

A new Placoderm, *Placolepis* gen. nov. (Phyllolepidae), from the Late Devonian of New South Wales, Australia

A. RITCHIE

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A rich concentration of Late Devonian (Frasnian) placoderm fish remains from a horizon low in the Devonian sequence on the western margin of the Budawang Range, southeastern New South Wales, Australia, contains abundant well-preserved plates of an antiarch, *Bothriolepis* sp., associated with a distinctive new genus and species of phyllolepid.

Placolepis budawangensis gen. et sp. nov. is closely related to, but readily distinguishable from, *Phyllolepis* ss. from the Late Devonian of Europe (including European U.S.S.R.), Greenland, Australia and Antarctica. The poorly known *Antarctaspis* White, from the Late Devonian of Antarctica is not considered here to be a phyllolepid, leaving *Phyllolepis* and *Placolepis* gen. nov. as the only two known genera of the family Phyllolepidae whose origins and affinities with other placoderms remain obscure.

A. Ritchie, Palaeontology Department, Australian Museum, 6-8 College St., Sydney, Australia 2000; manuscript received 8 September 1982, accepted for publication in revised form 22 June 1983.

INTRODUCTION

Phyllolepis, a Late Devonian placoderm, is a distinctive, specialized armoured fish whose remains are widely distributed in continental deposits in Greenland, Europe, Australia and Antarctica. Until recently *Phyllolepis* has been the sole genus in the family Phyllolepidae Woodward (1891) with seven described species and several more occurrences awaiting description. The only known articulated specimens have been those from northern hemisphere sites and the origins and relationships of *Phyllolepis* have been the subject of considerable discussion.

New discoveries of phyllolepid remains, including well-preserved articulated specimens, from sites in southeastern Australia throw new light on the morphology and relationships of this placoderm. From the Mount Howitt area east of Mansfield, Victoria (Marsden, 1976: 122) have come many fine specimens of a new species of *Phyllolepis* currently under preparation and study by Mr J. Long, Monash University. The other major new phyllolepid find, the subject of this paper, came to light in late 1980 from a site on the western margin of the Budawang Range, northeast of Braidwood in southern New South Wales.

From personal examination of the Mt Howitt and Budawang Range phyllolepid material the writer has confirmed that they represent two quite distinct taxa and the New South Wales material is sufficiently different from all known examples of *Phyllolepis* spp. that it must be placed in a new genus for which the name *Placolepis* is proposed. *Placolepis* gen. nov. is thus only the second genus recognized in the Phyllolepidae.

Until recently all known *Phyllolepis* occurrences came from the youngest Devonian continental deposits (Famennian) and there were even suggestions that it may have survived into Early Carboniferous times. From the Australian occurrences of phyllolepids it is now clear that the genus is present not only in the Famennian but also in the preceding Frasnian stage, reviving an earlier suspicion that the Phyllolepidae,

which make rather a sudden late appearance in the northern geological record, perhaps originated in the southern hemisphere (Young, 1974, 1981).

All authors with the exception of Denison (1978: 41) have regarded *Phyllolepis* as the sole genus in the Order Phyllolepidia. The writer does not accept Denison's claim that the very poorly known *Antarctaspis* White (1968) from the Late Devonian Aztec Siltstone of southern Victoria Land, Antarctica, should be included in the Phyllolepidia; *Phyllolepis* ss. is now known to be present in the Aztec Siltstone vertebrate fauna.

PREVIOUS DISCOVERIES OF *PHYLLOLEPIS*

Since its first discovery in Europe in the early 19th century the nature, origins and relationships of *Phyllolepis* have been in dispute. The first remains described came from the Late Devonian Rosebrae Beds (Upper Old Red Sandstone) of northeastern Scotland. *Phyllolepis concentrica* Agassiz (1844) was a moderately large species represented only by a few isolated plates. Isolated phyllolepid plates also came to light in the 1850s during the excavation of the famous Upper Old Red Sandstone (or Late Devonian) site at Dura Den, Fife, Scotland. As Woodward (1891: 313) pointed out these problematical plates were variously referred to 'Holoptychian Crossopterygii' and also to the 'head-bones of Palaeozoic Dipnoi'. Woodward himself preferred 'the suggestion of Newberry that the plates are truly referable to some so-called "Placoderm"', though we would compare them with *Coccosteus* and its allies rather than with *Pterichthys*'.

It is rather ironic, however, that when an almost complete specimen of *Phyllolepis* came to light during renewed excavation of the Dura Den site in 1912 and 1913 Woodward felt compelled to reinterpret it as a fossil agnathan (Woodward, 1915: 122-3, fig. 4). He concluded that 'there is, therefore, not much doubt that *Phyllolepis* is a genus of Ostracoderms most nearly allied to the Drepanaspidae or Psammosteidae' (see also Woodward, 1920: 31, fig. 3).

The earliest records of phyllolepid plates from continental Europe were of small isolated plates from the Famennian in two areas of Belgium. Lohest (1888: 157-167, pls 10, 11) described two genera and three species (*Phyllolepis undulata* Lohest, *P. corneti* Lohest and *Pentagonolepis konincki* Lohest).

In a re-examination of these forms Leriche (1930: 7-14, pls 1, 2) concluded that there was only evidence for one species *P. undulata* Lohest and that the other two, *P. corneti* and *Pentagonolepis konincki* were junior synonyms. Leriche accepted Woodward's interpretation of *Phyllolepis* as a heterostracan ostracoderm allied to the Drepanaspidae.

The discovery of abundant well-preserved Late Devonian fish remains in East Greenland in the late 1920s and early 1930s provided the solution. *Phyllolepis orvini* Heintz (1930: 31-46, pls 1-4) has subsequently become the best known species of this genus through the later discovery of abundant isolated plates and a few partly articulated individuals, and from the accounts of Stensiö (1934, 1936, 1939). Stensiö and Gross (1934) simultaneously came to the conclusion that *Phyllolepis* was not an agnathan and ostracoderm but a gnathostome and a placoderm.

Phyllolepis orvini Heintz (Figs 2A, B, 14A) was a large phyllolepid in which the head and trunk shields reached a length of over 40 cm. A second species, *P. soederberghi* Stensiö (1934) is now regarded as synonymous with *P. orvini*. Stensiö later (1939) described another species *P. nielseni* from the Lower Remigolepis Series of East Greenland.

Stensiö reviewed the Belgian material, at first (Stensiö, 1934: 34) accepting only *P. undulata* Lohest but later (Stensiö, 1939: 10, text figs 4B, 6B) resurrecting *P. konincki* (Lohest) as a valid species. Initially, he (Stensiö, 1934, 1936) accepted Traquair and

Woodward's original identification of the *Phyllolepis* material from the Scottish Dura Den fauna as *P. concentrica* Agassiz but later (Stensiö, 1939) placed it in a separate species, *Phyllolepis woodwardi* Stensiö.

Phyllolepis has also been recorded from the U.S.S.R. *P. tolli* Vasiliasukas (1963: 427-30, figs 3-6, pls 1-4; cf. also Obruchev, 1967: 255, pl. 4, fig. 4) is known from isolated plates from the Famennian of Latvia in the Baltic area and the genus is also reported from Northern Timan in northwestern U.S.S.R.

The only other records of *Phyllolepis* come from the Late Devonian of Australia and Antarctica but, until the recent discoveries, none has been sufficiently complete to warrant specific description.

Fragmentary plates attributed to *Phyllolepis*, largely on the basis of their distinctive ornament, come from the Late Devonian of Taggerty, central Victoria (Hills, 1931: 212-3, fig. 2; 1936: 164, pl. XII, figs 1, 2); from Hervey's Range, northeast of Parkes, central New South Wales (Hills, 1932: 852, pl. LVI, figs 2, 3); from Mansfield, central Victoria (Hills, 1936: 164, text fig. 4, pl. XII); and from the Dulcie Range, Northern Territory, 320 km northeast of Alice Springs, N.T. (Hills, 1959: 175, pl. VIII, figs D, E).

Another supposed *Phyllolepis* occurrence, from the Mulga Downs Group of western New South Wales (Rade, 1964) has since been shown to be mistaken. Placoderm plates with an ornament superficially similar to *Phyllolepis* were later shown to belong to an unusual Early-Middle Devonian genus, *Wuttagoonaspis*, whose relationships to *Phyllolepis* and to the Arthrodira *ss.* are still uncertain (Ritchie, 1969, 1973; cf. also Miles and Young, 1977; Young, 1980).

Elsewhere in eastern Australia isolated phyllolepid plates have been recovered from: the Cloghnan Shale, Jemalong Range, west of Forbes, N.S.W. (Ritchie, 1975; Campbell and Bell, 1977); Catombal Group, northwest of Canowindra, N.S.W.; 'Khan Yunis' near Krawaree, southeast of Captains Flat, N.S.W. (Johnson, 1964); near Pambula, southeast coast, N.S.W. (Young in Fergusson *et al.*, 1979); Freestone Creek, northeast of Briagolong, eastern Victoria (discovered by the writer, early 1981).

In Victoria however the most important phyllolepid occurrence is unquestionably that from the Frasnian Bindaree sequence, near the head of the Howqua River, east of Mansfield. The Mount Howitt fauna, as it is generally called, includes several genera of dipnoans, acanthodians and palaeoniscids in association with *Bothriolepis*, *Groenlandaspis* and phyllolepids. Many of the phyllolepid specimens are articulated and virtually complete.

It is now clear that, in eastern and central Australia, *Phyllolepis* spp. occur over a much greater stratigraphic range than in the northern hemisphere where the genus appeared suddenly in the Famennian and thus forms a useful index fossil for that stage. In Australia *Phyllolepis* occurs usually in association with species (mostly awaiting description) of *Bothriolepis*, *Remigolepis*, *Groenlandaspis* and others in various combinations which make it of more limited use for stratigraphic purposes, at least until the associated faunas and sequences have been studied in detail.

DISCOVERY OF *PLACOLEPIS* GEN. NOV.

In October 1980 a student party from the New South Wales Institute of Technology, Sydney, led by Dr R. Rogerson, discovered a rich Late Devonian fish site on the western limb of the Budawang Range Synclinorium in southeastern N.S.W. (Fig. 1). Several blocks containing abundant, well-preserved fish plates were forwarded for identification to the writer by Dr G. Gibbons, head of the department of Geology, N.S.W.I.T.

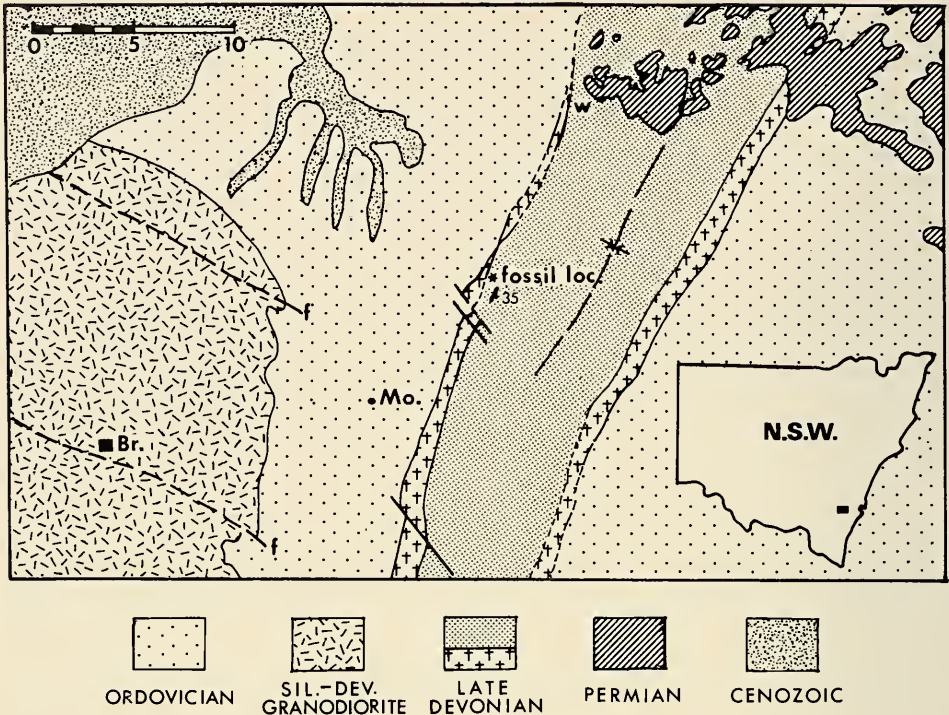


Fig. 1. Geology of the area east of Braidwood, New South Wales, showing the location of the *Placolepis/Bothriolepis* site on the west side of the NNE-SSW Budawang Range synclinorium. The fish bed occurs near the junction of the Comerong Volcanics (crosses), the basal Devonian formation in this area, and the overlying Merrimbla Group (fine stipple). Br. = Braidwood (surrounded by Braidwood Batholith); Mo = Mongarlowe; * = fossil fish site; w = Wog Wog marine invertebrate fauna (Frasnian). Scale in km.

The fossil site lies on the south bank of a northern tributary of Nettletons Creek, 9 km northeast of Mongarlowe, east of Braidwood, New South Wales (G.R. 014336; Corang sheet 8927-111-N).

The bulk of the material consisted of dissociated plates of two typical Late Devonian placoderm fishes, the antiarch *Bothriolepis* and what, at first sight, appeared to be *Phyllolepis*. In November 1980 a preliminary excavation, carried out by the writer, Mr R. K. Jones, Mr M. Leu and Dr Rogerson, producing most of the material described here. In January 1982 the writer, Mr Jones, Mr B. A. Ritchie and Mr T. Cogger re-excavated the site and clarified the position of the fish horizon in the section and its relationship to the marine invertebrate faunas of the overlying Merrimbla Group.

The fish plates occurred at various levels throughout a red and green mottled siltstone unit about 75 cm thick. Although *Bothriolepis* and phyllolepid plates predominated several specimens of crossopterygian plates and scales and an acanthodian fin-spine were also recovered. Some of the *Bothriolepis* trunk plates and pectoral fin skeletons were still articulated and the bulk of the fish material, although dissociated, had clearly not moved very far after death. One bedding plane almost completely covered with *Bothriolepis* plates also bore an assemblage of phyllolepid plates.

almost certainly derived from the head and trunk shield of a single individual, the first such occurrence of a phyllolepid from the Devonian of New South Wales. This specimen, AM F.61748 (Fig. 3A, B) has been selected as the holotype of a new genus and species of phyllolepid, *Placolepis budawangensis*, described here.

The Nettletons Creek phyllolepid material consists mainly of isolated head and trunk plates most of which were apparently complete at the time of burial and show little evidence of transport or abrasion. Many of the larger plates had been extensively fractured after burial, probably during the compaction of the sediment but, for the most part, even the smallest fragments have retained their original association. In the majority of specimens the original bone material, although still present, had either weathered or become so fragile as to be irrecoverable. The bulk of the material was therefore prepared as external moulds, the remaining bone being removed by dilute hydrochloric acid before casting in latex.

STRATIGRAPHIC SETTING

The Budawang Range Synclinorium, on the west flank of which the *Placolepis/Bothriolepis* assemblage was discovered (Fig. 1) forms the northern part of an extensive, elongate and narrow rift zone which extends some 300 km from south of Eden on the far southeast coast of New South Wales, northwards to Yalwal, west of Nowra, on the southern margins of the Sydney Basin.

McIlveen (1975: fig. 1, table 2) in an overall account of the Eden-Comerong-Yalwal Rift Zone, reviewed earlier work and demonstrated the clear similarities and correlations between the Eden-Merrimbula Devonian sequence and that of the more extensive Budawang Range Synclinorium. Both begin with a considerable thickness of acid, and some basic, volcanics of probable Givetian-Frasnian age, succeeded by a much thicker sedimentary sequence, the Merrimbula Group, of Frasnian-Famennian age. The Eden-Merrimbula area has since been shown by Fergusson *et al.* (1979) to be much more complex than had previously been thought. The earlier volcanic sequence, formerly the 'Eden Rhyolite' and the 'Locheil Formation', now renamed the Boyd Volcanic Complex, apparently formed in a terrestrial zone of extension before the whole area was blanketed by the Merrimbula Group.

Farther north, in the Budawang Range Synclinorium, the Devonian sequence is confined within a narrow belt 160 km long and 6-13 km wide. The basal volcanic suite, the Comerong Volcanics, consists of rhyolite, felsite, basalt, rhyolite breccia and interbedded sediments overlain, apparently conformably, by the sediments of the Merrimbula Group.

Earlier estimates of the thickness of the Merrimbula Group sediments in the Budawang Range (McElroy and Rose, 1962) have been shown to be conservative by Powell (*pers. comm.*). In early 1982 Powell and two students from Macquarie University measured detailed E-W sections through the Budawang Range along a line some 10 km north of the fish site. They were able to confirm that in this region the structure is a simple syncline with dips up to 70° on the eastern limb and 90° on the western limb. The total thickness of the Merrimbula Group here is estimated to be over 4 km, considerably greater than any recorded in the Eden-Merrimbula area where Steiner (1973) estimated it to be some 870 m thick.

The best evidence for the age of the lower part of the Merrimbula Group in the Budawang Range comes from a rich marine fossil assemblage recovered from Wog Wog, 8 km north of Nettletons Creek and the fish locality. Wood (*in* McElroy and Rose, 1962: 59, loc. U.P.4) identified *Orthis* sp., *Chonetes* sp., *Cyrtospirifer* sp.,

productids, *Bellerophon* sp., *Tentaculites* sp., *Pterinea* sp. and crinoid fragments, a characteristic Late Devonian assemblage but one that needs revision and detailed study. The presence of tentaculitids in abundance is particularly significant as this group is not known to have survived into Famennian times. The Wog Wog faunal assemblage is thus Frasnian in age. It is estimated to lie several 100 m above the youngest unit of the Comerong Volcanics in the same area.

In the tributary north of Nettletons Creek the only known exposure of the *Placolepis/Bothriolepis* fish bed lies less than 2 m above the youngest exposed rhyolite of the Comerong Volcanics. Powell (1983) and Jones (*pers. comm.*) measured the section independently and estimate that the fish bed lies in the lower part of the Comerong Volcanics, at least 350 m above the base and about 700 m below the junction with the overlying Merrimbula Group.

Mr R. K. Jones measured the Devonian section upstream from the fish-bed to establish its relationship with the later marine incursions in the Merrimbula Group. He located at least three distinct marine horizons containing abundant, but poorly preserved, shelly faunas none of which, at present, can be accurately correlated with the Wog Wog occurrence farther north.

The first marine band, 920 m above the fish-bed, produced abundant productid brachiopods, crinoid ossicles and small ramose bryozoans but none well enough preserved for specific identification.

The higher marine horizons, 1390 m and 1520 m above the fish-bed, contain abundant brachiopods (*Cyrtospirifer* cf. *subdisjunctus*, *Sinotectirostrum* sp. a new species of rhynchonellid and occasional productids) together with a bivalve similar to '*Lep-todesma*'. This assemblage is reminiscent of the Lambie facies marine faunas found at Mt Lambie and Gap Creek in central N.S.W. which are thought to be Famennian in age (R. K. Jones *pers. comm.*).

The Wog Wog Frasnian marine assemblage is certainly higher stratigraphically than the lower part of the Comerong Volcanics (containing the fish-bed) but older than the marine horizons located in the Nettletons Creek section. The latter section must therefore include the Frasnian/Famennian boundary although this cannot be precisely located on available evidence.

At the northern end of the Budawang Range Synclinorium the Devonian sequence is covered by the Permian of the Sydney Basin and is only exposed in rugged and relatively inaccessible tributaries of the Shoalhaven River. In two of these, Ettrema and Jones Creeks, a 30 m thick limestone unit has been shown to contain a late Frasnian conodont fauna associated with atrypid brachiopods, rare phillipsastreid corals and *Cyrtospirifer* (Pickett, 1973). The Ettrema Limestone Member, the only known Frasnian limestone in New South Wales, is believed to be equivalent to an horizon in the Merrimbula Group.

Other information relevant to the age of the *Placolepis/Bothriolepis* assemblage comes from the Eden-Pambula area of southeastern N.S.W. Young (*in* Fergusson *et al.*, 1979: 97-8, 102-3) reviewed the known, but still largely undescribed, Devonian fish finds from the Boyd Volcanic Complex and the Merrimbula Group. The earliest fish remains, from the Bunga Beds (Facies 2) in the lower part of the Boyd Volcanics, are thought to be late Givetian or early Frasnian (Young, 1982). Fragmentary remains of *Bothriolepis* sp. and *Phyllolepis* sp. first appear in the later Facies 3 (arkosic-volcanolithic clastic facies) in the Boyd Volcanics of the Pambula district and are interpreted as Frasnian from the presence of late Frasnian marine invertebrates in the overlying Merrimbula Group of the same region.

It is suggested here that the *Placolepis/Bothriolepis* assemblage from the Comerong Volcanics in Nettletons Creek must be either early or middle Frasnian in age.

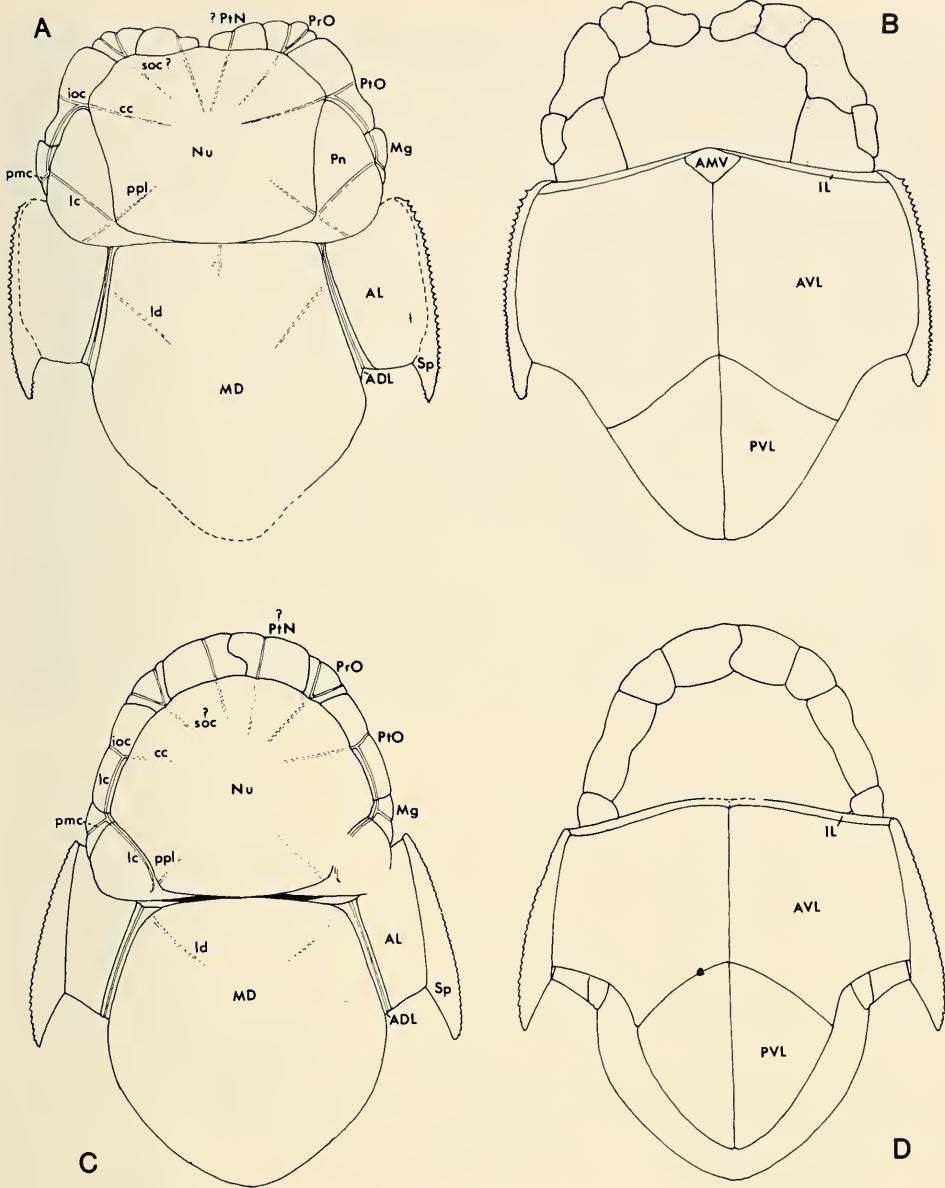


Fig. 2. Dorsal and ventral restorations on the head and trunk shields of *Phyllolepis orvini* Heintz and *Placolepis budawangensis* gen. et sp. nov. for comparison.

The *Phyllolepis* figures (A,B) are modified after Denison (1978: fig. 29) and Stensiö (1969: figs 132, 199). An attempt has been made, for the first time, to indicate the extent of the overlap areas in the ventral view of the headshield (B). In *Placolepis* (C,D) allowance has been made for the probable convexity of the dorsal and ventral shields (cf. also Figs 8, 14).

Abbreviations:— ADL — anterior dorsolateral plate; AL — anterior lateral; AMV — anterior median ventral; AVL — anterior ventrolateral; IL — interolateral; Mg — marginal; MD — median dorsal; Nu — nuchal; Pn — paranuchal; PrO — preorbital; ?PtN — ?postnasal; PtO — postorbital; PVL — posterior ventrolateral; Sp. — spinal; cc — central canal; ioc — infraorbital canal; lc — lateral canal; pmc — postmarginal canal; ppl — posterior pit-line; soc — supraorbital canal.

PREVIOUS INTERPRETATIONS OF *PHYLLOLEPIS*

Before describing *Placolepis* gen. nov., it is appropriate for comparative purposes to review briefly past and current interpretations of *Phyllolepis*, as the two genera are so alike in many respects.

The distinctive, ridged dermal ornament of *Phyllolepis* is so characteristic that hitherto even small fragments of plates have been confidently referred to this genus. The new material described here shows that ornament alone is not a reliable basis for such an identification.

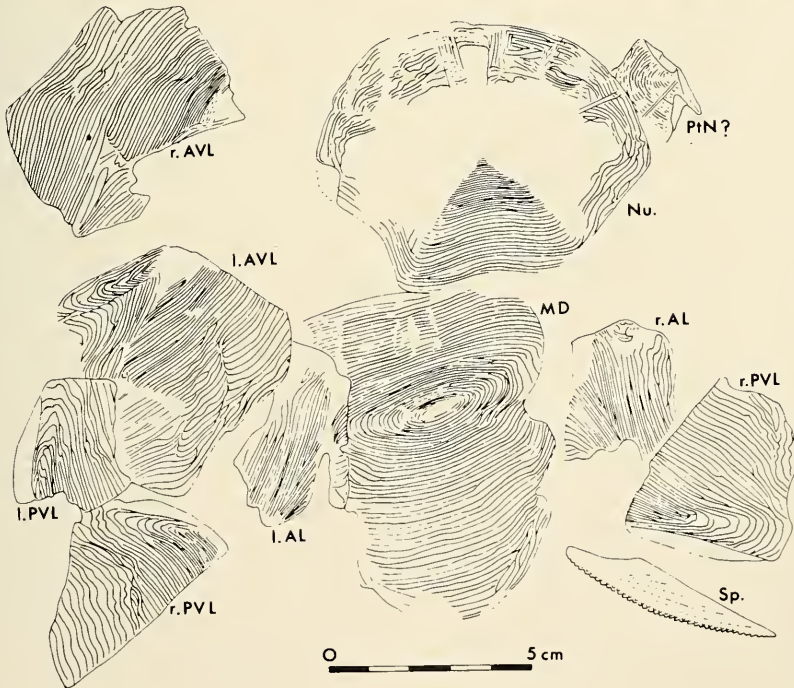
In the best known species from the Famennian of East Greenland, *Phyllolepis orvini* Heintz (1930; Stensiö, 1934, 1936, 1939, 1969: figs 132, 199a, b; Denison, 1978: fig. 29) and Scotland, *Phyllolepis woodwardi* Stensiö (1936: text figs 3, 5; 1939: text figs 2, 3) the fish was clearly dorsoventrally flattened in life. The headshield was broad and flat, consisting of a greatly enlarged nuchal plate bordered by a series of small paired plates. The latter, originally labelled 'marginals 1-5' by Stensiö (1934, 1936, 1939), have been variously interpreted by other authors to include the homologues of the arthrodiran paranuchals, marginals, postorbitals, preorbitals and (less certainly) the postnasals (Denison, 1978: fig 29, 41-42; cf. also this paper Figs 2, 8E, 8F).

The rostral and pineal plates are not developed in the Phyllolepidida and the anterior and lateral margins of the headshield were probably unarmoured. There is little evidence for the position and size of the eyes, and some disagreement about their probable position. It has even been suggested that *Phyllolepis* may have been blind (Westoll, 1979: 350). Stensiö (1969: figs 3B, 132; this paper Fig. 14A) depicted an extensive soft area in front of the headshield with the eyes anteriorly placed and directed, an interpretation accepted by Obruchev (1967: fig. 69), Romer (1966: fig. 34), Moy-Thomas and Miles (1971: fig. 8, 15) and others. However Denison (1978: 41-42, fig. 29) suggested that the eyes were more antero-laterally placed in a much narrower unarmoured marginal strip. This interpretation is accepted here in the closely related *Placolepis* gen. nov. (Fig. 14B).

The phyllolepid cranio-thoracic joint consists of simple flanges on the anterior margin of the trunk shield which underlie, and articulate with, the paranuchal plates of the headshield. The trunk shield is short, broad and comparatively flat. The component plates are well known (Fig. 7A, B). Posterior dorsolateral (PDL) and posterior lateral (PL) plates are not known in *Phyllolepis*. Opinions differ as to whether this absence is a primitive or derived condition in that genus. Although a very small triangular anterior median ventral (AMV) plate has been depicted in both *Phyllolepis orvini* and *P. woodwardi* the evidence for its presence in the former is regarded as equivocal, as discussed below. The only evidence for the presence of a posterior median ventral (PMV) plate in *Phyllolepis* was a minute sliver of bone in *P. woodwardi* (Stensiö, 1936: text fig. 5) but evidence for such a plate has recently come to light in the new Victorian material (J. Long *pers. comm.*).

The pectoral fin skeleton of *Phyllolepis* is unknown but it is obvious that the pectoral fenestra was open posteriorly and must have housed such a fin. The shape of the

Fig. 3. *Placolepis budawangensis* gen. et sp. nov. (holotype) and *Bothriolepis* sp.; this specimen (AM F.61748) and all other figured specimens from Late Devonian (Frasnian), tributary of Nettletons Creek, west flank of Budawang Range, New South Wales. A — above) latex cast whitened with ammonium chloride sublimate; bedding plane with abundant *Bothriolepis* plates and the slightly dissociated remains of a single *Placolepis* individual, selected as the holotype. Scale in millimetres. B) interpretation of *Placolepis* remains seen in A); abbreviations as in Fig. 2. Note that right posterior ventrolateral plate (r.PVL) lying adjacent to the spinal (Sp), and slightly obscuring a fine example of a *Bothriolepis* headshield, belongs to a second *Placolepis* individual.



trunk and tail posterior to the trunk shield is known only from remains of an ossified vertebral column in *Phyllolepis woodwardi* Stensiö (1936: text fig. 3) but more information should become available when the well-preserved, articulated material from the Mt Howitt fauna in Victoria is fully prepared and evaluated.

DESCRIPTION OF THE *PLACOLEPIS* GEN. NOV. MATERIAL

The holotype of *Placolepis budawangensis* gen. et sp. nov. (F.61748) consists of a localized concentration of dorsal and ventral plates (Fig. 3A, B), which are clearly derived from a single adult individual with the exception of an adjacent right PVL (cf. also Fig. 13F).

These form the basis for a complete restoration by providing the relative proportions for the major head and trunk plates. The individual plates are also represented by numerous isolated examples, covering a wide range.

CRANIAL SHIELD

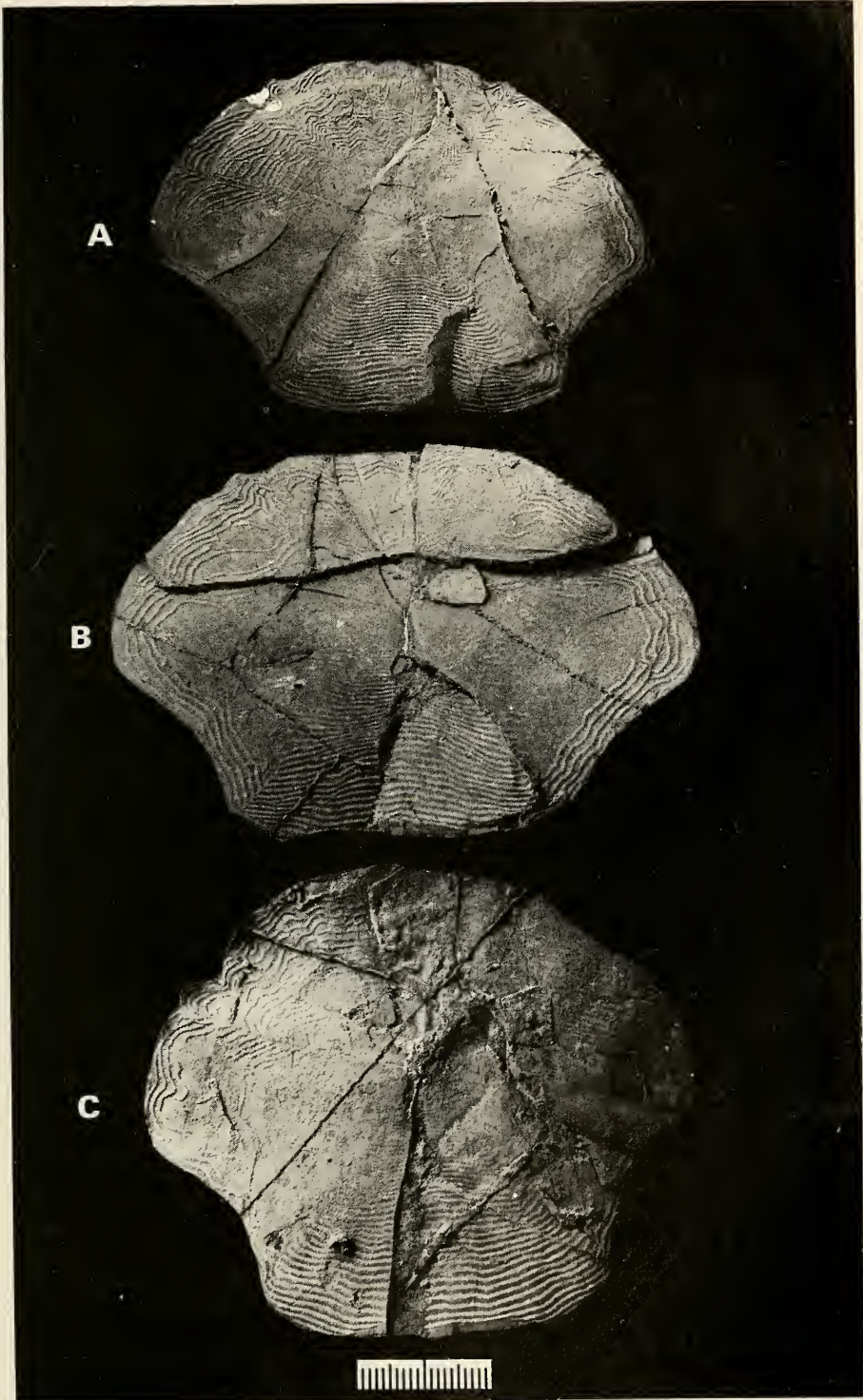
Before considering the cranial elements of *Placolepis* in detail an error in Stensiö's restoration of the headshield of *Phyllolepis* should be noted. The ventral plate boundaries of the headshield are always depicted as identical to those of the dorsal surface (Stensiö, 1969: fig. 199B, 503; Denison, 1978: fig. 29). In fact the nuchal plate overlaps all the smaller circum-nuchal plates and these overlap one another. The ventral plate pattern of the *Phyllolepis* (and *Placolepis*) headshield is thus quite different from that of the dorsal surface as indicated here (Figs 2, 8A, D).

Nuchal plate (Nu) — in addition to the type nuchal (Fig. 3) many other examples of the Nu of *Placolepis budawangensis* are available, covering a wide size range.

Both dorsal and ventral surfaces are displayed (Figs 4, 5, 6). The nuchal plate dominates the headshield of *Placolepis*, as in *Phyllolepis*, but its shape is markedly different. The widest part of the Nu in *Placolepis* lies opposite, or slightly posterior to, the centre of the plate; in *Phyllolepis* the greatest width is always considerably anterior to the midline. In addition, the general outline of the *Placolepis* Nu is less angular, with a broad rounded, sub-circular anterior and anterolateral margin. The posterolateral margins are gently concave and the posterior margin slightly convex. The posterior margin is around 0.6 of the maximum width. There is considerable variation in the length: width ratio of the nuchal plate ranging from 0.61-0.87; an intermediate figure (0.73) has been used in the reconstruction of the headshield (Fig. 8A) but some allowance for original curvature has been made in Figs 2C and 14B.

The *Placolepis* Nu carries the proximal portions of four pairs of sensory canals which converge on the centre of ossification as shallow, often indistinct grooves cutting across the subconcentric dermal ornament (Figs 2C, 4, 6A, 8A). These canals compare closely with those present in *Phyllolepis orvini* (Fig. 2A) and in *P. woodwardi*. From the rear they may be homologized with the posterior pit line (*ppl*), the central canal (*cc*), the supraorbital canal (*soc*) and an anteriorly directed pair whose homology remains uncertain. This interpretation of the various canals is basically in accord with that proposed by Denison (1978: fig. 29) but conflicts with that of Stensiö (1969: fig. 132).

Fig. 4. *Placolepis budawangensis* gen. et sp. nov., three nuchal plates (Nu) in dorsal view. A) AM F.61901a; B) F.61902a; C) F.61919; (same specimens as in Fig. 5). Latex casts whitened with ammonium chloride sublimate. Scale in millimetres.



The dermal ornament of the Nu of *Placolepis budawangensis* consists mainly of subconcentric, slightly undulating ridges whose regular arrangement breaks down completely in two subtriangular areas lying between the centre of ossification and the posterolateral margins. Here they zig-zag almost randomly or are largely undeveloped (Figs 4, 6A, 8A) leaving extensive smooth areas free of ridges. The region between the posterior margin of the Nu and the centre of ossification is occupied by a clearly demarcated triangular area of transverse parallel ridges bordered anterolaterally by the faintly developed left and right posterior pit-lines (*ppl*).

Smaller cranial plates — Stensiö (1934, 1936, 1939) recognized and described in detail five pairs of 'marginal' cranial plates bordering the Nu. He numbered them M1-M5 but only one pair of these plates (M5) is undoubtedly homologous to the true 'marginal' plates of Arthrodira. Stensiö's original nomenclature has long been discarded but was later (1969: fig. 132; 1971: 165) replaced with other names which have not been (or appear likely to be) widely accepted.

Denison's interpretation (Denison, 1978: fig. 29) is the one accepted and followed here but, for convenience, it may be useful to list the various names applied to these plates:

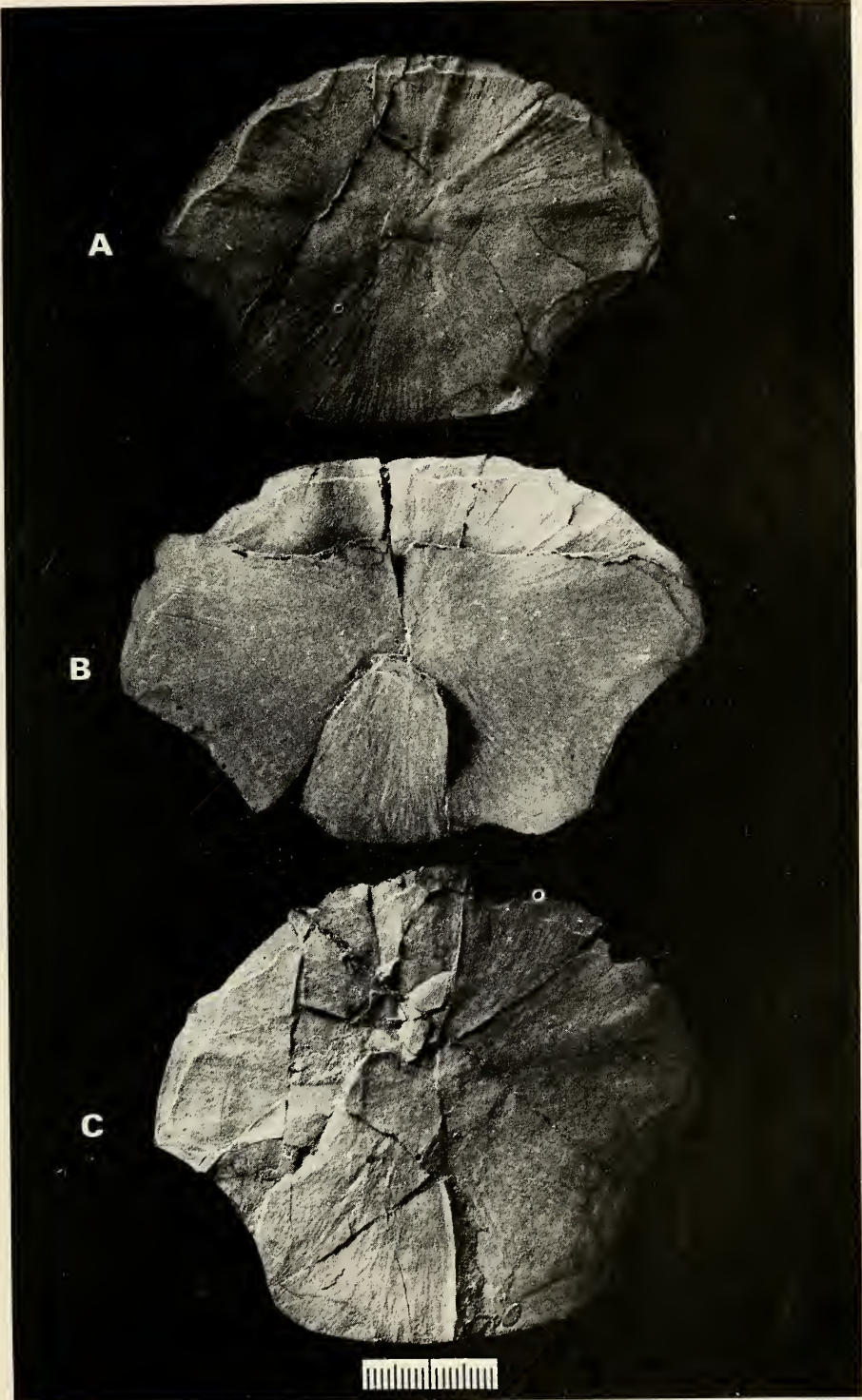
Stensiö (1934, 1936, 1939)	Stensiö	Denison	Abbrev.
Marginal 1	Preorbital	Postnasal?	PtN?
Marginal 2	Dermosphenotic	Preorbital	PrO
Marginal 3	Intertemporal	Postorbital	PtO
Marginal 4	Paranuchal	Paranuchal	Pn
Marginal 5	Intertemporal- supratemporal- extrascapular	Marginal	Mg

In *Phyllolepis orvini* and the other species each of these smaller plates, with the sole exception of the marginal, is overlapped by the nuchal whilst both the PtO and Mg plates are overlapped by the plates lying anterior and posterior to them (Figs 2B, 8F).

In *Placolepis budawangensis* the same five plates can be readily identified but their relative proportions and inter-relationships reveal important differences (Figs 2C, D, 6, 7, 8A, D, E). They will be considered in order beginning with the most posterior, the paranuchal.

Paranuchal (Pn) — many fine examples of the *Placolepis* Pn are available (Fig. 6 A-C, E-G). The *Placolepis* Pn is much shorter than that of *Phyllolepis* and lacks the broad ornamented area anterior to the lateral canal. In *Placolepis* the *lc* follows closely the nuchal/paranuchal margin and passes anteriorly off the Pn onto the small marginal plate and not midway along the lateral margin as in *Phyllolepis*. Posteriorly the *lc* curves sharply towards, but terminates short of, the cranio-thoracic articulation. There is no trace of a posterolaterally directed branch canal like that depicted in *Phyllolepis* (Fig. 2A) but it should be noted that this feature appears on only one of Stensiö's (1936: pl. 4, fig. 2) figured specimens. Along its entire inner margin the *Placolepis* Pn has a well-developed overlap area which underlay the posterolateral, and part of the posterior margin of the Nu. Immediately underlying the inner angle of the Pn there is a prominent rounded process (Figs 6E-G, 8D). From its shape and position this process

Fig. 5. *Placolepis budawangensis* gen. et sp. nov., three nuchal plates (Nu) in ventral view; (same specimens as in Fig. 4). A) AM F.61901b; B) F.61902b; C) F.61921. Latex casts whitened with ammonium chloride sublimate. Scale in millimetres.



was probably in contact with the concave anterior margin of the anterior dorsolateral (ADL) plate to form a relatively simple cranio-thoracic articulation with limited range of movement. In several *Placolepis* specimens this process has been crushed as if it were originally hollow, suggesting perhaps that it may have housed the ductus endolymphaticus, or the craniospinal process of the endocranium.

Marginal (Mg) — the course of the lateral canal of the Pn indicated that the smaller adjacent marginal plate was anteriorly placed and, unlike that of *Phyllolepis*, must have been in direct contact with the lateral margin of the Nu. This is confirmed by the presence of overlap areas on the Nu (Figs 5, 6D, 8D oa Mg). Three plates of the appropriate size and shape (Figs 7K-M, 8A, D, E) are regarded as left and right marginals. They are subcircular to ovate, 15-16 mm long and 12-13 mm wide with a triangular ornamented area. Each bears two sensory canal grooves, a very short, curved portion of the *lc* and, meeting it at right angles, a longer, radially-directed branch, the postmarginal (or preopercular) canal (Fig. 2C *pmc*). The Mg has well-developed anterior, posterior and proximal overlap areas for the PtO, Pn and Nu respectively.

Postorbital (PtO, Fig. 7 G-J). This plate is relatively long, narrow and subrectangular (Figs 2C, D, 8A, D, E). The lateral canal follows the nuchal margin until it meets, at an obtuse angle, the central canal (*cc*) leaving the Nu. The infraorbital canal (*ioc*), in *Placolepis* as in *Phyllolepis*, passes anterolaterally off the PtO onto the unarmoured lateral margin of the head.

On its visceral surface immediately underlying the *ioc*, the PtO displays a prominent rounded process which may be for the articulation of the hyomandibula. It is perforated transversely by a fine canal which emerges laterally, and immediately ventral, to a slight indentation in the outer margin of the PtO (Figs 7H, 8D). In *Placolepis* the PtO was in contact with, and overlapped by, the Nu over its full length, unlike the PtO of *Phyllolepis* which was partly separated from the Nu by an anterior extension of the Pn (Fig. 8F).

Preorbital (PrO) — immediately anterior to the PtO and overlapped by it was a smaller, subtriangular plate, here interpreted as the preorbital (Figs 2C, D, 7B-F, 8A, D, E). Like its homologue in *Phyllolepis* (Figs 2A, 8F) it differs from that of most other placoderms in bearing two well-developed sensory canal grooves which converge proximally and meet near the PrO/Nu border in line with the distal end of the supraorbital canal (*soc*). In *Placolepis* these converging canals are more symmetrically placed than are the same canals in *Phyllolepis* but with a few exceptions (Fig. 7F) one can readily distinguish between left and right PrOs.

Postnasal (PtN) — the anterior overlap areas on the *Placolepis* nuchal plate (Figs 5, 6D, 8D) show that the anterior margin of the headshield was formed by a pair of reasonably large, transversely oriented plates which met in the midline, much as in *Phyllolepis*. Although in *P. orvini* Heintz these plates have been depicted as more widely spaced and separate (Stensiö, 1936: text fig. 9) his figured specimens showing the dermal surface (1936: pl. 25) and the inner surface and overlap areas of the Nu (1936: pl. 5) indicate that the median gap was much smaller than shown in the reconstruction (this paper

Fig. 6. Placolepis budawangensis gen. et sp. nov., nuchal (Nu) and paranuchal (Pn) plates. Latex casts whitened with ammonium chloride sublimate. Scale in millimetres for A, B, C, D, E, F; G is $\times 2$. A, D) dorsal and ventral views of nuchal with associated paranuchal, AM F.63873 (dorsal); F.63874 (ventral); B, F) dermal and visceral surfaces of left paranuchal, F.61755a,b; C, E) dermal and visceral surfaces of right paranuchal, F.61756a,b; G) left paranuchal, visceral view, F.61925 ($\times 2$).

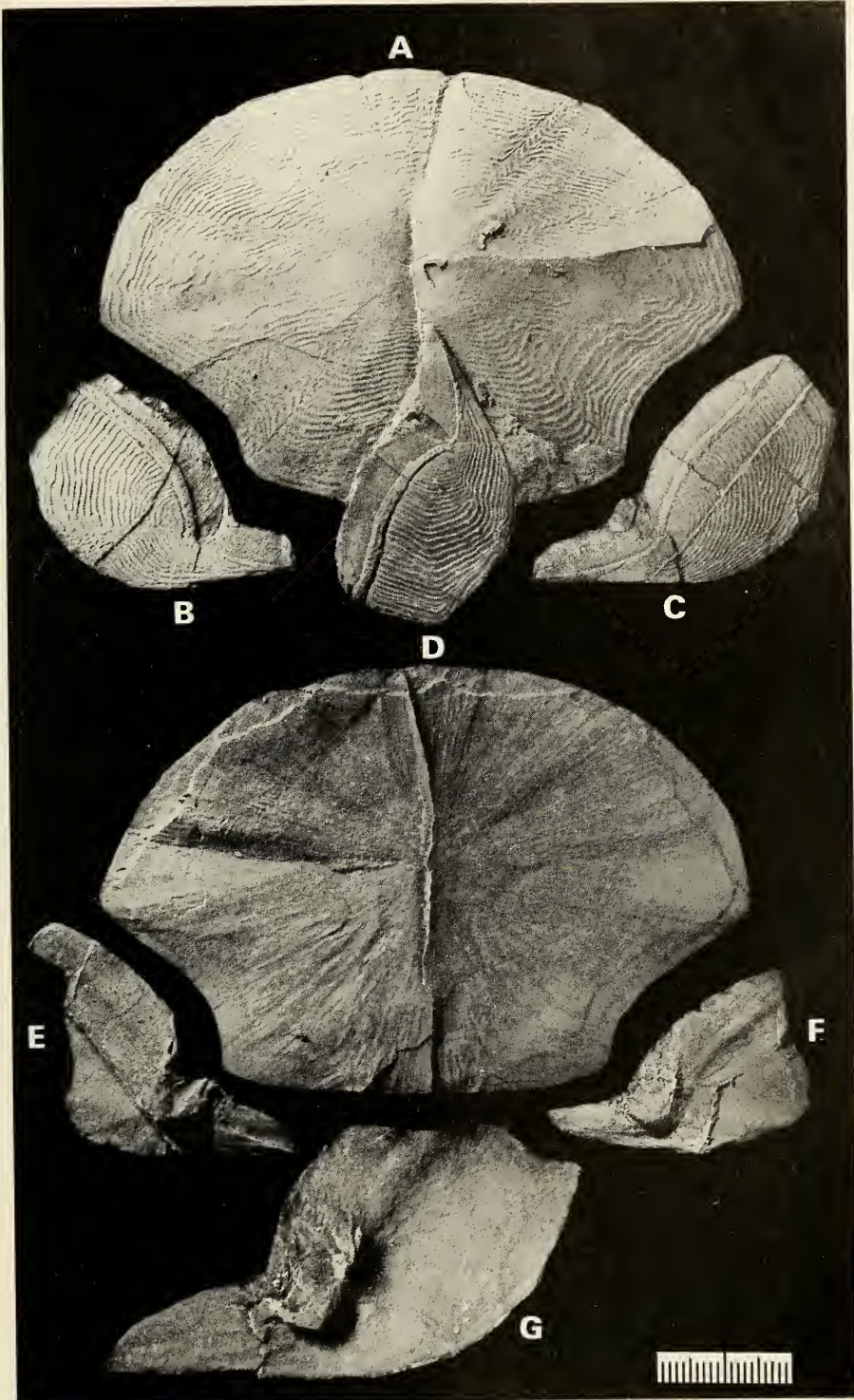


Fig. 2A, B) and the plates may have met and overlapped in the midline as in *P. woodwardi* (Stensiö, 1936: text fig. 3; 1939: text fig. 3).

There is little doubt that this was the condition in *Placolepis*. The plate interpreted here as the postnasal (F.61760, Fig. 7A) is much deeper than the PtN in *Phyllolepis orvini* (Figs 2A, B, 8F) and in the new Australian genus the left and right PtNs appear to have met along a sinuous median suture, each partly overlapping the other.

The PtN is traversed by a short straight canal which is clearly a continuation of one of the anterior pair of canals on the nuchal, the interpretation of which presents a problem. Denison (1978: 42, fig. 26A, roc) has suggested that it may be homologous to the short 'rostral' canal of *Lunaspis*.

TOOTHPLATES OF *PLACOLEPIS* GEN. NOV.

The Nettletons Creek material includes two small tuberculated plates which appear to be placoderm toothplates (Fig. 10 N-Q). The only other placoderm in the same fauna as *Placolepis* is the antiarch *Bothriolepis*, the gnathal elements of which are well known and quite different. Impressions of similar toothplates have been observed *in situ*, underlying the headshield, in several specimens of *Phyllolepis* sp. nov. from the Frasnian Mt Howitt fish fauna of central Victoria (Marsden, 1976: 79, 122). The isolated elements found with *Placolepis* appear to represent both superognathal and inferognathal elements.

The superognathal (Sg) is a small, flat, subtriangular plate 8 mm long and 5.5 mm wide, covered with 9 or 10 radiating rows of small conical denticles which increase in size distally (F. 61920, Fig. 10P, Q). The rows of denticles converge on one corner, possibly anteriorly, but because the original orientation of the plates remains uncertain it has been figured in two positions.

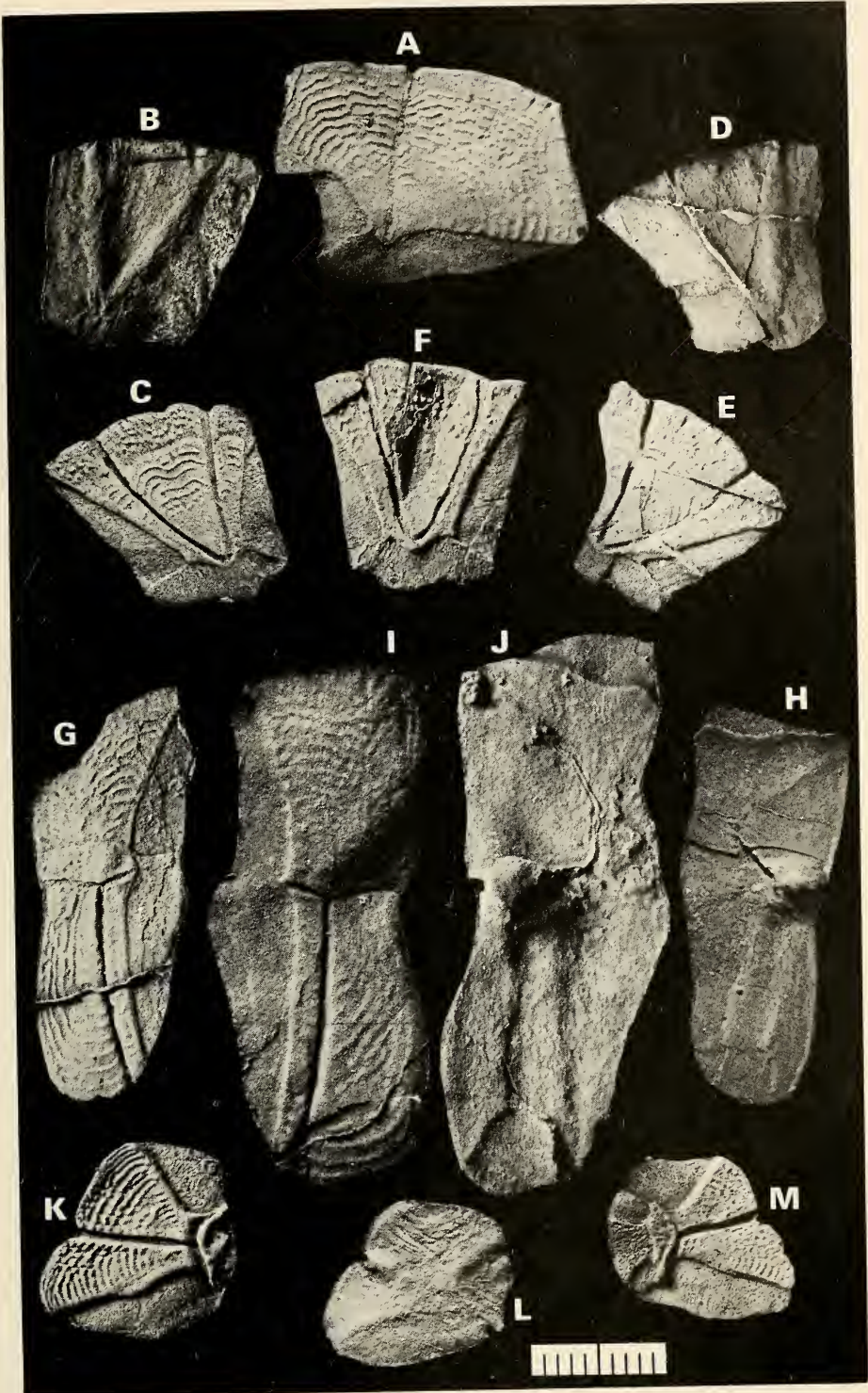
The second denticle covered plate, interpreted here as the inferognathal (Ig), is quite different in shape (F.61761, Fig. 10N, O). It is lenticular, 14 mm long and 4 mm wide in the middle and pointed at both ends. As with the Sg the small conical denticles are arranged in radial rows. Some 16 or 17 slightly curved rows of tubercles converge midway along the straighter of the lateral margins. Again the original orientation of the plates remains conjectural. The closest equivalent in other placoderms would appear to be the superognathal plate of the phlyctaeniid arthrodire, *Dicksonosteus arcticus* Goujet (1975: figs 3, 4).

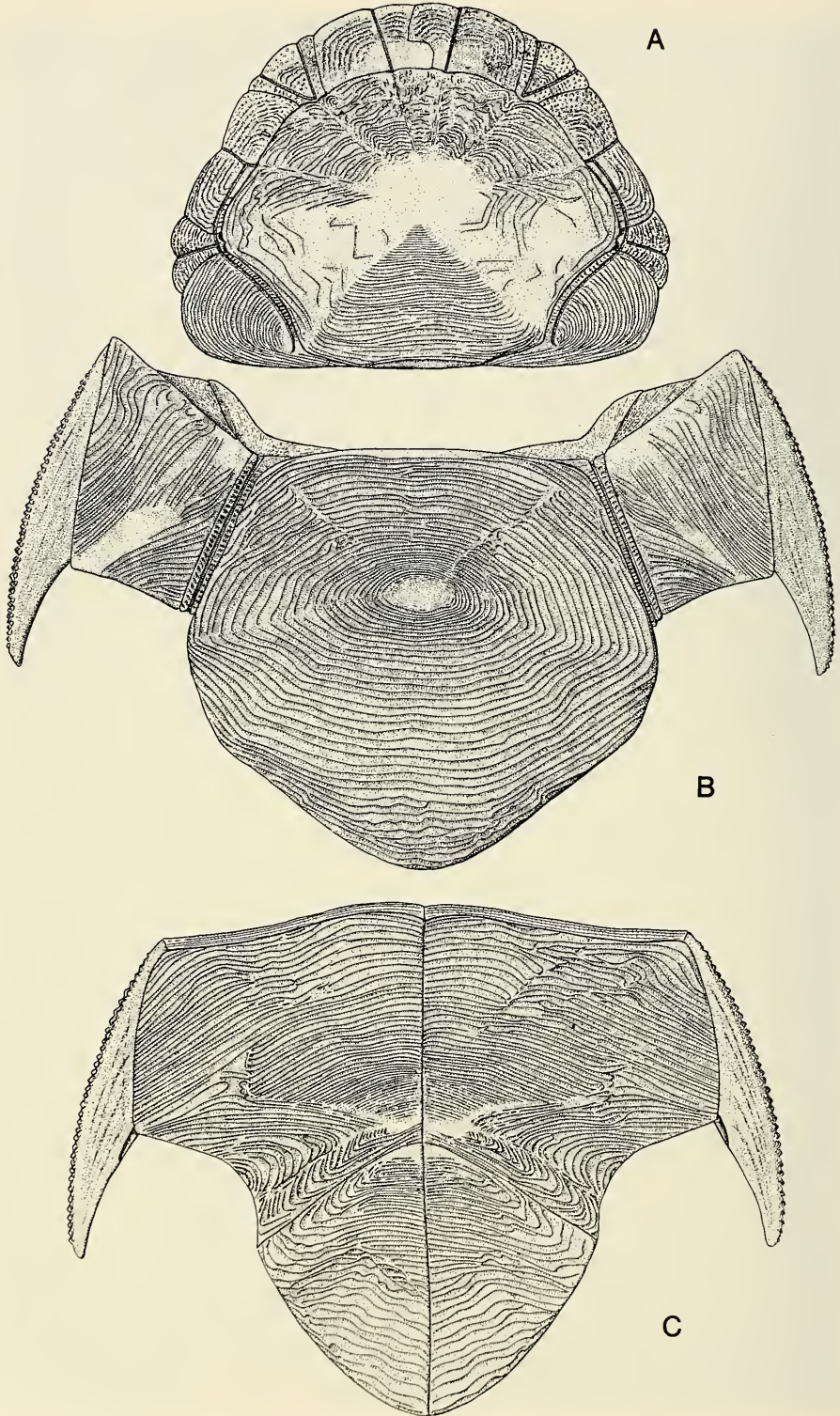
TRUNK SHIELD

The thoracic shield of *Placolepis* (Fig. 8B, C) is developed basically like that of the various species of *Phyllolepis* with several minor but significant differences.

Median dorsal (MD) — relatively complete and uncrushed specimens of the MD of *Placolepis budawangensis* indicate that this plate was more convex in cross section than the MD of *Phyllolepis orvini* as depicted by Stensiö (1936: fig. 12). The *Placolepis* MD (Figs 8B, 9A-E) is subpentagonal in outline but more rounded and less angular than that of

Fig. 7. *Placolepis budawangensis* gen. et sp. nov., smaller cranial plates. A) right ?postnasal (PtN), dermal surface, AM F.61760; B-E) left and right preorbitals (PrO) in visceral and dermal views; both specimens on same block (F.61915, counterpart F.61916) and probably from same individual; F) right ?preorbital, F.61921; G, H) left postorbital (PtO), dermal and visceral view, F.61757a,b; I, J) right postorbital, dermal and visceral view, F.61759a, b; K) left marginal (Mg), dermal surface, F.61758; L, M) right marginal, visceral and dermal views, F.63873, F.63874. Latex casts whitened with ammonium chloride sublimate. Scale in millimetres.





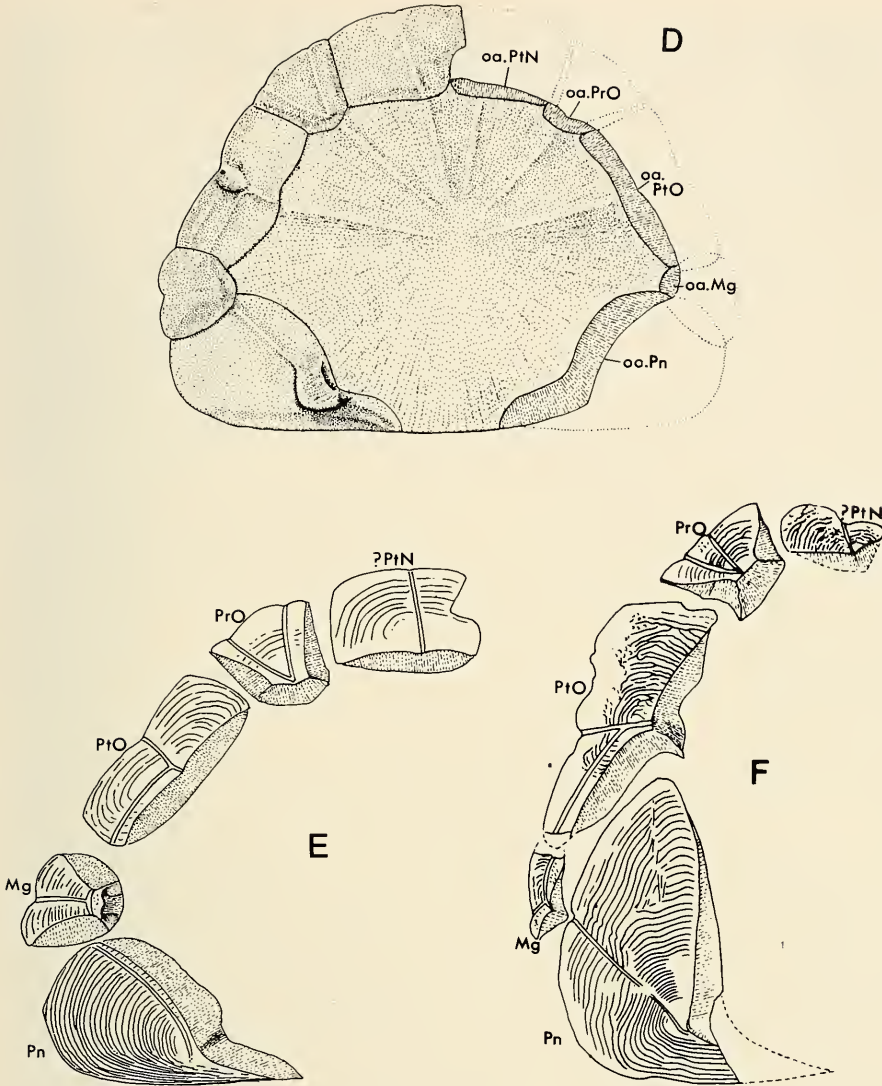


Fig. 8. *Placolepis budawangensis* gen. et sp. nov., restorations of head and trunk shields, dorsal and ventral. Approximately natural size.

A) headshield in dorsal view; nuchal shield based on information from several figured examples, of intermediate length: width proportions. Depicted as if flattened in horizontal plane; no allowance made for original curvature (cf. Figs 2C, D, 13).

B) dorsal trunk shield and **C)** ventral trunk shield, both in dermal view; depicted as if flattened in horizontal plane. Relative proportions based initially on relevant plates of the holotype (AM F.61748, Fig. 3A, B) with additional details from other, more complete, examples.

D) headshield in ventral view with left cranial plates removed to reveal extent of overlap areas on nuchal plate (cf. Fig. 5 A-C, Fig. 6 A,D). Abbreviations as for Fig. 2 with following additions: oa.PtN?, oa.PrO, oa.PtO, oa.Pn — overlap areas for relevant plates.

E, F) smaller cranial plates of *Placolepis* gen. nov. (**E**) and *Phyllolepis orvini* (**F**) separated to show relative positions and extent of overlap areas. The *P. orvini* plates are redrawn from Stensjö as follows:— Pn (1934: fig. 19 = M4); Mg (1936: fig. 15 = M5); PtO (1934: fig. 18 = M3); PrO (1934: fig. 17 = M2); PtN? (1936: fig. 13 = M1).

Phyllolepis orvini, *P. woodwardi* or either of the Belgian species, *P. konincki* or *P. undulata* (Leriche, 1930: pl. 1, figs 2a, 3a, pl. 2, fig. 1a; Stensiö, 1939: text fig. 5).

The length/width of the *Placolepis* MD varies between 0.8 and 1.0 perhaps partly as a result of post-mortem flattening and crushing.

The centre of ossification, and of the subconcentric ornament, is more anteriorly situated than in the various species of *Phyllolepis* where it is virtually central. In *Placolepis* about 35% of the plate length lies anterior to the ossification centre and 65% posterior to it. The strongly-developed, ridged ornament is less angular and zig-zag than that of *Phyllolepis* spp. As in *P. orvini* (Stensiö, 1969: fig. 132; this paper Fig. 2A) a branch of the lateral canal passes postero-dorsally onto the MD from the lateral canal on the ADL, but in *Placolepis* this canal emerges near the anterolateral corner of the MD and not farther back as in *Phyllolepis* (Figs 8B, 9A, B, D). This canal is not always clearly developed.

No trace has been found in *Placolepis* of a short 'canal' midway along the anterior margin of the MD as depicted in *Phyllolepis orvini* (Stensiö, 1969: fig. 32, dx) but it should be noted that in *Phyllolepis* this feature is only known from one specimen (Stensiö, 1936: pl. 10) and should probably be regarded as an individual aberration in the ornament.

The visceral surface of the *Placolepis* MD is smooth, completely lacking any development of a keel but with a short and very low median ridge lying just behind the anterior margin. The antero-lateral margins of the MD display an extensive L-shaped overlap area for the anterior dorsolateral (ADL).

Anterior dorsolateral (ADL) — in *Placolepis* (Fig. 10 A-C), as in *Phyllolepis*, the exposed portion of the ADL is extremely narrow. The anterior margin of the ADL is narrow in front of the MD but wider under in front of the AL where it forms part of an articular process.

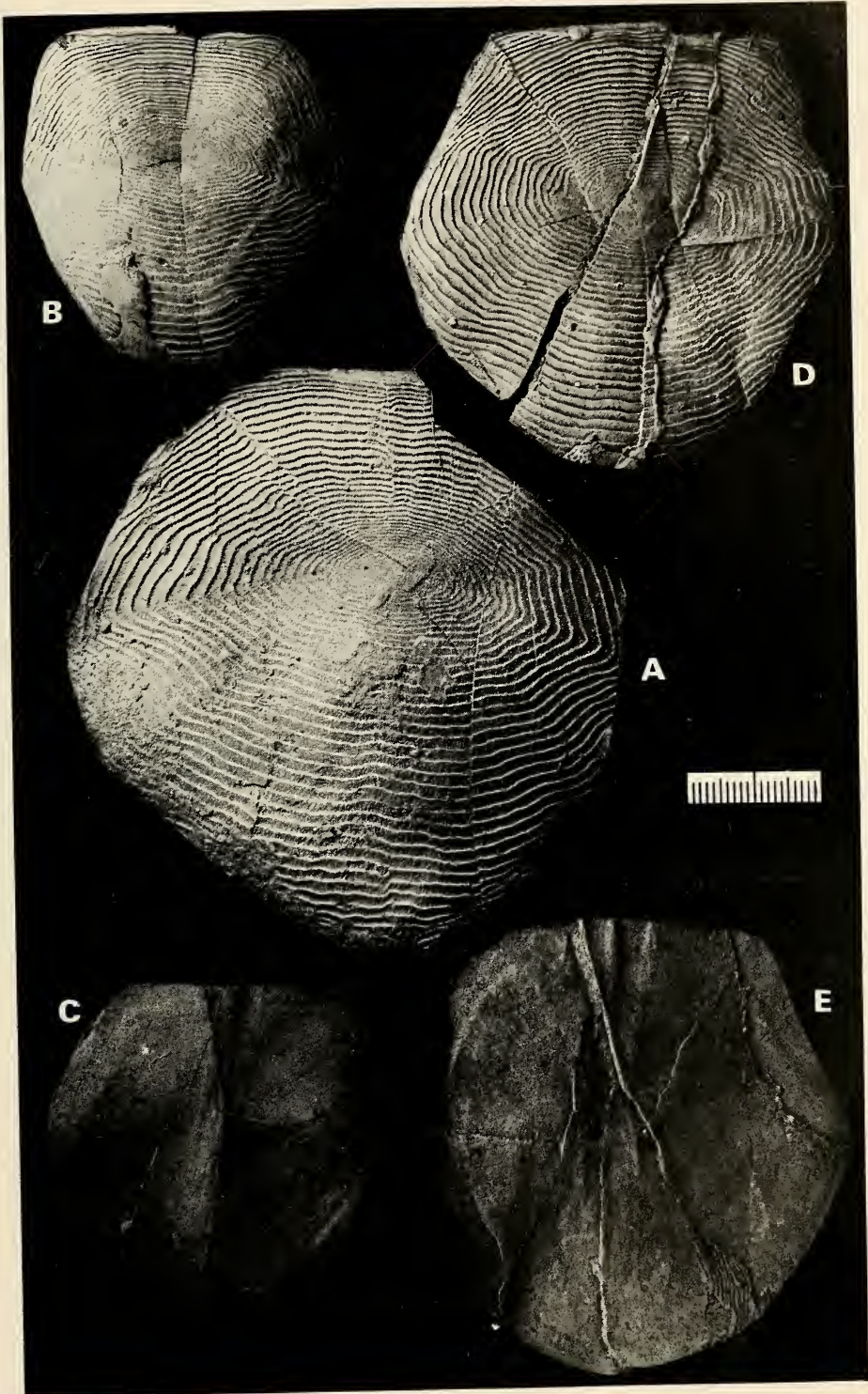
Anterior lateral (AL) — many well-preserved examples of the *Placolepis* AL plates have been recovered (Figs 3A, B, 10D-I). Although quite variable in shape and ornament the ALs are all longer than high with a steeply sloping anterior margin. This bears a subtriangular anterior projection which combines with, and buttresses, the anteroventral margin of the ADL to form a smooth, flattish articular lamina (Fig. 3B) which clearly extended under the posterior margin of the paranuchal plate of the headshield. The degree of free movement was obviously rather limited and the articulation is reminiscent of the sliding cranio-thoracic arrangement in actinolepid euarthrodires except that in the latter the glenoid process is formed almost entirely by the ADL with little involvement of the AL.

The *Placolepis* AL has an almost straight, sloping dorsal margin, a vertical, slightly concave posterior margin and a ventral margin (bordering the spinal plate) which varies from gently to strongly convex. The ornament consists of radiating longitudinal ridges which tend to converge on the posteroventral corner of the AL, as in *Phyllolepis orvini* (Stensiö, 1936: text fig. 10) and other species.

The dorsal and ventral thoracic shields are linked only by the spinal plates. Posterior dorsolateral (PDL) and posterior lateral (PL) plates were obviously absent in *Placolepis*, as in *Phyllolepis*, and the large posteriorly-directed fenestra for the pectoral fin was clearly open behind and not bridged posteriorly by the trunk shield.

Fig. 9. *Placolepis budawangensis* gen. et sp. nov., three isolated median dorsal plates (MD). Latex casts whitened with ammonium chloride sublimate. Scale in millimetres.

A) AM F.61766, dermal surface; B, C) F.61769a,b, dermal and visceral surfaces; D, E) F.61722a,b, dermal and visceral surfaces.



Anterior ventrolateral plate (AVL) — the AVLs of *Placolepis budawangensis* (Figs 3, 8C, 10J, K, 11A, B, F, G, 12A, B) are of typical phyllolepid type, large broad plates with proportions and ornament variable but not significantly different from the AVLs of *Phyllolepis orvini*, *P. woodwardi* (Stensiö, 1934, 1936), *P. tolli* Vasiliauskas (1963) and others. The *Placolepis* AVLs are ornamented with a variable pattern of transverse, obliquely directed, and slightly sinuous ridges. Towards the posterior margin the ridges alter direction abruptly several times and are also traversed by a prominent ridge parallel to, and a short distance anterior to the rear margin of the AVL. In this the *Placolepis* AVLs resemble those of *Phyllolepis neilseni* Stensiö (1939: text fig. 10, pl. 3) more than the AVL of *P. orvini*.

In several AVLs (Fig. 11A, B, F, G) a shallow but marked oblique groove traverses the plate from the AVL/PVL junction in the midline to the anterolateral corner of the AVL. The degree of convexity preserved in some of the *Placolepis* AVLs and the angle at which they met in the midline indicates a deeper profile than was estimated to be present in *Phyllolepis* and this is supported by the posterior ventrolateral plates.

Posterior ventrolateral plate (PVL) — the PVLs were fairly stout, subtriangular and strongly convex plates (Figs 3 A, B, 10 L, M, 11 H, I, 12 C, D). Their general proportions and ornament are so variable that many of them would be difficult to distinguish from those of various *Phyllolepis* species which are also individually variable. Some idea of the diversity of the PVLs in *Placolepis* may be obtained from Fig. 13A-F.

The oblique anterior margin displays a well developed overlap area for the AVL but the median suture is straight and non-overlapping like that of the AVLs. Experimental reassembly of the plates of the ventral trunk shield indicates that it was quite convex and that the trunk cross section immediately posterior to the thoracic shield was quite rounded (Fig. 14).

Median ventral plates (AMV, PMV) — an anterior median ventral plate has been reconstructed in various species of *Phyllolepis* (*P. orvini*, *P. woodwardi* Stensiö, 1934, 1936, 1939) but no such plate has been observed in *Placolepis*. The published evidence for such a plate in *Phyllolepis* appears to be based largely on the single articulated specimen of *P. woodwardi* from Dura Den, Fife, Scotland (Stensiö, 1934: text fig. 2D; 1936: text fig. 5), where a small triangular plate is identified as the AMV. The only evidence for the presence of a similar plate in *P. orvini* appears to be a slight rounding of the antero-mesial corners of the AVLs in a few of the figured specimens (Stensiö, 1936: text fig. 22, pls 19-21). It should be noted, however, that in many of the other figured specimens (Stensiö, 1934: text figs 24, 25, pl. 12; 1939: text fig. 10, pl. 3, fig. 3) there is

Fig. 10. Placolepis budawangensis gen. et sp. nov., dorsolateral, lateral, ventral and spinal plates of trunk shield and probable toothplates. Latex casts whitened with ammonium chloride sublimate. Millimetre scale for all except the toothplates (N-Q), which are $\times 2$.

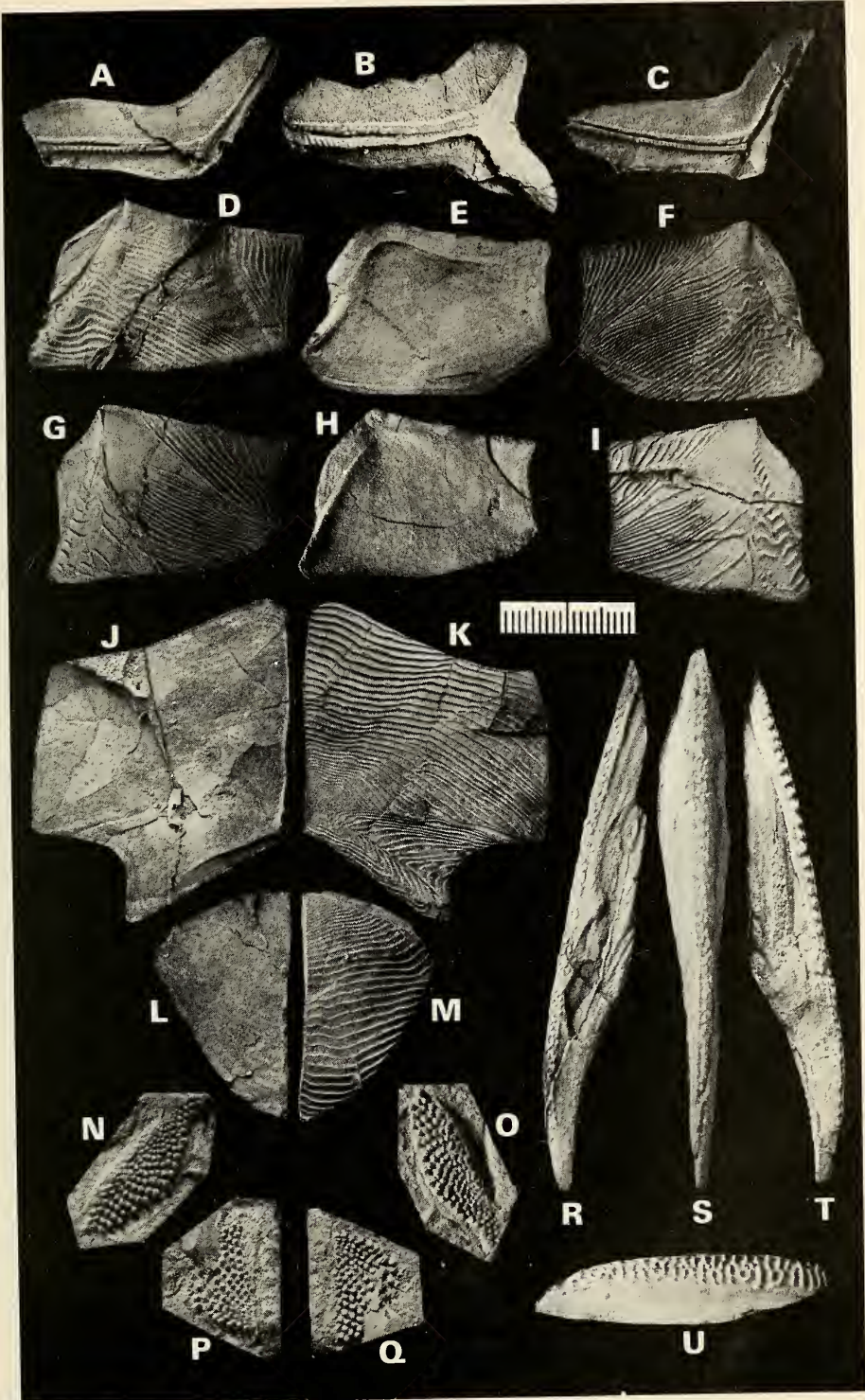
A-C) three right anterior dorsolateral (ADL) plates, in dermal view; A) AM F.61783, B) F.61782, C) F.61784.

D-I) anterior lateral (AL) plates; D) left AL, dermal surface, F.61919; E, F) right AL, visceral and dermal surfaces, F.61908b and counterpart, F.61908a; G, H) left AL, dermal surface and right AL, visceral surface, both plates closely associated on same specimen, F.61799, and probably from same individual; I) right AL, dermal surface, incomplete posteriorly, F.61781.

J-M) left AVL and PVL of small *Placolepis* individual, visceral and dermal surfaces; J, K) F.63878b, F.63878a; L, M) 63879b, F.63879a.

N-Q) ?inferognathal (Ig) and supragnathal (Sg) toothplates, each depicted in two possible orientations; N, O) Ig, F.61761, P, Q) Sg, F.61920; both twice natural size.

R-U) spinal (Sp) plates; R, S, T) ?right Sp, in ventral, lateral and dorsal views, F.61903a and counterpart F.61917; U) incomplete Sp to illustrate coalescence of tubercular ornament into short, transverse ridges, F.61912.



no trace of this supposed margin or of any overlap area for the AMV and the same applies to *Placolepis budawangensis* (Figs 10-12). The restoration given in Fig. 8C assumes that this plate is absent.

Stensiö (1934: text fig. 2D, *x*; 1936: text fig. 5, *Px*) also detected what appeared to be a small, extremely narrow, posterior median ventral plate (PMV) in the ventral shield of the holotype of *Phyllolepis woodwardi*. No trace of a PMV has been detected in any of the Greenland *Phyllolepis* material. In *Placolepis* the longitudinal median sutures are extremely straight, providing no support for the presence of such a median plate. J. Long, Monash University (*pers. comm.*) has informed the writer that the new species of *Phyllolepis* from the Mt Howitt fauna does possess a small but well-developed PMV plate. From this, and from the evidence of *P. woodwardi* described above, it would appear probable that both AMV and PMV plates formed part of the original complement of plates in the ancestral phyllolepid trunk shield and that they have been subsequently reduced and/or secondarily lost in most later representatives of the Phyllolepidae.

Interolateral plate (IL) — the single example of the IL is represented by moulds of its dermal and visceral surfaces on slabs F.63873 and F.63874 (Fig. 11C-E). The plate is partly obscured by a *Bothriolepis* plate but the visible portion is 37 mm long and 2-3 mm wide for most of its length. 8 mm from the distal end it flares to 5 mm wide before tapering to a point. The outer surface (Fig. 11E) is ornamented with extremely fine, longitudinal denticulate ridges. In general it compares closely with the IL of *Phyllolepis orvini* (Stensiö, 1936: text fig. 21, pl. 1, fig. 6, pl. 17, figs 1-3) and *P. woodwardi* (Stensiö, 1936: text fig. 5).

Spinal plate (Sp) — the spinal plate is long and well-developed, hollow throughout most of its length and with up to one third of its length projecting posteriorly and flanking the (presumed) pectoral fin (Figs 10R-T, 12E,F). The Sp is narrowest anteriorly, reaching its widest point at the posterior end of the AL and AVL junction. On the dorsal and ventral surfaces faint longitudinal ridges converge posteriorly. The outer, rounded margin is ornamented with a single longitudinal ridge flanked dorsally and ventrally by 2-3 rows of tubercles which sometimes coalesce into short, transverse ridges (Fig. 10U). The inner margin of the posterior spine may bear a single row of small tubercles.

Stensiö depicted the Sp as having been extensively overlapped dorsally and ventrally by the AL and AVL plates (Stensiö, 1936: 40, text fig. 20) but in *Placolepis* (and probably also in *Phyllolepis*) the AL/Sp and AVL/Sp sutures appear to have been simple, non-overlapping, edge-on contacts (Fig. 8B, C).

SYSTEMATIC DESCRIPTION

Order PHYLLOLEPIDA Stensiö 1934

Diagnosis: cranial roof relatively flat; nuchal plate enlarged, wider than long; central plates lost; rostral and pineal plates not developed. Orbits probably small and antero-

Fig. 11. Placolepis budawangensis gen. et sp. nov., ventral trunk plates, possibly from same individual, all present on two large slabs, F.63783 (C, E, F, G, I) and its counterpart, F.63874 (A, B, D, H), in close association with a fine nuchal and paranuchal plate (cf. Fig. 6 A, D). Latex casts whitened with ammonium chloride sublimate.

A, G) left anterior ventrolateral (AVL) plate, visceral and dermal surface; B, F) right AVL, visceral and dermal surface.

C-E) right interolateral (IL) plate, in dermal (C) and visceral (D) views, with enlargement, $\times 2$ (E).

H, I) right and left posterior ventrolateral (PVL) plates, dermal surfaces.



lateral. Lateral lines occupy shallow grooves; posterior pit-lines, central, supraorbital and rostral ?canals converge towards centre of nuchal. Cranio-thoracic joint formed by simple flanges. Median dorsal plate short and broad, lacking inner keel. Posterior lateral and posterior dorsolateral plates absent. Spinal plate moderately long. Anterior and posterior median ventral plates small or absent.

Family PHYLLOLEPIDAE Woodward 1891

Diagnosis: cranial shield broad and flat, nuchal wider than long, enlarged to cover much of cranial roof. Rostral and pineal plates not developed; central plates lost; marginal, postorbital and postnasal plates relatively small bordering nuchal and paranuchals laterally and anteriorly. Four pairs of shallow lateral line grooves converge on centre of nuchal. Orbits small and anterolateral, not expressed in cranial plates. Trunk shield broad and flat, moderately long; anterior dorsolaterals with long, narrow exposed face. Spinals moderately long, projecting posteriorly. Ventral shield short and broad, with large anterior ventrolaterals and shorter, subtriangular posterior ventrolaterals. Anterior and posterior median ventrals minute or absent. Ornament of concentric slightly undulating ridges, locally of elongate tubercles.

Genus *PHYLLOLEPIS* Agassiz 1844

Diagnosis: as for family with following additions. Nuchal subpentagonal, widest anteriorly. Paranuchals enlarged anteriorly, extending to widest part of nuchal, partly separating postorbitals and nuchal. Marginals small, lateral to paranuchal and bordered anteriorly by postorbital but not in direct contact with nuchal. Lateral canal diverges sharply from nuchal, traversing anterior lamina of paranuchal to meet marginal. Median dorsal subpentagonal, centre of ossification medially situated, ornament concentric, subpentagonal.

Genus *PLACOLEPIS* nov.

Name: from *plax*, *plakos* = broad, flat (Gr.); *lepis* = scale (Gr.).

Type species: *Placolepis budawangensis* sp. nov.

Diagnosis: as for family with following additions. Nuchal rounded anteriorly, widest opposite, or slightly posterior to, centre of ossification. Paranuchals relatively small, bordered anteriorly by marginals and not in direct contact with postorbitals; marginals with short but direct contact with nuchal at widest point. Lateral canal traverses paranuchals, marginals and postorbitals in close proximity to lateral margin of nuchal; paranuchal lacks lamina anterior to lateral canal. Median dorsal large, subpentagonal; ornament concentric with ossification centre situated anterior of midline. Spinals long, projecting posteriorly about one-third of total length. Anterior and posterior median ventral plates absent.

Placolepis budawangensis sp. nov.

Name: after the Budawang Range, southeastern New South Wales, Australia on the western flanks of which the type locality is situated.

Diagnosis: as for genus (only species).

Fig. 12. Placolepis budawangensis gen. et sp. nov., ventral trunk plates and spinal plates. Latex casts whitened with ammonium chloride sublimate. Scale in millimetres.

A) right anterior ventrolateral (AVL) plate, F.61505a; B) left AVL, F.61906a; C, D) right posterior ventrolateral (PVL) plate, dermal and visceral surfaces, F.61909a,b; E, F) spinal (Sp) plates, F.61787a, F.61748 (Holotype, cf. Fig. 3A,B).

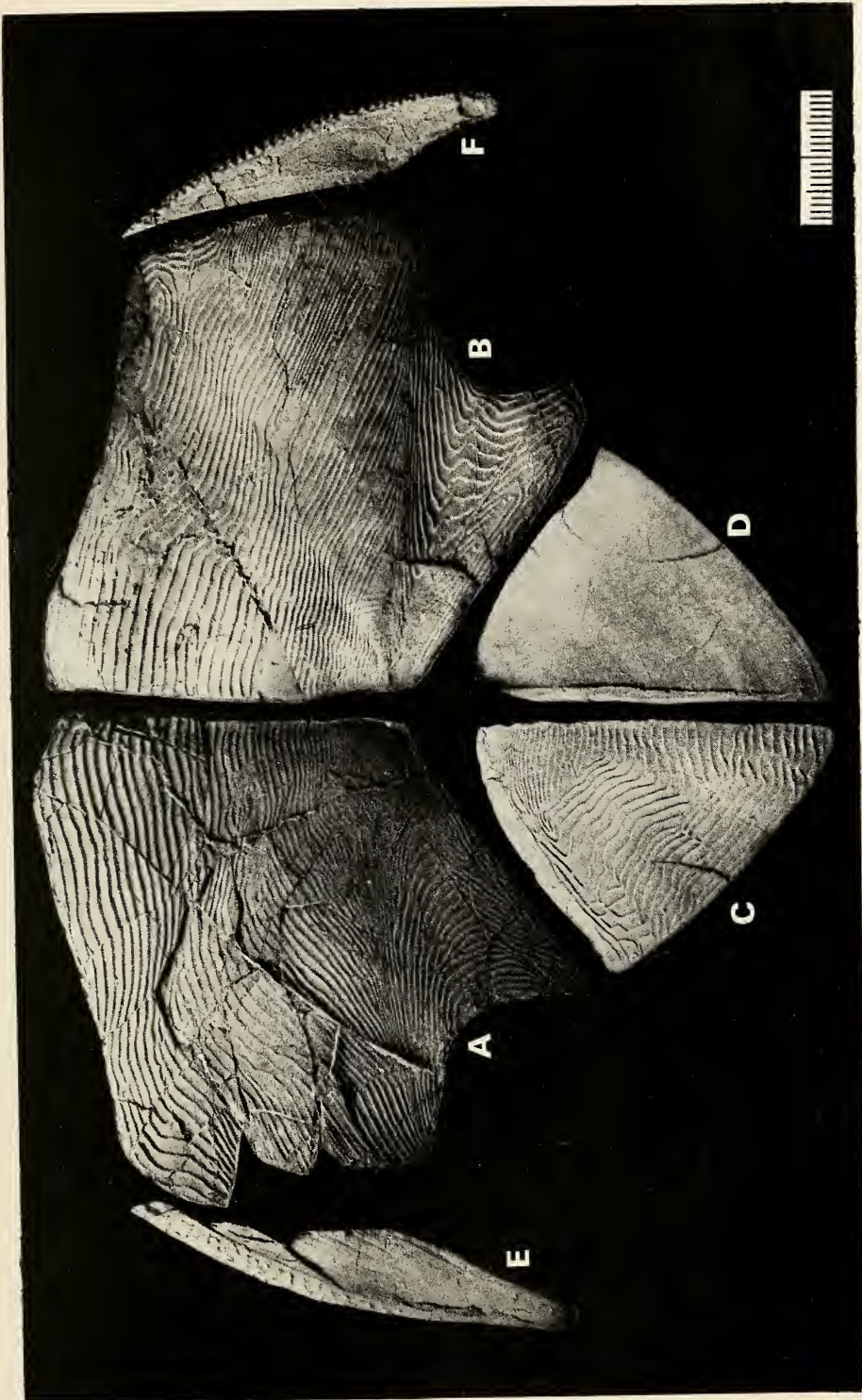


TABLE 1

Length and width of the most complete nuchal (Nu) and the median dorsal (MD) plates of Placolepis budawangensis gen. et sp. nov.

Nuchal Plates	Length (mm)	Width (mm)	% L/W
F.61751	47.5	62	76.6%
F.61901	55	75	73.3%
F.61752	55	80	68.8%
F.61753	55	90	61%
F.68373-4	64	94	68.1%
F.61903	65	95	68.4%
F.61748 (holotype)	68	85	80%
F.61919	70	80	87.5%
F.61750	70	100	70%
Median Dorsal Plates	Length (mm)	Width (mm)	% L/W
F.61769	50	50	100%
F.61913	64	80	80%
F.61772	66	66	100%
F.61768	80	90	88.9%
F.61766	85	92	92.4%
F.61764	90	90	100%
F.63875	93	94	99%

Holotype: AM F.61748, consisting of scattered plates of a single *Placolepis* individual (Nu, PtN?, MD, 2 ALs, 2 AVLs, 2 PVLs, Sp) associated with a right PVL of another *Placolepis* and numerous plates of *Bothriolepis* sp.

Referred material: large slab, in counterpart, AM F.63873, 63874, bearing scattered remains of at least two *Placolepis* individuals (Nu, Pan, Mg, PtO, MD, AL, 4 AVLs, 2 PVLs, IL, Sp) associated with at least four individuals of *Bothriolepis* sp.

Cranial plates: nuchals (AM F.61750, 61751, 61752, 61753, 61901, 61902, 61919, 61921, 63875); postnasals? (F.61760, 61756); preorbitals (F.61915, 61916, 61918, 61921); postorbitals (F.61757, 61759, 61763); marginals (F.61756, 61758, cf. also F.63873-4) paranuchals (F.61755, 61756, 61925); superognathal (F.61920); inferognathal (F.61761).

Trunk plates: median dorsals (F.61764, 61766, 61768, 61769, 61772, 61913, 63875, 63876); anterior dorsolaterals (F.61782, 61783, 61784); anterior laterals (F.61779, 61781, 61908, 61919); interolateral (only known specimen on slabs F.63873-4); anterior ventrolaterals (F.61505, 61776, 61777, 61906, 61907, 63878); posterior ventrolaterals (F.61909, 61910, 61912, 61923, 63879); spinals (F.61787, 61912, 61903/61917, pt. and ctp.).

RELATIONSHIPS OF PHYLLOLEPIDIDA TO OTHER PLACODERMS

Phyllolepis and *Placolepis* gen. nov. are closely related, very specialized Late Devonian placoderms characterized by a reduced complement of plates in the trunk shield and by an enormous enlargement of the nuchal plate at the expense of the other plates of the headshield, a pattern not readily comparable with that of the Arthrodira ss.

Phyllolepid relationships have been the subject of controversy since their discovery in the early 19th century. More recent discussions of their affinities with other placoderms are those of Westoll (1967), Stensiö (1969), Moy-Thomas and Miles

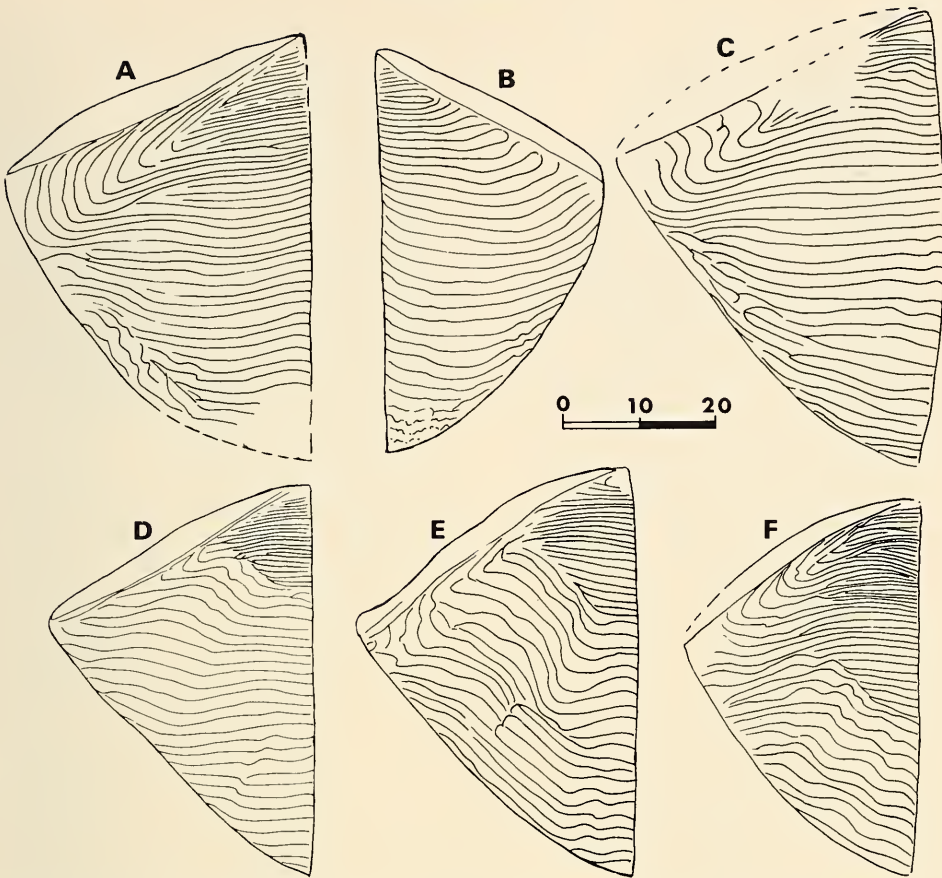


Fig. 13. *Placolepis budawangensis* gen. et sp. nov., six posterior ventrolateral (PVL) plates showing variation in ornament (for other examples cf. Fig. 11 H, I). All to same scale, shown in mm.

A) right PVL, holotype, F.61748 (cf. Fig. 3A, B); B) left PVL, F.61912; C) right PVL, F.61923; D) right PVL, F.61910a; E) right PVL, F.61909 (cf. Fig. 12C); F) right PVL, F.61748 (cf. Fig. 3A, B; extra right AVL not belonging to holotype).

(1971), Denison (1975, 1978), Miles and Young (1977), Young (1980, 1981) but it would be fair to state that a consensus is still far from being reached.

Westoll (1967: 96) suggested that placoderms formed two natural groups, divergently specialized in one important manner.

- a) placoderms with a long occipital region and two pairs of paranuchals in the skull roof — petalichthyids, rhenanids and stenioellids.
- b) placoderms with a short occipital region and only one pair of paranuchals — the euarthrodires (including the ptyctodontids and presumably the phyllolepid) and their probable derivatives, the antiarchs.

More recently the ptyctodontids and phyllolepid have generally been considered to belong outside the Arthrodira (or Euarthrodira) *ss.* and placed in their own separate orders.

Moy-Thomas and Miles (1971: 197) queried the use of these characters, pointing out that in most members of the first group the skull roof could not be interpreted with

a high level of confidence. Since then most attention has focused on shared or derived characters in the trunk shield rather than in the headshield. Moy-Thomas and Miles (1971: 198) considered that the earliest known members of most placoderm groups already showed the typical characters of the group to which they belonged, 'thus it is not possible to say whether the trunk shield ever extended posteriorly on the flank behind the pectoral fins in petalichthyids, ptyctodontids, phyllolepid and stenioellids, as it does in arthrodires and antiarchs, and we cannot say whether the long type found in primitive arthrodires is primitive for all placoderm groups'.

Denison (1975: 12-13) proposed that an anteroposteriorly short trunk shield was primitive. He maintained that this had remained short in stenioellids, pseudopetalichthyids, rhenanids and ptyctodontids and that the first steps in lengthening it were to be seen in the Acanthothoraci (Palaeacanthaspididae and Kolymaspidae) with the addition of posterior lateral (PL) and posterior dorsolateral (PDL) plates; (but cf. also (Denison, 1978: 34) where the evidence for the PLs is questioned).

The next stage was the development of a ventral shield composed of AVLs, PVLs, AMV, PMV, and ILs; this is seen in petalichthyids and arthrodires, the early members of which had a pectoral fenestra enclosed by union of the ventral and lateral shields. The evolutionary position of the phyllolepid — with a moderately long thoracic shield but lacking PLs and PDLs — presented a problem; was this condition original or by secondary reduction?

Miles and Young (1977: 126-8) criticized Denison's phylogeny on grounds of parsimony. Whilst admitting that, at present, it is not possible to produce a convincing hypothesis of placoderm taxa relationships they suggested alternative phylogenies, starting from the basis of Moy-Thomas and Miles (1971: 198) quoted above.

Miles and Young (1977: 135-6) recognized only one genus of phyllolepid, ruling out *Antarctaspis* as a close relative. *Phyllolepis* had 'only one paired paranuchal, no tesserae and a short trunk shield with a posterior ventrolateral plate. The pattern of plates in the headshield is in some respects unique, but there are no known specializations here which link this genus with many of the groups considered so far'. They considered, but rejected, Denison's reason for linking *Antarctaspis* with *Phyllolepis*, which was based apparently on the fact that the supraorbital canal (*soc*) and central canal (*cc*) passed onto the nuchal plate. They noted that the *soc* passed onto the Nu also in petalichthyids, ptyctodontids and *Wuttagoonaspis* and that the *cc* passed onto the nuchal in *Wuttagoonaspis* and in some specimens of the arthrodire *Baringaspis*. The evidence of the sensory canals did not, therefore, provide a sound reason to link *Antarctaspis* and *Phyllolepis*.

Miles and Young also suggested (1977: 136) that the phyllolepid canal pattern was either a) primitive for placoderms or b) subject to convergent evolution. They tentatively suggested 'that phyllolepid might be most closely related to the common ancestor of arthrodires and antiarchs. These three groups are unique in having posterior ventrolateral plates'. The recent discovery of a PMV in the new Victorian phyllolepid removes another point of difference.

It was suggested (Miles and Young, 1977: 131) 'that primitive placoderms possessed median dorsal, dorsolateral, anterior lateral, interolateral, spinal, anterior ventrolateral and anterior median ventral plates. Two types of trunk shields were proposed:

- a) a short shield with the plates listed above, primitive for placoderms, and in which there are no plates on the flank behind the pectoral fin; posterior laterals are absent (e.g. petalichthyids).
- b) a long shield in which the ventral and lateral plates meet on the flank to enclose the

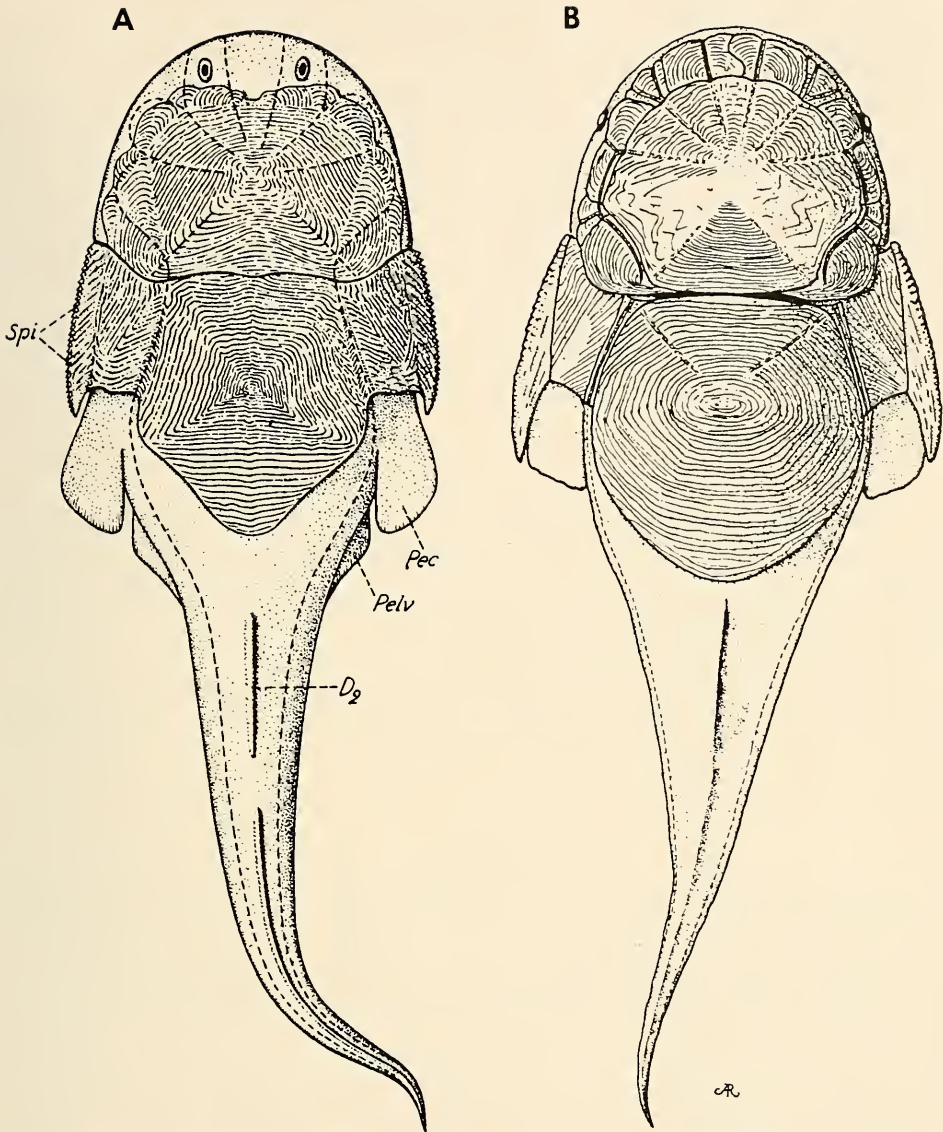


Fig. 14. *Phyllolepis orvini* Heintz and *Placolepis budawangensis* gen. et sp. nov. Restorations of the two genera in dorsal view illustrating alternative interpretations of the shape of the fins and trunk and the probable position of the eyes.

A. *Phyllolepis*, after Stensiö (1969: 77, fig. 3) and
 B. *Placolepis* (and, it is suggested, *Phyllolepis*) by the writer.

base of the pectoral fin; posterior laterals are present, either as separate plates or combined with posterior dorsolaterals to form mixilaterals (e.g. arthrodires and antiarchs).

On this basis *Phyllolepis* (and *Placolepis*) would fall in group a) but this would be

paraphyletic and would not accurately reflect its relationships, especially since we know that phyllolepid, arthrodires and antiarchs share not only posterior ventrolaterals but also posterior median ventrals.

The new genus, *Placolepis*, is not sufficiently different from *Phyllolepis* to throw much new light on the origins or relationships of the phyllolepid. Young (1980: 66, text fig. 27) included *Phyllolepis* in the Dolichothoracomorpha as the sister group of *Wuttagoonaspis*, antiarchs and euarthrodires. His analysis of the biogeography and interrelationships of placoderms 'suggests differentiation of certain more primitive placoderm taxa (*Antarctaspis*, *Phyllolepis* and *Wuttagoonaspis*) in the region of East Gondwana, and of more derived forms (actinolepid and phlyctaenioid euarthrodires) in Euramerica' (Young, 1981: 237).

The discovery of phyllolepid from the Middle Devonian or earlier rocks may provide a wider range of characters and a better understanding of which features are primitive; on present evidence Australia would appear to be the area most likely to yield earlier phyllolepid.

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