Timan in Russland. *Sitzungsberichte der Königlichen Böhmischen Gesellschaft der Wissenschaften, Mathematisch-naturwissenschaftliche Classe, 1899* (8), 1–77.

Schultze, H.-P. & Cloutier, R. 1996. Comparison of the Escuminac Formation ichthyofauna with other late Givetian/early Frasnian ichthyofaunas. *In* Schultze H.-P. & Cloutier R., *eds. Devonian fishes and plants of Miguasha, Quebec, Canada*. Munich: Verlag Dr Friedrich Pfeil, 348–368.

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.

Turner, S. 1997. Sequence of Devonian thelodont scale assemblages in East Gondwana. *Geological Society of America, Special Publications,* **321**, 295–315.

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

Vasiliauskas, V.M. 1963. *Phyllolepis tolli* sp. nov. and some problems concerning the stratigraphy of the Famennian deposits in the Baltic states. *In* Grigelis, A. & Karatajute-Talimaa, V., *eds. Geology of Lithuania*. Vilnius, 407–429. [in Russian].

Westoll, T.S. 1979. Devonian fish biostratigraphy. *Special Papers in Palaeontology,* **23**, 341–353.

White, E.I. 1968. Devonian fishes of the Mawson–Mulock area, Victoria Land, Antarctica, Trans-Antarctic Expedition 1955–1958. *Scientific Reports, Geology,* **16**, 1–26.

Woodward, A.S. 1921. Fish-remains from the Upper Old Red Sandstone of Granite Harbour, Antarctica. *British Antarctic* (*Terra Nova*) *Expedition, 1910. Natural History Report* (*Geology*)*,* **1**, 51–62.

Woolfe, K.J., Long, J.A., Bradshaw, M., Harmsen, F. & Kirkbride, M. 1990. Discovery of fish-bearing Aztec Siltstone (Devonian) in the Cook Mountains, Antarctica. *New Zealand Journal of Geology & Geophysics,* **33**, 511–514.

Young, G.C. 1974. Stratigraphic occurrence of some placoderm fishes in the Middle and Late Devonian. *Newsletters on Stratigraphy*, **3**, 243–261.

Young, G.C. 1979. Appendix: vertebrate palaeontology. *Journal of the Geological Society of Australia,* **26**, 102–103.

Young, G.C. 1982. Devonian sharks from south-eastern Australia and Antarctica. *Palaeontology,* **25**, 817–843.

YOUNG, G.C. 1983. A new asterolepidoid antiarch (Placodermi) from the Late Devonian of southeastern 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**, 239–254.

YOUNG, G.C. 1988a. New occurrences of phyllolepid placoderms from the Devonian of central Australia. *BMR Journal of Australian Geology & Geophysics,* **10**, 363–376.

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

YOUNG, G.C. 1989a. The Aztec fish fauna of southern Victoria Land - evolutionary and biogeographic significance. *In* CRAME, J.A., *ed. Origins and evolution of the Antarctic biota.* Geological Society of London Special Publications, **47**, 43–62.

YOUNG, G.C. 1989b. 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* MCKERROW, W.S. & SCOTESE, C.R., *eds. Palaeozoic biogeography and palaeogeography.* Geological Society of London Memoirs, **12**, 243–255.

YOUNG, G.C. 1991. Fossil fishes from Antarctica. *In* TINGEY, R.J., *ed. The geology of Antarctica.* Oxford: Oxford University Press, 538–567.

YOUNG, G.C. 1993. Middle Palaeozoic macrovertebrate biostratigraphy of eastern Gondwana. *In* LONG, J.A., *ed. Palaeozoic vertebrate biostratigraphy and biogeography.* London: Belhaven Press, 208–251.

YOUNG, G.C. 1996. Devonian (chart 4). *In* YOUNG, G.C. & LAURIE J.R., *eds. An Australian Phanerozoic timescale.* Melbourne: Oxford University Press, 96–109.

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**, 139–150.

YOUNG, G.C. 2003. North Gondwanan mid-Palaeozoic connections with Euramerica and Asia: Devonian vertebrate evidence. *Courier Forschungsinstitut Senckenberg,* **242**, 169–185.

YOUNG, G.C. 2005a. An articulated phyllolepid fish (Placodermi) from the Devonian of central Australia: implications for non-marine connections with the Old Red Sandstone continent. *Geological Magazine,* **142**, 173–186.

YOUNG, G.C. 2005b. New phyllolepids (placoderm fishes) from the Middle–Late Devonian of southeastern Australia. *Journal of Vertebrate Paleontology,* **25**, 261–273.

YOUNG, G.C. & BURROW, C. 2004. Diplacanthid acanthodians from the Aztec Siltstone (late Middle Devonian) of southern Victoria Land, Antarctica. *In* YOUNG, G.C., *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**, 23–43.

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**, 1–85.

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., LONG, J.A. & RITCHIE, A. 1992. Crossopterygian fishes from the Devonian of Antarctica: systematics, relationships and biogeographic significance. *Records of the Australian Museum Supplement,* **14**, 1–77.

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**, 755–761.

YOUNG, G.C. & TURNER, S. 2000. Devonian microvertebrates and marine–nonmarine correlation in East Gondwana: Overview. *Courier Forschungsinstitut Senckenberg,* **223**, 453–470.

ZHU, M. 2000. Catalogue of Devonian vertebrates in China, with notes on bio-events. *Courier Forschungsinstitut Senckenberg,* **223**, 373–390.