

A NEW ANTIARCHAN FISH (PLACODERMI) FROM THE LATE DEVONIAN OF SOUTHEASTERN AUSTRALIA

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A new asterolepidoid antiarch is described from sediments of probable Late Devonian (Frasnian) age in the Boyd Volcanic Complex, on the south coast of New South Wales. It occurs as a rare element in an assumed freshwater assemblage with abundant *Bothriolepis* and *Phyllolepis*, and less common rhipidistian, acanthodian, and possible onychodontid remains. *Pambulaspis cobandrahensis* gen. et sp. nov. resembles *Remigolepis* in possessing separate posterior dorsolateral and lateral plates and a prominent postorbital crista, and resembles *Asterolepis* in having an elongate postorbital process and prominent

suborbital area, and lacking the posterior oblique pit-line groove in the adult. It differs from both in that the posterior dorsolateral completely overlaps the anterior median dorsal, and the lateral line canal crosses the posterior lateral plate instead of the posterior dorsolateral. The preorbital region of the skull, certain plates of the trunk, and the basic structure of the pectoral fin are not known. It is suggested that *Pambulaspis* is closely related to *Asterolepis* and *Remigolepis*, and may be a sister taxon to the latter. The most recent common ancestor of these genera must have been Eifelian or older.

Introduction

Diverse faunas of Devonian fishes were discovered in the Eden-Pambula area of southeastern New South Wales during detailed mapping of the area in 1978. The mapping was undertaken to investigate the relation between intrusive and extrusive igneous rocks and associated sediments of Mid-Late Devonian age, which are widespread in the region. A preliminary study of a small collection of fish material from eight new localities (Young, *in* Fergusson & others, 1979) indicated that four assemblages were probably represented, ranging in age possibly from the latest Middle Devonian (Givetian) through to the end of the Late Devonian (Famennian). The fact that the fishes occur stratigraphically above and below a marine formation with an invertebrate fauna of Frasnian age and that granites intruding the sequence have been dated isotopically suggested that more detailed study of the fishes might provide information of biostratigraphic significance. Accordingly, the area was revisited in 1979 and much new material was collected from the original and some additional localities. Elasmobranchs in this new collection from Bunga Head, north of Pambula, have recently been described (Young, 1982).

In this paper, a new antiarch belonging to the suborder Asterolepidoidei is reported from sediments of probable Frasnian age. The occurrence is of interest in filling out the record of this major subgroup of antiarchs in Australian rocks, a group that, until fairly recently, appeared to be poorly represented. Previous assignments include Hills' (1936, 1958) determination of an antiarch plate from Gilberton in Queensland as belonging to *Asterolepis*, although this specimen is not diagnostic and may belong instead to the much more common form, *Bothriolepis*. Other material from Western Australia (*see* Young, 1974, p. 252) can, however, be referred with confidence to the suborder, but the material is insufficient to determine conclusively whether it belongs to *Asterolepis* or *Remigolepis*. The latter genus, first described by Stensiö (1931) from near the top of the Devonian vertebrate succession in east Greenland, has been known to occur in Australia since Hills (1932) reported plates of a new species from the Upper Devonian Hervey Group (Connolly, 1965), north of Parkes in central western New South Wales. *Remigolepis* has since been reported (but not described) from other localities in southeastern Australia (Tomlinson, 1968; Young, 1974; Ritchie, 1975; Campbell & Bell, 1977), and it also occurs abundantly in the youngest known vertebrate horizon in the Eden-Pambula area (the Worange Point Formation; *see* Fergusson & others, 1979). These occurrences have generally been regarded as Late Devonian in age, by comparison with the European occurrences of *Remigolepis*, considered to be latest Late Devonian (Famennian) or even

Early Carboniferous (e.g. Westoll, 1951, 1979; Jarvik, 1961; Andrews, 1978). However, the possibility of an earlier age for *Remigolepis* in Australia has not been discounted (Tomlinson, 1968; Young, 1974).

In Europe, the suborder Asterolepidoidei is also well represented in Middle Devonian deposits, but equivalent occurrences were unknown in Australia until fairly recently. Young & Gorter (1981) described a new form *Sherbonaspis hillsi* from a Middle Devonian fauna near Wee Jasper, New South Wales, and reported similar remains from the Broken River area of Queensland. The earliest known asterolepidoid occurrence in Australian rocks, and one of the earliest yet recorded, is from the Early Devonian of the Georgina Basin, central Australia (Young, *in* preparation). The new member of this group, described below as *Pambulaspis cobandrahensis* gen. et sp. nov., fills a gap between the Middle Devonian occurrences in New South Wales and Queensland and the Late Devonian *Remigolepis* occurrences of southeastern Australia.

Dermal bone terminology and antiarch classification used here generally follow those of Miles (1968). Measurement of dermal bones is in accordance with the system of Karatajute-Talimaa (1963). All described and figured specimens are deposited in the Commonwealth Palaeontological Collection (prefix CPC), housed in the Bureau of Mineral Resources, Canberra.

Stratigraphy

In a revision of previous stratigraphic schemes, based on more detailed mapping, Fergusson & others (1979) proposed a new stratigraphic unit, the Boyd Volcanic Complex, for the interbedded volcanic and sedimentary rocks of the Eden-Pambula area (Fig. 1). Of the nine facies identified within this complex, two contain fish faunas (Fig. 2). The age relation between these is uncertain; similar plants have been reported from both facies, but the fish faunas have few elements in common, and the Facies 2 fauna may be slightly older. The Boyd Volcanic Complex is overlain by sediments of the Merimbula Group, at some locations without apparent discordance, but elsewhere with a high angular unconformity. However, the fault movements that caused the unconformity were probably contemporaneous with deposition of the Boyd Volcanic Complex (Fergusson & others, 1979, p. 97). Three formations are recognised in the Merimbula Group (Fig. 2): the Bellbird Creek Formation contains a marine invertebrate fauna, including Frasnian brachiopods (Talent, 1969), and the overlying Worange Point Formation and underlying Twofold Bay Formation contain Late Devonian fish faunas. In the southern part of the area the Gabo Island Granite intrudes other facies of the Boyd Volcanic Complex, and is also overlain by

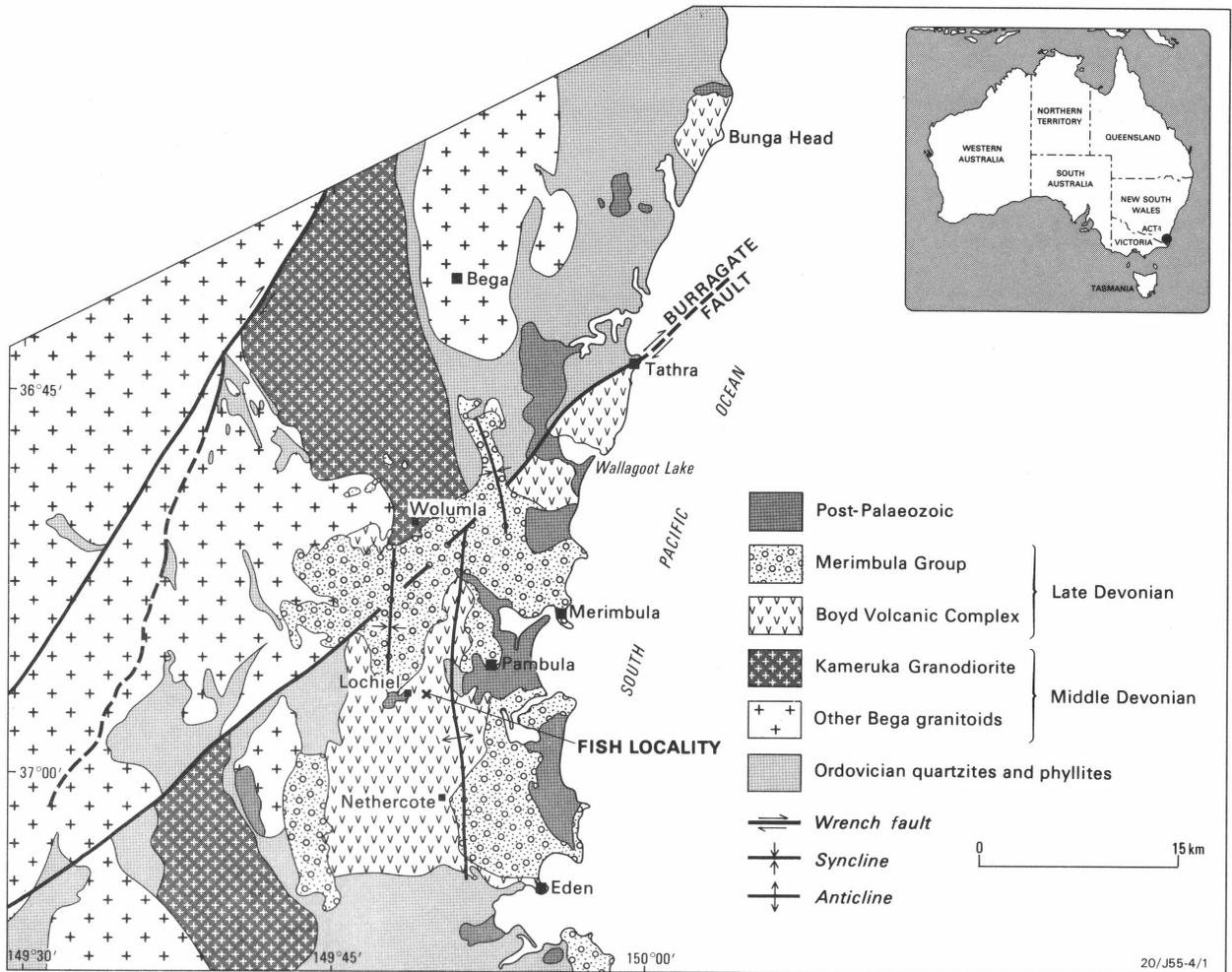


Figure 1. Regional geology of the Eden-Pambula District, south-eastern New South Wales (after Fergusson & others, 1979).

FAMENIAN	WORANGE POINT FORMATION	<i>Remigolepis</i> sp. <i>Groenlandaspis</i> sp. holoptychiid rhipidistian
	BELLBIRD CREEK FORMATION	MARINE
FRASNIAN	TWOFOLD BAY FORMATION	<i>Bothriolepis</i> sp. ? <i>Remigolepis</i> sp. <i>Phyllolepis</i> sp.
	ARKOSIC - VOLCOLITHIC CLASTIC FACIES (FACIES 3)	<i>Pambulaspis cobandrahensis</i> gen. et sp. nov. <i>Bothriolepis</i> sp. <i>Phyllolepis</i> sp. holoptychiid rhipidistian osteolepid rhipidistian Antiarcha indet. Acanthodii indet. ? Osteichthyes indet.
GIVETIAN	FLYSCHOID FACIES (FACIES 2 = BUNGA BEDS)	<i>Antarctilamna prisca</i> Young 1982 holoptychiid rhipidistian Acanthodii indet.

Figure 2. Summary of the stratigraphy and vertebrate faunas in the Middle (?) and Late Devonian rocks of the Eden-Pambula district.

sediments of the Merimbula Group. An isotopic age of 363 ± 12 m.y. for this intrusion (Fergusson & others, 1979) is not inconsistent with Ziegler's (1978, fig. 1) estimate of about 370 m.y. for the Givetian/Frasnian boundary.

The specimens described below come from Facies 3 of the Boyd Volcanic Complex, from the same locality (GR 7510E 59081N, Pambula 1:25 000 Sheet) that previously yielded *Bothriolepis* plates, remains of a smaller antiarch and a possible osteichthyan, and striated and tuberculate acanthodian spines (Fergusson & others, 1979, p. 103). The considerable quantity of new material from here, collected in 1979, has yielded much additional *Bothriolepis* material, abundant *Phyllolepis*, other indeterminate antiarch remains, acanthodian spines, osteolepid and holoptychiid rhipidistian remains, and other ornamented bones, referred to previously as osteichthyan (Fergusson & others, 1979), but which may be acanthodian (J. Long, Monash University, personal communication, 1982).

Current knowledge of the faunal content of vertebrate assemblages in the Eden-Pambula and Bunga Head regions is summarised in Figure 2. Only eight specimens of *Pambulaspis* have been identified in a collection of over 180 specimens, and it was a relatively rare element in the fish fauna.

Systematic palaeontology

Subclass Placodermi

Order Antiarcha

Suborder Asterolepidoidei Miles 1968**Definition.** See Young & Gorter (1981, p. 100)**Genus *Pambulaspis* nov.*****Pambulaspis cobandrahensis* sp. nov.****Name.** After the town of Pambula, and the Greek *aspis* (a shield). The fossil locality is on the property 'Cobandrah', about 5 km west of Pambula.**Holotype.** CPC 22559, an incomplete skull-roof in part and counterpart.**Other material.** Three anterior median dorsal plates (CPC 22560–22562), associated posterior dorsolateral and incomplete posterior lateral and posterior ventrolateral plates (CPC 22563), an isolated posterior lateral (CPC 22564), and a lateral marginal plate from the pectoral fin, (CPC 22565). An associated incomplete posterior ventrolateral and probable median ventral plate (CPC 22566) are tentatively referred to the species.**Locality.** Grid reference 7510E 5908IN on the Pambula 1:25 000 Sheet, about 5 km west of Pambula, on the south coast of New South Wales, Australia.**Horizon and age.** Facies 3 of the Boyd Volcanic Complex (Fergusson & others, 1979), probably Frasnian in age (early Late Devonian).**Diagnosis.** An asterolepidoid antiarch of medium size, with trunk armour attaining a mid-dorsal length of about 130 mm. Skull-roof with convex posterior and narrow rostral margins, a relatively large orbital fenestra, and well-developed suborbital and obducted nuchal areas. Breadth/length index of nuchal plate about 150. Lateral plate long and narrow. Endocranial postorbital process extending as far forward as the maximum width of the orbital fenestra. Postorbital crista strongly formed, and a prominent ventral process developed inside the anterior margin of the post-pineal plate. Anterior median dorsal plate with a breadth/length index ranging from 80 in small specimens to 55 in large, the anterior division of the plate slightly longer than the posterior, and a low median crest sometimes developed. Posterior dorsolateral plate with a breadth/length index of about 45, and posterior lateral plate slightly less than three times as long as deep. Ornament of tubercles normally coalesced into anastomosing ridges.**Remarks.** In erecting the genus *Remigolepis*, Stensiö (1931) noted the following features by which it could be distinguished from *Asterolepis* Eichwald: the absence of a distal joint in the pectoral fin, the presence of separate posterior lateral and posterior dorsolateral plates instead of a single mixilateral, the overlap relations between the anterior median dorsal and posterior dorsolateral plates — with a prominent dorsal process on the latter — and the absence of median grooves, ridges, processes, tuberosities, or pits on the visceral surface of the anterior and posterior median dorsal plates. In other respects *Asterolepis* and *Remigolepis* exhibit a general similarity, and there are said to be fairly detailed resemblances in the preorbital region of the skull (Stensiö, 1931, pp. 31–34). Apart from Stensiö, most authors since Gross (1965) have accordingly regarded the two genera as closely related, on the assumption that the absence of the distal joint in the pectoral fin in *Remigolepis* is secondary. Unfortunately, the new material described here is insufficient to establish the presence or absence of a distal joint in the pectoral fin, and, otherwise, this new species exhibits characters previously regarded as typical of either *Asterolepis*, or *Remigolepis* together with several peculiarities of its own.Points of resemblance with *Asterolepis* are the more elongate postorbital processes of the endocranium, the absence in the adult of posterior oblique pit-line grooves on the anterior median dorsal plate, the bilobed form of the paranuchal trochlea, the configuration of the posterolateral region of the skull, with well-developed suborbital areas, and the grooves on the anterior median dorsal plate crossing the contact faces for the anterior dorsolaterals. However, information on the last three characters is not available for *Remigolepis*, and in the new Chinese species *R. zhongningensis*, the posterior oblique pit-line groove is said also to be weakly developed or absent (Pan & others, 1980), even though this groove is prominent in Greenland species of the genus.In common with *Remigolepis* the new form described here has a strong postorbital crista and associated ventral process on the postpineal plate of the skull, and retains separately ossified posterior dorsolateral and lateral plates. In addition, openings for the endolymphatic ducts are not visible externally, although in *Remigolepis* this feature is poorly known. Other antiarchs and euarthrodires have separate posterior dorsolateral and lateral plates, which is, therefore, probably a primitive feature, and the same may apply to the postorbital crista, which is also well developed in *Yunnanolepis* (e.g. Liu, 1963). Neither character can, therefore, be used to proposed close affinity between *Remigolepis* and this new form. However, the pronounced rounded thickening on the visceral surface of the postpineal is a feature apparently absent in *Asterolepis* (e.g. Stensiö, 1931, fig. 12; Karatajute-Talimaa, 1963), but clearly developed in one well-preserved skull of *Remigolepis* (Stensiö, 1948, fig. 16).Finally, the new form differs from both *Asterolepis* and *Remigolepis* in that the posterior dorsolateral overlaps the anterior median dorsal over the length of their common suture, and the main lateral line groove on the flank crosses the posterior lateral rather than the posterior dorsolateral. The former condition is seen in several other asterolepidoids (e.g. *Pterichthyodes*, *Gerdalepis*, *Sherbonaspis*), but these are all forms with a short, high trunk-armour. The presence of the main lateral line groove on a discrete posterior lateral plate is, however, unique to this form, which I therefore propose as a new genus and species of asterolepidoid antiarch, possibly closely allied with *Remigolepis*.**Description.** Of the skull-roof, only the postorbital region is known, although an impression of part of the anterior margin of the orbital fenestra is preserved. There is no information on the form of the rostral, pineal, and sclerotic plates. On the right side, the paranuchal and postmarginal plates have been broken away, and the specimen has been subject to some distortion. An attempted restoration is shown in Figure 3B & 3D. The posterior margin is gently convex, and the skull was apparently somewhat narrower anteriorly than in the postorbital region. In general shape it thus resembles particularly the skull of *Asterolepis* sp. figured by Murphy & others (1976) from the Late Devonian of Central Nevada. In other species of *Asterolepis* the rostral margin also tends to be narrower than the posterior margin, but the difference may be less pronounced (e.g. Karatajute-Talimaa, 1963). The skull-roof outline in *Remigolepis* is less well known (e.g. Stensiö, 1931), but published figures suggest that the orbital fenestra was relatively smaller than in *Pambulaspis*. Although the orbital fenestra is (*f. orb*) incompletely preserved, it is also clear that it was larger than the suborbital fenestra in *Pambulaspis*. This is a character that distinguishes both *Asterolepis* and *Remigolepis* from *Bothriolepis* (Stensiö, 1948, p. 48).The unornamented obducted nuchal area (*nm*, Fig. 3B) is broadly developed, especially in the region of the nuchal plate.

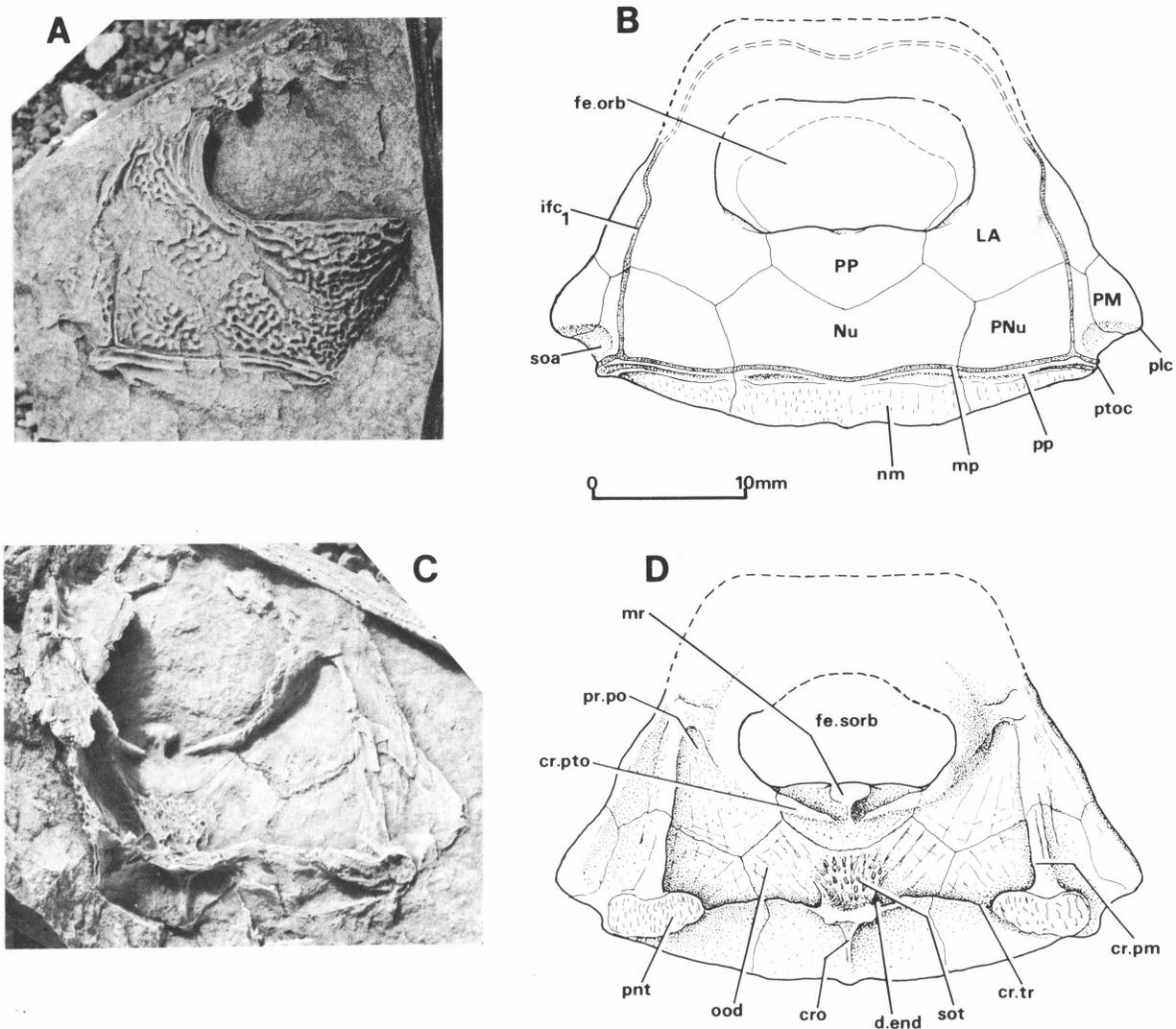


Figure 3. *Pambulaspis cobandrahensis* gen. et sp. nov.

The holotype, CPC 22559, an incomplete skull roof in dorsal (A) and ventral (C) views. B, D, restorations of the skull in dorsal and ventral views, based on the holotype. *cro*, median occipital crista; *cr.pm*, *cr.pto*, paramarginal and postorbital crista; *cr.tr*, transverse nuchal crista; *d.end*, endolymphatic duct opening; *fe.orb*, orbital fenestra; *fe.sorb*, suborbital fenestra; *ifc₁*, infraorbital sensory groove; *LA*, lateral plate; *mp*, middle pit-line; *mr*, median thickening beneath postpineal plate; *nm*, obtected nuchal area; *Nu*, nuchal plate; *ood*, otico-occipital depression; *plc*, preobstantic corner; *PM*, postmarginal plate; *PNu*, paranuchal plate; *pnt*, paranuchal trochlea; *PP*, postpineal plate; *pp*, posterior pit-line; *pr.po*, postorbital process; *pt.oc*, postobstantic corner; *soa*, subobstantic area; *sot*, supraotic thickening.

It is noteworthy that in many species of *Asterolepis* this area is densely covered with ornament (e.g. Pan, 1964; Murphy & others 1976; Lyarskaya, 1981). Two transverse grooves cross the paranuchal and nuchal plates. The posterior one (*pp*) is distinct and continuous laterally, but less clearly defined on the nuchal plate. It lies along the anterior edge of the obtected nuchal area. The anterior groove (*mp*) lies at the posterior margin of the ornamented region of the skull, and passes laterally off the skull-roof in front of the postobstantic corner (*ptoc*). Following Stensiö's (1931) interpretation of similar grooves in *Asterolepis*, these are termed the middle and posterior pit-lines. The external openings of the endolymphatic ducts could not be discerned on the specimen. Only the posterior part of the infraorbital sensory groove is preserved (*ifc₁*). A noteworthy feature of the skull is the small but distinct subobstantic area (*soa*), which is similarly developed to this area in other asterolepidoids (e.g. Hemmings, 1978, fig. 1). The subobstantic area is not preserved in previously described *Remigolepis* material.

As restored, the nuchal plate has a breadth/length index estimated at 150, which is comparable to that in *Remigolepis*

zhongningensis (see Pan & others, 1980), but broader than in some *Remigolepis* species from Greenland (e.g. *R. acuta*, *R. cristata*; see Stensiö, 1931). In another Greenland species (*R. kochi*) the nuchal is broader, and similar variation is seen in species of *Asterolepis* (e.g. Stensiö & Save-Söderbergh, 1938), although many species have comparable values to that reported here (e.g. *A. radiata*, *A. sinensis*; see Karatajute-Talimaa, 1963; P'an, 1964). The paranuchal and postpineal plates are similarly developed to other species in both genera. The posterolateral corner (*plc*) is not clearly preserved, but the postmarginal plate was probably less elongate than in *Asterolepis* or *Pterichthyodes* (e.g. Nilsson, 1941; Karatajute-Talimaa, 1963; Hemmings, 1978; Lyarskaya, 1981). This bone is poorly known in *Remigolepis* (Stensiö, 1931). Enough of the lateral plate is preserved to indicate its narrow form, as in some Greenland species of *Remigolepis* (Stensiö, 1931, pl. 4, fig. 2), although, in others, this plate was considerably broader (Stensiö, 1948, fig. 16; Pan & others, 1980). The lateral plate is also elongate in *Asterolepis*.

Structures on the visceral surface of the skull-roof are well displayed on the counterpart of the holotype (Fig. 3C, D). The

transverse nuchal crista (*cr.tr*) is strong, with a roughened elevation laterally (*pnt*), which in its bilobed form is reminiscent of the paranuchal trochlea in *Asterolepis ornata* (Karatajute-Talimaa, 1963, fig. 26). The median occipital crista (*cro*) is prominent, and the supraotic thickening (*sot*) forms an elevated area of cancellous texture in the centre of the nuchal plate. The internal endolymphatic duct openings occupy deep depressions lateral to the junction of this thickening with the transverse nuchal crista. Other prominent structures are the paramarginal and post-orbital cristae (*cr.pm*, *cr.pto*), which delineate the otico-occipital depression (*ood*). As previously reported for *Remigolepis* (Stensiö, 1931), this depression in *Pambulaspis* is much broader and deeper than in *Bothriolepis*. However, in *Pambulaspis* the anterolateral corner of the depression (*pr.po*), which housed the dorsal face of the endocranial postorbital process, extends farther forward than previously reported for *Remigolepis* (Stensiö, 1948, fig. 16). A more elongate postorbital process is also seen in *Asterolepis* (Stensiö, 1931; Karatajute-Talimaa, 1963). The postorbital crista is strongly developed on the visceral surface of the postpineal plate, which at its anterior margin bears a conspicuous thickening. Both features are typical of *Remigolepis* (Stensiö, 1948, fig. 16); in *Asterolepis* they are only slightly developed (Stensiö, 1931, fig. 12; Karatajute-Talimaa, 1963, pl. 8).

The trunk-shield of *Pambulaspis cobandrahensis* is represented by a small number of disarticulated plates. The three examples of the anterior median dorsal plate (Figs. 4, 5) differ considerably in size, and show some variation in morphology and proportions, which may be ontogenetic features. On available evidence the breadth/length index decreases considerably with size (Table 1), although the opposite trend has been recorded in *Bothriolepis* (Stensiö, 1948, p. 287), and in *Asterolepis* no such variation is evident (see Karatajute-Talimaa, 1963, p. 160). In the two smaller examples of this bone there is a low median crest developed behind the tergal angle. In the largest specimen, however, this crest is reduced to a prominent median dorsal ridge (Fig. 4A). A third feature possibly related to growth is the development of sensory grooves on the plate. In the smallest specimen the posterior and anterior oblique abdominal pit-line grooves are clearly seen (*dlg₁*, *dlg₂*, Fig. 4A), although the anterior one is manifested as a ridge rather than a groove. In the larger specimens these grooves are inconspicuous or absent. In *Bothriolepis* the strong development of the anterior pit-line groove is a juvenile character (Stensiö, 1948, p. 185), and the same can be assumed here. The poor development of the posterior oblique pit-line groove in the larger plates is in contrast to the situation in the Greenland species of *Remigolepis*, in which they are well developed (Stensiö, 1931). However, these grooves are also absent or poorly developed in the Chinese species *Remigolepis zhongningensis* (Pan & others, 1980). Both grooves are normally absent in *Asterolepis*, although there are exceptions (e.g. Karatajute-Talimaa, 1963, pl. 1, fig. 13; Lyarskaya, 1981, pl. 1, fig. 2).

In all three examples of this plate the anterior division is slightly longer than the posterior, the anterior and posterior margins are of similar length, and the tergal angle lies in the anterior half, but not the anterior third, of the plate. The broad anterior margin and the tendency to develop a low median dorsal crest are resemblances to the Greenland species *Remigolepis cristata* (Stensiö, 1931). The overlap area for the posterior dorsolateral plate (*oa.PDL*) is clearly developed in each specimen, but, in contrast to the situation in *Remigolepis*, it extends along the posterolateral margin almost to the lateral corner. This condition is typical of *Bothriolepis*, and amongst other asterolepidoids is seen in *Pterichthyodes* and *Sherbonaspis* (Hemmings, 1978; Young & Gorter, 1981). The

remigolepid condition typical of species of *Remigolepis* occurs also in *Byssacanthus* and *Stegolepis*, and occasionally in *Sherbonaspis* and *Bothriolepis* (e.g. Miles, 1968). In *Asterolepis* the anterior median dorsal completely overlaps the posterior dorsolateral, whereas some of the Chinese yunnanolepids also have the remigolepid overlap arrangement (Zhang, 1978). The taxonomic significance of this character at the suprageneric level is obscure, but at least in *Remigolepis* it is consistently developed in all known species.

Other features of the anterior median dorsal in *Pambulaspis* include the slight postnuchal notch (*npr*) and external postlevator process (*pr.pl*); this feature is absent in CPC 22562), and on the visceral surface a distinct supranuchal area (*sna*) and postlevator thickening (*alr*). Beneath the external postlevator process on the visceral surface is a groove (*f*) on the contact face for the anterior dorsolateral plate, similar to that observed in the Baltic species *Asterolepis estonica* (Gross, 1940, p. 34; Karatajute-Talimaa, 1963, fig. 14). The presence or absence of this feature in the Greenland *Remigolepis* has not been determined (Stensiö, 1931).

The posterior dorsolateral plate is represented by one incomplete specimen from the right side, closely associated with incomplete right posterior lateral and posterior ventrolateral plates. These are assumed to come from the same individual. Total preserved length of the posterior dorsolateral is 60 mm. The relatively smaller anterior median dorsal plate from the same block (CPC 22561) is assumed to belong to a different individual. As restored (Fig. 7A), the posterior dorsolateral is fairly elongate, but proportions of this plate are known to vary considerably in species of *Remigolepis* (Stensiö, 1931, pp. 186, 191), so inclusion of this character in the diagnosis is only tentative. Some irregularities in the plate margins are due to oblique distortion, as evidenced by slight crenulations of the ornamented surface of the plate (Fig. 6A). These have been rectified in the reconstruction. Only one overlap area is well preserved on the specimen (*oa.PL*, Fig. 7A), but overlap areas for the posterior median dorsal and anterior dorsolateral plates have been restored after the condition in other asterolepidoid antiarchs. The small section of the overlap area for the anterior dorsolateral, as preserved near the anterodorsal corner (*adc*), has a plate margin that suggests it abutted against the contiguous plate without overlap. However, such a condition is not known in other forms, and further specimens are required to clarify this point of structure. Near its posterior end the ventral overlap area for the posterior lateral has a distinct notch (*vn*, Fig. 7A), as in *Remigolepis* (Stensiö, 1931, fig. 85). The contact face on the posterior lateral is correspondingly developed. A notable feature of the plate is the apparent absence of the sensory canals and pit-line grooves normally situated on the posterior dorsolateral in other placoderms. As described below, the lateral line groove is situated on the posterior lateral plate in *Pambulaspis*.

The external surface of the plate is gently arched dorsoventrally, without a clearly developed dorsolateral ridge or keel. The visceral surface is poorly preserved, the only significant feature being an impression of the crista transversalis interna posterior, which extends dorsally from the region of the ventral notch. The posterior margin of the plate is not well shown, but was, presumably, short.

The posterior lateral plate associated with the specimen just described is too fragmented to show details of structure, but in another specimen (CPC 22564) the morphology of this plate is well displayed, although again it is incomplete posteriorly (Figs. 6C, 6D, 7B, 7C). Total preserved length of this example is 52 mm. It comes from the right side, as indicated by the

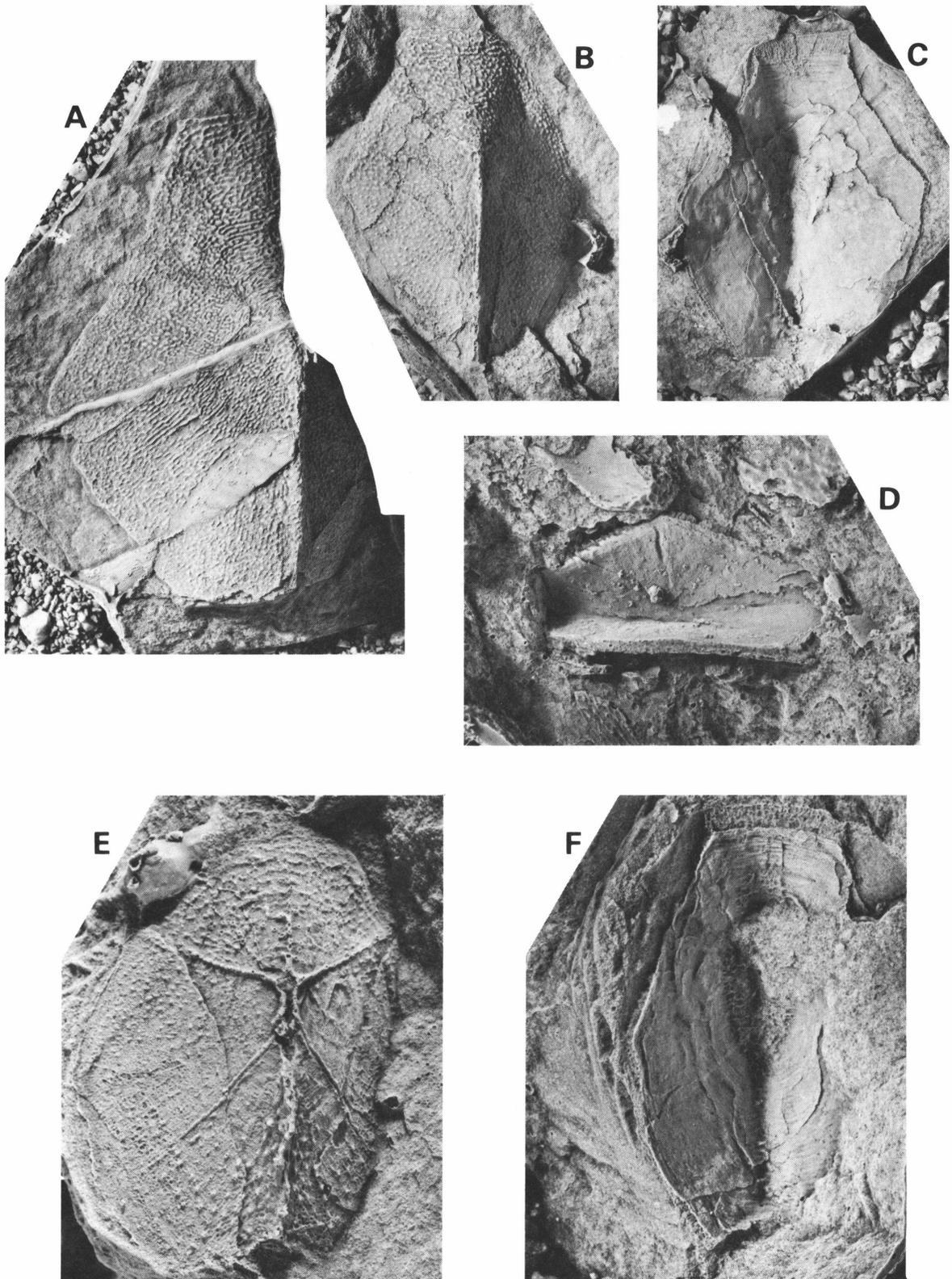


Figure 4. *Pambulaspis cobandrahensis* gen. et sp.nov.

A, anterior median dorsal plate in dorsal view, CPC 22562 (x1); B, C, anterior median dorsal in dorsal and ventral views, CPC 22561 (x 1.5); D, lateral marginal plate from the pectoral fin, CPC 22565 (x 3); E, F, anterior median dorsal in dorsal and ventral views, CPC 22560 (x 3).

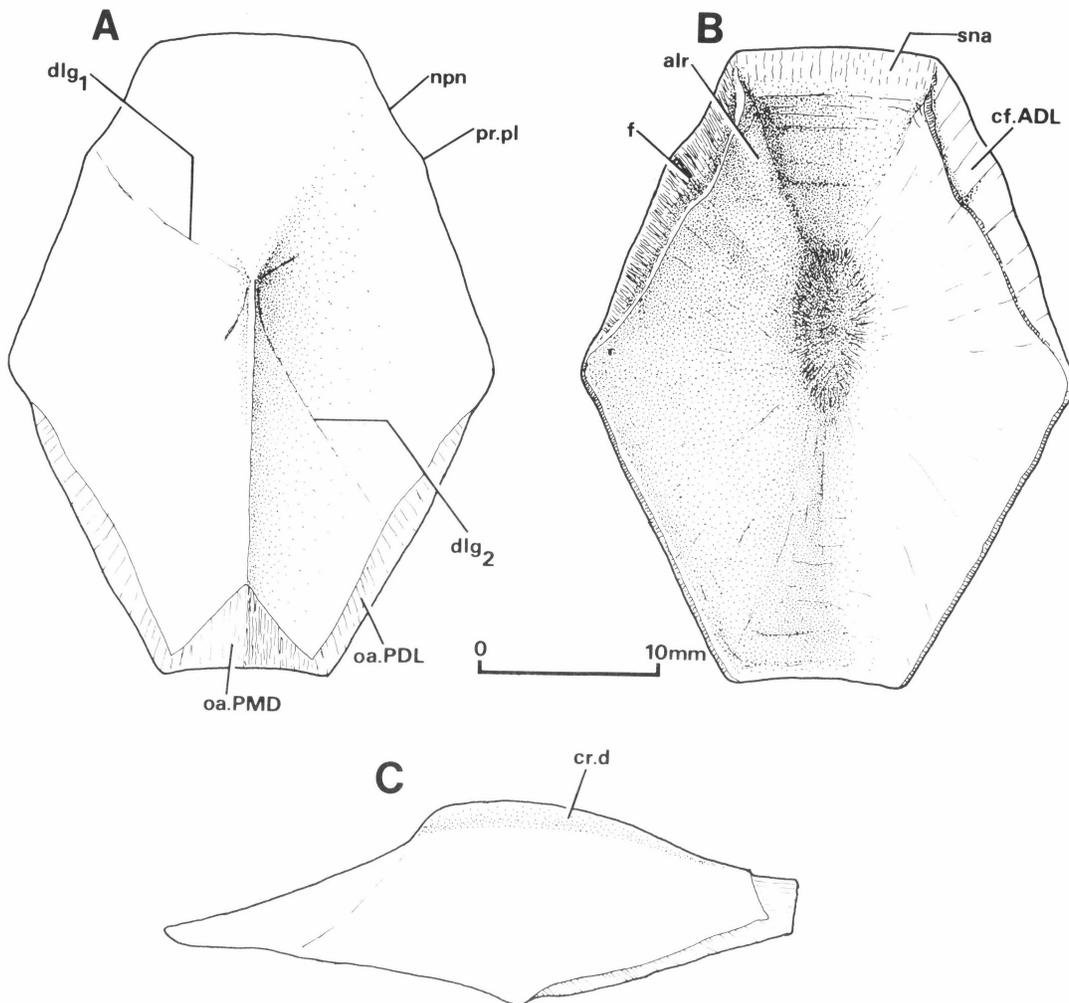


Figure 5. *Pambulaspis cobandrahensis* gen. et sp. nov.

Reconstruction of the anterior median dorsal plate in dorsal (A), ventral (B), and left lateral (C) views. After CPC 22560, 22561. *alr*, postlevator thickening; *cf.ADL*, contact face for anterior dorsolateral; *cr.d*, median dorsal crest; *dl_g1, dl_g2*, anterior and posterior oblique abdominal pit-line grooves; *f*, groove crossing contact face for anterior dorsolateral; *nnp*, postnuchal notch; *oa.PDL*, *oa.PMD*, overlap areas for posterior dorsolateral and posterior median dorsal plates; *pr.pl*, postlevator process; *sna*, supranuchal area.

ventral overlap area for the posterior ventrolateral, and the dorsal contact face for the posterior dorsolateral (*oa.PVL*, *cf.PDL*, Figs. 7B, 7C). This overlap relation to the posterior dorsolateral and ventrolateral plates is also seen in some other antiarchs with a separate posterior lateral (e.g. Malinovskaya, 1973, fig. 3; Zhang, 1978, fig. 1), and in euarthrodires (e.g. Denison, 1958, fig. 111). It is likely, therefore, that this is the primitive relation between these plates in both groups. Other narrow overlap areas are developed anteriorly for the anterior dorsolateral and ventrolateral plates (*oa.ADL*, *oa.AVL*). The plate is slightly angled dorsoventrally about a line running from the presumed position of the dorsal angle (*d*) to the anterior margin, just ventral to the anterior corner (*arc*). However, no distinct keel or ridge is developed. On the visceral surface the dorsolateral and ventrolateral laminae of the plate are separated by a shallow depression, with an adjacent short ridge (*ri*, Fig. 7C) near the anterior margin.

Along the length of the preserved dorsal margin of this plate is a clearly defined sensory groove for the main lateral line canal (*lc*, Figs. 6C, 7B). In some other antiarchs (e.g. *Gerdalepis*, *Stegolepis*, *Sherbonaspis*) showing incipient fusion of the posterior dorsolateral and lateral plates to form a mixilateral, the sensory groove and the bone suture appear coincident (Gross, 1965; Malinovskaya, 1973; Young & Gorter, 1981). On the other hand, in the *Remigolepis* material described by Stensiö (1931) the sensory groove lies adjacent to the ventral margin of the posterior dorsolateral, thus retaining its primitive

position. As noted above, sensory grooves are apparently completely absent from the posterior dorsolateral, and *Pambulaspis cobandrahensis* is, therefore, the only antiarch clearly showing displacement of the lateral line onto a separately ossified posterior lateral plate.

On the visceral surface of the plate (Fig. 7C) the contact face for the posterior dorsolateral is not clearly delineated, except posteriorly, where it is expanded to occupy the notch described above on the ventral margin of the posterior dorsolateral.

Little is known of the remaining plates of the trunk-shield in *Pambulaspis*. The posterior ventrolateral associated with the posterior dorsolateral described above is represented only by the anterior parts of its ventral and lateral laminae, which show no significant features. The second fragmentary posterior ventrolateral (CPC 22566) is only tentatively referred to this

Table 1. Measurements (in millimetres) and indices for three anterior median dorsal plates of *Pambulaspis cobandrahensis* gen. et sp. nov.

	CPC 22560	CPC 22561	CPC 22562
<i>total length</i>	18.8	36	80
<i>total breadth</i>	15	27	44
<i>length of anterior division</i>	10	18.5	43
<i>length of anterior margin</i>	7	10.5	37
<i>breadth/length index</i>	80	75	55

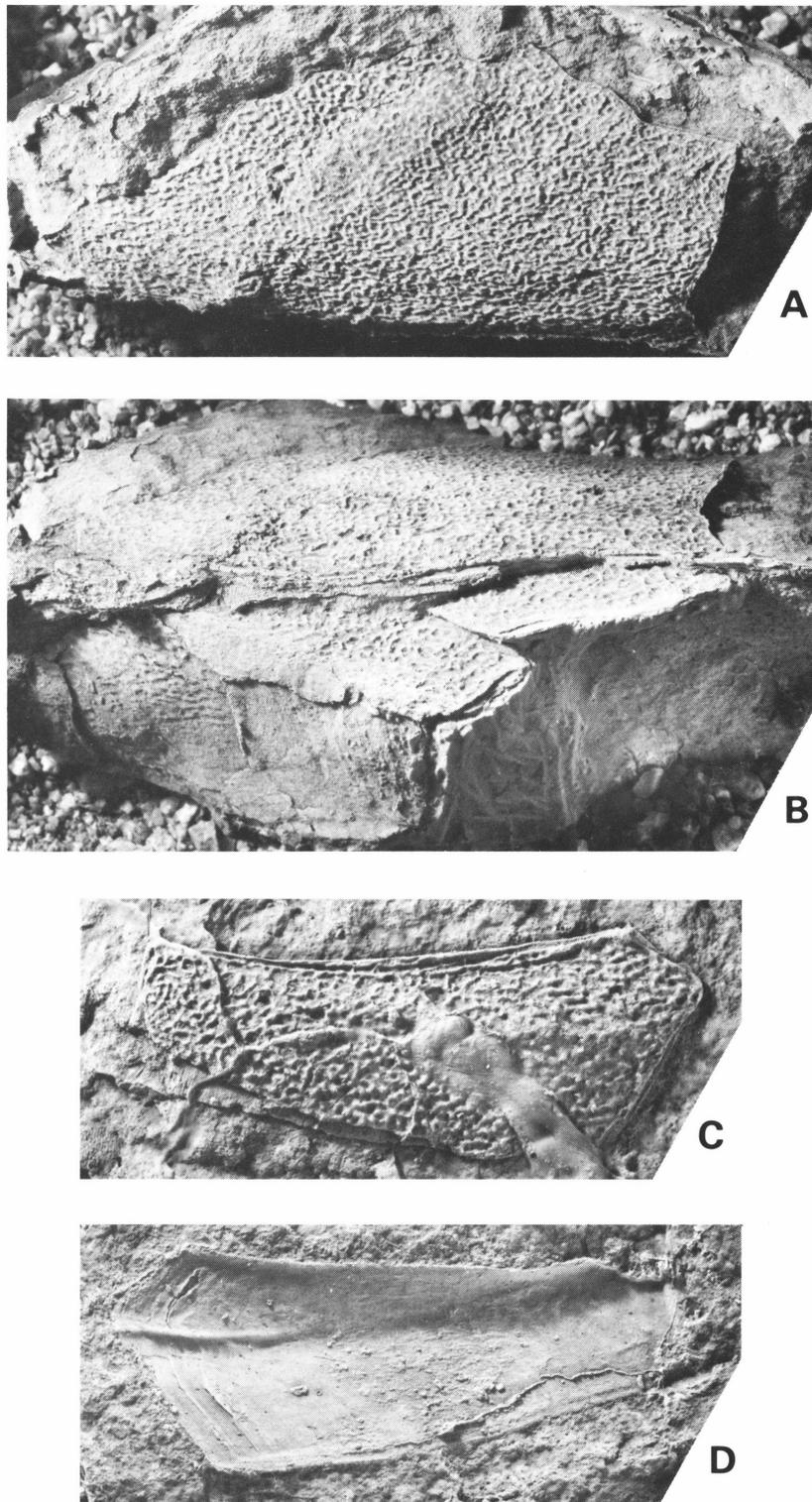


Figure 6. *Pambulaspis cobandrahensis* gen. et sp. nov.

A, right posterior dorsolateral plate, CPC 22563 (x 1.5). B, the same plate in ventral view, showing the overlap area for the posterior lateral plate, and part of this plate and the posterior ventrolateral (x 1.5). C, D, right posterior lateral plate in lateral and mesial views, CPC 22564 (x 1.5).

species on the basis of ornament (coarser than in the associated *Bothriolepis* material). The posterior margin of the lateral lamina, as preserved in this specimen, is normal to the ventrolateral ridge. The dorsal corner of the lateral lamina, and mesial and anterior margins of the ventral lamina are missing. Associated is another plate fragment, tentatively identified as a median ventral plate. The posterior median dorsal, anterior dorsolateral, anterior ventrolateral, and semilunar plates are unknown.

The pectoral fin is represented by a single disarticulated plate (Fig. 4D), probably the lateral marginal plate from a proximal pectoral fin segment. In its short, broad proportions, this plate is more reminiscent of *Pterichthyodes* than *Asterolepis* (e.g. Hemmings, 1978). However, it is also possible that the plate is one of a lateral marginal series, as occurs in *Remigolepis* (e.g. Stensiö, 1931, fig. 88). Thus, the important question of whether the pectoral fin had a distal joint cannot be answered on available evidence.

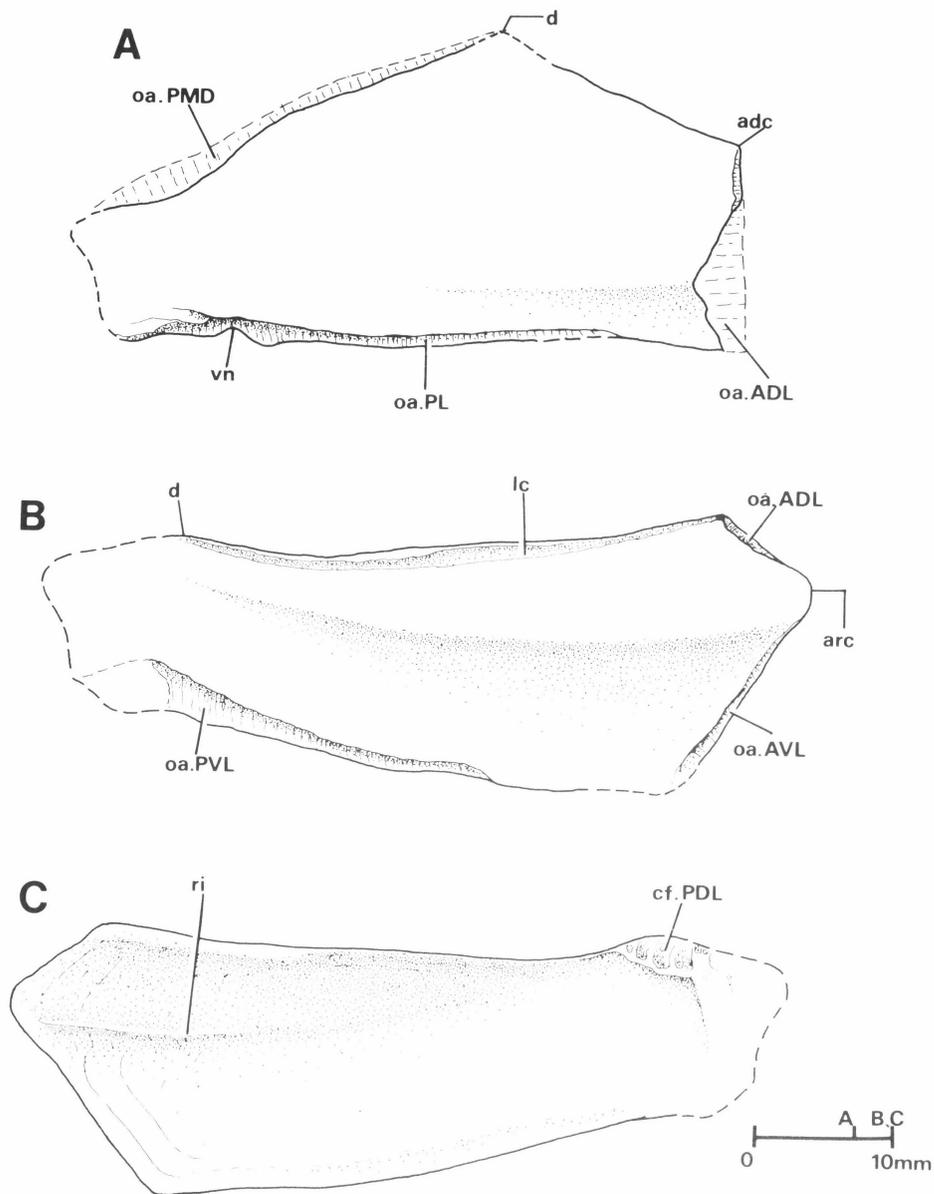


Figure 7. *Pambulaspis cobandrahensis* gen. et sp. nov.

A, reconstruction of posterior dorsolateral plate in lateral view, after CPC 22563. B, C, reconstruction of posterior lateral plate in lateral and mesial views, after CPC 22564. *adc*, anterodorsal corner; *arc*, anterior corner; *cf.PDL*, contact face for posterior dorsolateral; *d*, dorsal corner; *lc*, lateral line sensory groove; *oa.ADL*, *oa.AVL*, overlap areas for anterior dorsolateral and ventrolateral plates; *oa.PL*, *oa.PMD*, *oa.PVL*, overlap areas for posterior lateral, posterior median dorsal, and posterior ventrolateral plates; *ri*, ridge; *vn*, ventral notch.

The dermal ornament of *Pambulaspis cobandrahensis* typically forms short anastomosing ridges (Figs. 2, 4, 6). Similar ornament is seen in some species of *Asterolepis* (e.g. Pan, 1964), although, in others, the ornament tends to be coarser and more tuberculate (e.g. Wells, 1964; Murphy & others, 1976). The same applies to the various species of *Remigolepis*, described by Stensiö (1931). In one small plate of *Pambulaspis*, fine widely spaced tubercles are developed (Fig. 4E), and this is possibly a juvenile feature. In CPC 22562, a slight tendency to alignment of ridges is evident (Fig. 4A). The dermal ornament of *Pambulaspis* is generally readily distinguishable from the more delicate ornament of the associated *Bothriolepis* material.

Discussion

The antiarchs were one of the most successful and widespread groups of placoderm fishes, and have been recorded from Middle and Upper Devonian rocks in most regions of the world. An analysis of their distribution in space and time

during the Devonian Period poses many problems of biostratigraphic and biogeographic importance (e.g. Young, 1981; Janvier & Pan, in press). In the European vertebrate succession, asterolepidoid antiarchs were predominant during the Middle Devonian (e.g. Young, 1974), but were apparently largely replaced in the Late Devonian by *Bothriolepis*. However, one asterolepidoid, *Remigolepis*, persisted in the Late Devonian of east Greenland and southeastern Australia, and has recently been reported also from Scotland (Andrews, 1978) and China (Pan & others, 1980). Another, *Asterolepis*, is now definitely known to range through to the late Frasnian in the Baltic succession (e.g. Lyarskaya, 1981), and it occurs in rocks of similar age in the United States (Wells, 1964; Murphy & others 1976; Gregory & others, 1977) and Iran (Janvier, 1979). However, the Chinese species *A. sinensis* P'an, 1964, is apparently of latest Devonian age (Pan, 1981).

As noted above, it has been suggested, on the basis of similarity in overall structure, that *Remigolepis* and *Asterolepis* are closely related, the former being derived from the latter (or

a close relative) by loss of the distal joint in the pectoral fin. One of the difficulties with this idea is that *Remigolepis* is more primitive than all known species of *Asterolepis*, in retaining separate posterior dorsolateral and lateral plates. The picture is further complicated by the fact that some Early Devonian antiarchs from Yunnan, China, also had an unjointed fin, said by Zhang (1978) to be similar in structure to that of *Remigolepis*. The detailed arrangement of plates in the yunnanolepid pectoral fin is not known, and there is no evidence on whether a ventral central series of plates was present, as in antiarchs generally, or whether this series was absent, as in *Remigolepis* (Stensiö, 1931). It has been argued, however, (Young & Gorter, 1981, p. 100) that acceptance of similarities in the preorbital region of the skull as shared specialisations of *Asterolepis* and *Remigolepis* implies that the unjointed pectoral fin in *Remigolepis* is a secondary condition. The new form, *Pambulaspis*, described here may be accommodated within this hypothesis as an assumed close relative of the most recent common ancestor of *Asterolepis* and *Remigolepis*. There is also some slight evidence (similar development of the visceral surface of the postpineal plate) suggesting a closer relation between *Pambulaspis* and *Remigolepis* than either has with *Asterolepis*. This suggestion would be confirmed by the demonstration that the pectoral fin in *Pambulaspis* lacks a distal joint, but would not be refuted if *Pambulaspis* was shown to possess such a joint, this feature then being interpretable as a symplesiomorphy of *Asterolepis* and *Pambulaspis*. However, the demonstration that in *Pambulaspis* the rostral region and jaws were specialised in the same way as in *Asterolepis* and *Remigolepis* would be important evidence corroborating the suggested close relationship between these three genera. Further information on the morphology of *Pambulaspis* is required to resolve these issues.

Since *Asterolepis* first occurs as early as Eifelian in the Baltic sequence (e.g. Lyarskaya, 1981), the above hypothesis implies also that the *Pambulaspis*-*Remigolepis* lineage must have differentiated in the Eifelian or earlier. Biogeographic considerations in relation to a period during which these groups were isolated from each other (perhaps the duration of the Middle Devonian) will be considered in detail elsewhere.

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