# AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

# The Sinolepidae, a Family of Antiarchs (Placoderm Fishes) from the Devonian of South China and Eastern Australia

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ABSTRACT. Two new antiarchs are described, from the Late Devonian Hunter Siltstone near Grenfell in south-eastern Australia (*Grenfellaspis branagani* n.gen., n.sp.), and from the Early - Middle Devonian Dayaoshan Group in Guangxi, south-eastern China (*Dayaoshania youngi* n.gen., n.sp.). New material is described of *Xichonolepis qujingensis* P'an & Wang, 1978 from the Middle Devonian of Yunnan, and new interpretations are presented for *Sinolepis* Liu & P'an, 1958 from the Late Devonian of Jiangsu. All four genera are placed in the family Sinolepidae Liu & P'an, of which the most obvious defining character is the much reduced ventral laminae of the anterior and posterior ventrolateral plates of the trunk armour, and the presumed absence of a median ventral plate. Emended diagnoses are presented for the family Sinolepidae and the genera *Xichonolepis* and *Sinolepis*. It is suggested that *Grenfellaspis* and *Sinolepis* are immediately related, and the biostratigraphic, biogeographic, and palaeogeographic implications of this relationship are discussed. The vertebrate fauna from the Hunter Siltstone is regarded as the youngest nonmarine vertebrate horizon known from the Devonian of south-eastern Australia. A close palaeogeographic connection between south-eastern Australia and South and North China is indicated for the latest Devonian and earliest Carboniferous (late Famennian-early Tournaisian), which contrasts with the distinctive Devonian vertebrate faunas from the two regions in earlier strata. Other Devonian fossil groups showing a similar biogeographic pattern are considered in the context of competing hypotheses concerning the palaeogeographic relationships of Gondwana and Asia during the Middle Palaeozoic.

## Contents

The group of primitive fishes dealt with here first became known when Liu & P'an (1958) described some unusual antiarch remains from the Late Devonian Wutung Series near Nanjing (Fig.1, loc.2) as two new species in a new genus, *Sinolepis* Liu & P'an, which they referred to its own family, the Sinolepidae. This important paper provided the first indication of the highly endemic character of the early vertebrate fauna from the Devonian of China. Preliminary descriptions of other endemic groups soon followed (Early Devonian antiarchs, and galeaspid agnathans by Liu, 1963, 1965), and since then many publications have established the Devonian vertebrate fauna from South China as of central importance in understanding the early evolution of most of the major groups of Devonian agnathan and gnathostome fishes (for a recent review of the Devonian vertebrates of China see Pan & Dineley, 1988).

Gross (1965) was the first western scientist to attempt to incorporate *Sinolepis* into a general classification of the antiarchs. Gross divided the antiarchs into two major subgroups of ordinal rank, the Asterolepiformes and the Bothriolepiformes. He noted that the broad lateral plate of the skull in *Sinolepis* suggested bothriolepid affinity, and that the rectangular shape of the anterior median dorsal plate was reminiscent of the bothriolepid *Grossilepis*, but that the anterior median dorsal overlap relations, and the shape of the premedian, postmarginal, and opercular plates in the skull, were more similar to those of asterolepid antiarchs. Accordingly he placed the family Sinolepididae within his order Asterolepiformes. Miles (1968) followed this opinion, but Hemmings (1978) removed *Sinolepis* to the bothriolepididoids

because of apparent similarities in pectoral fin structure. The distinctiveness of *Sinolepis* was recognised in the classification of Denison (1978), who divided the antiarchs into three major groups of equal rank, the Bothriolepidae, the Asterolepidae, and the Sinolepidae.

In Australia the discovery of sinolepid remains resulted from an investigation by AR in 1972 of a new fish locality in the Upper Devonian Hunter Siltstone near Grenfell in east central New South Wales (Fig.2A). The arthrodire *Groenlandaspis* from this locality was reported by Ritchie (1975), but a diverse associated fauna was also recovered, including remains of other placoderms, dipnoans, crossopterygians, and acanthodians. The placoderm material included bones belonging to the antiarchs *Bothriolepis* and *Remigolepis* (Ritchie, 1975), as well as other isolated plates with a distinctive tubercular ornament, which could be identified by their internal structure to be median dorsal plates from the trunk armour of an unknown antiarch. They resembled both *Sinolepis* and *Grossilepis* in the somewhat rectangular shape of the anterior and posterior median dorsal plates. But the most unusual bones were the ventral plates of the trunk armour, which in other antiarchs always have an extensive ventral lamina forming a complete ventral wall to the trunk armour. In this new antiarch the ventral lamina on both the anterior and posterior ventrolateral plates was reduced to two narrow strips running transversely and longitudinally along the ventral wall.

Photographs of these very distinctive bones were taken by GY to China in 1981. During discussions with Chinese colleagues Pan Jiang and Zhang Guorui in

Beijing, and examination of antiarch material held in the Institute of Vertebrate Paleontology and Paleoanthropology, and the Museum of Geology, it became clear that similar features were present in the ventral wall of the trunk armour in two Chinese genera, *Sinolepis* Liu & P'an, and *Xichonolepis* P'an & Wang. *Xichonolepis qujingensis* was erected by P'an & Wang (1978) for a few distinctive antiarch bones from the

Middle Devonian of Yunnan Province, which they provisionally referred to the Bothriolepidae. Zhang (1980) described additional material, but concluded that *Xichonolepis* was an asterolepid antiarch. Young (1981, fig.5) proposed a scheme of antiarch interrelationships in which sinolepids were placed as the sister group of bothriolepiforms and asterolepiforms, with the Early Devonian yunnanolepids as the plesiomorphic sister
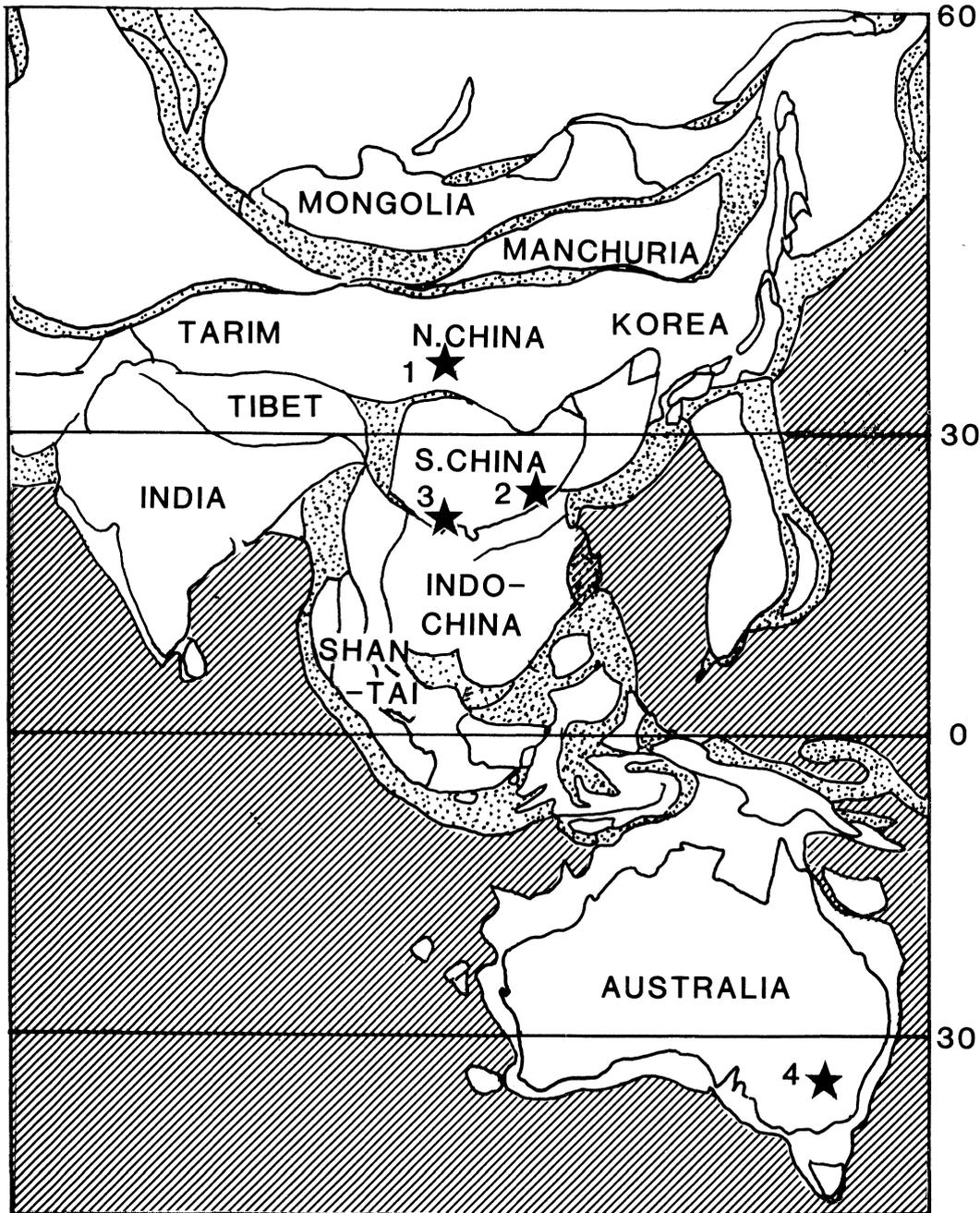
**Fig.1.** Distribution of Devonian Sinolepidae (Antiarchi). 1 - Ningxia Province, North China block (*Sinolepis*); 2 - Nanjing region (*Sinolepis*); 3 - Yunnan-Guangxi region (*Xichonolepis, Dayaoshania, Liujiangolepis*) and north Vietnam (*Vanchienolepis*; see Tong-Dzuy & Janvier, 1990), South China block; 4 - Grenfell region, Tasman Fold Belt, East Gondwana (*Grenfellaspis*). Modified from Scotese (1986) showing terranes comprising Asia and south-east Asia; *cf.* also Figure 35A,B.
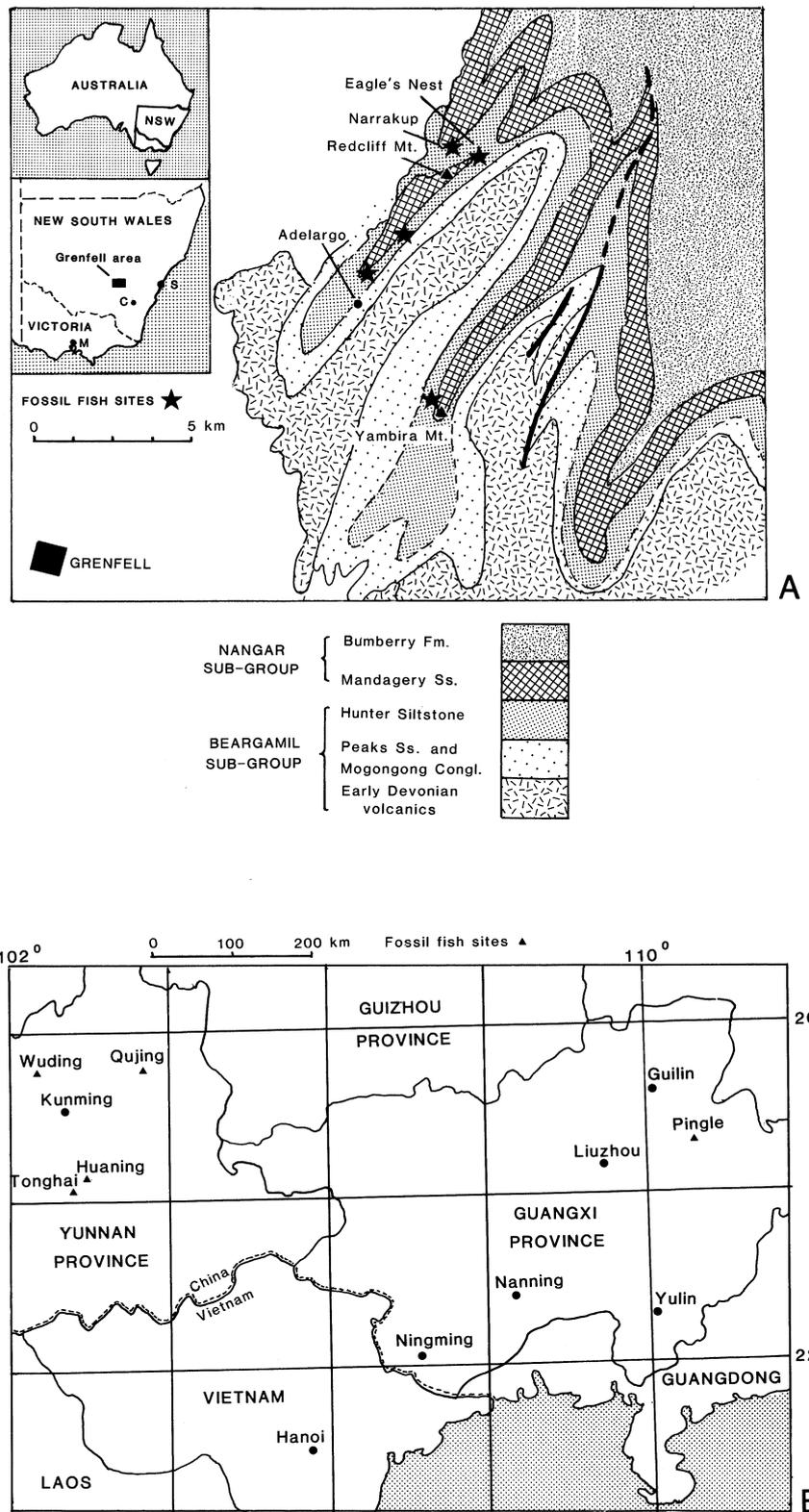
**Fig.2.** Sinolepid antiarch sites in Australia and South China. A - geological map of Grenfell area, eastern central NSW, Australia, showing Devonian succession (after Conolly 1965, fig.11) and fossil fish sites. S - Sydney; C - Canberra: M - Melbourne. B - sinolepid sites in Yunnan province (Wuding, Qujing, Huaning, Tonghai) and Guangxi province (Pingle), South China.

group to all remaining antiarchs. Janvier & P'an (1982) proposed a similar scheme, and distinguished non-yunnanolepids (sinolepids, bothriolepids, asterolepids) as a major group, the euantiarchs, characterised by a well developed brachial process. A similar opinion was expressed by Zhang (1979). They suggested that *Xichonolepis* may belong to the stem Bothriolepida, or that it may be the sister-taxon of the Bothriolepida. Long (1983) elevated the group to subordinal rank (the Sinolepidoidei), and tentatively included *Xichonolepis*, as did Young (1984c), who however suggested that sinolepids were the sister group of bothriolepidoids only.

It is evident that there has been considerable confusion as to the precise phyletic relationships of *Xichonolepis* and *Sinolepis*, and of the relationships of sinolepids as a group to other antiarchs, even though the distinctiveness of this group has been acknowledged since the initial descriptions of Liu & P'an (1958). Also of great interest are the biogeographic implications of the presence of a sinolepid in the Late Devonian of eastern Australia (see Young, 1981, 1984c, 1990a,b; Burrett *et al.*, 1990), this being the only occurrence outside of eastern Asia of an otherwise strictly endemic Chinese group. (A sinolepid recently reported from Vietnam by Tong-Dzuy & Janvier, 1990 comes from the southern edge of the South China Block).

The primary prerequisite to clarifying the phyletic relationships of sinolepids, and properly assessing their biogeographic implications, was seen to be an adequate description of the new Australian form. In this paper we describe this form as *Grenfellaspis branagani* n.gen., n.sp., and we describe another new form (*Dayaoshania youngi* n.gen., n.sp.) from material collected by Wang Shitao, Zhang Zhenxian and others in 1984. We complement these descriptions with an account of new material of *Xichonolepis* obtained since the earlier publications of 1978 and 1980, and we present emended diagnoses of *Xichonolepis* and *Sinolepis*, and provide a reinterpretation of the latter. These descriptions provide the background for a discussion of the interrelationships and relationships of sinolepids, and their biostratigraphy and biogeography. Higher classification of placoderms follows that of Denison (1978). The term 'Euantiarchi' is used in the sense of Janvier & Pan (1982) and Young (1984c). Throughout the text standard abbreviations are used for the dermal bones of antiarchs which mainly follow the terminology of Stensio (1948) and Miles (1968). Zhang (1984) has suggested new homologies for some of the bones of the antiarch pectoral fin, but for ease of comparison with earlier descriptions we use the older terminology here. Abbreviations for morphological structures used in the text and figures are listed in Appendix II. In the descriptions bone proportions are generally expressed as the ratio of length to breadth or breadth to length times 100 (abbreviated to B/L or L/B index). Bone measurements (Tables 1-6) are given in Appendix I.

Specimens described or discussed below are housed in various institutions, identified by prefix as follows: AMF – Australian Museum, Sydney; CPC –

Commonwealth Palaeontological Collection, Australian Geological Survey Organisation, Canberra; IVF – Institute of Geology, Academy of Geological Sciences, Beijing; V – Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing; L, MGV – Museum of Geology, Ministry of Geology, Beijing.

## Systematic Descriptions

### Class PLACODERMI

### Order ANTIARCHI

### Suborder SINOLEPIDOIDEI Long, 1983

### Sinolepidae Liu & P'an, 1958

**Diagnosis.** Orbital fenestra of head shield small; premedian plate wide, preorbital depression developed, triangular; postorbital division long; lateral plate large, wide, polygonal. Trunk armour low; dorsal wall slightly arched; ventral wall flat; ventral lamina of anterior and posterior ventrolateral plates greatly reduced, very narrow; median ventral plate absent and a large subrectangular ventral aperture present; ventrolateral margin of trunk armour developed as low ridge; prepectoral corners developed on ventral wall of trunk armour. Semilunar plates paired; subanal division short, posterior margin straight or concave. Anterior median dorsal overlaps anterior and posterior dorsolaterals; posterolateral margins of AMD short. Pectoral fin segmented, with flat articular processes on the dorsal and ventral central plates, no dorsomesial crest or mesial lamina on the dorsal central plate, a dorsal lamina on the first mesial marginal plate, and a small articulation on the first ventral central plate. Central sensory line groove, posterior oblique cephalic pit-line groove and posterior oblique abdominal pit line groove all absent.

**Remarks.** The defining characters of the suborder and family are discussed below in the section on sinolepid relationships.

### *Grenfellaspis* n.gen.

**Etymology.** After the town of Grenfell, NSW, Australia, about 20 km from the type locality, and *aspis* (Gk), shield.

**Diagnosis.** Head shield small, broader than long, less than half as long as trunk armour; postpineal and nuchal plates do not overlap lateral plate; trunk armour long, narrow; processus obstans developed; anterior margin of AMD as broad as posterior margin. PMD lateral process not developed. Crista transversalis

interna posterior strongly developed, with the anterior margin of its median dorsal part united with the median ventral ridge; posterior ventral pit separate with posterior ventral process. AVL with one transverse crest on visceral surface; ventral wall of AVL and PVL straight, narrow, widest between prepectoral corners; semilunar plate(s) large; posterior marginal area of PMD well developed, bearing posterior ventral pit and process; ventral fossa articularis pectoralis small, shallow; axillary foramen small, triangular; pectoral fin slender, ventral area narrow, small and circular in shape. Boundary line between marginal and external articular areas not clear.

**Remarks.** The characters used to distinguish the new genus are discussed below in the section on sinolepid interrelationships.

### *Grenfellaspis branagani* n.sp.

### Figs 3-17

'undescribed form from eastern Australia' Young, 1981: 236, 237.
'antiarch from Grenfell' Long, 1983: 311.
'sinolepid nov.' Young, 1984c: fig.2.
'sinolepid nov.' Young, 1988a: fig.68.
'sinolepid' Young, 1990a: 247.
'sinolepid...from...near Grenfell' Burrett et al., 1990: 168.
'new Australian genus' Young & Zhang, 1992: 448, fig.7C.

**Type material.** HOLOTYPE, AMF 78680, a left AVL in part and counterpart.

**Other material.** Head plates: PrM (AMF 54346, 56156, 56291, 78724, 79207, CPC 29102, 29103); PP (AMF 56295); Nu (AMF 56116, 56273, 56290, 56291, 56374, 78682, 78686, CPC 29105); L (AMF 56275, CPC 29106-29108); PNu (AMF 56346, 61457, 78681, CPC 29104, 29109). Trunk plates: AMD (AMF 56147, 56360, 56367, 56370, 61424, 61447, 78684, 78690, 78691, 78695, CPC 29110-29117); PMD (AMF 56136, 56136, 56174-5, 56282, 56292/56294, 56295, 56324, 56328, 56362, 56364, 56371, 78688, 78697, 78698, CPC 29118-29122); ADL (AMF 55308, 56146, 56148/56274, 56283, AMF 56295, 56363, 61438, 61433, 63891, 78682); PDL (AMF 56145, 56294, 61438, 78692, 78694, CPC 29123, 29125); AVL (AMF 56148, 56346, 61433, 61445, 61450, 78680, 78683, CPC 29126, 29127); PVL (AMF 55308, 56121-2, 56280-1, 56355-6, 56371/56374, 61451/56346, 78695, 78696, CPC 29128); Pectoral fin plates (AMF 56148/56274, 56280-1, 78693, CPC 29129-29131).

**Type locality.** Redcliff Mountain, about 20 km north-east of Grenfell, NSW (see Fig.1). Also collected from other localities in the vicinity (Mount Yambira, Narrakup, Eagle's Nest; Fig.2A).

**Horizon.** Hunter Siltstone of the Beargamil Sub-Group of the Hervey Group (Connolly, 1965).

**Age.** Late Late Devonian (late Famennian).

**Etymology.** After Dr David Branagan, Dept of Geology, University of Sydney, who drew the attention of A. Ritchie to this occurrence, and whose contributions to Australian geology are wide ranging.

**Diagnosis.** As for genus (only species).

**Description.** The material occurs as isolated bones scattered across bedding planes in a hard grey-green siltstone. Bedding planes are commonly completely covered with bone remains, mostly deeply weathered, which have been removed by etching in 20% hydrochloric acid, to allow casting with latex rubber of impressions. Much of the material is distorted, so estimates of proportions are only approximate. Strong distortion may be indicated by the elliptical shape of tubercles, but for moderate or slight distortion this is not a reliable criterion. For bilaterally symmetrical bones restoration of original shape has been carried out for selected examples using the techniques outlined by Ramsay & Huber (1983), and these have been used in preparing reconstructions of the whole armour (Figs 16,17).

**Headshield.** Of the bones from the headshield only the postmarginal has not been identified in the material. The premedian (PrM) plate (Fig.3E-J) is represented by six examples, each showing a triangular preorbital depression on the posterior division of the plate as in *Sinolepis* and *Xichonolepis* (see below), which takes the place of the preorbital recess of bothriolepid antiarchs. The PrM is broader than long (breadth/length index 162-217), and widest at the rostral margin, which is much wider than the orbital margin. The ornament continues to the rostral margin which is slightly convex. The posterior margin is occupied by the preorbital depression which reaches forward to the centre of the plate and is suggestive of Yunnanolepiformes. The depression is smaller than in *Yunnanolepis* and differs in that it does not reach the lateral plate. The lateral margins of the PrM are slightly convex, but less so than in *Sinolepis*.

In all specimens the infraorbital sensory canal groove can be clearly seen extending onto the plate from the middle of the lateral margin (ifc, Fig.5A). It forms a commissure (soc) in front of the preorbital depression. There is a strong ridge behind the sensory canal, but the left and right ridges do not meet in the midline. Two specimens show the visceral surface of the plate. In AMF 78724 the ventral surface of the preorbital depression is strongly convex (Fig.5B). A keyhole-shaped median depression, bordered by a ridge, extends anteriorly beyond the centre of the plate, and there is no sign of a premedian ridge and other structures seen in most other antiarch genera. CPC 29102 is similar but the median depression is relatively broader (Fig.3G). The ventrolateral margins of the PrM are vertical, and there is no ventrolateral notch.

There are four lateral (L) plates, each represented only by its dorsal impression (Fig.3A-D). The L was
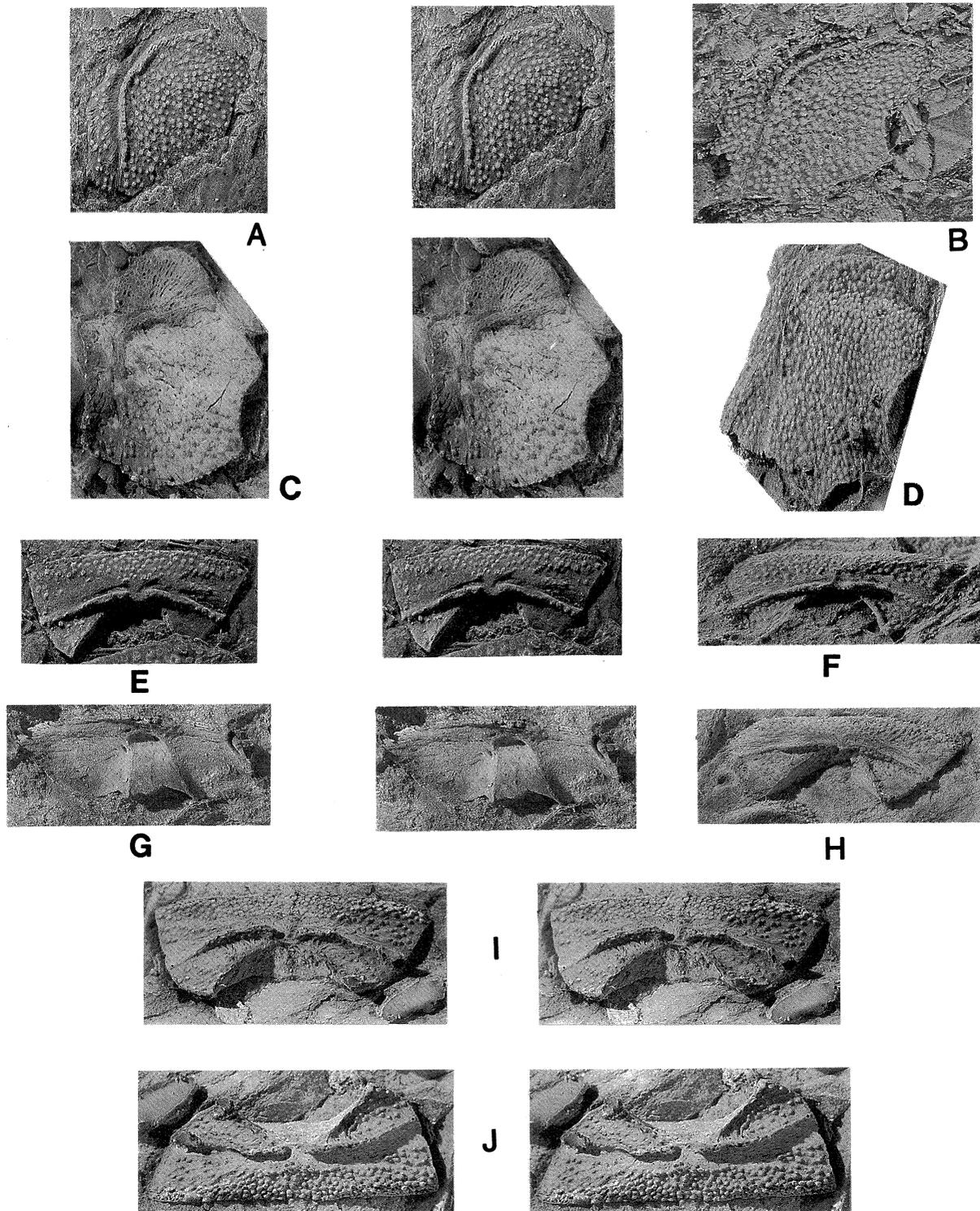
**Fig.3.** *Grenfellaspis branagani* n.gen., n.sp.; Hunter Siltstone, Late Devonian, near Grenfell, NSW, Australia. Premedian (PrM) and lateral (L) plates of headshield. Latex casts whitened with ammonium chloride. All specimens twice natural size (x2). A - left lateral plate, AMF.56275 (stereo pair); B - left lateral plate, AMF.78679; C - left lateral plate, CPC 29106 (stereo pair); D - left lateral plate, CPC 29107; E - premedian, AMF.56156 (stereo pair); F - premedian, AMF.79207; G-H - premedian, CPC 29102; G - ventral surface (stereo pair), H - dorsal surface; I - premedian, CPC 29103, dorsal view (stereo pair); J - premedian, CPC 29103, anterior view (stereo pair).

apparently a broad plate, the largest bone in the skull, and multilateral in shape. It was evidently similar to that of *Sinolepis* and *Yunnanolepis* in the very small orbital notch (Fig.5C), but details remain unclear. The orbital notch is only poorly preserved in the most complete specimen (CPC 29106, Fig.3C), and is missing from the
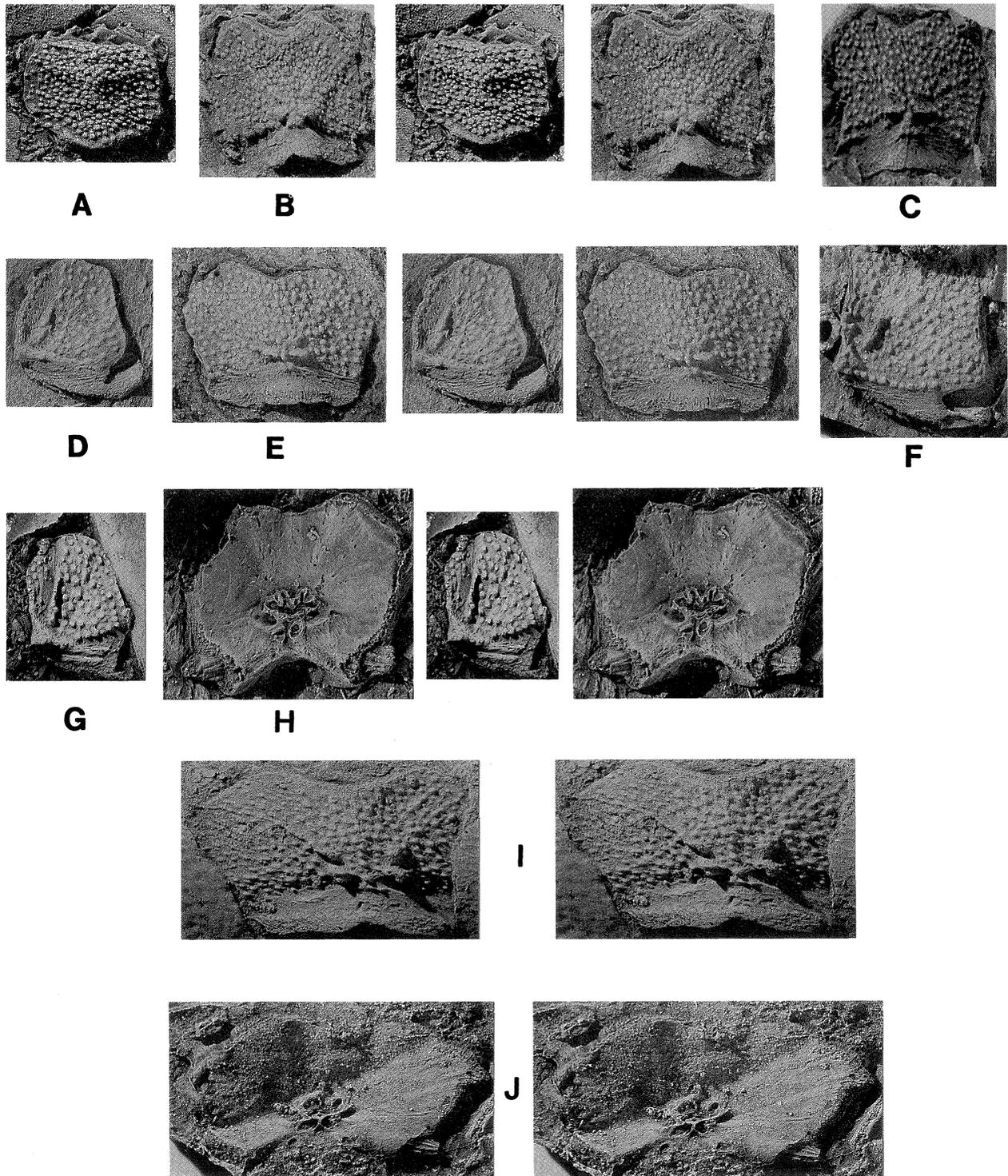


**Fig.4.** *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Posterior and posterolateral plates of headshield. Latex casts whitened with ammonium chloride. All specimens twice natural size (x2). A - postpineal, AMF.56295 (stereo pair); B - nuchal, AMF.56273 (stereo pair); C - nuchal, AMF.78686; D - left paranuchal, AMF.79210 (stereo pair); E - nuchal, AMF.78682 (stereo pair); F - left paranuchal, CPC 29104; G - left paranuchal, AMF.78681 (stereo pair); H - nuchal (visceral surface), CPC 29105 (stereo pair); I-J - nuchal, AMF.78685 (stereo pairs: I - dorsal; J - ventral).

other examples. CPC 29106 is a nearly complete left plate (49.5 mm long, 36 mm wide; L/B index 138), which judging from tubercle shape has been somewhat distorted anteroposteriorly. It shows an expanded anterior part lacking ornament, and a distinct anterolateral notch (nprl, Fig.5C) not clearly preserved on other specimens. The orbital margin (om) is indicated as a notch on the ventral edge of the mesial margin, but the dorsal edge is straight so this was either abraded off or not developed. The anterior and lateral margins are convex. The anterolateral corner is indistinct, and the prelateral notch (nprl) as preserved in CPC 29106 is large (Fig.3C), but this is due to upward flattening of the margins. AMF 56275 and CPC 29107 show suggestions of a notch, but both are incomplete anteriorly. Behind the notch in CPC 29107 is a short pointed lateral process projecting downward. This specimen has a well-preserved lateral margin which thickens towards the posterior. The postmarginal contact is ill-defined immediately lateral to the sensory groove, and must have been small, even though the lateral division of the PNu is narrow. A slight notch mesial to the groove accommodated the anterior corner of the PNu. The Nu contact is straight in CPC 29106 but concave in CPC 29107, and the PP margin is concave in both. The orbital margin is short on the

L plate, and the contact with the nuchal plate is oblique. It is clear that *Grenfellaspis* lacked the overlapping areas for the PP and Nu plates seen in *Sinolepis*. The infraorbital sensory groove (ifc) is near the lateral margin, with a strong ridge developed inside the groove as on the PrM. A shallow depression is variably developed behind the anteromesial section of the sensory groove. The bone is smooth with a few sparse tubercles lateral to the sensory groove in CPC 29106 and AMF 56275, but has normal ornament in CPC 29107 and 29108.

The postpineal (PP) plate is only known from one specimen, AMF 56295, a complete dorsal impression (Fig.4A). It differs from the PP of *Sinolepis* and Yunnanolepiformes in its slightly convex lateral margin, without overlap onto the L plate. Orientation of this specimen is based on the posterior margin, which is convex with a blunt medial angle corresponding to the shape of the postpineal notch on the Nu plate (Fig.4E). Compared with Nu plates of corresponding size, it was more than two thirds the length of the Nu plate. It is a subpentagonal plate (Fig.5D), and broader than long (L/B index 80). The anterior margin is straight to slightly concave.

The nuchal (Nu) plate is 'crown-shaped', and similar in outline to that of *Asterolepis* and *Pterichthyodes*, but
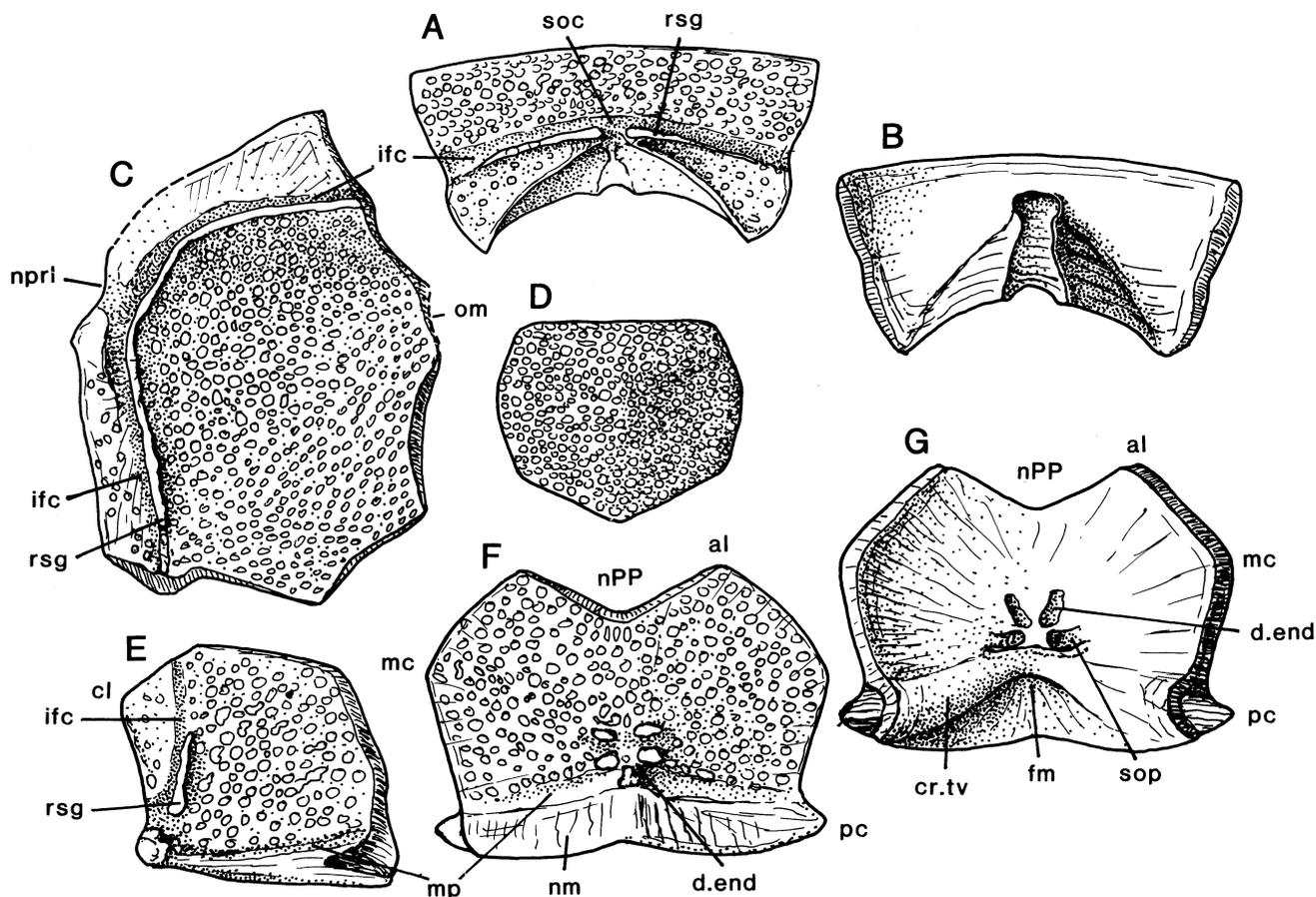


**Fig.5.** *Grenfellaspis branagani* n.gen, n.sp. Restoration of head plates: A,B - premedian (dorsal and ventral); C - left lateral; D - postpineal; E - paranuchal; F,G - nuchal (dorsal and ventral).

in its greater elongation it resembles the Nu of *Sinolepis* or *Yunnanolepis* (Fig.33C,D). The figured specimens (Fig. 4B,C,E,H-J) illustrate well the range of distortion in the material, with AMF 78686 elongated longitudinally, and 78685 elongated laterally. AMF 78682 and CPC 29105 appear relatively undistorted (based on ornament and intermediate proportions) and have been used for the restoration (Fig.5F). The L/B index is estimated at about 80 (measured range 76-105), based on the three best specimens (AMF 56157, 78582, CPC 29105).

The anterior division of the plate is shorter than the posterior division (Fig.5F). The anterolateral (al) and lateral corners (mc) are well developed, and the postpineal notch (nPP) is broad and shallow. The anterolateral margin is strongly oblique but the posterolateral margin tapers more gradually. The posterior margin is seen to be slightly concave in uncrushed specimens, which show the plate to be arched transversely at its posterior margin. Most specimens lack a posterior median process, but one is present in AMF 56290. The obtected nuchal area (nm) is not depressed far below the ornamented surface. The central sensory line groove is not developed, but part of the middle pit-line groove can be seen on AMF 78682 (Fig.4E) and other specimens (mp). Over the ossification centre of the plate there may be one (e.g., AMF 78682) or two (AMF 78685) pairs of enlarged tubercles, separating four shallow unornamented sulci, of which the posterior pair presumably represents the endolymphatic duct openings (d.end). However, no specimen shows a clear foramen here, and considering the detailed preservation of the material it seems that the duct may not have opened to the surface. The inner surface of the Nu (Figs 4H,J, 5G) shows two pairs of pits, as in other antiarchs, the anterior being the internal endolymphatic openings, and the posterior the supraoccipital pits (sop). The posterolateral corners (pc) are well developed and project beyond the lateral margins in AMF 56290, a large plate (20.5 mm across), and also the only one showing a posterior median process. AMF 78685 is the largest available Nu (28 mm across) but the posterolateral corners are obscured in external view. All other examples lack the posterolateral corners in external view (Fig.4B,C,E), but they are visible in specimens showing the visceral surface (Fig.4H,J), and fitted into a socket on the PNu. The visceral surface of the Nu plate, best seen in CPC 29105, shows a well developed transverse nuchal crista (cr.tv, Fig.5G), which forms a strong, anteriorly convex arc for the levator fossa (fm). The rounded contact margin across the crista for the PNu plate contrasts with the development of this area in *Bothriolepis* (e.g., Stensiö, 1948, fig.25), where the PNu forms a strong mesial process overlapped by the Nu. The posterior surface of the crista displays the well-developed fossa for insertion of the levator muscles of the headshield, but there is no median occipital crest.

The paranuchal (PNu) plate is represented by several almost complete examples (Fig.4D,F,G). It is a quadrilateral bone, as long as, or longer than, broad (L/B index 100, 120 in AMF 79210, 78681), with a convex anterior margin. The main difference in shape from the corresponding bone of *Bothriolepis* is the absence of the strong mesial process which underlies the transverse nuchal crista on the Nu plate in that form (see Stensiö, 1948, fig.27). The PNu is divided into a very narrow lateral division and wider mesial division by the infraorbital sensory canal groove (ifc, Fig.5E), which is a broad shallow groove as in *Sinolepis*. All available specimens show a short ridge of coalesced tubercles defining the mesial edge of the groove along its posterior half (rsg). Another shallow groove passing across the anterior edge of the obtected area may be the middle pitline (mp). At the posterolateral corner is a marked elevation of coalesced tubercles. The anteriorly situated lateral corner (cl) shows that the obstantic margin was more anterolaterally directed than in *Bothriolepis*. A marked notch and/or socket on the mesial margin received the posterolateral corner of the Nu.

No example of the postmarginal plate of *Grenfellaspis* has yet been located in the material, nor have any cheek plates (submarginal, suborbital, infragnathal) been identified.

**Trunk shield.** The bones of the trunk armour of *Grenfellaspis* are generally well represented, although as noted above no posterior lateral or median ventral plates have been found, and these are presumed to have been absent.

The anterior median dorsal (AMD) plate is strikingly long and narrow (Fig.6), with a B/L index ranging between 47 and 62 (Table 1), making it amongst the narrowest for known genera of Antiarchi. In some specimens (AMF 61447, 78684) both the dorsal and visceral surfaces are represented by complete impressions. The dorsal wall is slightly convex along the dorsal median line, but lacks a crest or median ridge. The tergal angle lies very close to the anterior margin of the plate and has an obliquely transverse depression. The lateral corner is not always distinct in dorsal view, but anterolateral and posterolateral margins are easily divided based on the overlapping areas seen on the visceral surface (Fig.6B,C).

The AMD is broadest posteriorly across the lateral corners. The anterior division of the plate is much longer than the posterior division (Table 1). The overlapping areas for adjacent bones are narrow. The anterior margin is straight, and about the same width as the posterior margin. The external postlevator process is weakly developed and situated near the anterolateral corner. The posterolateral margin of the plate is slightly arched. The posterior margin is concave, with a short posterior median process, and the overlap for the PMD restricted to the central part. Laterally the ornamented part of the AMD projected back to form a butt joint with the PMD.

On the visceral surface (Fig.6B,C,E) the postlevator thickening is strongly developed, but there is no
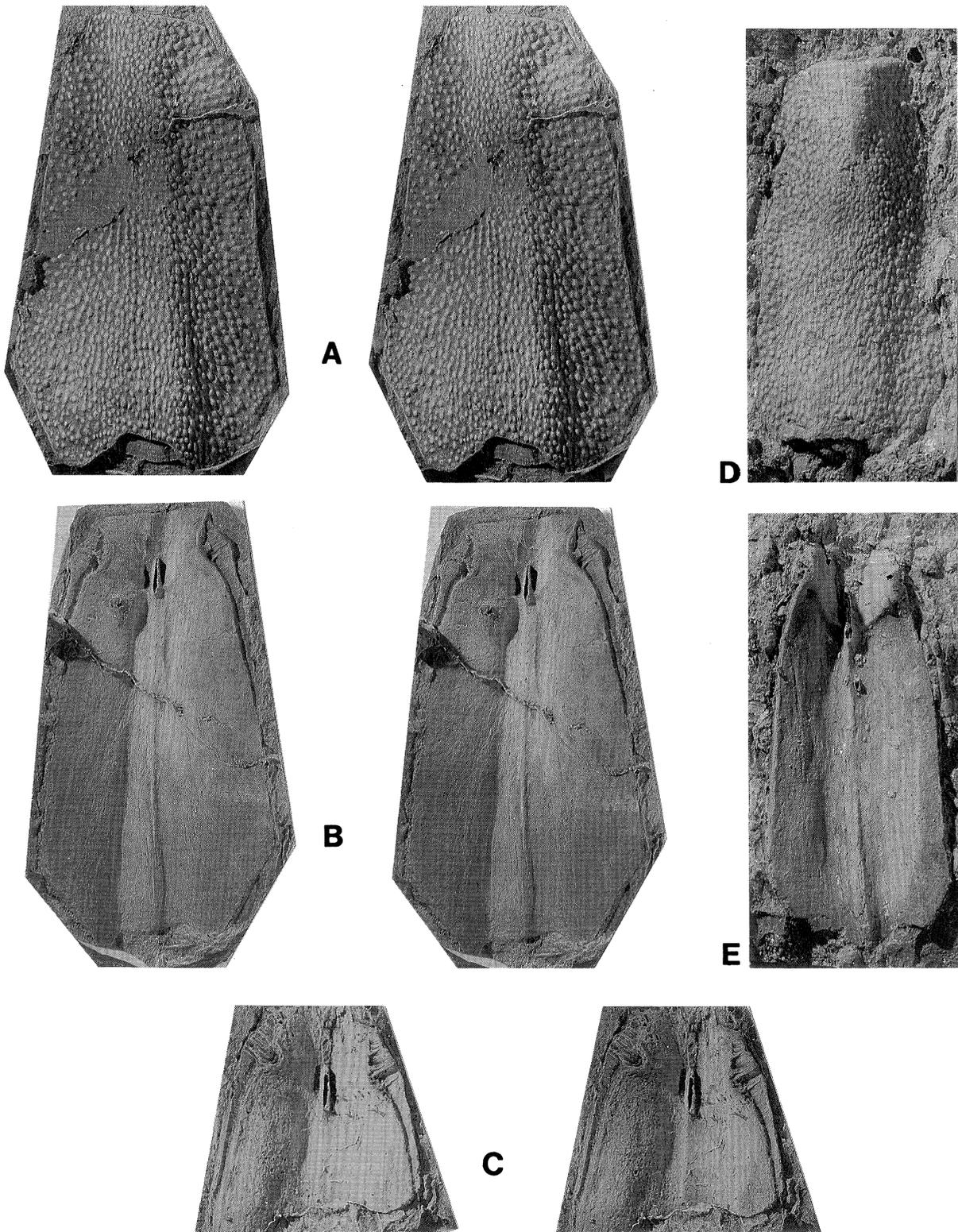
**Fig.6.** *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Anterior median dorsal plates (AMD) of trunk shield. Latex casts whitened with ammonium chloride. All specimens 1.5 times natural size. A-B - anterior median dorsal, AMF.78684; A - dermal surface, B - visceral surface (stereo pairs); C - anterior median dorsal, AMF.56370, anterior part of visceral surface (stereo pair); D-E - anterior median dorsal, AMF.61447a,b; D - dermal surface, E - visceral surface.

postlevator crista. The levator fossa is short, about one sixth the length of the AMD. The anterior ventral process and pit are narrow and long, and situated at the posterior end of the levator fossa, between the posteromesial ends of the two postlevator thickenings.

The ventral median ridge is strongly developed, and extends backwards from the anterior ventral process to the posterior margin.

The posterior median dorsal (PMD) plate is also long and narrow, and similar to the AMD in size and outline
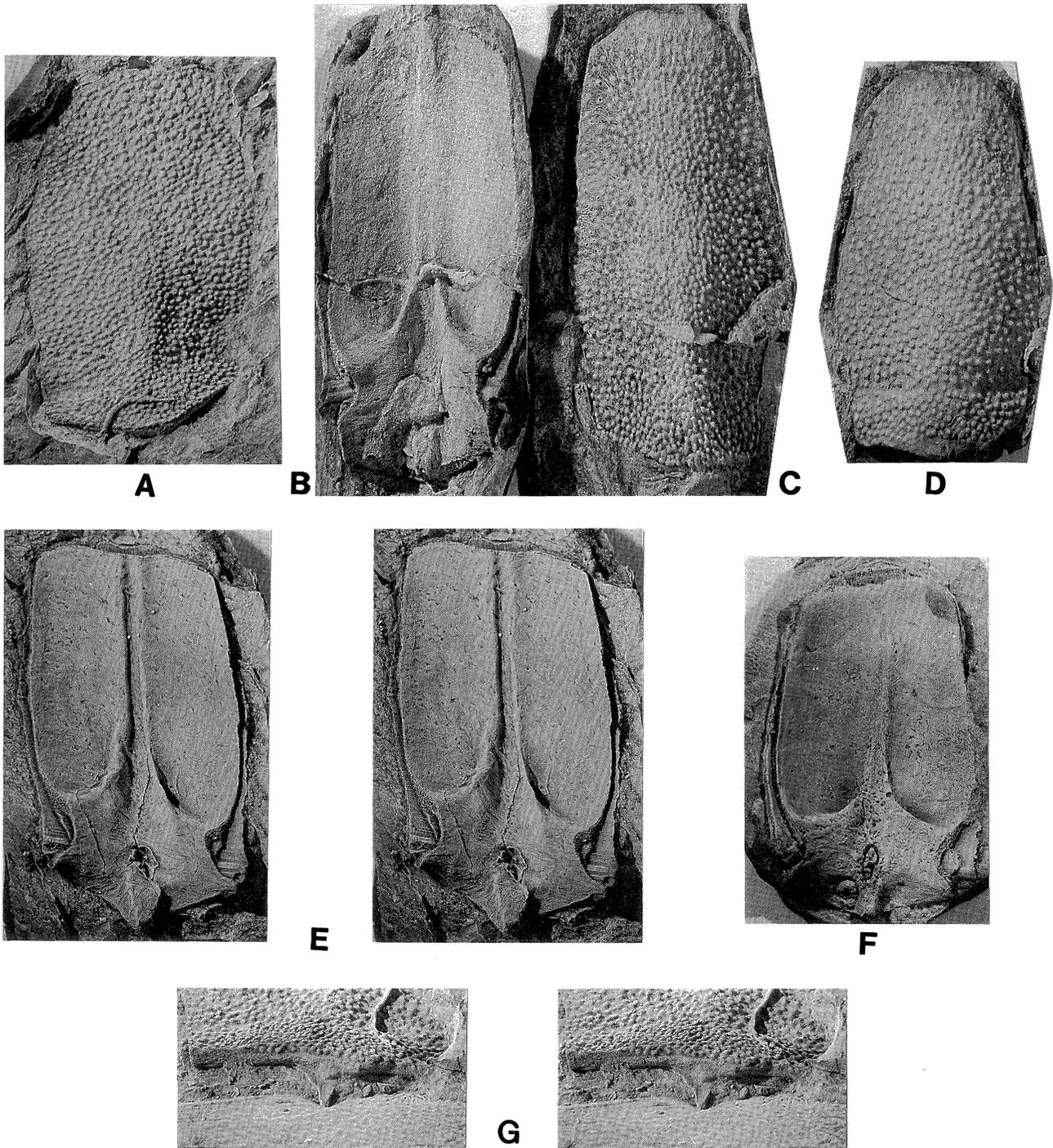


**Fig.7.** *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Posterior median dorsal plates (PMD) of trunk shield. Latex casts whitened with ammonium chloride. All specimens 1.5 times natural size. A - posterior median dorsal, AMF.79203a; B-C - posterior median dorsal, AMF.56175; B - visceral surface, C - dermal surface; D - posterior median dorsal, AMF.56316; E - posterior median dorsal, AMF.79203b, visceral surface (stereo pair); F - posterior median dorsal, AMF.56324, visceral surface; G - posterior median dorsal, AMF.79202; posterior margin showing well-developed posterior process (stereo pair).

(Fig.7). In the most complete specimens (AMF 56136, 78678, 56294, 56328) the B/L index is between 43-55, but some examples are much more elongate (Table 2), possibly due to distortion. In shape the PMD compares with that of *Xichonolepis*, except in the absence of lateral processes (see below), which give it a quadrilateral shape. The anterior margin is strongly convex, but lacks an anterior angle. It is straight in the middle of this margin, as indicated also by the posterior margin of the AMD plate (e.g., AMF 56175, 78684). The long lateral margins are slightly convex, with narrow overlap areas in visceral view (Fig.7B,E,F). In contrast to *Xichonolepis* (see below) the lateral processes and corners are not well developed, and the plate is about the same width along its length. The posterior margin is rounded, but with a prominent angular median ventral process (Fig.7E-G), which is homologised with the posterior ventral process of the PMD in other antiarchs (see below).

On the visceral surface of the PMD the posterior internal transverse crista is very strongly developed, with a distinct anterior and rounded posterior margin (Fig.7E,F). The posterior marginal area takes the form of a paired shallow depression behind the crista on either side of the posterior ventral process, which projects back to the posterior margin of the bone. A prominent ventral median ridge with a ventral groove extends from the anterior margin of the PMD back to the posterior transverse crista, where it broadens to form the oblique anterolateral margin of the crista. The posterior ventral pit lies on the posterior part of the crista, and immediately in front of the posterior ventral process, situated entirely behind the crista. This arrangement differs from that of typical antiarchs (e.g., *Bothriolepis* or *Yunnanolepis*), in which the posterior marginal area is unpaired, and the posterior ventral pit and process lie in front of the transverse crista. However Zhang (1980) noted a similar arrangement in *Xichonolepis*, with both the posterior ventral pit and process lying behind the crista. The main difference between the two genera can be attributed to the slight development of the transverse crista in *Xichonolepis*, and correspondingly broader posterior marginal area (see below), such that both the pit and process lie behind the crista. In addition the pit and process are not separated as they are in *Grenfellaspis*.

The anterior dorsolateral (ADL) plate of *Grenfellaspis* is basically quadrilateral in shape (Fig.8A), but the absence of a well-developed dorsolateral ridge makes it difficult to distinguish the dorsal and lateral laminae. AMF 56148 is an almost complete but flattened ADL, with a B/L index of 60, but this value may be slightly high due to compression. In outline and proportions the *Grenfellaspis* ADL differs from that of both Bothriolepidae and Asterolepidae. The dorsal surface of the plate is widest anteriorly, and in dorsal view the anterior margin of the dorsal lamina is straight, with a convex obstantic process developed laterally. The mesial margin of the plate is slightly concave, reflecting the absence of a strong external postlevator process or

postnuchal notch on the AMD. The posterior margin of the ADL is convex, with a posterior corner developed on the dorsal lamina. The lateral margin is convex anteriorly and straighter posteriorly. The well-developed lateral line groove is bordered dorsally by a prominent ridge of coalesced tubercles, as on the PNu, L, and PrM bones of the skull. The groove is broad and ill-defined laterally, grading into the narrow, depressed margin of the lateral lamina, which tends to be sparsely ornamented posteriorly (Fig.8C). The overlap area for the AVL plate is only developed at the anterior end (Fig. 8F). Whether or not there was contact with the PVL plate, as described below in *Dayaoshania* and *Xichonolepis*, is not clear in the available specimens.

As seen on AMF 56292 (Fig.8D-F) the crista transversalis interna anterior is strongly developed, with the articular fossa for the paranuchal trochlea of the headshield well displayed (Fig.8E). The fossa is bordered below by a well-developed infra-articular crest, but a supra-articular crest is absent.

The posterior dorsolateral (PDL) plate, like the ADL, is long and narrow (Fig.9). It is broadest across its dorsal corner, which is developed much as in *Xichonolepis*. Posteriorly the plate becomes gradually narrower, also as in *Xichonolepis*. As with the ADL the boundary between the dorsal and lateral laminae is not clear, the external surface of the plate being gently convex, without a dorsolateral ridge. One uncrushed specimen (CPC 29123) reveals that the lateral lamina is very low and of equal height throughout its length, as on the ADL. The ventral margin is straight and the main lateral line groove is clearly marked just inside the margin (Fig.9B,E). The posterior margin of the PDL is short and concave, and in visceral view shows a strongly developed crista transversalis interna posterior (Fig.9F,G).

The PDL is overlapped anteriorly by the ADL as in all other known antiarchs. Dorsomesially it is overlapped anteriorly along a short margin by the AMD, and posteriorly along a much longer margin by the PMD. CPC 29123 shows a strong buttress of cancellous bone which fitted against the strong transverse posterior thickening developed on the PMD as described above. The narrow overlap area on the ventral margin is only developed posteriorly, and is assumed to be for the PVL, because the low lateral wall provides no space for a separate posterior lateral plate, and no such element has been identified in the material.

The most unusual plate in the trunk armour of *Grenfellaspis* is the anterior ventrolateral (AVL) plate (Fig.10). The most complete example in the Australian Museum collection (AMF 78680, a left AVL) has been selected as the holotype of *Grenfellaspis branagani* n.gen., n.sp. It is preserved as an external and internal impression showing virtually all the features of this distinctive and definitive plate (Fig.11).

As in other Antiarchi the AVL of *Grenfellaspis* is made up of lateral and ventral laminae, but it differs strikingly from previously described antiarch genera in the very low lateral lamina, and the greatly reduced

posterior part of the ventral lamina, which has a deep, almost right-angular mesial embayment (m3, Fig.11). The holotype is 72 mm long and 28 mm wide anteriorly (L/B index 257), but behind the level of the brachial articulation the ventral lamina is reduced to only 7 mm wide, and posteriorly it narrows to 5 mm. The ventral lamina thus comprises a broad anterior subcephalic division comparable to that of other antiarchs, and an elongate narrow posterior division, which enclosed only the lateral side of the ventral surface of the trunk (Fig.17).

On the ventral lamina the subcephalic division has the anterolateral corner strongly developed (c.al, Fig.11),

and there is a slight anteromesial corner (c.am) on the free anterior margin, which is concave and very short. The anterior division (m1) of the mesial margin is comparatively long and wide, forming a deep rectangular notch. Its shape is somewhat similar to that of the Early Devonian *Yunnanolepis*, but in *Grenfellaspis* it is much deeper, with its posterior margin level with the prepectoral corner (prc). The middle division (m2) which met the opposite (right) AVL is straight and very short (in the holotype 11 mm long, only about 16% of total length). A well-developed corner of the middle division was present on the right plate where it overlapped the left, as shown by the shape of the overlap area
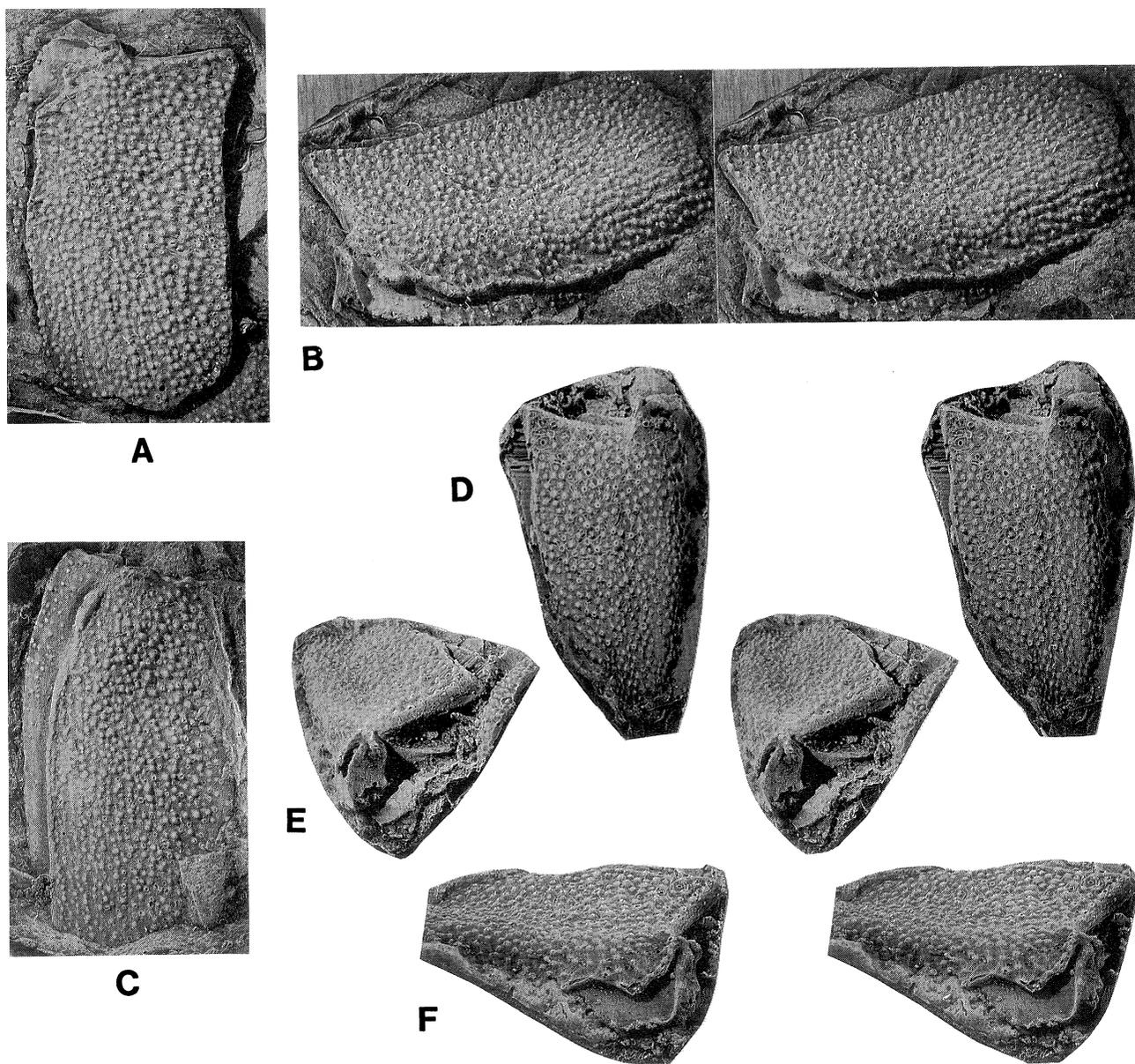


**Fig.8.** *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Anterior dorsal lateral plates (ADL) of trunk shield. Latex casts whitened with ammonium chloride. All specimens 1.5 times natural size. A-B - left anterior dorsolateral, AMF.56148; A - dorsal view, B - oblique anterolateral view (stereo pair). C - left anterior dorsolateral, AMF.56295, dorsal view; D-F - right anterior dorsolateral, AMF.56292; D - dorsal view, E - anterior view, F - dorsolateral view (stereo pairs).

(oa.AVL), but the left plate has no corner developed. The posterior division (m3), corresponding to the margin with the median ventral plate in other antiarchs, is very specialised as a deep rectangular embayment. In the holotype it is 54 mm long (measured from corners c4 to c5).

The well-developed prepectoral corner (prc) is best preserved on AMF 61446. The AVL is broadest between this corner and the median contact between left and right plates. The subcephalic division is relatively shorter than in other known antiarchs. In the holotype it is about 13 mm long, and only 20% of the length of the plate.

The anterior margin of the lateral lamina is essentially
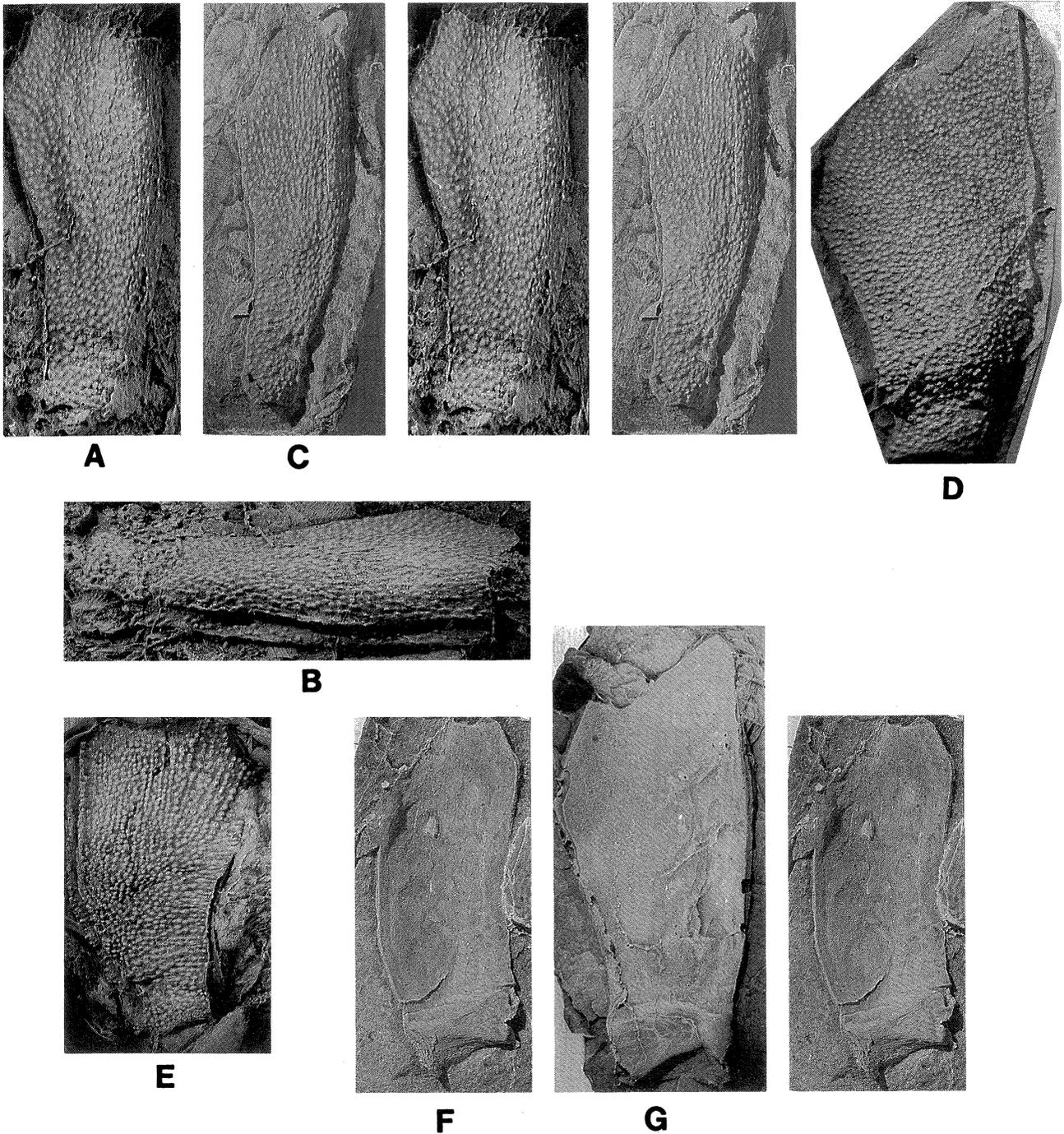


**Fig.9.** *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Posterior dorsolateral plates (PDL) of trunk shield. Latex casts whitened with ammonium chloride. All specimens 1.5 times natural size. A-B - right posterior dorsolateral, CPC 29123. A - dorsal view (stereo pair), B - lateral view; C - right posterior dorsolateral, AMF.79208, dorsal view (stereo pair); D - right posterior dorsolateral, AMF.78694, dorsal view; E - left posterior dorsolateral, CPC 29124, dorsal view; F - right posterior dorsolateral, AMF.79209, visceral surface (stereo pair); G - left? posterior dorsolateral, AMF.61438, visceral surface.
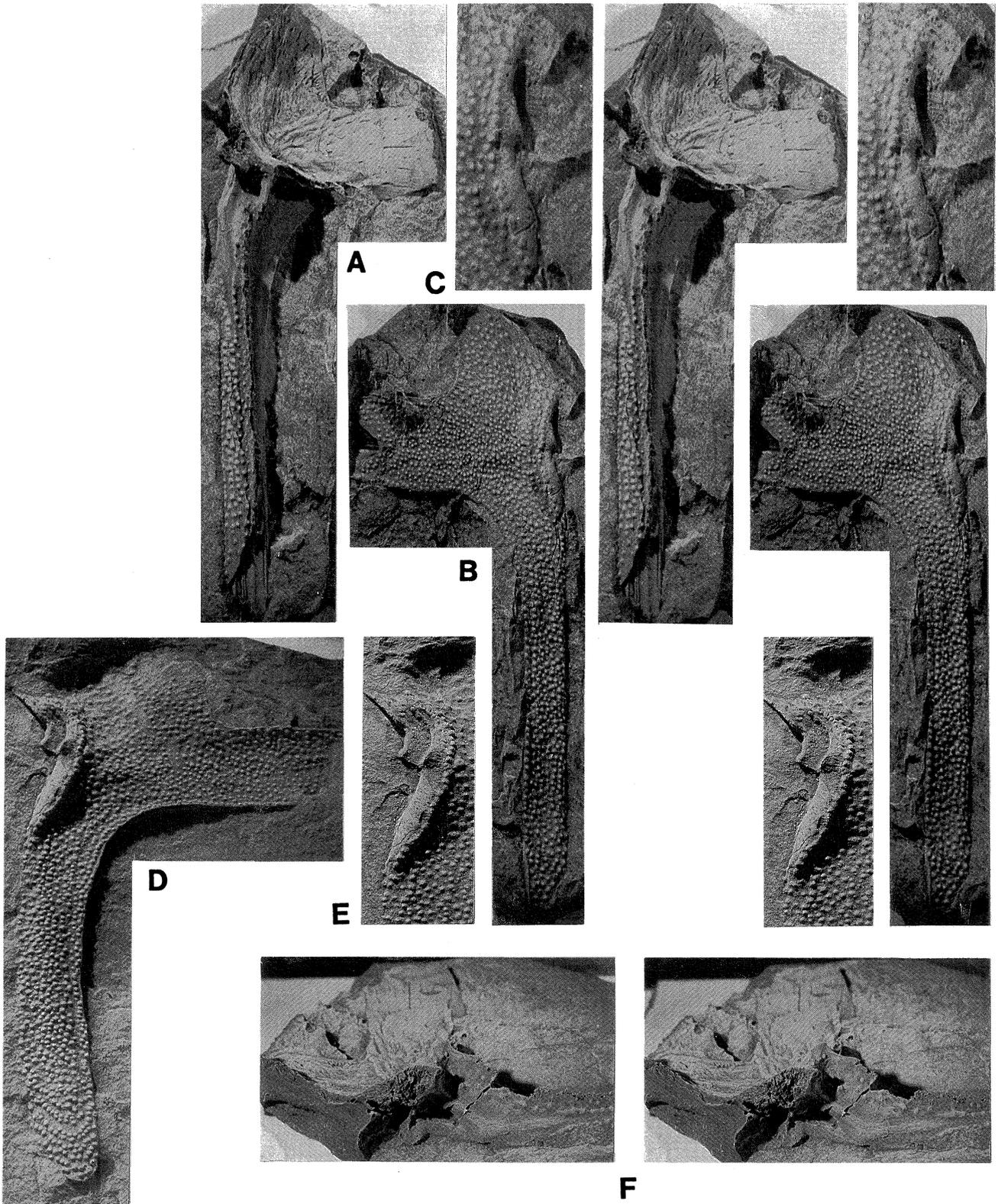
**Fig.10.** *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Anterior ventrolateral plates (AVL) of trunk shield. Latex casts whitened with ammonium chloride. All specimens 1.5 times natural size. A-C,F - left anterior ventrolateral, AMF.78680 (HOLOTYPE); A - dorsal (visceral) view (stereo pair), B - ventral (dermal) view (stereo pair), C - detail of brachial region (stereo pair), F - dorsolateral view of brachial region in AMF.78680 (stereo pair). For interpretation *cf.* Fig.11A-C. D-E - right anterior ventrolateral, AMF.78683, ventral view; D - whole AVL, E - detail of brachial area (stereo pair).

as in other Antiarchi, passing ventrally from the dorsal corner (dc, Fig.11C) into the free lateral margin of the subcephalic division. The dorsal margin of the lateral lamina shows a somewhat more complex development than in other forms but the overlap relationship to the ADL is comparable. In front of the dorsal corner a triangular rugose articular area faces dorsolaterally (art.d,

Fig.11C), separated by a narrow neck of ornamented bone from a groove (cf. ADL, Fig.11B). This groove runs down the inside of the dorsal corner onto the anterior transverse crista (cit2), which formed the anterior overlap onto the ADL. Posteriorly is a short section of rounded margin without overlap surfaces, behind which the straight dorsal margin carries a shallow groove
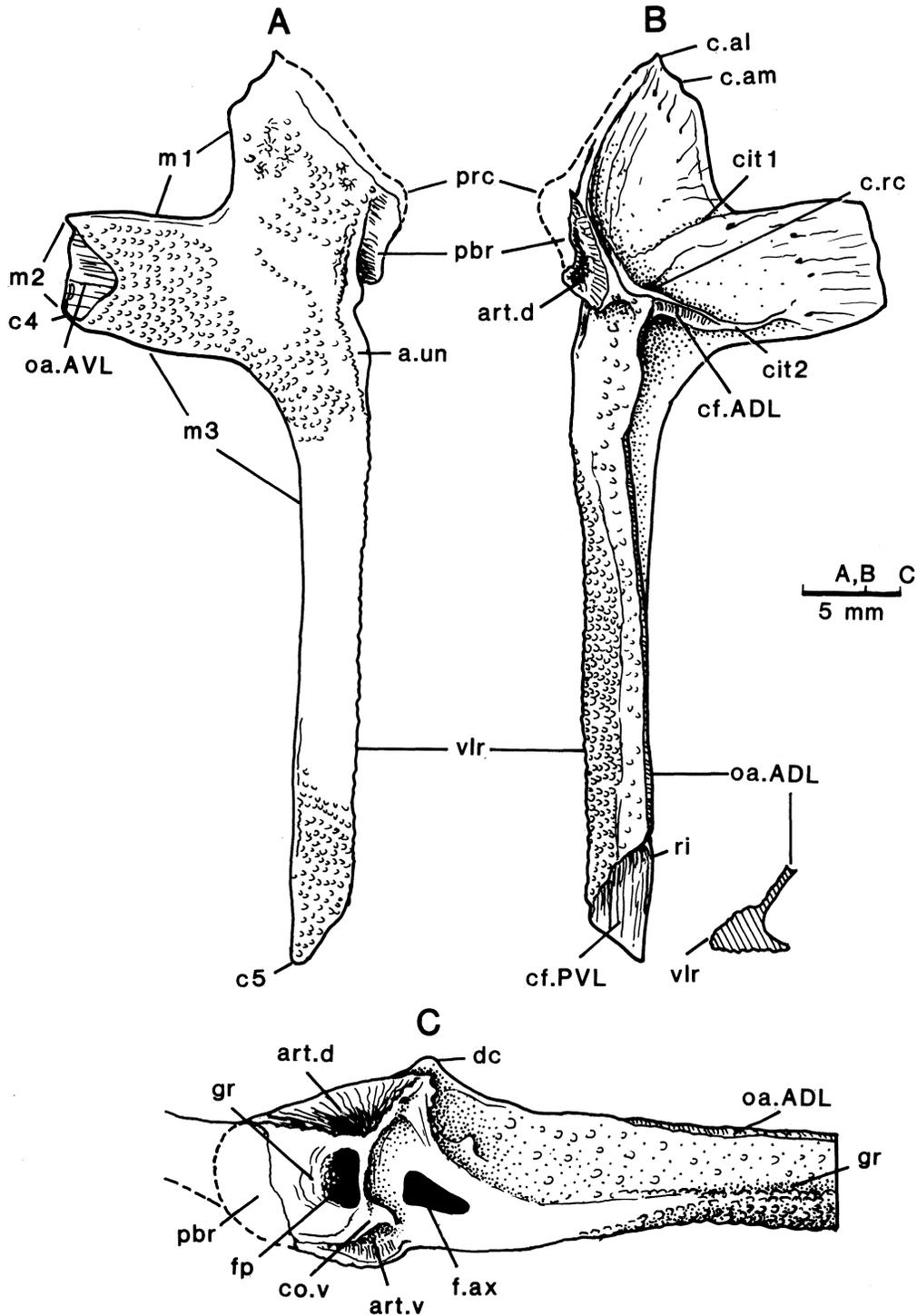


**Fig.11.** *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Holotype, AMF.78680. Left anterior ventrolateral plate (AVL), *cf.* Fig.10A-C,F. A - ventral, B - dorsal (with cross-section at the level shown) and C - lateral views.

into which the ventral margin of the ADL abutted (oa.ADL). The external surface of the lateral lamina comprises a dorsolaterally facing ventral part with crowded tubercles (forming the rounded dorsal surface of a strong ventrolateral ridge or keel formed jointly by the ventral and lateral laminae), and a laterally facing dorsal part on which tubercles are sparse. The two regions are separated by a shallow groove (gr).

On the internal surface of the plate the main branch of the crista transversalis interna anterior is well developed (cit2). It is fairly high and sharp-edged, and decreases in height mesially to terminate before the midline, and does not join up with the crista on the opposite AVL. A weaker anterior branch of the crista transversalis (cit1) runs anteromesially from the inside of the dorsal corner straight to the posterolateral corner of the semilunar notch. Between the two branches a large foramen (c.rc) opens into a shallow groove running anteromesially behind the anterior branch of the crista, which corresponds presumably to the 'rostro-caudal canal' described by Stensiö (1931: 97).

In the midline the right AVL overlaps the left, and posteriorly the AVL overlaps the PVL, as in other antiarchs. The internal lateral margin of the semilunar notch displays an overlap area but the posterior division of the medial margin (m3, Fig.11) lacks any trace of an overlap. No example of a large rectangular median ventral plate required to fill this space has been

identified in the abundant material recovered from several sites near Grenfell, and we suggest therefore that the median ventral plate was not developed in Grenfellaspis. Posteriorly the contact face for the PVL (cf. PVL) has its mesial margin delineated by a narrow ridge (ri), which is consistent with this suggestion.

A rudimentary processus brachialis of unusual form (pbr) is incompletely preserved in the holotype, and clearly seen in ventral view (Fig.10B,C). Similar preservation is seen in AMF 61445 and 78683 (Figs 10D,E,12). In lateral view these specimens show the foramen axillare (f.ax) to be small and triangular in shape, with its long axis horizontal. A ventral fossa articularis pectoralis (art.v) of unusually small size is visible in lateral and ventral views immediately anteroventral to the axillary foramen. This small fossa is placed near the ventral margin and must have received the articular process of the first ventral central plate of the pectoral appendage described below (Figs 14,15). It lies beneath a thickened ventral part of a vertical lamina forming the posterior boundary of the funnel pit (fp). By comparison with the corresponding partition between the axillary foramen and funnel pit in Bothriolepis (e.g., Stensiö, 1948, fig.51A), this ventral thickening (co.v) must be a rudimentary ventral portion of the brachial process (ventral pars condyloidea). The triangular dorsal articular area mentioned above (art.d) must have received the articular process of the first dorsal central plate of the pectoral appendage described below, with the fin pivoting around a single axis passing through the dorsal and ventral articulations.

In the articulation of the pectoral fin Grenfellaspis thus differed markedly from more advanced antiarchs with a large helmet-shaped processus brachialis, such as Bothriolepis, Asterolepis and Remigolepis. In these forms the dorsal and ventral articulations are deep hemispherical grooves separated anteriorly by the narrow pars pedalis of the brachial process. In Grenfellaspis however, as far as can be determined, there was no pars pedalis, the anterior edge of the brachial process being continuous with the prepectoral corner of the AVL (best seen in AMF 61445, 61446; Fig.12). The ventral position of the ventral articular fossa is reminiscent of the brachial articulation in Hyrcanaspis bliecki from the Middle Devonian of Iran (Janvier & Pan, 1982), but that form also had a large normally developed brachial process. Similar discrete dorsal and ventral articulations are seen in the brachial fossa of Procondylolepis (Zhang, 1984), but they differ in being closer together and in front of the funnel pit. In Grenfellaspis the articular areas of the pectoral fin are more widely separated, lying above, below and slightly behind the funnel pit. This implies a high proximal brachial aperture to the fin, of the type seen in advanced antiarchs (abp, Stensiö, 1948, fig.196).

The posterior ventrolateral (PVL) plate superficially resembles the AVL, but in reverse (Fig.13). The PVL
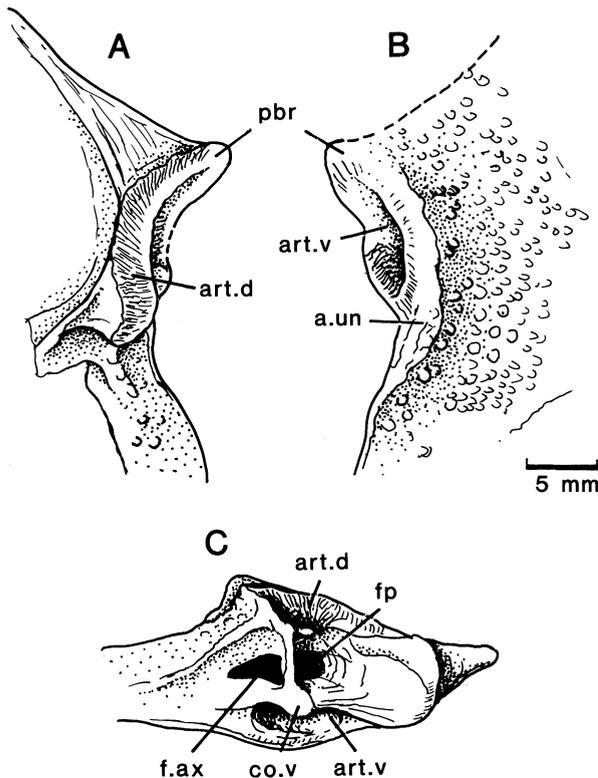


**Fig.12.** *Grenfellaspis branagani* n.gen, n.sp. Late Devonian, NSW, Australia. Right anterior ventrolateral plate, AMF.61445-6. Detail of brachial area in A - dorsal, B - ventral and C - right lateral view.
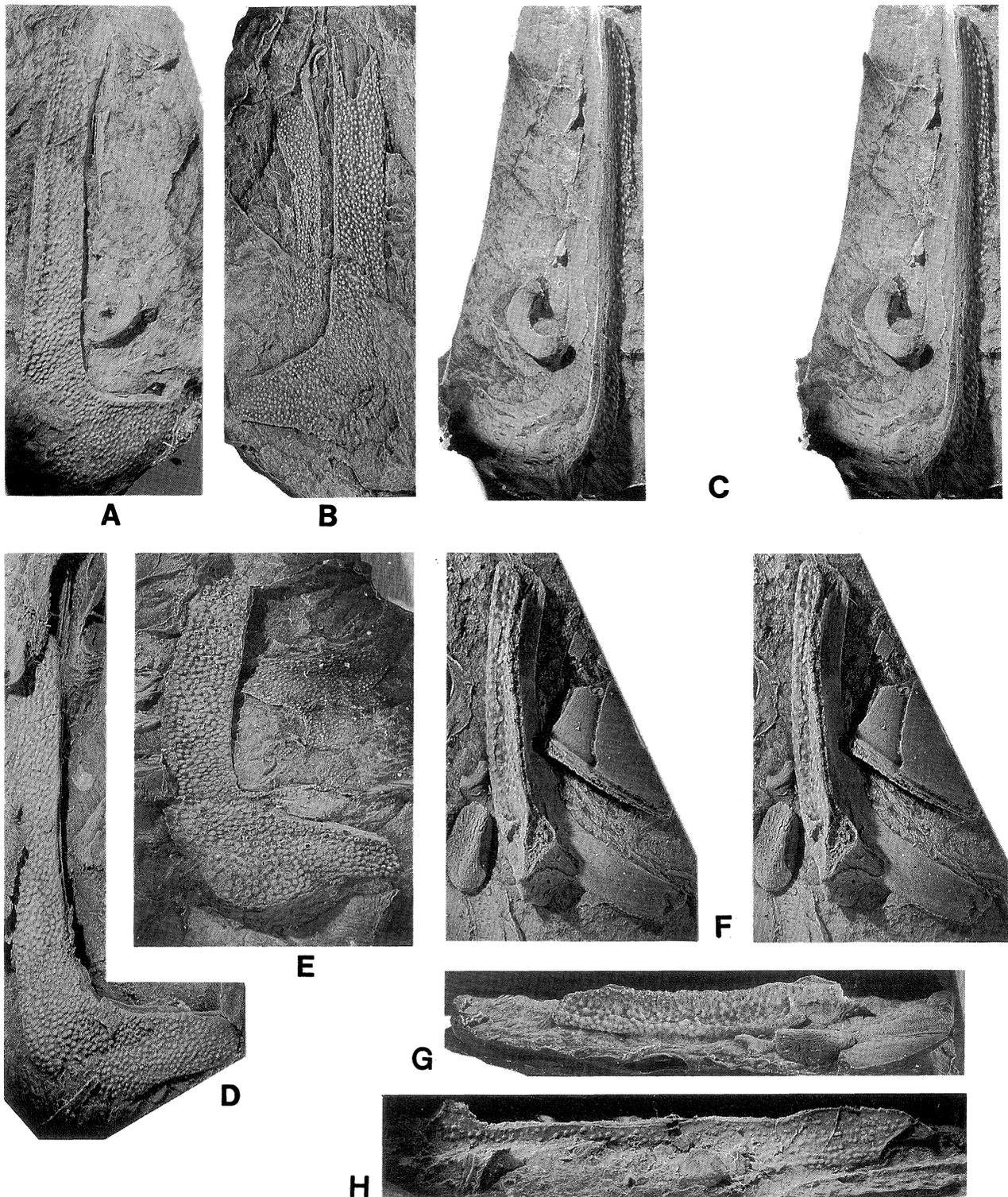
**Fig.13.** *Grenfellaspis branagani* n.gen.,n.sp. Late Devonian, NSW, Australia. Posterior ventrolateral (PVL) plates of trunk shield. Latex casts whitened with ammonium chloride. All specimens 1.5 times natural size. A - right posterior ventrolateral, AMF.56356, ventral (dermal) surface; B - left posterior ventrolateral, AMF.78695, ventral surface (NB also posterior lamina of associated ? left AVL); C - right posterior ventrolateral, AMF.56355 (counterpart of AMF.56356 (A), visceral surface (stereo pair); D - right posterior ventrolateral, AMF.56371, ventral surface; E - right posterior ventrolateral, CPC 29128, ventral surface; F-G - left posterior ventrolateral, AMF.56346, F - dorsal view (stereo pair), G - right lateral view; H - right posterior ventrolateral, AMF.56355, right lateral view of PVL seen in 'C' above.

consists of a long, narrow anterior division and a short, wide posterior division. AMF 56371 is a well preserved right PVL (62 mm long, 25 mm broad; L/B index 248). The anterior division of its ventral lamina is 49 mm long but only 7 mm wide. The posterior division, where the left PVL slightly overlaps the right, is narrowest at the midline (about 6.5 mm across). The lateral lamina of the PVL is very low, with a straight dorsal margin and of equal height throughout, except for a posterior dorsal corner (Fig.13G,H).

The anterior margin of the PVL plate is overlapped by the AVL, and the anterior division of the mesial margin, which in other antiarchs overlapped the median ventral plate, lacks an overlap area, as does the posterior division of the medial margin of the AVL just described. The overlap relationship with the PDL was similar to that between the AVL and ADL, with a dorsal groove which received the ventral edge of the PDL, with a developed overlap area only present in the posterior part of the margin (seen in AMF 56335). This type of overlap is suggestive of more primitive antiarchs (Yunnanolepiformes; also in *Remigolepis*; see Stensiö, 1931: 177,178).

Several specimens (AMF 56355, 56371, 56346) show the lateral and ventral laminae to be of equal length, and indicating that the subanal division of this plate which occurs in *Bothriolepis* is not developed in *Grenfellaspis*. Instead, the posterior margin of the trunk

armour was concave (Fig.17), due to the lateral convexity on the posterior margin of the ventral lamina of each PVL (Fig.13D,E).

The visceral surface of the PVL plate shows the crista transversalis interna posterior strongly developed and very close to the posterior margin (Fig.13F). The contact surface of the PVL with the PDL is well preserved in AMF 56371, 56346 and 56355. The transverse crista runs vertically inside the lateral lamina and curves ventromesially to meet its antimere.

Last to be described are remains of the pectoral fin. No complete pectoral fin of *Grenfellaspis* has been located, and its structure is determined only from isolated plates.

Four types of pectoral appendage bones with terminal articulations have been identified (Fig.15), which are presumed to correspond to the four bones of the proximal segment of the fin in euantiarchs which carry articular processes. That identified as a Cd1 is represented by several examples (AMF 56274/148; 78693, 78778; CPC 29129, 29130). These vary somewhat in shape and proportions (Fig.14C,E), probably due to distortion, but three measured specimens are just over twice as long as broad. All show a prominent flattened articular process projecting at an angle to the long axis of the bone (ar3d, Fig.15A), and separated from it by a constricted neck. In two
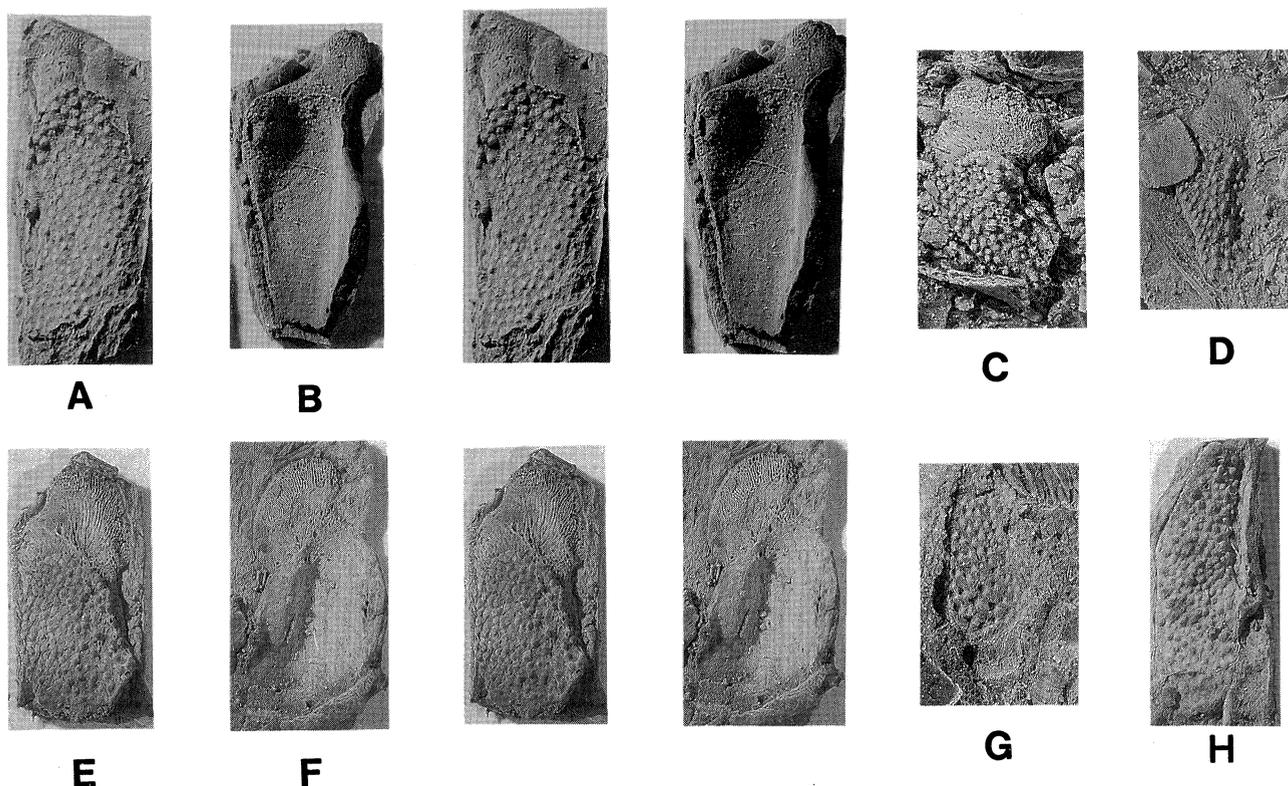


**Fig.14.** *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Pectoral fin elements. Latex casts whitened with ammonium chloride. All specimens twice (x2) natural size. A-B - Cv1 plate, AMF.56280 (dermal) and 56281 (visceral) (stereo pairs); C - Cd1 plate, CPC 29129; D - Cv1 plate, AMF.79211; E-F - Cd1 plate, E - AMF.56148, dermal, F - AMF.56274, visceral (stereo pairs). G - ?Cd2 plate, AMF.79213; H - ?Cv2 plate, AMF.56148.

measured specimens the width of the process was 63-70% of total width. AMF 78693 (Fig.15A) in its short broad form is reminiscent of the Cd1 of *Remigolepis*, but its ornament of stellate tubercles is distinctive, and it differs from the Cd1 of *Remigolepis* or *Asterolepis* in the absence of a dorsomesial crest dividing the plate into dorsal and mesial laminae. A strong tubercular ridge at the mesial margin of the ornament in several specimens (r.dm) may be an equivalent feature. In asterolepids and bothriolepids generally the mesial lamina meets the main lamina of the bone at a right or acute angle, but in *Grenfellaspis* the ornamented part lies in a single plane (Fig.15B). All well preserved

examples show three distinct margins for adjacent bones, which by comparison with other forms must be the Ml2 laterally, and Mm1 and Mm2 mesially. Thus, in contrast to *Asterolepis* (Gross, 1931, pl.5), the Mm1 must have formed part of the dorsal surface of the fin, a condition otherwise only reported in the Early Devonian *Procondylolepis* from China (Zhang, 1984). A distal angle indicates either point contact, or lack of contact, with the Cd2. One distorted specimen preserved in part and counterpart (AMF 56274) shows the inner surface of the articular process (Fig.14F). This carries an articular pad, but its surface is flat, in contrast to the strongly concave articular area of
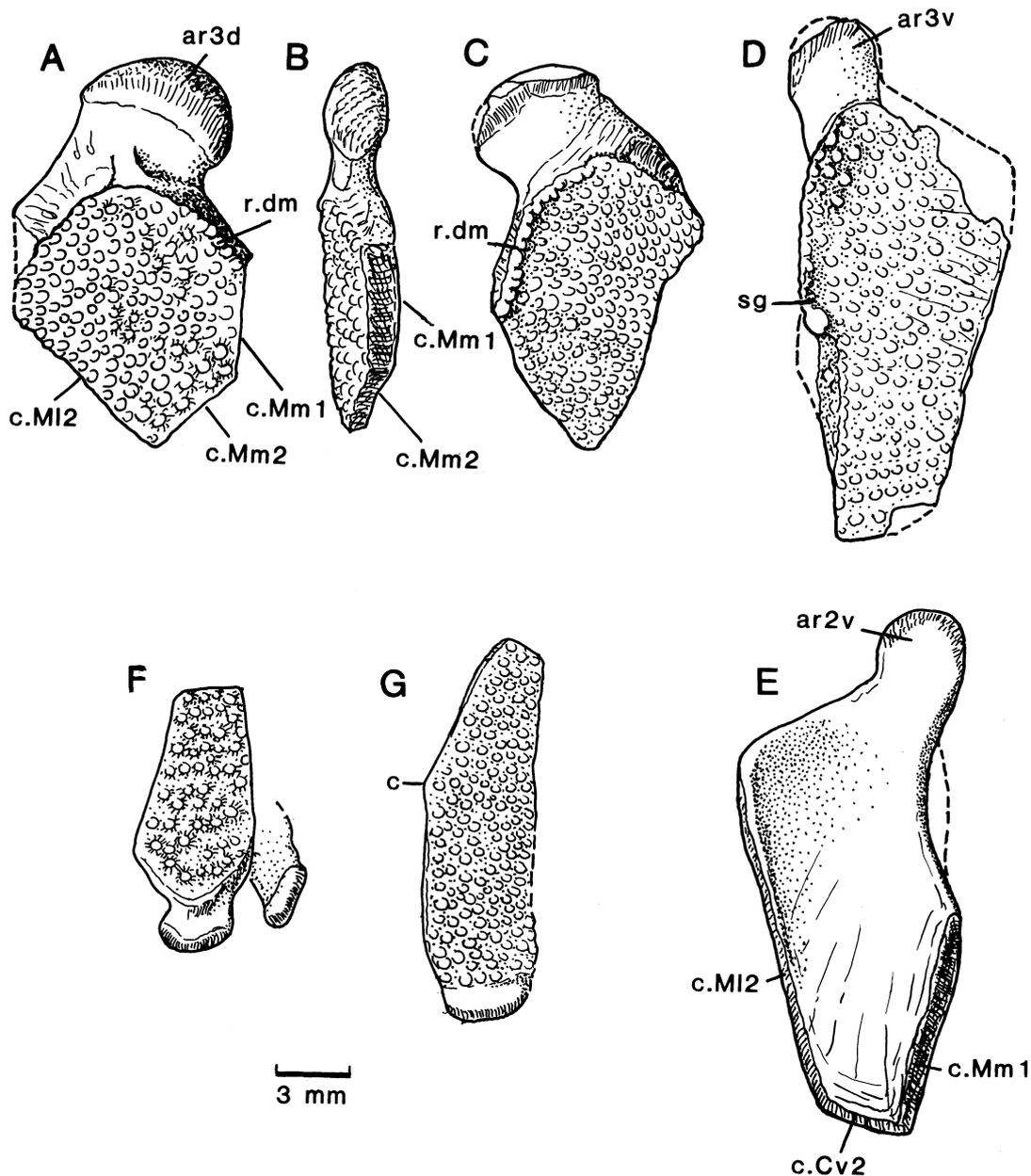


**Fig.15.** *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Interpretation of pectoral fin elements in Figure 14. A-B - Cd1 plate, in external and side views, AMF.78693; C - Cd1?, CPC 29130; D - Cv1 plate, AMF.56280 dermal (Fig.14A); E - Cv1 plate, AMF.56281 visceral (Fig.14B); F - ?Cd2, AMF.79213 (Fig.14G); G - ?Cv2 plate, AMF.56148 (Fig.14H).

advanced antiarchs, in which both the Cd1 and Cv1 fit around the large hemispherical brachial process.

Two other specimens (AMF 56280,281; 79211) are interpreted as Cv1 plates. They have a much smaller narrow articular process than the Cd1, in the most complete specimen (Fig.14A,B,15D,E) only 19% of total width. Again the process projects strongly from the main part of the bone in what must be a mesial direction. A *siebknochen*-type surface is seen on dorsal and ventral surfaces, both of which are slightly convex (ar2v, ar3v, Fig.15D,E). The external impression is incomplete (Fig.15D), but shows an ornamented crest running down the mesial edge of the dorsal lamina, with a notch adjacent to a large tubercle which leads into a shallow groove, possibly sensory (sg). In *Asterolepis* a sensory groove crosses the Cv2, not the Cv1, but AMF 56280, with its two distinct and unequal laminae meeting at a high angle, has quite a different morphology to the Cv2 of *Asterolepis* (cf. Stensiö, 1931, fig.65).

The counterpart (Figs 14B,15E) shows the anteromesial margin to be a long concave margin to the mesial lamina of the plate, which did not contact other bones and thus must have formed a border to the

proximal brachial aperture of the fin. This free margin is about half the length of the bone itself, and its large size, together with the fact that the bone narrows towards the end opposite the articulation, demonstrates that this was part of the proximal articulation. That the proximal brachial aperture of the fin was large can also be inferred from the structure of the brachial articulation on the AVL (see above). Other margins of the Cv1 show contact with three adjacent bones, which by direct comparison with *Asterolepis* (Gross, 1931, pl.5) must be the Mm1 mesially, the Cv2 distally, and the Ml2 laterally. In *Asterolepis* a sensory groove crosses the Mm1 to pass distally onto the ventral surface of the fin across the Cv2, but in *Grenfellaspis* the sensory groove apparently passed off the Mm1 onto the Cv1. The bone is nearly 1.2 times as long as broad. AMF 79211 is a right Cv1 incompletely preserved in external view (Fig.14D).

The third type of articular element (Figs 14G,15F) is represented by only one specimen (AMF 79213). This is an elongate bone (L/B index 217) with a small articular process, which differs from the Cv1 in that the process projects from the broader end in the direction of the long axis of the bone, in its more elongate
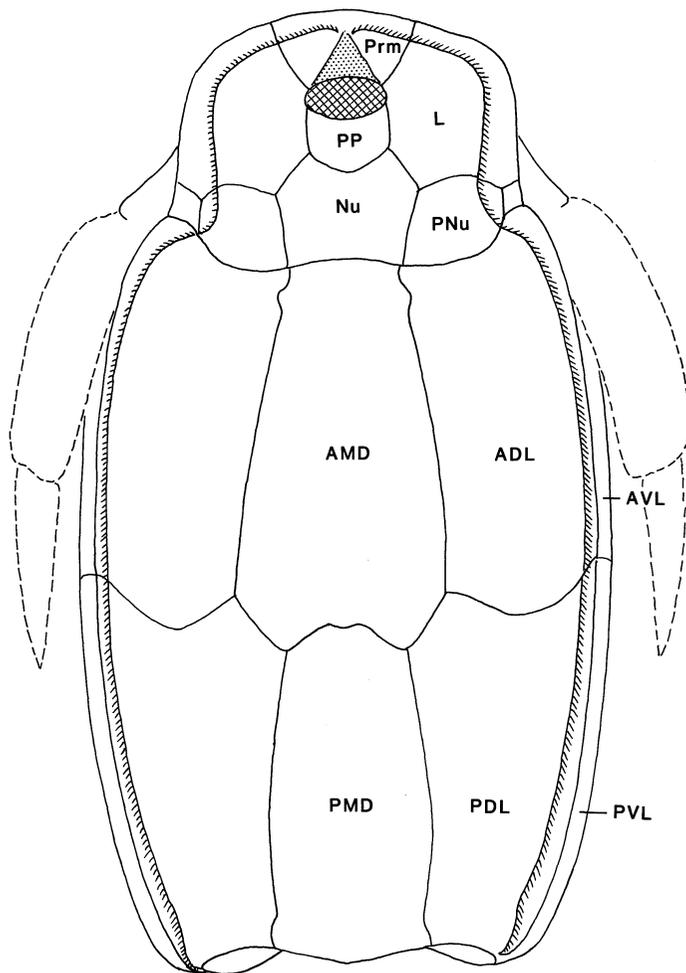


**Fig.16.** *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Reconstruction of head and trunk shield in dorsal view. x1 actual size.

proportions, and in the relative size of the process (slightly smaller width than in the Cv1, but more than half the total breadth of the plate). The bone is flat with two long contact margins at each side and a short one at the opposite end to the articulation. By comparison with *Asterolepis* (Gross, 1931, pl.5) the longer free margin adjacent to the distal articular surface of the fin is mesial, and together with the marked corner near the articulation (c) suggests that this is a Cd2 from the right fin (*cf.* Stensiö, 1931, fig.64). An adjacent articular process exposed in visceral view may be the Cv2 from the same fin.

The fourth type of articular element (Figs 14H,15G) is again represented by a single example (AMF 56148). This is a more elongate bone (L/B index 280) with a small articular process of similar size to the previous specimen, but less distinct from the rest of the bone. One long margin is poorly preserved but appears fairly straight. The other has a slight angle about half way along (c), and there is a short terminal margin. This bone is assumed to be a Cv2 from the left side, by direct comparison with the corresponding plate of *Asterolepis* (Stensiö, 1931, fig.65).

In summary, the pectoral appendage of *Grenfellaspis* shows several special features compared to other euantiarchs: 1) distinct neck on the articular processes of the Cd1 and Cv1; 2) flat shape of their articular surfaces; 3) absence of a dorsomesial crest and mesial lamina on the Cd1, implying that Mm1 formed part of the dorsal surface of the fin; 4) much smaller articulation on the Cv1; 5) extension of sensory groove onto the Cv1 rather than the Cv2.

In these features *Grenfellaspis* shows a more primitive type of brachial articulation than in advanced antiarchs, in which the Cd1 and Cv1 of the pectoral appendage have large semicircular articular areas, of similar size and closely integrated to the ornamented part of the bone. In all known euantiarchs these features are always associated with a large hemispherical brachial process, and a mesial lamina on the Cd1.

On the other hand various features just described correspond to those seen in the pectoral appendage of *Asterolepis*, and presumably originated earlier in antiarch phylogeny: 6) Cv1 was longer than Cd1; 7) Cd2 was broader than Cv2; 8) there was a short or point contact between Cd1 and Cd2; 9) the articulations on Cd2 and Cv2 are of similar size.

The ornament of *Grenfellaspis* consists of crowded but randomly distributed tubercles often showing stellate bases. Only occasionally do the tubercles show slight linear alignment (Figs 6A,9E). A radial alignment is present in some examples of *Sinolepis* (see below). The ornament is often sparse in some regions (e.g., lateral to the sensory groove on the PNu, and L plates, and adjacent to the brachial articulation on the AVL), but this is variable amongst individuals.
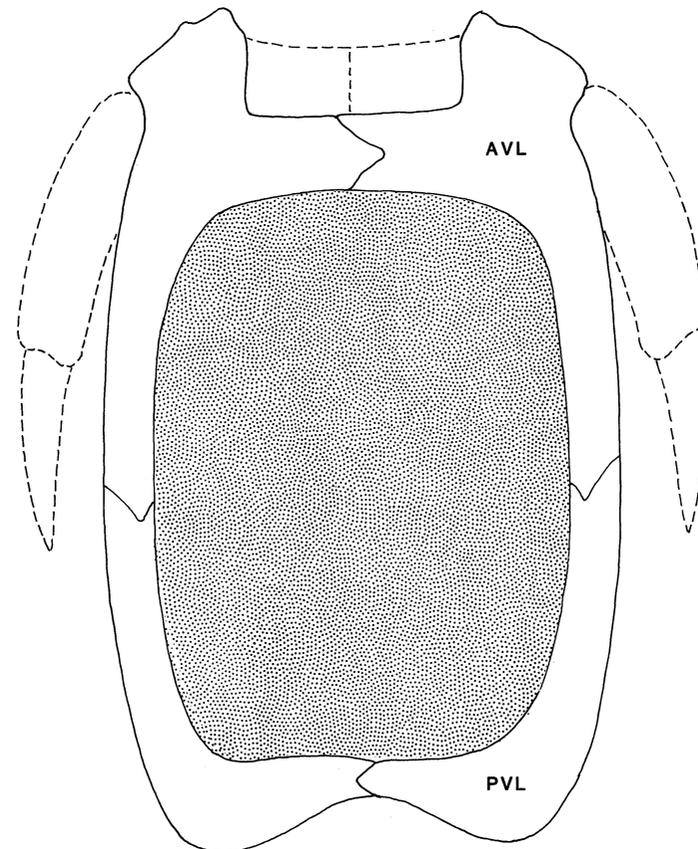


**Fig.17.** *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Reconstruction of ventral trunk shield. x1 actual size.

## *Dayaoshania* Wang n.gen.

**Etymology.** From Dayaoshan Mountain of north-east Guangxi, China, the type locality.

**Diagnosis.** Middle sized Sinolepidae, with the skull broader than long (B/L index 140), and about or slightly over one third the length of the trunk armour. Rostral margin convex. Orbital fenestra small, and about one third the width of the skull. Trunk armour flat, with low lateral walls. AMD and PMD in the dorsal wall narrower than ADL and PDL. AMD with a B/L index of 50-60, the anterior margin narrower than the posterior, and the anterior division of the plate longer than the posterior. PMD plate smaller than AMD, with posterior and lateral corners developed. Levator fossa, postlevator thickening, and median ventral grooves apparently not developed, but anterior and posterior pits present on the ventral aspect of the shield. Semilunar plates small. Pectoral appendage robust, and almost as long as the ventral wall of the trunk armour, with a distal segment almost as long as the proximal. Arrangement of pectoral appendage bones of pterichthyodid type, with long Cd1 and Ml2, and large Mm1 comprising dorsal and mesial laminae. Spines on the inner margin of the proximal segment. Main lateral line sensory groove passes dorsally to dorsolateral ridge of trunk armour.

**Remarks.** Some of the features included here (such as overall size) may be specific rather than generic characters. The latter are discussed below in the section on sinolepid inter-relationships. *Dayaoshania* shares many features with *Grenfellaspis* described above, but differs in the proportions of the AMD and PMD plates (wider in *Grenfellaspis*), and the strongly developed anterior and posterior ventral pits and processes. *Dayaoshania* differs from *Sinolepis* (Liu & P'an, 1958) in the much smaller size of the head shield relative to the trunk armour, the ornament, and the distinct overlap of the L onto the PP and Nu plates. Various other characters of *Dayaoshania* are no doubt primitive features for sinolepids or antiarchs generally. These may include the absence of a median ventral ridge and groove on the trunk armour, the small orbital fenestra situated close to the rostral margin, and the large size of the Mm1 in the dorsal surface of the pectoral appendage.

The basis for distinguishing *Dayaoshania* from *Xichonolepis* is discussed below in the 'Remarks' section for the latter genus.

## *Dayaoshania youngi* Wang n.sp.

### Figs 18-22

**Type material.** HOLOTYPE, MGV 1947, 1948, an almost complete external mould of the headshield and dorsal trunk armour, with the dorsal trunk shield preserved in the counterpart (MGV 1948).

**Other material.** An articulated individual with pectoral appendages preserved in part and counterpart (MGV 1950,51), and incomplete remains of the dorsal shield (IVF 2,4,5).

**Locality and horizon.** Yuantou, Pingle County, Guangxi Province, from a single horizon in the upper part of the Dayaoshan Group, of Lower or Middle Devonian age (?Emsian-Eifelian). Associated fossils include abundant polybranchiaspids (a new genus and species) and rare arthrodires.
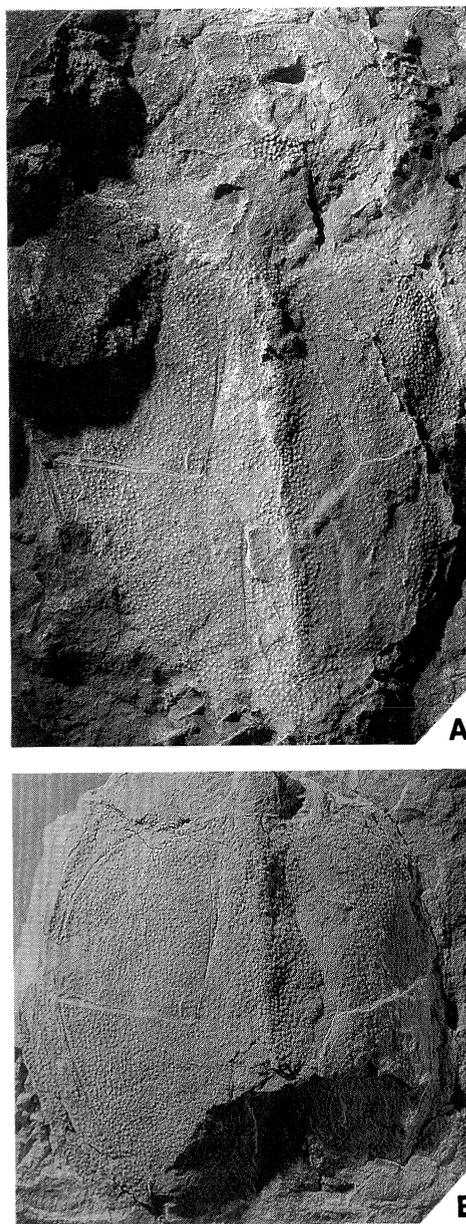


**Fig.18.** *Dayaoshania youngi* n.gen., n.sp. Dayaoshan Mountain, Pingle County, Guangxi Province, China. Dayaoshan Group, Early or Middle Devonian (?Emsian-Eifelian). A - holotype, dorsal impression of head and trunk shield, MGV.1947. Latex cast, whitened with ammonium chloride. x1.7 natural size. B - holotype, dorsal surface, trunk shield, V.1948. Original specimen, whitened with ammonium chloride. x1.3 natural size.

**Etymology.** In honour of the late eminent Chinese vertebrate palaeontologist Professor Young Chung-chien.

**Diagnosis.** As for genus (only species).

**Description.** The five known specimens of *Dayaoshania youngi* n.gen., n.sp. are all of similar size (Table 3), and were closely associated on one horizon. We assume, for the present, that the species did not attain a large size. The holotype (Fig.18A) shows the head and trunk shields preserved in association, but slightly dislodged. The combined head and trunk length as preserved is 71 mm, with an estimated original length of about 68 mm. MGV 1950 (Fig.19) is 56 mm in total length, and 48 mm wide, with the AMD and some plates of the pectoral appendage displaced.

The **head shield** is reasonably preserved as an external mould in the holotype. It is flat, and slightly hexagonal in shape, with a convex rostral margin (22 mm long) and lateral margin 12 mm long. Obstantic and posterior margins are not preserved, but the length of the posterior margin is estimated at about 20 mm. Total length of the head shield is 20 mm, and its greatest width (between lateral corners) is 28 mm. The margins of the PrM and L plates are distinct. The anterior margin of the PNu and anterolateral margin of Nu are seen on both sides, but the posterior part of the Nu is not preserved. The anterior margin of the PP apparently forms only the middle part of the posterior margin of the orbital fenestra, in contrast to *Grenfellaspis* or *Sinolepis* where it forms most or all of this margin. However the anterolateral margins of the PP are unclear, and its posterior margin is not preserved.

The orbital fenestra is small and elliptical in shape, and more than twice as broad as long (B/L index 180). It is anteriorly placed (7.2 mm from the rostral, and about 9 mm from the posterior margin).

The PrM plate is 13.3 mm wide at its anterior margin, and 7.6 mm long (B/L index 57). The orbital margin is 7.4 mm across. The infraorbital canals do not meet in the midline, as is normal in antiarchs. The preorbital depression is preserved in MGV 1947, and appears triangular in shape with rounded corners.

The L plate is a large polygonal bone, 13 mm long and 8.2 mm wide (B/L index 63). As in other antiarchs the ifc crosses this plate from the PrM to the PNu. On the right side of the holotype a prelateral notch is seen, but on the left the lateral margin is obscured by the SM plate (Fig.18A). The lateral corners on the PP (Fig.21) are not comparable to those on the PP of *Sinolepis*, which are formed by the unique overlap of this bone onto the L in that form.

The Nu plate was apparently large and hexagonal in shape (Fig.21), but only the anterior division of one lateral margin is clearly seen. The PNu is smaller and squarish in shape, and is crossed by the ifc.

The submarginal (SM) plate of the cheek, preserved on the left side of the holotype (Fig.18A), is 11 mm long and 4.5 mm wide, and of elongate elliptical shape. There is no evidence of a separate prelateral (PrL) plate.

The postmarginal (PM) plate is not well preserved, but its mesial borders are seen on the right side of the holotype.

The ventral aspect of the head shield is partly preserved in MGV 1950, but only the rostral margin is clear (Fig.19). The posterior part is obscured by the impression of the semilunar plates, and on the counterpart by the subcephalic division of the AVL plates (Fig.20).

There are five examples showing the structure of the **trunk shield** in dorsal view, of which the holotype (Fig.18) shows the complete dorsal wall. The PMD is incomplete in IVF 4, but in this specimen the overlap relations of the AMD are well shown. The AMD and PDL are also preserved on MGV 1950, and most of the PMD is seen on MGV 1951. These specimens show the dorsal wall of the trunk armour to have been rather flat, but with a convex median dorsal ridge. The lateral wall is low. In the holotype the dorsal wall is 53 mm long and 45 mm wide.

The AMD is longer than wide (Table 3), with well-developed lateral corners situated about three quarters of the length from the narrow, straight anterior margin. The external posterior margin is wider than the anterior. The internal posterior margin shown on MGV 1950 (Fig.19B) appears to be convex, whereas in *Xichonolepis* it is transverse. The ratio of external length of AMD to PMD (106-117) is comparable to *Xichonolepis*, but in *Dayaoshania* this is affected by the much stronger posterior process on the PMD. Taking this into account the PMD in *Dayaoshania* is proportionally smaller compared to the AMD.

The ventral structures of the dorsal wall can only be seen in MGV1950, which shows the impression of the anterior ventral pit and process on the displaced AMD (pt1, Fig.19B). The anterolateral thickening appears weak or absent, and a weak median ventral groove is developed posteriorly, as in small *Xichonolepis*.

The PMD is well preserved in the dorsal impression of the holotype (Fig.18A). It is similar in shape to *Xichonolepis*, but with a stronger posterior process. The posterior ventral pit and process are not preserved on any specimen, but presumably were developed as in other sinolepids. Proportions are given in Table 4.

The overlap relationships between the AMD and PMD are not clearly preserved on the holotype, but are more distinct on V.1950, IVF 2 and IVF 4, where the anterior margin of the PMD overlaps the posterior margin of the AMD.

The ADL is broad (B/L index 60). The dorsal lamina in the holotype is 23 mm long and 18 mm wide, but the lateral lamina is very low (only about 2 mm high), and difficult to measure with any accuracy. In the holotype the left obstantic process of the ADL is broken. No other specimen shows the anterior inner transverse ridge or obstantic process. The main lateral line canal passes across the plate, and in MGV 1948 (Fig.18A) and other specimens is clearly seen to lie dorsomesial to the lateral margin of the plate, on its dorsal lamina, and there is no clear dorsolateral ridge or lateral lamina. In contrast, in bothriolepids the lateral line sensory groove
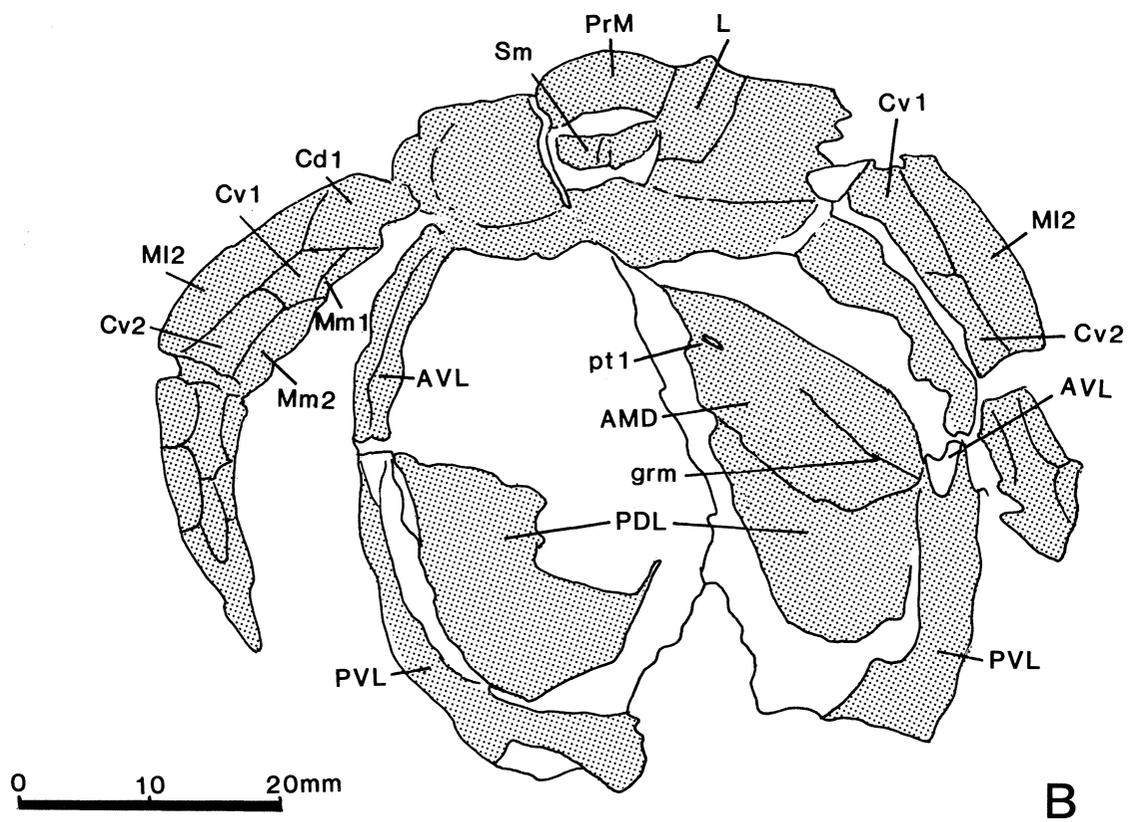
**Fig.19.** *Dayaoshania youngi* n.gen., n.sp. Dayaoshan Mountain, Pingle County, Guangxi Province, China. Dayaoshan Group, Early or Middle Devonian (?Emsian-Eifelian). A - almost complete specimen, MGV.1950, in dorsal view. B - interpretation of MGV.1950.
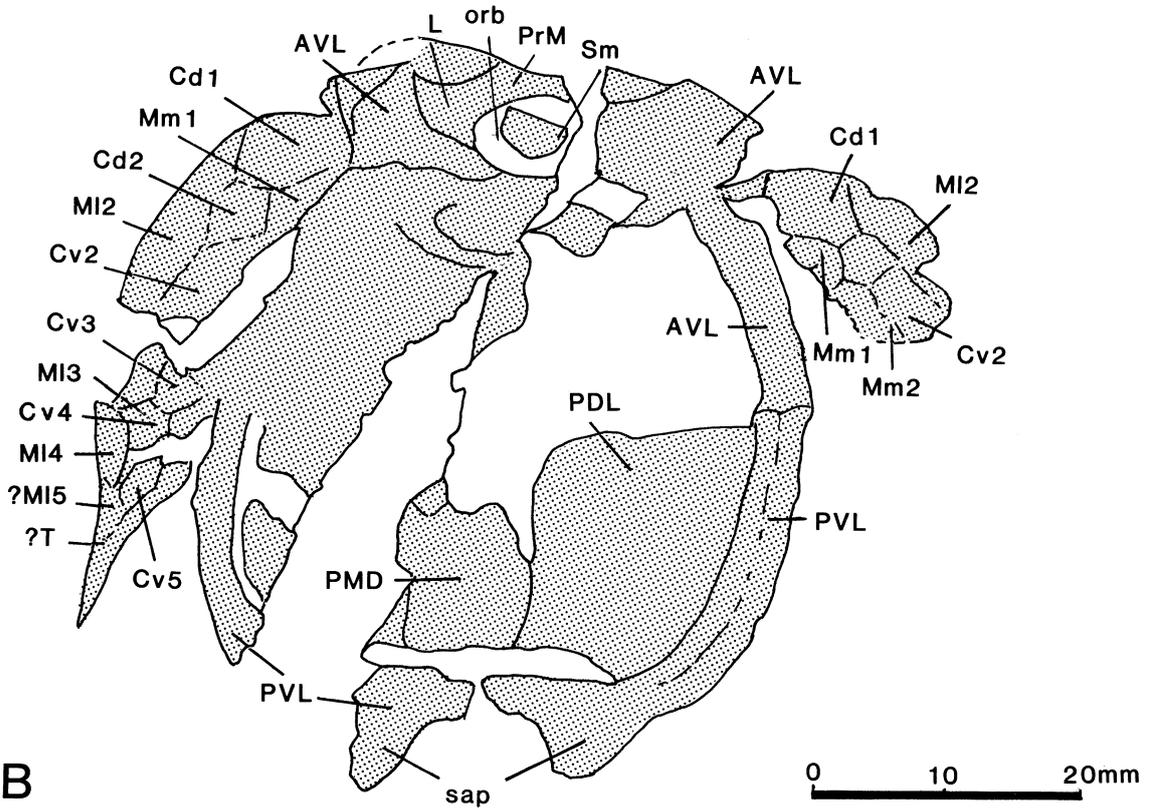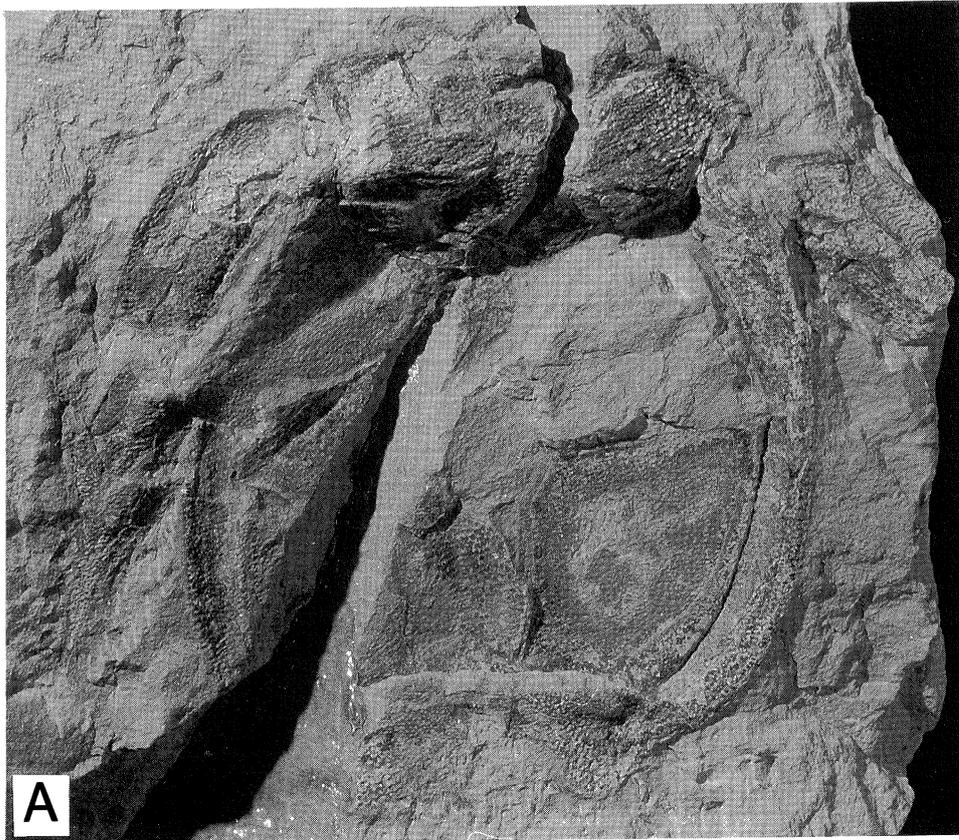
**Fig.20.** *Dayaoshania youngi* n.gen., n.sp. Dayaoshan Mountain, Pingle County, Guangxi Province, China. Dayaoshan Group, Early or Middle Devonian (?Emsian-Eifelian). A - almost complete specimen, MGV.1951 (counterpart of MGV.1950, Fig.19), seen in ventral view. B - interpretation of MGV.1951.

crosses the lateral lamina of the ADL. The dorsal margin of the ADL is overlapped by the anterolateral margin of the AMD, as is normal, but the overlap area is very narrow, particularly the      posterior part. Posteroventrally on the left side of MGV 1948 is a short margin in contact with the PVL, as in *Xichonolepis*.

The PDL has a large and broad dorsal lamina, 22 mm long in the holotype, with greatest breadth (18 mm) through the dorsal corner (B/L index 82). On the left side of MGV 1948 (Fig.18A) the suture with the PVL plate is clearly seen immediately lateral to the groove for the lateral line canal. Thus the PDL lacked a distinct dlr and lateral lamina, as is also the case in smaller individuals of *Xichonolepis* (see below). Whether the PDL and PL plates are fused to form a MxL plate is not clear from the available specimens. The overlap relations with surrounding bones is the same as in *Xichonolepis*. The area overlapped by the ADL is very narrow, and that overlapped by the PMD is narrow, and similar to *Xichonolepis* and *Grenfellaspis*. The lateral line sensory groove is much closer to the lateral margin than on the ADL (Figs 18B,21).

On the second articulated specimen (MGV 1950, 51) the skull bones are largely obscured by the AVL plates and are difficult to interpret, but the specimen is important in showing the ventral wall of the trunk armour and the pectoral appendage. MGV 1950 (Fig.19) exhibits the internal mould of dorsal trunk shield bones (AMD, PDL), the anterior and posterior parts of the

ventral wall preserved as incomplete external moulds of the AVL and PVL plates, and a part impression of the almost complete left pectoral appendage. The exposed skull bones in this specimen (PrM, L, Fig.19B) are problematic in that their surfaces show impressions of the ornament, as on the adjacent AVL plates, and we must presume therefore that the skull was turned over before preservation. In MGV 1951 the preservation is reversed, and this specimen shows most clearly the subcephalic and subanal divisions of the ventral wall, and the distal segment of the right fin (Fig.20). Both specimens were flattened during burial. On the available evidence there was no MV plate in *Dayaoshania*, as was suggested above for *Grenfellaspis*, and inferred also for *Xichonolepis* and *Sinolepis* (see below). The ventral wall consists only of the narrow and elongate ventral laminae of the ventrolateral plates, with apparently no dermal armour over the central part. In external view the ventral laminae of both AVL and PVL are 4 mm wide; the former is 30 mm long, and the PVL slightly longer (34 mm). The AVL overlaps the PVL, and the shape of the overlap is most clearly seen on the left side of MGV 1950 (Fig.19B). The subcephalic division of the AVL is distinct in both specimens, but the overlap relationship between right and left plates at their median suture could not be determined. The paired semilunar plates are preserved in both specimens compressed against the orbital fenestra (Sm, Figs 19B, 20B). Their small size, and the smaller semilunar notch, are clearly different
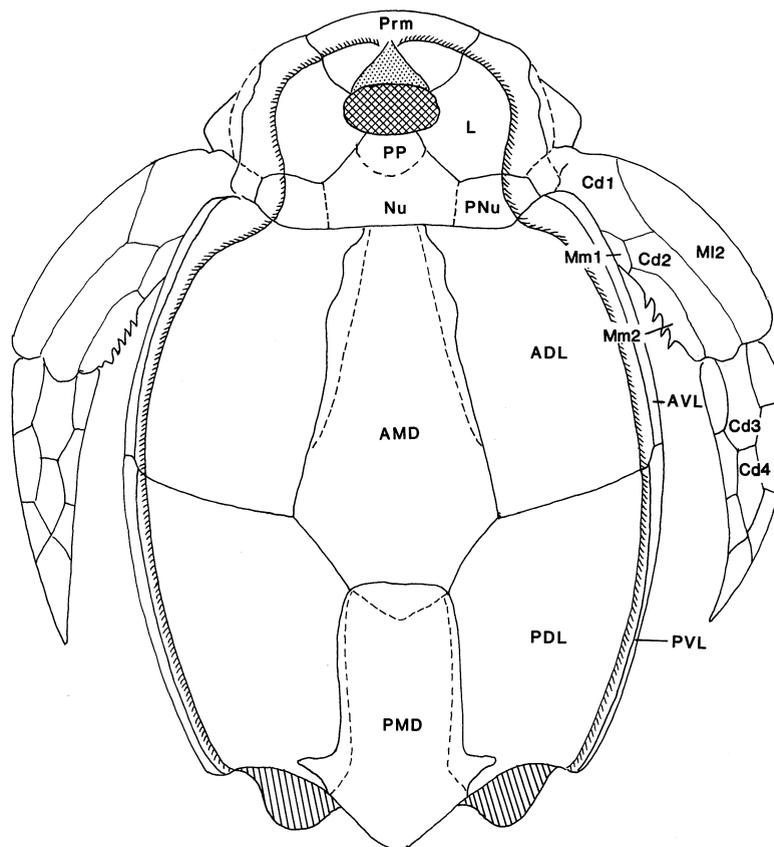


**Fig.21.** *Dayaoshania youngi* n.gen., n.sp. Devonian, China. Reconstruction of dorsal surface x1.8.

from the condition in *Grenfellaspis* or *Xichonolepis* (Figs 17,31). The PVL in MGV 1951 is 4 mm wide and 34 mm long. The posterior part of the PVL is wide, with the left plate meeting and overlapping the right in the midline. The posterior margin is strongly concave with prominent, rounded lateral subanal processes (sap, Fig.20B). A similar shape is seen in *Grenfellaspis* and *Xichonolepis* (Figs 17,31), but in *Dayaoshania* the lateral processes are much stronger. There is no true subanal division with extensive midline suture as is seen in bothriolepid and asterolepid antiarchs. *Dayaoshania* and other sinolepids may be primitive in this respect since yunnanolepids also lack a true subanal division.

In MGV 1950 the left pectoral appendage is preserved mainly as an impression of the ventral surface, with part of the dorsal surface preserved as bone (Fig.19). The right appendage shows part of the external impression of the ventral surface, and part of the internal surface of the dorsal wall, but the distal segment is incomplete. For the complete left fin, the proximal segment is 21 mm long and 9.1 mm wide, and the distal segment is 22 mm long and 6 mm wide at its proximal end. The left proximal segment displays the Cd1, which is apparently a short plate, as shown by the suture on the counterpart (MGV 1951), in which the bone is preserved (right side of Fig.20). The Ml2 on this specimen is preserved as an external impression of the dorsal ornament. The mesial side of the fin is occupied

by two bones separated by a clear suture, which must be the Mm1 and Mm2 plates (Fig.20B). Although not very clear, it seems that their dorsal surfaces are preserved as impressions, with the spinose margin therefore representing the dorsomesial ridge of the fin (cr.dm). At the incomplete distal end of this fin the bone adjacent to the Mm2 shows ornament, and must be the Cv2. Its mesial edge presumably approximates to the mesial margin of the ventral surface of the fin (displaced laterally), as in *Bothriolepis* (e.g., Stensiö, 1948, fig.195). The suture between the Mm1 and Mm2 divides laterally to give the appearance of an additional small bone, but the proximal side of this suture is with the Cd1, and the distal side sutures with the Cv2, indicating that dorsal and ventral surfaces of the fin have been compressed together. Thus this specimen shows that the Cv1 was longer than the Cd1, as in other antiarchs. The Cd1 on this specimen is preserved mainly as an impression of the ornamented surface. An articular head of the fin is present as poorly preserved bone (right side of Fig.20B). This projects mesially, and its relatively small size compared to most other antiarchs recalls the Cv1 of *Grenfellaspis* described above. A trace of bone connecting this articular process to the AVL is probably a remnant of the brachial process. The opposite side of MGV 1951 again preserves the inner bone surface of the dorsal side at its proximal end, which confirms that the Cd1 was short. The inside of the Ml2 is clear, and
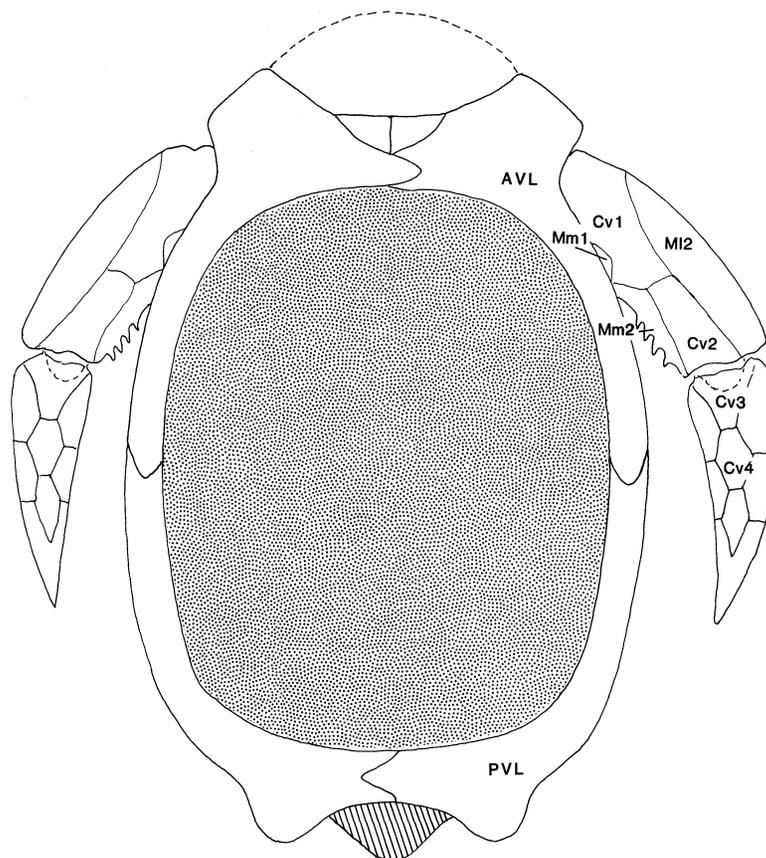


**Fig.22.** *Dayaoshania youngi* n.gen., n.sp. Devonian, China. Reconstruction of ventral surface. x1.8.

the Mm1 again shows the same suture on its dorsal lamina, partly obscured by the ventral lamina. However the distal part of the dorsal wall is covered by the well preserved ventral bone surface. On the basis of the similar suture pattern displayed on both sides of MGV 1951, we interpret the Cd2 of *Dayaoshania* to have been longer than the Cd1, and of unusual shape with an expanded proximal end (Fig.21). The distal end and articular surface of the Cd2 are not preserved.

The distal part of the ventral wall of the proximal segment is well preserved as bone showing the ornamented surface on the more complete (right) fin of MGV 1951 (Fig.20). A clear suture down the middle of the fin separates two bones. The lateral one must be the ventral lamina of the Ml2, and the mesial one is the Cv2, with no indication of the Mm2 on this specimen. The counterpart of this fin on MGV 1950 (right side of Fig.19B) shows the proximal end of the Cv2 and the suture between the Ml2 and Cv1, but the proximal end of the Cv1 is missing. The impression of the left fin of this specimen shows the Cv2 with its distal articulation, and a narrow strip of the Mm2 exposed along the mesial edge of the fin.

In MGV 1950 the impression of the ventral aspect of the distal segment is preserved for the left fin, but sutures between bones are unclear. The distal segment for the right fin in MGV 1951 shows the bones slightly displaced, with apparently three bones in the ventral central and lateral marginal series (Fig.20B).

The ornament of *Dayaoshania* comprises fine stellate tubercles evenly distributed over the external surface of the bones, with coarser ornament on the median dorsal ridge of the trunk armour. The sensory canal system shows no special features except that the main lateral line groove on the trunk runs back across the dorsal wall because the dorsolateral ridge is absent.

### *Xichonolepis* P'an & Wang, 1978

**Emended diagnosis.** Sinolepid of large size. Head shield much shorter than trunk armour; postpineal and nuchal plates do not overlap lateral plate. Trunk armour broad, dorsal wall flat, lateral wall convex; dorsal median and dorsolateral ridges generally not developed. Semilunar plate(s) large. AMD large, six-sided, lateral corners well developed, wider than ADL or PDL; anterior margin of AMD slightly narrower than posterior margin. Postnuchal notch and external postlevator process of anterolateral margin of AMD developed. PMD narrower than AMD; lateral process long, extending beyond lateral margins. Posterior marginal area wide and long, with straight anterior margin, posterior ventral pit and posterior ventral process on posterior marginal area.

**Remarks.** Some characters, such as large size, are probably specific features, but until more than one species is described no attempt is made to separate them.

The characters used here are discussed generally in the section on sinolepid inter-relationships.

*Xichonolepis* resembles *Dayaoshania* in the shape of the PrM, AMD and PMD bones, and in the general morphology and proportions of the trunk armour. However, *Dayaoshania* differs as follows (Table 6): 1) the slight anterior median ventral groove and ridge; 2) the more elongate AMD in *Dayaoshania* (B/L index 50-60, compared to 60-80 for *Xichonolepis*); 3) the small semilunar plates; 4) the convex internal posterior margin of the AMD; 5) the stronger posterior process on PMD, which is proportionately shorter compared to the AMD; 6) the broader PDL; 7) the stronger lateral subanal process on the PVL; 8) a different shape in the overlap between the AVL and PVL plates; 9) a presumably smaller adult size of *Dayaoshania*.

### *Xichonolepis qujingensis* P'an & Wang

### Figs 23-31

*Xichonolepis qujingensis* P'an & Wang, 1978: 334, pl.33, figs 1-6.
*Xichonolepis qujingensis.–*Zhang, 1980: 272-280, pls 1-3.

**Type material.** HOLOTYPE, an incomplete PMD (MGV 1546) collected from Xichong, near Qujing, and first described by P'an & Wang (1978: 324-325, pl.33, figs 1,2) as an AMD (see Zhang, 1980, pl.2, fig.3).

**Other material.** Original material collected from Xichong by P'an & Wang (1978), and subsequently by Wang (three PrM plates, MGV 1547, IVF 501, 502; one PNu, MGV 1549; a possible L, MGV 1548, an Ml2 from the pectoral fin , MGV 1550); one specimen collected from Dashishan near Kunming (AMD, V 4440.1a); an AMD (V 9058) and PDL (V 4442.14a) from Panxi, Huaning (collected by IVPP members; Zhang, 1980); an AMD (V 5077) from Zhangjiaying, Qujing; material collected from Zhaojiazhuang and the nearby cement quarry near Wuding by IVPP members and Zhang and colleagues (AMD, V 2965.9, 9057.8; PMD, V 2965.1,2, V 5076.2a; ADL, V 9056.1, 9057.4; PDL, V 2965.4, 9057.1.2; AVL, V 9057.7a,b; PVL, V 9056.2, 9057.3; complete dorsal wall of trunk armour, V 5076.1a,b; subcephalic division of ventral wall of trunk armour, V 5076.6; incomplete ventral wall of trunk armour, V 2965.7; distal segment of pectoral fin, V 2965.7).

**Localities and horizon.** From the following localities in Yunnan Province: Xichong and Zhangjiaying, near Qujing; Dashishan, near Tonghai; Panxi, near Huaning; Zhaojiazhuang and the nearby cement quarry near Wuding (Fig.2). All in sandstones or dolomitic limestones beneath the Haikou Formation (Middle Devonian), and equivalent to the Sanshuanghe and Chuandong Formations of Yang *et al.* (1981, table 4). At Zhaojiazhuang the same fish fauna (including *Dianolepis* and *Bothriolepis tungseni*) occurs in the limestone and underlying sandstones. The fish horizon is considered to be older than the typical Haikou Formation in the vicinity of Kunming, which is Givetian in age.

**Diagnosis.** As for genus (only species).

**Remarks.** *Xichonolepis qujingensis* was established by P'an & Wang (1978) and later amended and amplified by Zhang (1980). The material then available for study consisted of a few individual plates of the skull and dorsal wall of the trunk armour, but the morphological characters of the ventral and lateral walls of the trunk armour remained largely unknown. On this evidence *Xichonolepis* was tentatively allocated to two different antiarch families, the Bothriolepidae and Asterolepidae.

New material collected in recent years from the original localities and horizons of Yunnan include examples of the ventral wall of the trunk armour and AVL and PVL plates. They show clearly that *Xichonolepis* belongs neither to the Bothriolepidae nor to the Asterolepidae, but is closely related to the genera *Grenfellaspis* n.gen. and *Dayaoshania* n.gen.,
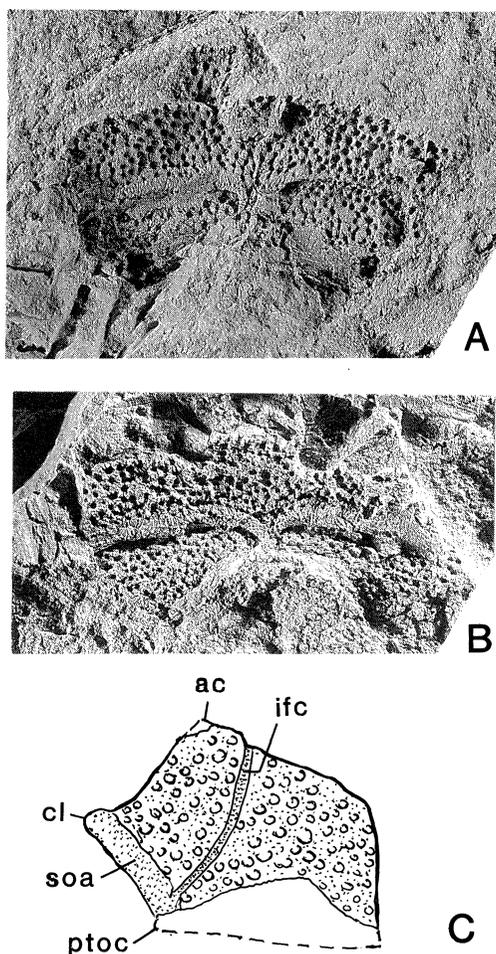


**Fig.23.** *Xichonolepis qujingensis* P'an & Wang; Xichong, near Qujing County, Yunnan Province, South China. Sandstones or limestones beneath Haikou Formation, Middle Devonian (Givetian). A,B - 2 premedian plates (IVF 501,502), preserved as natural moulds. Both x2.4. C - outline of right PNu, based on reinterpretation of specimen MGV.1549 from Qujing County; figured by P'an & Wang (1978, pl.33, fig.5).

described above, and to *Sinolepis* (Liu & P'an, 1958).

**Description.** The headshield of *Xichonolepis qujingensis* is represented only by isolated bones. MGV 1547 (originally figured as a Nu plate) is an inverted PrM, and MGV 1549, described by P'an & Wang (1978) as a L plate, is regarded as an inverted PNu (Fig.23C). The PrM is known from three external impressions (Fig.23A,B; P'an & Wang, 1978, fig.13). Two are almost complete (MGV 1547, IVF 501), and show that the plate is broader than long (B/L indices 206 and 210 respectively), and somewhat broader than in *Dayaoshania*. The anterior margin is much broader than the posterior, and in IVF 501 is convex (Fig.23A). The straight margin on the previously figured specimen (P'an & Wang, 1978, pl.33, fig.3) is probably incomplete. The lateral margin is convex. On the whole the plate is very similar in shape to that of *Sinolepis*, except that the anterior division of the plate in *Sinolepis* is very short, with the infraorbital groove much closer to the rostral margin. All three specimens exhibit clearly the triangular preorbital depression. The infraorbital canal passes onto the plate from the middle of the lateral margin. Behind it is a deep groove which shows that the sensory ridge was strongly developed, as in *Grenfellaspis* described above. The ornament is evenly distributed on both sides of the sensory groove.

MGV 1549 was originally described as an incomplete L plate by P'an & Wang (1978, pl.33, fig.5), but we now consider the specimen to be an inverted dermal impression of a right PNu (Fig.23C). The posterior margin is missing, but the position of the sensory groove indicates that the posterolateral corner is nearly complete. In its pentagonal shape the plate is generally similar to the PNu of bothriolepids (Stensiö, 1948, fig.27). The lateral division is broad, in contrast to *Grenfellaspis* and *Sinolepis* (and asterolepids) in which it is very narrow. A conspicuous anterior corner (ac) is developed on the anterior margin between lateral and mesial divisions. The lateral margin, which contacted the PM plate, has an oblique anterolateral orientation, and is about the same length as the obstantic margin. The obstantic margin and subobstantic area (soa) are long, and the anterolateral corner (cl) is therefore situated much further anteriorly than in asterolepid antiarchs. This indicates that the obstantic process of the trunk armour was well developed, and that the PM plate of *Xichonolepis qujingensis* was of bothriolepid type, and similar to *Grenfellaspis* and *Dayaoshania* as described above. The infraorbital sensory groove is very clear. As preserved this plate resembles the PNu of *Dayaoshania* in being short and broad, whereas in *Grenfellaspis* and *Sinolepis* (see below) the PNu is more elongate.

The incomplete external impression of the L plate (MGV 1548) figured by P'an & Wang (1978, pl.33, fig.4) is apparently a left plate showing a broad lateral division. It is similar to that of *Dayaoshania*, and differs from *Grenfellaspis* and *Sinolepis* in which the lateral

division is very narrow. Based on the previously published figure the ridge adjacent to the sensory groove may also be present.

New information on the trunk armour of *Xichonolepis* comes from additional specimens of separate bones collected from the Haikou Formation at Wuding (preserved in limestone and mostly exposed in internal view), and preparation of latex casts of internal and external impressions of the trunk armour in previously described specimens (V5076.1, 6), collected from the underlying sandstone unit (which contains the same fish fauna). A latex cast of V 5076.1b (Fig.24) shows the broad and flat dorsal wall of the trunk armour, which is only slightly elevated, and lacks both a median dorsal ridge and sensory groove. The lateral wall is very low (Fig.25B). This specimen lacks the anterior margin of the trunk armour, and the processus obstans of the ADL plate is missing (Fig.25A). Preserved trunk armour length is 210 mm and breadth 174 mm (B/L index 83). The right lateral wall is relatively complete, 184 mm long and 13 mm high, and

thus 13.5 times as long as high. The laminae meet at an obtuse angle. The main sensory canal runs back just beneath the dlr. The AMD is large and broad with well-developed lateral corners. The narrow anterior and broad posterior margins are well shown in other specimens (Fig.26A,B). In shape the plate is strikingly different from the AMD of *Sinolepis* or *Grenfellaspis*, and is the broadest bone in the dorsal wall. The anterior division is three times the length of the posterior division, and the posterolateral margin is short. The PMD of V 5076.1 (Figs 24,25) is narrow and slightly shorter than the AMD. The dorsal lamina of the ADL is quadrilateral, with the anterior end slightly broader than the posterior. Its lateral lamina is long (96 mm), very low (8 mm high) and of constant height throughout its length. The PDL has a prominent dorsal corner as in the corresponding plate of *Grenfellaspis*, or the mixilateral of *Bothriolepis*. The sutures between plates of the lateral wall are well seen in V.5076.1b (Fig.25B). The plates are preserved in natural association, and both dorsal and ventral margins of the lateral wall



**Fig.24.** *Xichonolepis qujingensis* P'an & Wang; Zhaojiazhuang near Wuding, Yunnan Province, South China. M. Devonian, dorsal wall of trunk armour, dermal surface, V.5076.1b. Specimen figured in Zhang (1980, pl.1, fig.2). Latex cast whitened with ammonium chloride (x0.6).

are continuous. It is clear from this specimen that *Xichonolepis* had no independent PL plate.

The isolated trunk armour plates include five AMD plates ranging in length from 41 to 103 mm. B/L index increases with size (Table 5). V 5076.1a and 5077 are two larger examples showing the inner surface, with a clear supranuchal area, strong postlevator thickening, but rather indistinct postlevator crista (Figs 25A,26B). The median ventral ridge and groove are well developed (Fig.26A,B). In the smallest specimen (V 9058, Fig.26C) the supranuchal area, postlevator crista and median ventral groove are poorly developed, which may reflect immaturity. The AMD shows the same overlap relations to the dorsolateral plates as in *Grenfellaspis*, with the anterolateral margin overlapping

the ADL and the posterolateral margin overlapping the PDL (also seen in asterolepids except *Remigolepis*, and possibly the primitive condition). The AMD has only a median overlap area for the PMD in V 5076.1b, and other specimens showing the visceral surface (e.g., V 9057.8, Fig.26A) show no contact face for the PMD on the posterolateral projections, indicating a non-overlapping lateral section of the posterior margin, as described above for *Grenfellaspis*.

The PMD is narrow and long (B/L index about 66), and the articulated specimen shows it is only slightly shorter than the AMD in the dorsal wall. Its anterior margin is broad and convex, but with a slight median concavity. The lateral margins are gently convex (Fig.26D,E). The PMD overlaps all adjacent plates, as
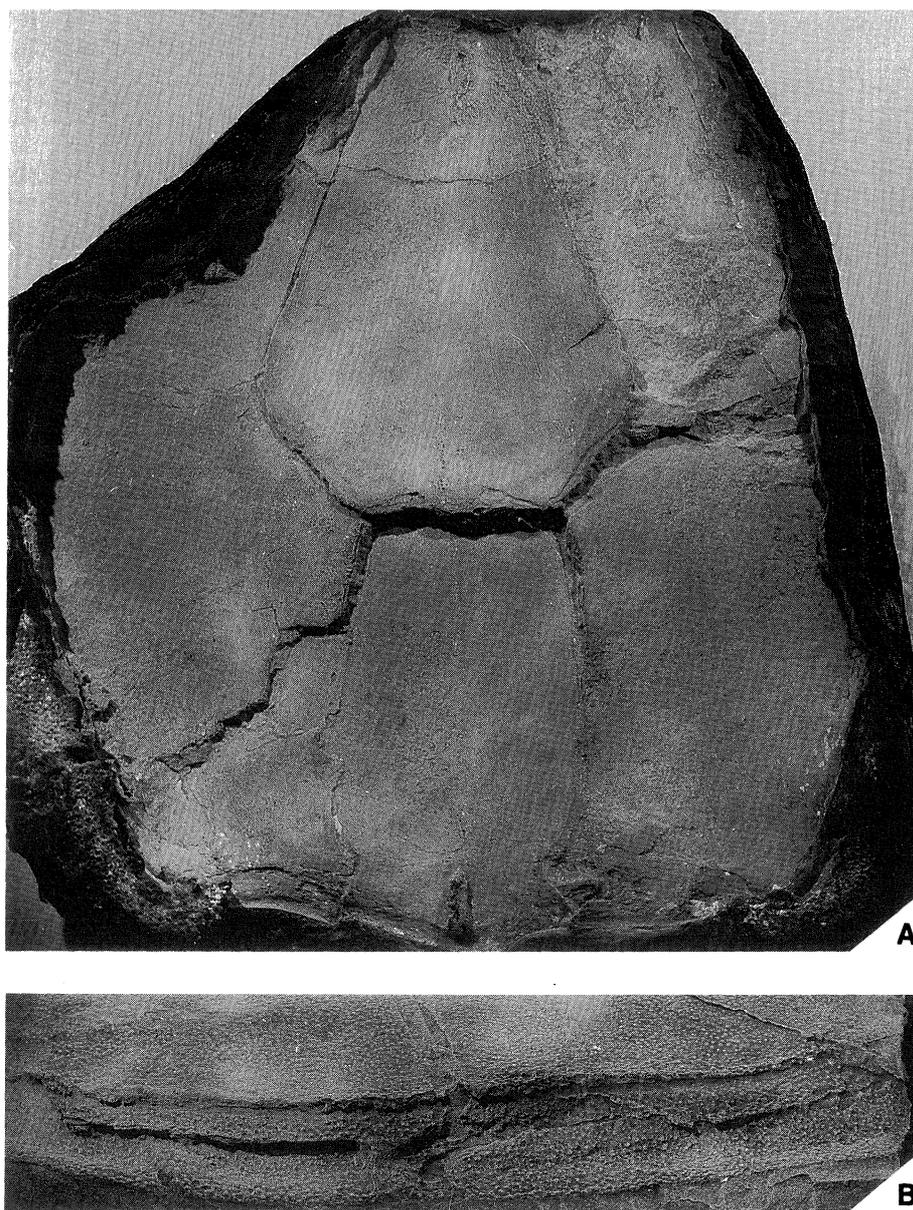


**Fig.25.** *Xichonolepis qujingensis* P'an & Wang; Zhaojiazhuang near Wuding, Yunnan Province, South China. M. Devonian. A - dorsal wall of trunk armour, visceral surface, V.5076.1a. Specimen figured in Zhang (1980, pl.1, fig.1). Latex cast whitened with ammonium chloride (x0.7). B - right lateral wall of trunk armour, V.5076.1b (*cf.* Fig.24), in lateral view (x0.9).

in all other known antiarch genera. The overlap area for the PDL is narrow but the bone is rather thick. There is only a slight overlap or the PMD may form a butt joint with the PDL. Lateral processes are very strongly developed, but otherwise the PMD is of similar breadth throughout its length, and just slightly narrower anteriorly. The posterior margin is convex, but lacks a posterior corner (Fig.30). The PMD is thus different in shape to that of *Grenfellaspis* (and

*Sinolepis*; see below), and most closely resembles the PMD of *Dayaoshania*. The visceral surface as exposed on V 2965.1, 2 shows the median ridge very well developed from the anterior margin backward (Fig.26D,E). Posteriorly it broadens to form a groove, but in the larger V 5076.2a there is an anterior groove and posterior ridge, and in V 5076.1a a shallow groove extends from the posterior division of the AMD across the PMD (Fig.25A), so these structures are variably
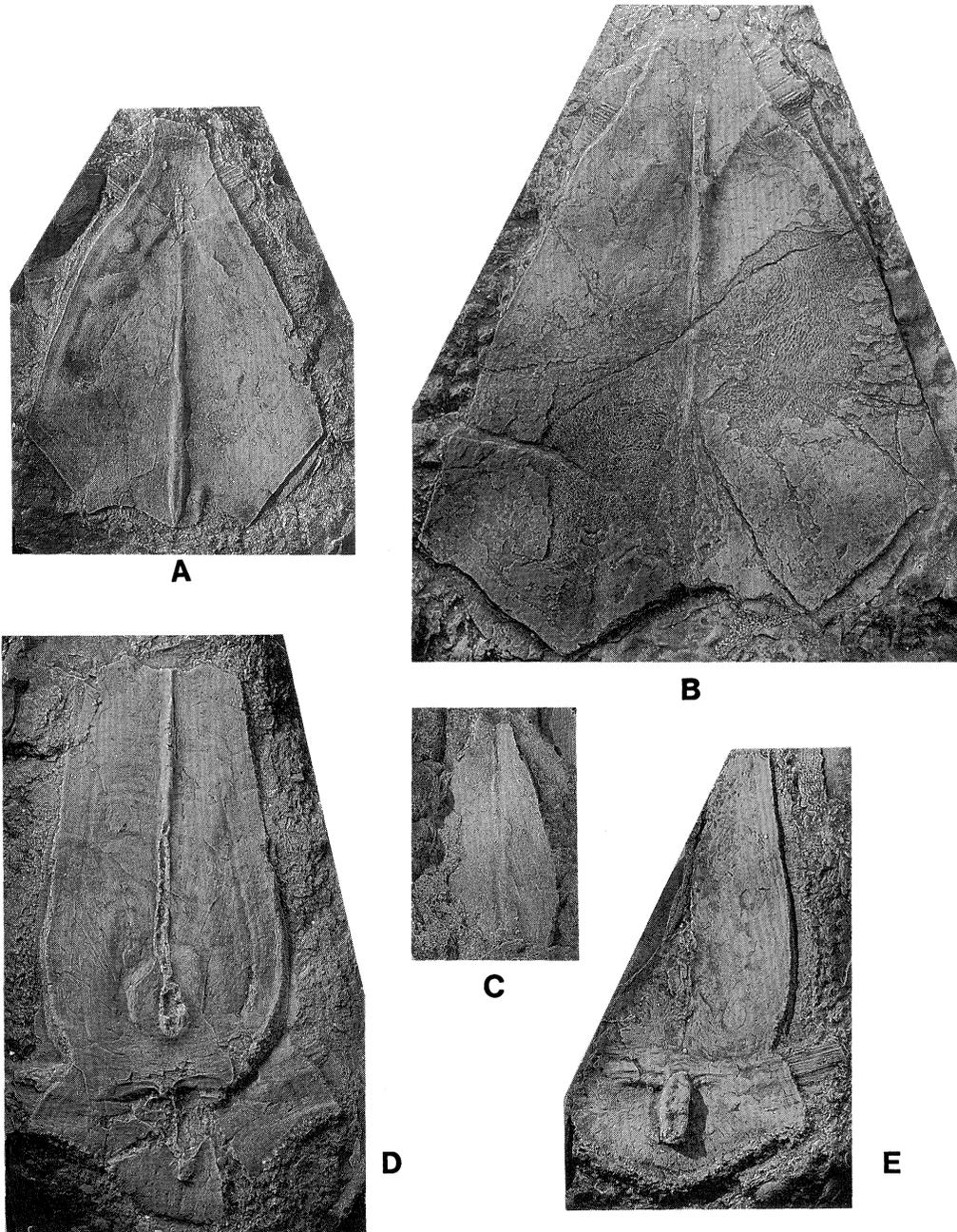


**Fig.26.** *Xichonolepis qujingensis* P'an & Wang; Middle Devonian, Devonian, Yunnan Province, South China. Median dorsal trunk plates, some of which were figured by Zhang (1980) as indicated below. Plaster casts whitened with ammonium chloride. x0.8 natural size. A-C - anterior median dorsals (AMD), visceral surface. A - V.9057.8; (Wuding, Yunnan). B - V.5077 (1980, pl.2, fig.5); (Qujing, Yunnan). C - V.9058; (Wuding, Yunnan). D,E - posterior median dorsals (PMD), visceral surface. D - V.2965.1 (1980, pl.2, fig.1); (Wuding, Yunnan). E - V.2965.2 (1980, pl.2, fig.2); (Wuding, Yunnan).

developed. The posterior marginal area is relatively long, and the posterior ventral pit and process are placed behind the crista near the posterior margin, and thus in a similar position to that of *Grenfellaspis* (except that in the latter the crista is much broader, and includes the pit). The state of this character is unknown in *Dayaoshania* and *Sinolepis*.

The ADL plate was previously known from V 5076.1, but two new specimens (V 9056.1 and 9057.4) provide more information on the visceral surface. The better specimen (V 9057.4, Fig.27A) is very flat, longer (60 mm) than broad (B/L index 60), and quadrilateral in shape. There is no clear division between dorsal and lateral laminae. The cit is broken laterally but shows normal development. The dorsomesial margin is overlapped by the AMD as already described. The overlap area along the posterior margin is narrow, and lacks the posterior corner seen in bothriolepids. The

ventral margin shows an oblique surface, presumably a contact for the AVL, although the main overlap area must have been on the external surface (not known), as in other antiarchs including *Grenfellaspis* described above. Posteroventrally is a short margin which formed a contact with the PVL, and shows that the AVL and PDL were separate. The same arrangement occurs in V 5076.1, and may be developed in some bothriolepids (e.g., variably present in *B. canadensis*; Stensiö, 1948).

Two new complete PDL plates are also preserved in visceral view (Fig.27B,C). The PDL has a distinct dorsal corner and dorsomesial process (Fig.30). It is broadest through the dorsal corner, and in shape resembles the PDL of *Grenfellaspis* rather than that of *Sinolepis*. The visceral surface in both specimens is flat, with no differentiation of dorsal and lateral laminae, and no contact faces developed for overlapping
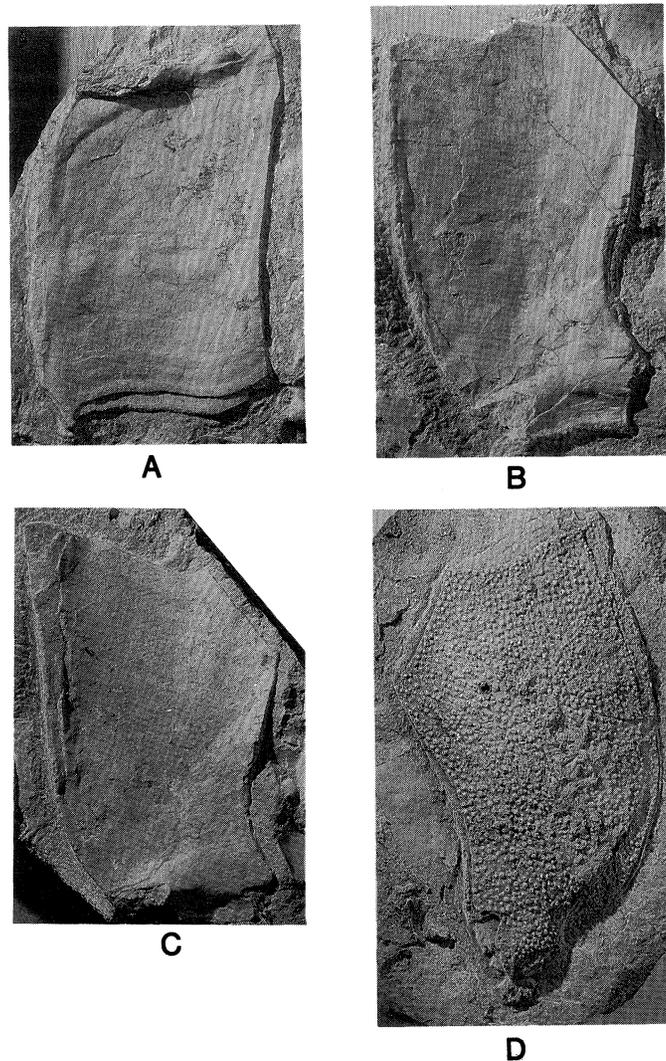


**Fig.27.** *Xichonolepis qujingensis* P'an & Wang, Middle Devonian, A-C - near Wuding, Yunnan Province, South China; D - from Panxi, near Huaning, Yunnan Province, South China. A-C - dorsolateral trunk plates, visceral surface. Original specimens, uncoated. x0.8 natural size. A - right anterior dorsolateral (ADL), V.9057.4; B - right posterior dorsolateral (PDL), V.9057.2; C - right posterior dorsolateral, V.9057.1. D - right posterior dorsolateral, V.4442.14b (Zhang 1980, pl.3, fig.4). Latex cast whitened with ammonium chloride (x1).

adjacent plates. V 4442 (Fig.27D) is a right plate showing the flat external surface, which lacks a dlr, and has a narrow overlap area along its lateral margin for the PVL. The lateral line groove runs just inside this margin. Since in the somewhat larger V 5076.1 the dlr is clear, its absence is assumed to be a juvenile characteristic in *Xichonolepis*. Two complete examples of the PDL have similar proportions (V 9057.1, 4442.14; length 77 and 70.5 mm, B/L indices 57, 58).

New information on the ventral wall of the trunk armour is provided by several specimens (Fig.29). V 9057.7a,b is part and counterpart of a large right AVL showing most of the inner surface of the bone (9057.7a), with the counterpart displaying the external surface of the lateral lamina and its dorsal margin. Posteriorly the contact face for overlapping the PVL is clearly preserved (Fig.29B), and is longer mesially than laterally, with a distinct mesial ridge just as described above for *Grenfellaspis*. In addition the specimen includes the subcephalic division showing some structures of the brachial articulation. V 9057.7a (Fig.29C) shows the dorsal aspect of a rounded process lying anterolateral to the ventral margin of the foramen axillare, and thus corresponding to the structure in *Grenfellaspis* labelled co.v in Figures 11 and 12. On the counterpart (V 9057.7b) the dorsal margin of the axillary foramen is not well preserved but the foramen seems to be longer than high, and possibly of triangular shape as in *Grenfellaspis*. Above the foramen the concave dorsal surface of the fossa axillaris extends up to the dorsal corner of the AVL (not preserved). The rest of the processus brachialis, fossa articularis pectoralis, and funnel pit are not preserved. Behind the prepectoral corner is a smooth margin 8 mm long which must be the ventral margin of the axillary foramen. The prepectoral corner is not completely preserved. Behind the brachial articulation an obtuse angle is clearly preserved between lateral and ventral laminae of the plate. V 9057.7b shows the

dorsal margin of the lateral lamina of the AVL to be fairly straight, and slightly higher at its anterior end. It is about 110 mm in length but only 10.5 mm high. The contact with the ADL is not clear, but presumably the AVL overlapped the ADL as in other antiarchs.

V 5076.6 (Fig.28) is a complete cast of the subcephalic division of the trunk armour, previously figured by Zhang (1984). It is 150 mm wide, with a length of 57 mm, so it came from a large individual. The prepectoral corners are well developed, and the right AVL overlapped the left as in all known antiarchs except yunnanolepids. The semilunar notch is large (81 mm across, 42 mm deep), occupying over half the total breadth of the subcephalic division. We consider therefore that *Xichonolepis* probably possessed paired semilunar plates, as known in *Dayaoshania*, but they must have been much larger than in that form, and of comparable size to those of *Grenfellaspis*. Both sides show a short free margin leading to the anterolateral corner of the AVL (poorly preserved), of similar shape to this region in *Grenfellaspis*. The transverse posterior margin to the subcephalic division in this specimen demonstrates that *Xichonolepis* had a similar morphology of the ventral trunk armour to that described above in *Grenfellaspis*. However, the narrow posterior part of the AVL plates have been broken off this specimen. On the left plate is an unornamented notch, corresponding to the similar structure in *Grenfellaspis* (a.un, Fig.11A).

Another specimen collected in 1962 from Wuding and previously difficult to interpret can now be understood in the light of the new information provided by *Grenfellaspis*. V 2965.7 is a long narrow strip of bone with a convex lateral and concave mesial margin, some 218 mm in preserved length and 23 mm across (Fig.29A). Both ends of the specimen are missing, but it is now clear that this represents the ventral laminae of an AVL and PVL in natural association, which from the overlap relationship must
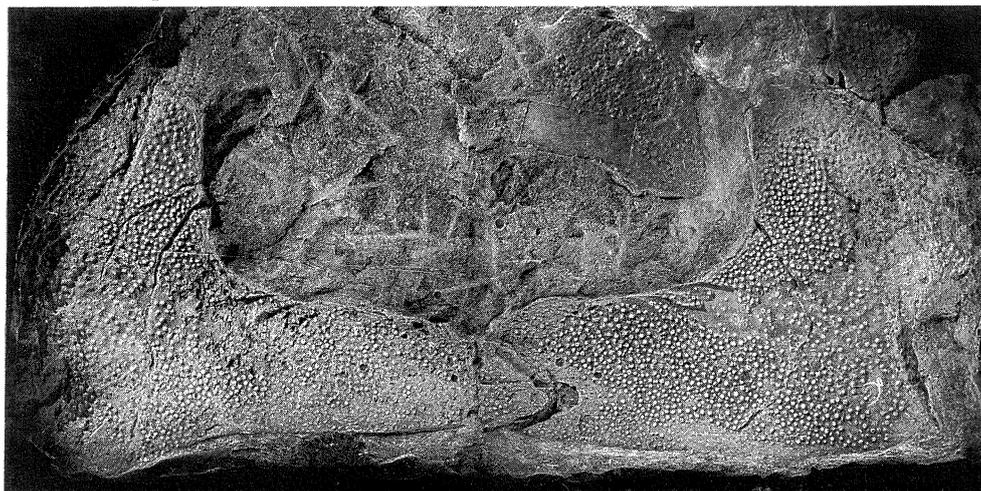


**Fig.28.** *Xichonolepis qujingensis* P'an & Wang; near Wuding, Yunnan Province, From below Haikou Formation, Middle Devonian. Anterior portion of ventral trunk shield, showing right and left AVLs in association (right overlaps left) and semilunar notch. V.5076.6. Latex cast whitened with ammonium chloride, from impression figured by Zhang (1980, pl.3, fig.1) (x0.8).

be from the left ventrolateral wall of the trunk armour.

V 9057.3 (Fig.29D) is the ventral lamina of a right PVL showing the visceral surface, and complete except for its anterior end. No posterior overlap is seen for the left PVL, but in all known antiarchs the right PVL is normally overlapped by the left, so this would not be seen on the inner surface. The subanal division is short, and shows the posterior margin of the trunk armour to have been concave (Fig.31), as in the other genera described above. However, the lateral subanal process described above in *Dayaoshania* is less pronounced in *Xichonolepis*. The process in this specimen displays a dorsally facing ornamented area extending mesially as a narrow strip inside the posterior margin (Fig.29D). This shows that the tail of *Xichonolepis* must have been much narrower than the trunk armour. The lateral lamina of this specimen
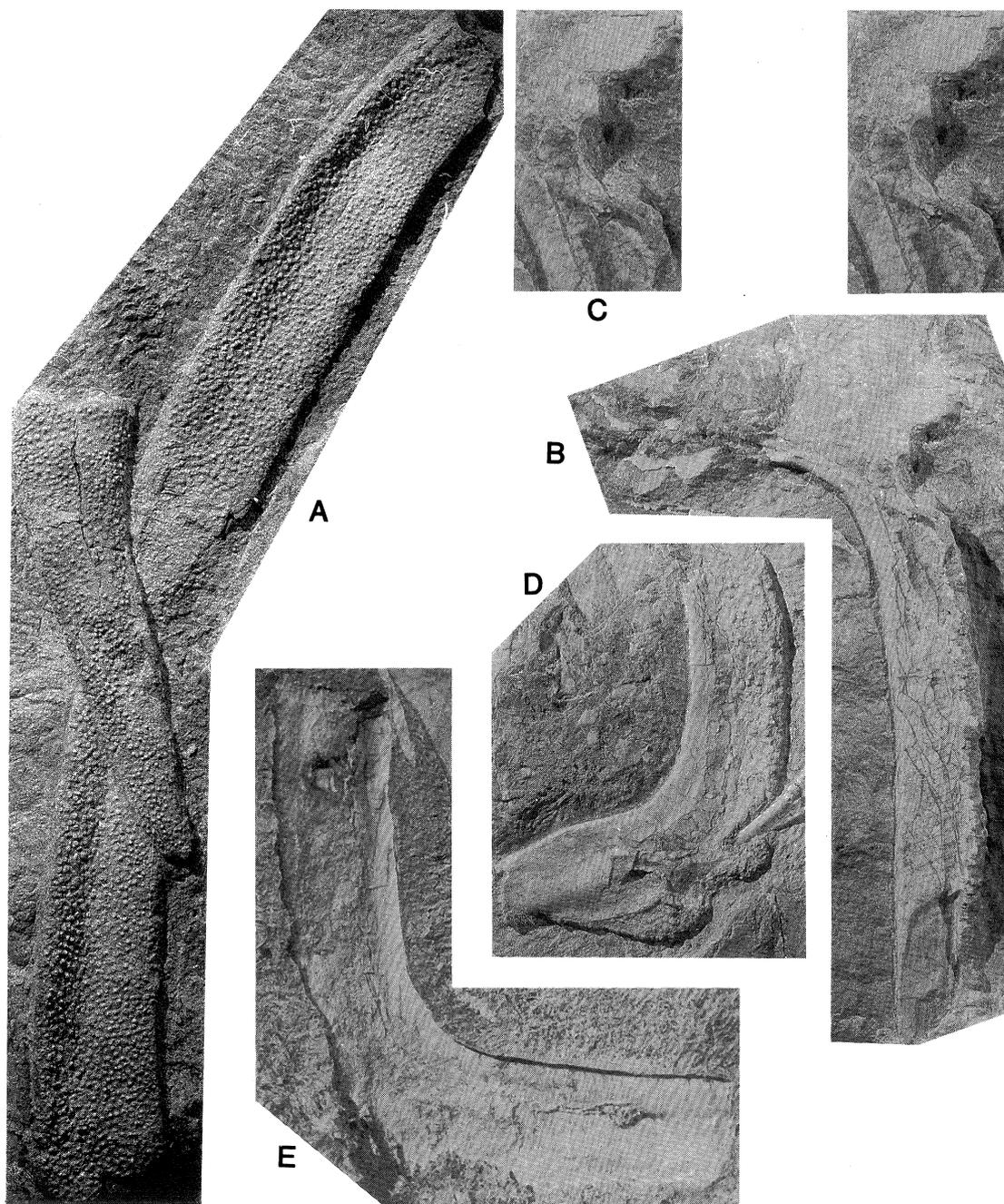


**Fig.29.** *Xichonolepis qujingensis* P'an & Wang; from near Wuding, Yunnan Province, South China. Middle Devonian. Ventral trunk plates (AVL,PVL). Original specimens. x0.8 natural size. A - associated right anterior (AVL) and posterior (PVL) plates (V.2965.7), partly overlain by the distal segment of a *Xichonolepis* pectoral fin (V.2965.8); B - right anterior ventrolateral, ventral view, V.9057.7a; C - detail of brachial area in V.9057.7a (stereo pair); D - right posterior ventrolateral, V.9057.3, dorsal view. E - left posterior ventrolateral, V.9056, dorsal view.

is broken off, but outside the broken edge is another dorsally facing ornamented surface, which indicates that the rim around the ventral wall in V 5076.1b is not an artefact of preservation. This rim is formed from the expanded ventrolateral ridge of the trunk armour. A second possible PVL (V 9056.2) is from the left side, but only the mesial margin is well preserved (Fig.29E).

P'an & Wang (1978, pl.33, fig.6) figured an incomplete Ml2 from the pectoral fin of *Xichonolepis*, and the only new pectoral fin specimen is a distal segment associated with the left ventral wall of the trunk armour just described (Fig.29A). From their relative sizes and closely similar ornament these associated remains are clearly conspecific and probably come from the same individual. The pectoral fin segment is complete except for the articular region at the proximal end which is slightly broken. It is 84 mm long and 20 mm wide proximally, and slightly curved with a flat exposed surface. In its broad and robust development it is very different from the elongate distal segment of the fin of *Bothriolepis*, or the associated *Dianolepis*. The sutures between bones cannot be traced, so it is not possible to decide whether the dorsal or ventral surface is exposed, and whether the segment comes from the left or right side. It is displaced relative to the associated

trunk remains because the distal end points anteriorly towards the AVL plate (Fig.29A).

As previously described (Zhang, 1980), the ornament of *Xichonolepis* is of crowded stellate tubercles, with no obvious alignment into rows. It is difficult to distinguish from the ornament of the associated bothriolepidoid *Dianolepis*.

### *Sinolepis* Liu & P'an, 1958

**Emended    diagnosis.** Headshield    large, subrectangular, as long as trunk armour; premedian plate with very short anterior division; postpineal and nuchal plates overlap lateral plate. Trunk armour broad, short, widest anteriorly, tapering posteriorly. Anterior median dorsal plate broad and quadrangular with straight anterolateral and short posterolateral margins. Posterior median dorsal shorter and narrower than AMD. Anterior dorsolateral plate as long as AMD. Subanal margin of ventral trunk wall straight. Pectoral fin as long as trunk armour.

**Remarks.** The diagnosis presented by Liu & P'an (1958) has been amended in the light of new information
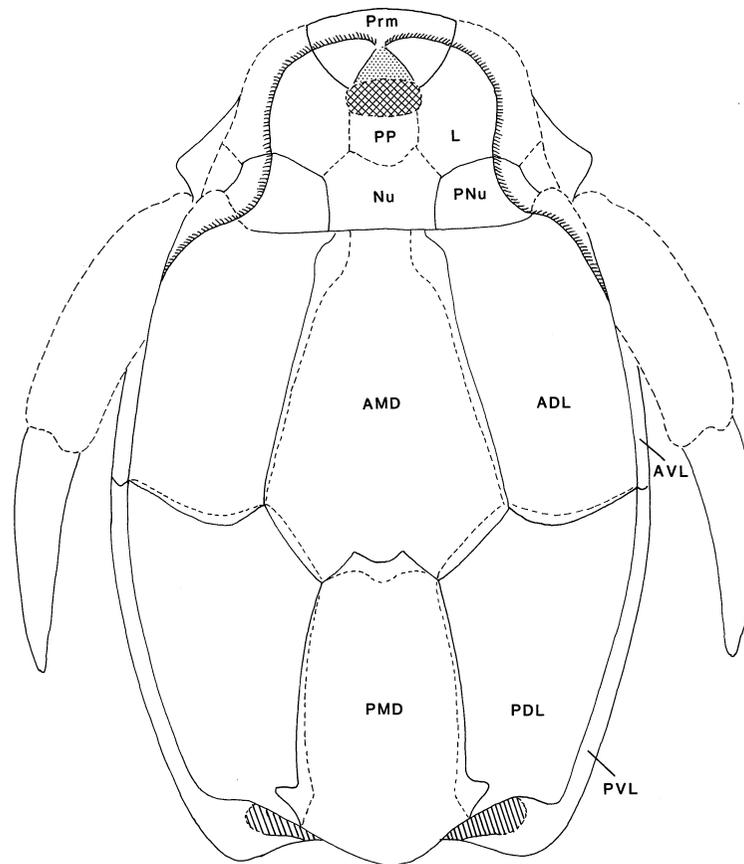


**Fig.30.** *Xichonolepis qujingensis* P'an & Wang, Middle Devonian, Yunnan Province, China. Reconstruction of armour in dorsal view (approximately two thirds natural size).

provided by the above descriptions. The characters used here are discussed below in the section on sinolepid inter-relationships.


### *Sinolepis macrocephala* Liu & P'an, 1958

### Figs 32,33C


**Type material.** HOLOTYPE, L41-4 (Liu & P'an, 1958, pl.1; pl.4, fig.1).

**Other material.** Material referred to this species was listed by Liu & P'an (1958).

**Type locality.** Luntan, near Nanjing, in the lower Yangtze Valley, Jiangsu Province (see Fig.1).

**Horizon and age.** Wutung Series (Late Devonian, Famennian).

**Diagnosis.** A *Sinolepis* with a maximal head shield length of about 65 mm, with a B/L index ranging between 100-120, and decreasing with size. AMD with straight anterior margin. Tubercular ornament partly replaced by anastomosing ridges.

**Remarks.** Three species of *Sinolepis* have been named: *S. macrocephala* (the type species), *S. wutungensis* Liu & P'an, 1958, and *S. szei* Pan *et al.*, 1987. *S. wutungensis* was based on a single small AMD plate from the type locality which was said to differ from the type species in being broader than long, with a concave anterior margin and less distinct median dorsal ridge (Liu & P'an, 1958: 40). More material is required to confirm the validity of this species. *Sinolepis szei* from the Upper Devonian of Ningxia was diagnosed by its large size (head shield 106 mm long), with an elongate postorbital part of the head shield (Pan *et al.*, 1987: 184). Like *S. wutungensis*, the AMD has a concave anterior margin, but it was evidently of more elongate proportions (Pan *et al.*, 1987, fig.48). Large size in itself is not a convincing difference, since the type species is known from only one collecting site, where most specimens collected are much smaller, and of similar size. However the largest known skull of *S. macrocephala* (Liu & P'an, 1958, pl.5, fig.1; the paratype, length about 63 mm) has more elongate proportions (B/L index about 104) than smaller specimens (B/L index up to 120; Liu & P'an, 1958: 31), suggesting a decrease in B/L index with size
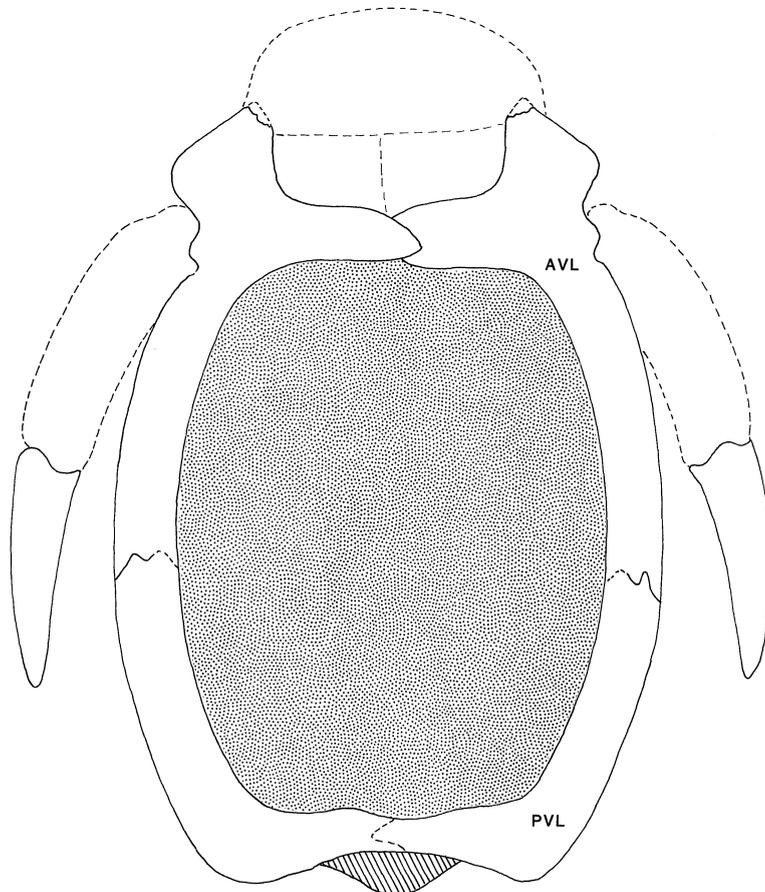


**Fig.31.** *Xichonolepis qujingensis* P'an & Wang, Middle Devonian, Yunnan Province, China. Reconstruction of armour in ventral view (approximately two thirds natural size).

as included in the above diagnosis. In contrast the larger more coarsely ornamented skull of *S. szei* has a greater B/L index (about 138), and although based on a single specimen this difference in proportion suggests that it is a valid species.

New interpretations presented below are all based on the type species, *S. macrocephala*.

**Description.** The type collection includes two nearly complete articulated individuals preserved in dorsal view, two other fishes with head and trunk preserved, and a few isolated plates, and was fully described and figured by Liu & P'an (1958). Here we comment on some problematic aspects of morphology arising from the above descriptions of *Grenfellaspis*,

*Dayaoshania*, and *Xichonolepis*. One specimen (L41-10) showing the AVL plate from the trunk armour is redescribed, and the structure of the pectoral fin is reinterpreted.

New restorations of the skull of *Sinolepis* have been presented by Long (1983), Young (1984c), and Pan *et al.* (1987). The most significant change from the original reconstruction is the long obstantic margin with an anteriorly placed PM plate, which gives the skull a hexagonal shape similar to that of bothriolepids and yunnanolepids, rather than asterolepids (Fig.33). The former condition is regarded as primitive for antiarchs generally (Young, 1984c). *Sinolepis* resembles *Grenfellaspis* in various skull features, for example the broad shallow grooves for the sensory canals.
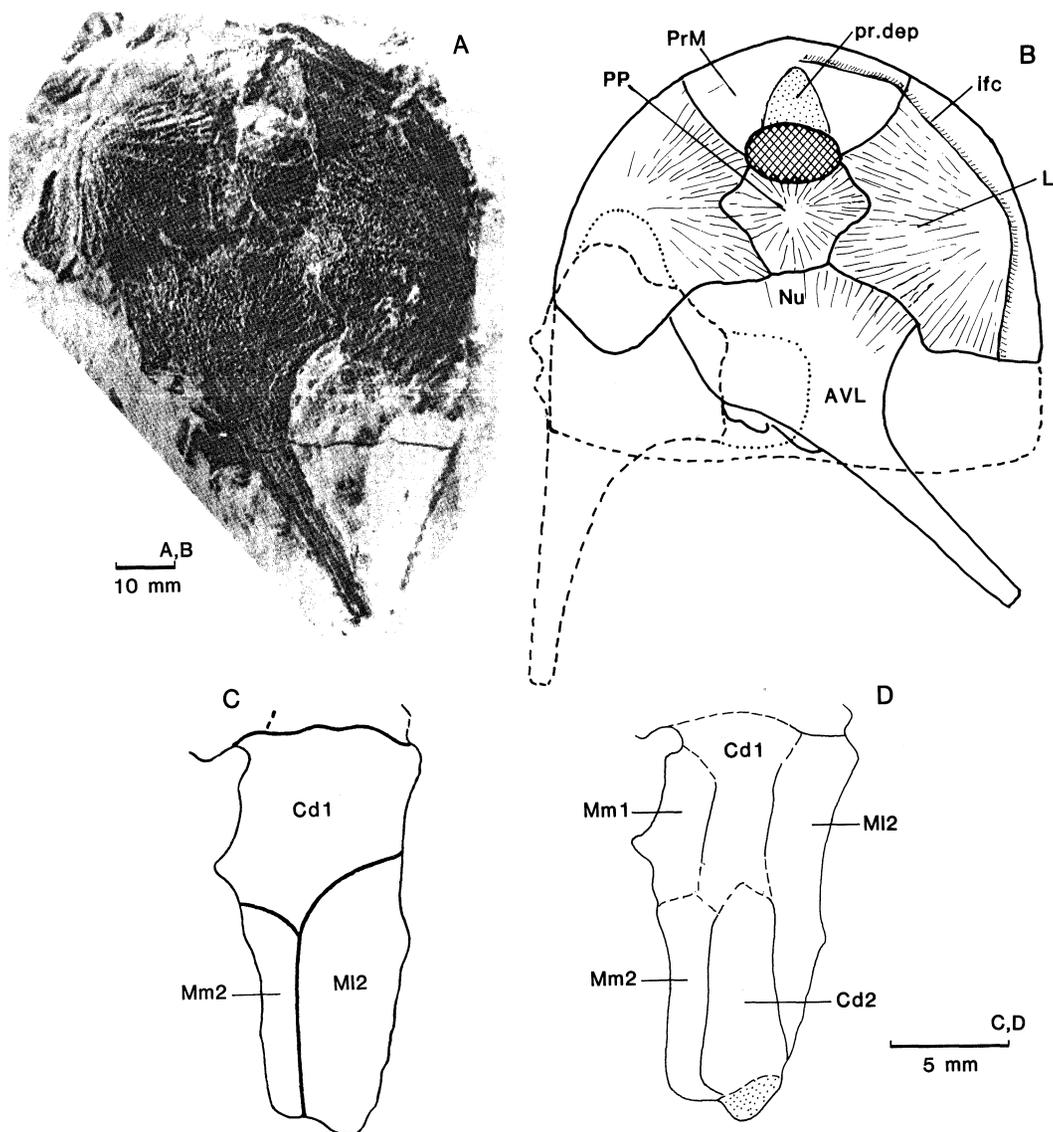


**Fig.32.** *Sinolepis macrocephala* Liu & P'an. A - headshield and right AVL, in ventral view. (specimen no. L41-10, refigured from Liu & P'an, 1958, pl.VII, fig.2b) B - reinterpretation of same specimen with original position of displaced AVL indicated by broken line; after information from *Grenfellaspis*, *Xichonolepis* and *Dayaoshania*. C - Liu & P'an's (1958) interpretation of the pectoral fin in specimen no. L41-6 (1958, pl.2). D - new interpretation of pectoral fin, traced from Liu and P'an's illustration, but based on new information from the pectoral fins of *Dayaoshania* and *Grenfellaspis*.

The ventral wall of the trunk armour was one aspect of the morphology of *Sinolepis* on which the type material provided little information. Liu & P'an (1958: 34,36) noted the presence of a clearly defined rim around the edges of the trunk armour as preserved in the holotype and paratype, which suggested that the ventral wall was probably broader and longer than the dorsal wall. A similar condition was described above for *Xichonolepis*. The long and low lateral laminae of the AVL and PVL plates were identified on the holotype (Liu & P'an, 1958, pl.1), but no other information was provided on the ventral wall, because both specimens are preserved in dorsal view.

In a re-examination of the material in 1981 it was discovered that another specimen described and figured as showing the anterior part of the headshield (Liu & P'an, 1958: 32, pl.7, fig.2) includes a displaced right AVL. In view of the highly unusual shape of the AVL and PVL plates in the three genera described above, it is not surprising that the AVL was not recognised in the original description of this specimen as an element of any significance. Without the benefit of comparative material of *Grenfellaspis* as described above, the elongate projection behind the small head-shield in specimen L41-10 has the appearance of a very incomplete fragmentary plate (Liu & P'an, 1958, pl.7, fig.2). This specimen (Fig.32A) demonstrates conclusively that the AVL of *Sinolepis macrocephala* was developed essentially as in *Grenfellaspis*, *Dayaoshania* and *Xichonolepis*. The much

reduced ventral lamina is represented only by a mesially directed transverse process (pr.tr) which was in contact with its antimere in the region of the crista transversalis interna anterior, and a narrow posterior process (pr.p) representing the ventrolateral ridge of the trunk-armour. However, the transverse process is somewhat broader than in *Xichonolepis* or *Grenfellaspis* (Figs 17,31). The semilunar notch is poorly seen but evidently of similar size and shape to that of *Grenfellaspis* or *Xichonolepis*. Incomplete remains of the brachial process (pbr) are also seen inside the prepectoral corner (prc).

Pan *et al.* (1987, fig.49) attributed an incomplete right AVL and associated pectoral fin to their new species *Sinolepis szei*, but, as preserved, this specimen has a more typical antiarch morphology and, on the evidence presented above, cannot belong to *Sinolepis*. The elongate pectoral fin suggests instead that it may belong to a bothriolepid antiarch. The fin itself is too poorly preserved to reveal details of suture pattern.

The suture pattern on the pectoral fin of *S. macrocephala* as originally restored by Liu & P'an (1958) has been of central importance in all previous considerations of the relationships of the genus. In their restoration in dorsal view (Liu & P'an, 1958, fig.5) the fin was shown to resemble that of *Bothriolepis*, with lateral and mesial marginal plates in contact with an extensive suture, and widely separating first and second dorsal central plates. It was noted that 'at the distal end
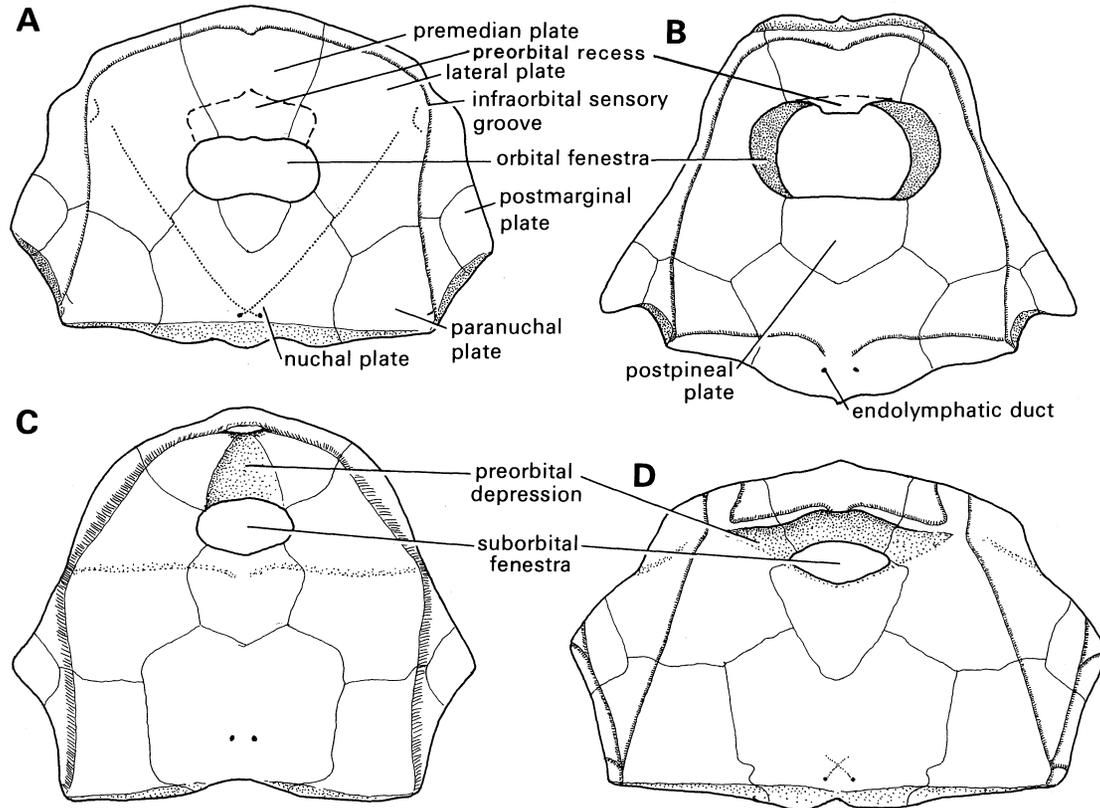


**Fig.33.** Skull roof patterns of representatives of the four major antiarch subgroups. Not to scale. (modified after Young 1984, fig.1) A - *Bothriolepis* (after Stensiö, 1948); B - *Asterolepis* (after Karatajute-Talimaa, 1963); C - *Sinolepis* (after Liu & P'an, 1958; Long, 1983); D - *Yunnanolepis* (after Zhang, 1978)

there is probably a small plate corresponding to the Cd2 of *Bothriolepis*, but being too ill-defined, a description of it is superfluous' (Liu & P'an, 1958: 34). Largely based on this description of the pectoral fin, and its similarity to that of bothriolepids, the sinolepids were placed as a sister group to bothriolepidoids in the phylogenetic scheme of Young (1984c).

The description of Liu & P'an (1958) is at variance with the structure of the pectoral fin as described above in *Grenfellaspis* and *Dayaoshania*, but from the published figures an alternative interpretation of the fin of *Sinolepis* can be suggested. Bone sutures are most clearly seen in the specimen illustrated by Liu & P'an (1958, pl.2), which shows the proximal part of the pectoral fin on the right side, with the elements labelled Cd1 and Ml2 clearly confined only to the central part of the dorsal surface of the fin. The large lateral element must be the Ml2 (Fig.32D), but the distal half of the preserved portion has two clear longitudinal sutures, not a single one as interpreted by Liu & P'an (1958). These sutures surely delineate an elongate Cd2 reaching proximally to meet with the Cd1, as described above in *Dayaoshania*. Along the mesial margin of the preserved portion two plates can be inferred. A well defined suture shows a dorsal lamina of the Mm1 attached to the Cd1, just as in *Dayaoshania* and inferred for *Grenfellaspis*. Preservation is less clear on the holotype of *Sinolepis*, but the more incomplete left fin Liu & P'an (1958, pl.1) suggests a Cd1 similarly restricted to the central part of the dorsal fin surface. We suggest therefore that restudy of the material of *Sinolepis* will reveal a pectoral fin structure essentially the same as that described above for *Grenfellaspis* and *Dayaoshania*.

## Discussion

**Inter-relationships of sinolepids.** Of the many morphological characters dealt with in the above descriptions, those relevant to a consideration of the interrelationships and relationships of sinolepids are further discussed here. Distribution amongst the various antiarch subgroups of characters proposed as synapomorphies in the cladograms of Figure 34 are summarised in a data matrix in Table 6. (A new sinolepid genus, *Vanchienolepis*, was recently erected by Tong-Dzuy & Janvier, 1990; it clearly belongs to the Sinolepidae on the evidence of the trunk armour, but has not been included in this discussion. The skull and pectoral fin are unknown.)

As will be seen from this matrix, the condition of many characters for many taxa is unknown. These gaps in knowledge are inevitable when dealing with incompletely preserved fossil taxa. As discussed by Zhang & Young (1992), such gaps prevent any rigorous parsimony analysis, unless unknown character states are incorporated as predictions of the preferred cladogram. However, the data matrix serves as a guide for future research in two ways: as a summary of

known and predicted character distributions within the context of a preferred phylogeny; and to focus collecting effort on reducing the proportion of missing character states for the group in question.

Antiarchs were highly specialised fishes, and for some characters, for example those concerned with the dermal pectoral articulation (a unique condition amongst vertebrates), decisions regarding character polarity are clear cut. Similarly, the major antiarch subgroups are supported by a number of good synapomorphies, and areas of disagreement in the current literature mainly concern structures for which we lack information in some of the taxa in question. Current phylogenetic schemes for placoderms generally (e.g., Young, 1986) and antiarchs as a major placoderm group (e.g., Janvier & Pan, 1982; Long, 1983; Pan *et al.*, 1987; Young, 1984c, 1988a), provide a phylogenetic framework for interpreting the new characters or character combinations arising from the above descriptions. Arguments supporting character polarity, mainly using outgroup comparisons, are given below for each of the 11 characters used in this analysis. The two instances of homoplasy in the analysis are also commented on below (for characters 1,2).
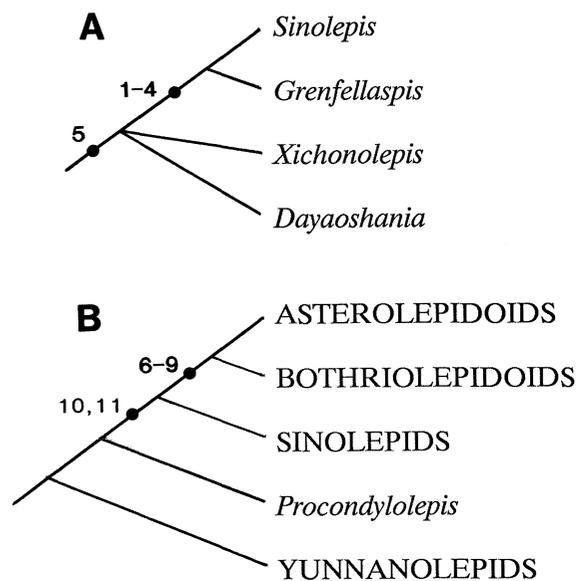


**Fig.34.** A - scheme of inter-relationships of sinolepid genera; B - suggested relationships of sinolepids to other major antiarch groups. Characters 1-10 as follows: 1 - lateral position of ifc on PNu and La, forming narrow lateral divisions; 2 - broad anterior margin to AMD; 3 - short posterolateral margin of AMD; 4 - square shape of PMD, with reduced lateral processes; 5 - large rectangular aperture in ventral trunk wall; median ventral plate absent; AVL and PVL reduced to narrow ventral laminae; 6 - Cd1 and Cv1 have large semicircular articular areas, similar in size and closely integrated to ornamented part of bone; 7 - mesial lamina on Cd1; 8 - Mm1 restricted to mesial wall of pectoral fin; 9 - brachial articulation with large, helmet-shaped processus brachialis; 10 - distal joint of pectoral fin; 11 - nerves and vessels to pectoral fin passing through a single axillary foramen.

First, various similarities observed in the above descriptions of the four sinolepid taxa may be separated into symplesiomorphies and synapomorphies. The genera *Dayaoshania* and *Xichonolepis* resemble each other in the following characters not seen in *Grenfellaspis* or *Sinolepis*: a) the broad lateral division on the paranuchal and lateral plates; b) the elongate anterior division of the premedian plate; c) the shape of the anterior median dorsal plate, with a narrow anterior margin, and pronounced lateral corners; d) the shape of the posterior median dorsal plate, with pronounced lateral processes. However, outgroup comparisons suggest that these are symplesiomorphies, because they also occur in other antiarch groups which on other evidence are monophyletic (e.g., a + b in yunnanolepids and bothriolepids; c in yunnanolepids and asterolepids).

*Sinolepis*, *Xichonolepis* and *Grenfellaspis* resemble each other, and differ from *Dayaoshania*, in having a deep semilunar notch and large apparently paired semilunar plate. By outgroup comparison this is also regarded as a symplesiomorphy, being seen in yunnanolepid and asterolepid antiarchs.

There are no obvious similarities of *Xichonolepis* and *Sinolepis* to the exclusion of the other taxa. However *Grenfellaspis* and *Sinolepis* resemble each other in several features which are possible synapomorphies (numbered as in Fig.34A): 1) lateral position of the infraobital sensory groove on the paranuchal and lateral plates, giving these bones narrow lateral divisions; 2) broad anterior margin to the anterior median dorsal plate; 3) short posterolateral margin of the anterior median dorsal; 4) square shape of the posterior median dorsal plate, with reduced lateral processes.

We interpret the lateral position of the infraobital sensory groove to be specialised, because the sensory groove arrangement which results in the broad lateral division in *Yunnanolepis* (Fig.33D) is also primitive in pattern, by comparison with an outgroup such as arthrodires. In addition *Yunnanolepis* is the most primitive known antiarch in several other major respects (e.g., pectoral fin articulation) although it is acknowledged that primitiveness in one feature does not necessarily imply primitiveness in another. Our interpretation predicts that the paranuchal and lateral plates of *Procondylolepis*, when described, will have narrow lateral divisions, and requires that the lateral position of the groove in asterolepidoids (Fig.33B) is independently acquired.

Similarly, character 2 is interpreted as independently acquired in bothriolepidoids and the two youngest sinolepid genera, because a narrow anterior margin to the anterior median dorsal plate occurs in the primitive *Yunnanolepis*. This argument is not supported by any clear-cut outgroup comparison, because other placoderm groups have both broad and narrow median dorsals. However, the fact that all known Early Devonian antiarch taxa, and most Middle Devonian taxa, have a narrow anterior division, provides a biostratigraphic argument in support of the interpretation adopted here. Characters 3 and 4 are regarded as

specialised by outgroup comparison with other antiarchs, since the alternative interpretation is less parsimonious in requiring independent loss of this character in *Xichonolepis* and *Dayaoshania*, yunnanolepids, and the common ancestor of bothriolepidoids and asterolepidoids. The validity of this argument depends on the monophyly of the Sinolepidae, discussed next.

Young (1984c, fig.2) proposed six possible synapomorphies defining sinolepids as a group, but new evidence now suggests that most of these are probably symplesiomorphies. Only one distinctive character is used here to define the group (Fig.34A): **5)** the large rectangular aperture in the ventral wall of the trunk armour, formed by the much reduced ventral laminae of anterior and posterior ventrolateral plates, and the absence of the median ventral plate.

Since all other placoderms with a long trunk armour (i.e., all other antiarchs, arthrodires, petalichthyids, phyllolepids, etc.) had one or two median ventral plates, and the ventrolateral plates were always developed with extensive ventral laminae, we consider this character to strongly support the monophyly of the Sinolepidae.

**Relationships of sinolepids.** Earlier views on the relationship of sinolepids to other antiarchs were summarised in the introduction. Most recently Young (1984c, fig.2; 1988, fig.68A) suggested a sister group relationship to bothriolepidoids, whilst Pan *et al.* (1987, fig.51) reiterated an earlier view of Janvier & Pan (1982, fig.12) and Long (1983, fig.11) that sinolepids were the sister group to bothriolepids plus asterolepids. The two synapomorphies of sinolepids and bothriolepidoids proposed by Young (1984c: 446) were: '12) elongation of the proximal part of the pectoral fin, with reduction of dorsal central plate 2 ; 13) PVL and posterior lateral plate fused to form (or replaced by) a single plate (*sensu* Janvier & Pan, 1982)'.

In the light of the new descriptions presented above neither can now be maintained. There is no evidence to support the view that sinolepids had a mixilateral plate, and the simplest explanation of the observed morphology is that they lost their posterior lateral plate with the development of a very low lateral wall to the trunk armour, leaving only the posterior dorsolateral plate. Unlike asterolepids, there is no evidence that the posterior lateral plate was fused to adjacent plates. In the pectoral fin it is now demonstrated that in *Grenfellaspis*, *Dayaoshania*, and presumably *Xichonolepis* and *Sinolepis*, the second dorsal central plate was not reduced as in bothriolepids, but was a large bone of the type seen in asterolepids, this being reasonably considered on morphological grounds to be the primitive condition (Young, 1984a).

That sinolepids are relatively primitive antiarchs is indicated by their retention of the preorbital depression, as in yunnanolepids, a structure which, in euantiarchs, is replaced by the preorbital recess (Janvier & Pan, 1982; Young, 1984c). Thus, in sinolepids, yunnanolepids and other groups with the preorbital depression, the central opening in the skull

is homologous with the suborbital fenestra of advanced antiarchs (Fig.33). The new material also confirms that sinolepids were more primitive than either bothriolepidoids or asterolepidoids in the structure of the brachial articulation and pectoral fin.

From our detailed knowledge of *Grenfellaspis* this genus may be regarded as typifying sinolepids, an assumption corroborated by the more limited evidence currently available from the other three genera. The pectoral appendage of *Grenfellaspis* is regarded as primitive in the following four respects: a) flat shape of the articular processes on the first dorsal and ventral central plates (Cd1, Cv1); b) absence of a dorsomesial crest and mesial lamina on the first dorsal central plate; c) presence of a dorsal lamina on the first mesial marginal plate (Mm1); d) much smaller articulation on the first ventral central plate.

The polarity of these states is based on the pectoral fin of *Procondylolepis*, which is the oldest and least complex armoured pectoral appendage known, with small dermal articulations on both the first ventral and first dorsal central plates. In contrast, the appendage of more advanced antiarchs is characterised by the following (numbered as in Fig.34B): **6**) the first dorsal central ventral central plates have large semicircular articular areas, of similar size and closely integrated to the ornamented part of the bone; **7**) a mesial lamina on the first dorsal central plate; **8**) the first mesial marginal plate restricted to the mesial wall of the pectoral fin.

The pectoral articulation on the anterior ventrolateral plate of sinolepids is also of primitive structure. In *Grenfellaspis* it comprised a triangular dorsal and a small ventral articular area respectively for the first dorsal and ventral central plates of the pectoral appendage, which pivoted around a single axis passing through these articulations. This is very different from the brachial articulation of more advanced antiarchs (bothriolepidoids, asterolepidoids), which possess: **9**) a large helmet-shaped processus brachialis, with the dorsal and ventral articulations developed as deep hemispherical grooves separated anteriorly by the narrow pars pedalis of the brachial process.

A dermal pectoral articulation is not recorded in any other vertebrates, and its greatest complexity is seen in the more advanced antiarchs (bothriolepidoids and asterolepidoids), so both outgroup and complexity arguments support the monophyly of euantiarchs based on character 9. In contrast, in sinolepids there was apparently no pars pedalis, and the anterior edge of the brachial process was continuous with the prepectoral corner of the anterior ventrolateral plate, this presumably representing the primitive condition, by outgroup comparison with *Procondylolepis* (Zhang, 1984). In addition, the sinolepids demonstrate that the complete brachial process appeared after the jointed pectoral fin was acquired.

We consider therefore that there is now ample evidence for placing sinolepids outside the asterolepidoids and bothriolepidoids (euantiarchs), as proposed by Janvier & Pan (1982), but the character they used to support euantiarch monophyly (presence of a 'brachial process') is no longer valid, because a rudimentary process is already present in *Procondylolepis* and sinolepids. Pan *et al.* (1987: 118) proposed that Euantiarchi be extended to include *Procondylolepis*, but the structure of the brachial articulation is very different from that in *Bothriolepis*, *Asterolepis* or *Remigolepis*, where the brachial process is fully formed, and this remains a valid character for euantiarchs in the original sense (and is thus equivalent to the Holocondylolepiformes of Zhang, 1984).

Sinolepids are more advanced than either yunnanolepids or *Procondylolepis* in possessing a distal joint in the pectoral fin (Young & Zhang, 1992). This structure had evolved at least by the end of the Early Devonian, as evidenced by *Liujiangolepis* recently described from Guanxi (Wang, 1987; the ventral armour of this form is not well known but, as described, the ventral armour wall is wider than the dorsal wall and the semilunar may be paired)*. Since the possession of a distal joint is a more complex condition than the unsegmented appendage of *Procondylolepis*, it may be assumed to be the specialised condition, and thus the following is proposed as a synapomorphy supporting a sister group relationship of sinolepids to asterolepidoids plus bothriolepidoids (Fig.34B): **10**) a distal joint in the pectoral fin.

An axillary foramen was previously inferred to have been present in the pectoral fin articulation of *Procondylolepis* (Zhang, 1984). However, a reinterpretation based on new material (Young & Zhang, 1992) now shows that the nerves and vessels to the fin passed through several small foramina, the primitive condition by outgroup comparison with arthrodires. The larger single axillary foramen is seen in only three groups: sinolepids, asterolepidoids and bothriolepidoids. Like Long (1983) therefore, we put forward the following as an additional synapomorphy at this level in the cladogram (Fig.34B): **11**) nerves and vessels to pectoral fin passing through a single axillary foramen.

## Biostratigraphy

**Middle Devonian.** The age of the Dayaoshan Group containing *Dayaoshania* is poorly constrained (Hou, Wang *et al.*, 1989). There are no marine horizons nor any palynological evidence of age in overlying strata which are very poorly exposed beneath Givetian marine beds higher in the sequence. The Dayaoshan Group is primarily a sandstone

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* *note added in press*: Further preparation of the specimen figured by Wang (1987, pl.2, fig.3) has recently confirmed that this form is also a sinolepid.

sequence, and is completely unfossiliferous except for the fish horizon (containing *Dayaoshania*) near its top. Its lower part rests unconformably on pre-Devonian rocks. The provisional Emsian-Eifelian age is based on general comparisons of the fish fauna.

**Late Devonian.** The only detailed consideration of the stratigraphic relationships of the Upper Devonian sediments of the Grenfell area is based on the mapping of J.R. Connolly, who presented a synthesis (1965) of the stratigraphy and correlation of the Hervey Group of central NSW. Connolly (1965, table 1) recognised three major lithological sequences which he formalised as subgroups of the Hervey Group: a lower Beargamil Subgroup of mainly red beds, lithic sandstones and arkoses; a middle Nangar Subgroup mainly comprising a rhythmic succession of white and red sandstones, and an upper Cookamidgera Subgroup, again mainly of red siltstones and shales. Correlation between the three main synclinal belts containing Hervey Group sediments was based primarily on lithological grounds, but also took into account the occurrence of placoderm plates from various localities and horizons (mainly within the sandstones of the Nangar Subgroup), referred to by Connolly as the 'bothriolepid fish assemblage'. This was based on the work of Hills (1932, 1936), who identified the antiarchs *Bothriolepis* and *Remigolepis* in a fish fauna from Gingham Gap in the Hervey Syncline, about 100 km north of the Grenfell area. However, Hills did not formally describe and name these species, and this and most other localities from which fish plates have been recorded remain very poorly known.

In the Grenfell area the Hunter Siltstone containing the *Grenfellaspis* fauna overlies a sandstone unit (the Peak Sandstone) which rests unconformably on Lower Devonian volcanics (Connolly, 1965, fig.11), and these formations were therefore referred to the lowermost Beargamil Subgroup. However detailed work on the vertebrate fauna and on other vertebrate occurrences in the Upper Devonian of NSW, currently in progress, suggests that the Hunter Siltstone is considerably younger than the stratigraphy indicates, and indeed may be one of the youngest Devonian vertebrate faunas known from eastern Australia. A preliminary faunal list is as follows:

| | |
|---|---|
| antiarchs | *Grenfellaspis branagani* n.sp. |
| | *Bothriolepis* sp. |
| | *Remigolepis* sp. |
| arthrodires | *Groenlandaspis* spp. |
| acanthodian | ischnacanthid jaw bones indet. |
| dipnoans | cf. *Ctenodus* (Long, 1987: 310) |
| crossopterygians | porolepiform scales |
| | ?*Eusthenodon* sp. |

A noteworthy feature is the absence of phyllolepid placoderms, which occur widely in other Famennian fish faunas in NSW (e.g., Ritchie, 1984). The associated *Groenlandaspis* is a new species with unornamented dermal bones, which also occurs on the south coast of NSW in the Worange Point Formation (Ritchie, in preparation), where again it is associated with antiarchs (*Bothriolepis, Remigolepis*) and crossopterygians (a

holoptychiid porolepiform, but with different scale morphology to that from the Grenfell fauna). Phyllolepid remains occur lower in this sequence, but not in the Worange Point fauna (Young, 1983), which suggests that both this and the Grenfell fauna represent a younger horizon than the upper limit of *Phyllolepis*, which occurs in the Famennian of Europe, and is regarded as a reliable index fossil for the late Famennian (e.g., Westoll, 1979; Lelievre & Goujet, 1986; Young, 1988b). The different crossopterygian, and absence of *Grenfellaspis*, suggest that the Worange Point fauna may be slightly older than the *Grenfellaspis* fauna. Evidence from borehole data in western New South Wales suggests that the *Bothriolepis-Remigolepis* assemblage approximates to the *Retispora lepidophyta* palynofloral zone of Playford (1976, 1982), which crosses the Devonian-Carboniferous boundary. Thus an earliest Carboniferous age for the Grenfell assemblage cannot be excluded. Janvier *et al.* (1984) regarded *Groenlandaspis* as also extending possibly into the earliest Carboniferous. This assessment based on the vertebrate assemblages is supported by palynological evidence of the age of the Chinese sinolepid occurrences.

Cai *et al.* (1987) have recently discussed the age and correlation of the Devonian - Carboniferous transitional sequences of south China. Before the discovery of placoderms in the late 1950's the upper part of the Wutung Formation (Leigutai Member) of the lower Yangtze Valley was regarded as Early Carboniferous in age on the evidence of plant macrofossils (e.g., Gothan & Sze, 1933; Sze, 1956). The macroplants include *Leptophloeum rhombicum, Cyclostigma kiltorkense*, and *Archaeopteris* sp. which are associated with the *Sinolepis* fish fauna in the lower part of the Leigutai Member. Pan (1981) placed the *Sinolepis-Asterolepis sinensis* assemblage as the youngest antiarch assemblage known from China, of late Upper Devonian age. In addition the Leigutai has recently yielded abundant miospores in which three assemblage zones have been recognised by Ouyang & Chen (1987): the lower *Retispora lepidophyta-Apiculiretusispora hunanense* (LH) zone (including the fish horizon) is placed in the late Famennian (Fa2d), and the overlying (LC) Zone may be Tournaisian (Tn1a to early Tn1b), although a latest Devonian age is preferred by Cai *et al.* (1987).

This evidence is consistent with that from the upper part of the Sanmentan Formation in Jiangxi Province, where the same *Sinolepis - Jiangxilepis* fish fauna (Zhang & Liu, 1991) is associated with a similar suite of macroplants, and (from the Changyi and Quannan localities in southern Jiangxi) a miospore assemblage including *R. lepidophyta* (Cai *et al.*, 1987). The lower part of the Sanmentan has a marine *Yunnanella* fauna, and the underlying Zhongpeng Formation contains several *Bothriolepis* and macroplant horizons.

In summary, the *Sinolepis* beds of south-eastern China are apparently of similar age to the *Grenfellaspis* fauna of south-eastern Australia. However, *Remigolepis* is apparently absent (although a new remigolepid occurs in the Sanmentan Formation, and *Remigolepis* sp.

is known from Hunan Province) perhaps indicating that the *Sinolepis* beds of south-east China lie above the range of *Remigolepis*. In contrast, *Remigolepis* is known to be associated with *Sinolepis* in north China, but there is other evidence that this fish assemblage may be older. The Middle-Upper Devonian continental sequence in Ningxia Province, and its contained flora and fauna, has been dealt with in an important monograph by Pan *et al.* (1987). From the uppermost Devonian formation, the Zhongning Formation, comes a fish fauna which includes indeterminate galeaspid agnathans and sarcopterygians, six species of *Remigolepis*, and one species of *Sinolepis*. Associated are macroplants including *Leptophloeum rhombicum*, *Sublepidodendron mirabile*, *Eolepidodendron wusihense*, *Sphenopteris taihuensis*, and *Ningxiaphyllum trilobatum*. A miospore assemblage of 20 genera and 32 species includes *Calamospora atava*, *C. nigrata*, *Retusotriletes distinctus*, *Verruciretusispora robusta*, and *Geminospora lemurata*.

The evidence of the plants and spores is cited by Pan *et al.* (1987) in support of a Famennian age for the Zhongning Formation, but the spore assemblage is somewhat different from that listed above for the Wutung Formation. Dr G. Playford (*in litt.*) has commented that this palynoflora "...is certainly older than the latest Devonian *Retispora lepidophyta* Assemblage and could even be pre-Late Devonian ... (and) datable within the interval mid-Givetian to Frasnian. Biostratigraphically significant components include *Apiculatisporites microconus*, *Geminospora lemurata*, *Verruciretusispora magnifica*, and *Archaeozonotriletes variabilis*..." Thus there may be evidence that the Ningxia *Sinolepis* horizon is somewhat older than the type locality for the genus in the lower Yangtze region.

## Biogeography

The distribution of sinolepid antiarchs in apparently non-marine environments in eastern Australia and China but nowhere else is of biogeographic interest, as has been noted by several workers (e.g., Young, 1981, 1984c, 1990a; Long, 1983; Burrett *et al.*, 1990). The fact that *Grenfellaspis* is only known from one locality in eastern Australia could be considered to place doubt on the adequacy of sampling of late Devonian vertebrate faunas for biogeographic purposes. However, as just discussed, other evidence of the vertebrate faunal succession in eastern Australia indicates that the Grenfell fauna is one of the youngest Devonian vertebrate assemblages so far known from the area, so the absence of *Grenfellaspis* itself from other faunas is assumed to be due to an age difference. It seems reasonable to infer from their earlier history in South China that sinolepids only dispersed to Australia in the latest Devonian. Many aspects of the Early Devonian fish faunas of the two regions indicate little communication between non-marine faunas, although there is some evidence of shallow marine similarity (e.g.,

*Buchanosteus* in eastern Australia, *Kueichowlepis* in China). Primitive bothriolepid antiarchs in the Middle Devonian of eastern Australia (*Monarolepis*) and South China (*Dianolepis*), and closely related species of *Bothriolepis* in the Givetian-Frasnian of Antarctica, Australia, and China (Young, 1988a), suggest closer biogeographic ties in the late Middle and Late Devonian. From the wide distribution of *Bothriolepis* (cosmopolitan in the Late Devonian) it seems clear that its range enlargement resulted from a greater capacity to cross
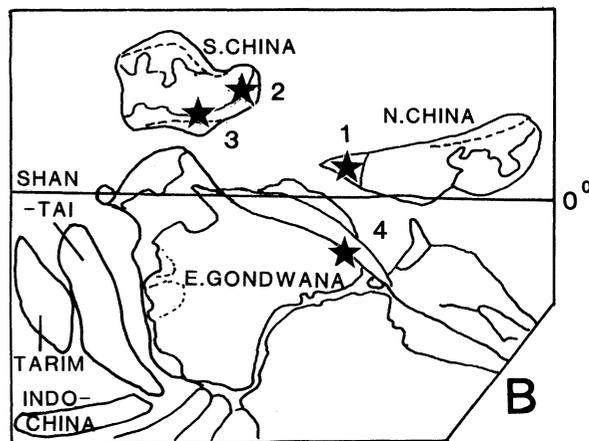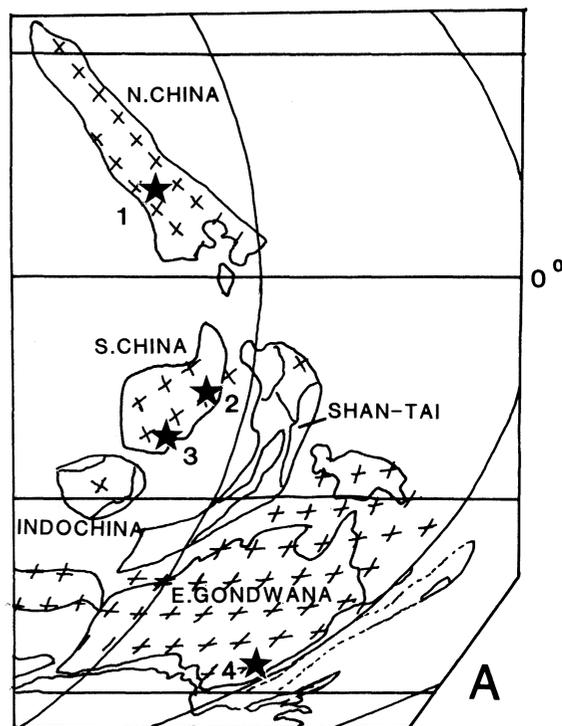




**Fig.35.** Suggested palaeogeographic relationships between North and South China and East Gondwana in the Late Devonian, showing the four main areas for sinolepid antiarchs (*cf.* Fig.1). 1 - Ningxia Province, North China block *(Sinolepis)*; 2 - Nanjing region *(Sinolepis)*; 3 - Yunnan-Guangxi region and north Vietnam, South China block (*Xichonolepis*, *Dayaoshania* etc.); 4 - Grenfell region, Tasman Fold Belt, East Gondwana (*Grenfellaspis*). A - after Scotese 1986; B - after Burrett *et al.* (1990).

marine barriers than some other placoderm groups, such as sinolepids or phyllolepids. The complete absence of phyllolepid placoderms from the Devonian of China has been taken to indicate persistent (probably marine) barriers between it and east Gondwana, but as noted in the previous section the Grenfell fauna appears to be younger than the upper biostratigraphic range of phyllolepids in eastern Australia. Thus it may be postulated that the palaeogeographic changes which permitted sinolepids to disperse into east Gondwana were events which postdated the extinction of the Phyllolepida.

Various palaeogeographic reconstructions have been proposed for the Palaeozoic configuration of the tectonic units of east Asia. Figure 35 shows two recent proposals. The maps of Scotese (1986) show the North China block with a similar orientation but much closer to the north-western margin of Australia in the Early Devonian, with an oceanic barrier of increasing width separating North China from South China and Australia in the Late Devonian. This shows no consistency with the biogeographic evidence of sinolepid distribution. Burrett *et al.* (1990) show a northward excursion of east Gondwana towards the palaeoequator, and of North China away from the palaeoequator to 30° north, during



**Fig.36.** A - accretionary sequence for Asian terranes (after Talent *et al.*, 1987); B - accretionary sequence for three regions based on the following faunal evidence. 1 - occurrence of Givetian quasipetalichthyids and Late Devonian galeaspids and sinolepids in Ningxia; 2 - occurrence of Late Devonian sinolepids in Australia.

the Early - Middle Devonian interval. North China returns to an equatorial position in the Late Devonian to lie adjacent to Australia and South China (Fig.35B). This reconstruction was proposed to take account of the sinolepid evidence, and the occurrence of a similar Late Devonian flora in Ningxia and South China, but as noted above there may be palynological evidence that the Zhongning Formation is older (?Frasnian) than the Wutung and Sanmentan Formations of South China. This is consistent with an earlier faunal exchange of *Remigolepis* between China and Australia - this genus is known from older deposits in eastern Australia than the *Grenfellaspis* assemblage, possibly as old as Frasnian, and undescribed *Remigolepis* species from the Hervey Group of central NSW (generally regarded as early Famennian in age) include very similar and presumably closely related species to those described by Pan *et al.* (1987) from Ningxia (Zhang Guorui, personal observation). In contrast the sinolepids are generically distinct between China and Australia.

The palaeogeographic history of the areas under consideration here may also be represented as area cladograms. Talent *et al.* (1987) present an accretionary sequence for Asian terranes which in South China and North China come together in the Triassic (Fig.36A). A Mesozoic closure has been accepted in the literature for some time (e.g., Burrett, 1974; McElhinny *et al.*, 1981), but the vertebrate evidence discussed here strongly indicates coalescence by the late Middle Devonian (Fig.36B). Resolution of this inconsistency is complicated by the fact that the Zhongning Basin of Ningxia (Pan *et al.*, 1987, figs 2,9) may have had a separate Palaeozoic history (the Hexizoulang Terrane of Li *et al.*, 1985), detaching from South China sometime after the Devonian (Burrett *et al.*, 1990). If correct then the sinolepid biogeographic evidence has no bearing on the palaeogeographic history of the North China terrane. Wang (1985: 141) shows the area of the Zhongning Basin to lie on the south-east margin of their geotectonic unit IIB3 (Alxa Massif), at the edge of the North Qilian fold zone (IIG1), but make no suggestions as to its separate palaeogeographic history in relation to the North China block.

A second complicating factor is the suggestion (Hsu *et al.*, 1988) that the South China fold belt may have been a separate terrane which did not coalesce with the Yangtze block until Mesozoic time. The sinolepid and other evidence (similar vertebrate, macroplant and miospore assemblages in the Sanmentan and Wutung Formations on either side of the proposed suture) is completely inconsistent with this hypothesis.

To conclude, some other faunal evidence consistent with the sinolepid distribution pattern may be briefly summarised. In the latest Devonian-Early Carboniferous close affinity between Australia and China is also indicated by freshwater leaiid ostracods, which are known in the Devonian only from China, but appear in the Early Carboniferous of north-western (Anderson Formation) and north-eastern (Drummond Basin) Australia, and only become widespread later in the Carboniferous,
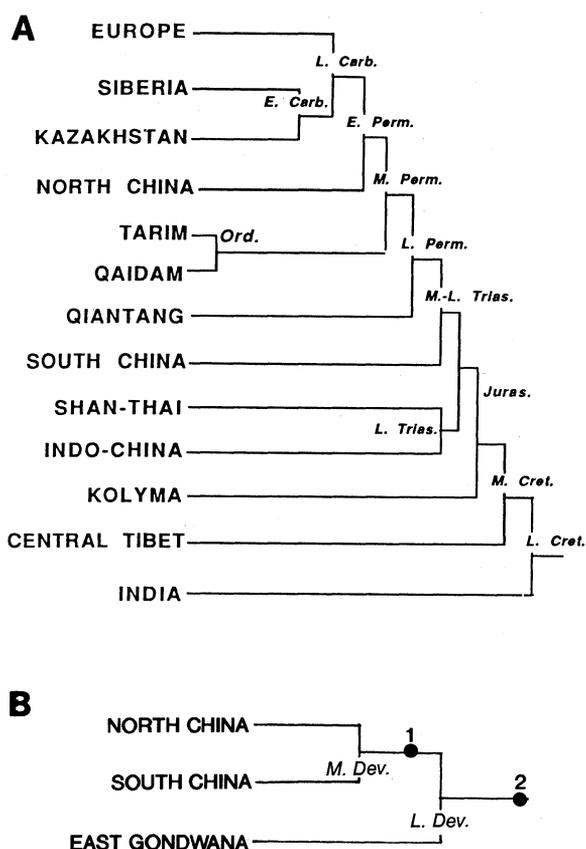
in Namurian and younger strata (P.J. Jones, personal communication). Some groups of Early Carboniferous brachiopods show a similar pattern (K.S.W. Campbell, personal communication; the sister taxa *Eochoristes* and *Ectochoristes*; see Chu, 1933; Campbell, 1957). A conodont species from the Bonaparte Basin of north-western Australia, originally described as *Polylophodonta* sp. A, which has a restricted range within the late Famennian Buttons Beds (Jones, 1985, fig.2), is probably conspecific (P.J. Jones, personal communication) with *Rhodalepis polylophodontiformes* of Wang & Yin (1985), only known from the Xiakou section of the Rongxian Formation, in Guangxi Province (lower-middle *praesulcata* Zone). Other examples showing a similar pattern are likely to be forthcoming, since this preliminary evidence suggests that both non-marine and shallow marine organisms were controlled by similar biogeographic factors.

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## APPENDIX I

Abbreviations:-  L.ad - length of anterior division; L.pd - length of posterior division; L.am - length of anterior margin; L.pm - length of posterior margin.

Table 1. Measurements and ratios of the AMD of *Grenfellaspis* (unit : mm)

| spec.no. | Length (L) | Breadth (B) | B/L | L.ad | L.pd | L.ad/L.pd | L.am | L.pm |
|---|---|---|---|---|---|---|---|---|
| AMF 56328 | 59 | 28 | 47 | 45 | 14 | 3.2 | 16 | 13 |
| AMF 61447 | 50 | 30 | 60 | 39 | 10 | 3.9 | 13 | 15 |
| AMF 78684 | 51 | 30 | 59 | 40 | 11 | 3.6 | 14 | 14 |
| AMF 78695 | 47 | 23 | 49 | – | – | – | 15 | – |
| CPC 29110 | 37 | 23 | 62 | 27 | 10 | 2.7 | 11 | 12 |

Table 2. Measurements and ratios of the PMD of *Grenfellaspis* (unit : mm)

| spec.no. | L | B | B/L | L.am | L.pm |
|---|---|---|---|---|---|
| AMF 56136a | 54 | 25 | 46 | 16 | 22 |
| AMF 56136b | 43 | 23 | 54 | 11 | 19 |
| AMF 56175 | 53 | 24 | 45 | 18 | 14 |
| AMF 56282a | 31 | 17 | 55 | 11 | 16 |
| AMF 56282b | 33 | 15 | 45 | – | – |
| AMF 56294b | 43 | 21 | 49 | 15 | 17 |
| AMF 56324 | 31 | 23 | 74 | 15 | 19 |
| AMF 56328a | 49 | 22 | 45 | – | 21 |
| AMF 56328b | 41 | 19 | 46 | 10 | 15 |
| AMF 56362 | 50 | 22 | 44 | – | – |
| AMF 56364 | 40 | 22 | 55 | 14 | 19 |
| AMF 79202 | 48 | 33 | 69 | 24 | 21 |
| AMF 79203 | 38 | 25 | 66 | 17 | 21 |

Table 3. Measurements of AMD  of *Dayaoshania* (unit : mm)

| spec.no | L# | B | B/L | L.ad | L.pd | L.ad/L.pd | L.am | L.pm |
|---|---|---|---|---|---|---|---|---|
| MGV 1947 | 30 | 15 | 50 | 22 | 8 | 2.8 | 5 | 9 |
| MGV 1950 | 24 | 11 | 46 | 20 | 6 | 3.3 | – | 5 |
| IVF 2 | 30 | 17 | 57 | 24 | 5 | 4.8 | 5 | 11 |
| IVF 4 | 27 | 15 | 56 | 22 | 5 | 4.4 | 5 | 10 |
| IVF 5 | 30 | 15 | 50 | 24 | 8 | 3.0 | 6 | 10 |

# external measurement excluding posterior *oa*

Table 4. Measurements of PMD of *Dayaoshania* (unit : mm)

| spec.no | L | B | B/L | L.am | L.pm |
|---|---|---|---|---|---|
| MGV 1947 | 26 | 17 | 65 | 8 | 18 |
| IVF 2 | 26 | 16 | 62 | 11 | – |
| IVF 4 | 26 | 18 | 69 | – | 17 |

Table 5. Measurements of AMD of *Xichonolepis* (unit : mm)

| spec.no | L. | B. | B/L | L.ad | L.pd | L.ad L.pd | L.am | L.pm |
|---|---|---|---|---|---|---|---|---|
| V 2965.3 | 98 | 80 | 82 | 68 | 30 | 2.3 | – | 28 |
| V 5076 | 115 | 85 | 74 | 87 | 28 | 3.1 | – | 43 |
| V 5077 | 103 | 90 | 87 | 85 | 25 | 3.4 | 14 | 43 |
| V 9057.8 | 66 | 49 | 74 | 51 | 15 | 3.4 | 10 | 26 |
| V 9058 | 41 | 20 | 49 | 31 | 11 | 2.8 | 6 | 16 |

Table 6. Data matrix for 11 characters used in constructing the cladograms of Figure 34. Character polarity is discussed in the text. For list of characters see caption to Figure 34. (0 = primitive character state; 1 = derived character state; – = character state unknown).

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ASTEROLEPIDOIDS | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| BOTHRIOLEPIDOIDS | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Sinolepis* | 1 | 1 | 1 | 1 | 1 | – | 0 | 0 | – | 1 | – |
| *Grenfellaspis* | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Xichonolepis* | 0 | 0 | 0 | 0 | 1 | – | – | – | – | 1 | 1 |
| *Dayaoshania* | 0 | 0 | 0 | 0 | 1 | – | – | – | – | 1 | – |
| *Procondylolepis* | – | – | – | – | – | 0 | 0 | 0 | 0 | 0 | 0 |
| YUNNANOLEPIDS | 0 | 0 | 0 | 0 | 0 | – | – | – | 0 | – | 0 |

# APPENDIX II

Abbreviations used in text and figures

| | |
|---|---|
| ADL | anterior dorsolateral plate |
| AMD | anterior median dorsal plate |
| AVL | anterior ventrolateral plate |
| ac | anterior corner of PNu |
| al | anterolateral corner of Nu |
| ar3d | external articular area of Cd1 |
| ar2v | internal articular area of Cv1 |
| ar3v | external articular area of Cv1 |
| art.d | dorsal articular area |
| art.v | ventral articular area |
| a.un | unornamented area beneath fossa articularis pectoralis |
| Cd1-5 | dorsal central plates 1-5 of pectoral fin |
| Cv1-5 | ventral central plates 1-5 of pectoral fin |
| c4 | corner between middle and posterior divisions of mesial margin of ventral lamina of AVL |
| c5 | posteroventral corner of AVL |
| c.al | anterolateral corner of subcephalic division of ventral lamina of AVL |
| c.am | anteromesial corner on anterior margin of ventral lamina of AVL |
| c.Cv2 | margin in contact with Cv2 plate |
| c.Ml2 | margin in contact with Ml2 plate |
| c.Mm1,2 | margin in contact with Mm1 or Mm2 plates |
| c.rc | rostro-caudal canal |
| cf.ADL | area overlapping ADL |
| cf.PVL | area overlapping PVL |
| cit | crista transversalis interna anterior |
| cit 1,2 | anterior and posterior divisions of cit |
| cl | anterolateral corner of PNu |
| co.v | ventral thickening of brachial condyle |
| cr.dm | dorsomesial ridge of pectoral fin |
| cr.tv | transverse nuchal crista of head |
| dc | dorsal corner of lateral lamina of AVL and PVL |
| d.end | opening of canal for endolymphatic duct |
| dlr | dorsolateral ridge of trunk-armour |
| f.ax | foramen axillare of AVL |
| fm | unpaired insertion fossae on head-shield for levator muscles |
| fp | funnel pit of processus brachialis |
| gr | groove |
| grm | ventral median groove on dorsal wall of trunk armour |
| ifc | infraorbital sensory line on head-shield |

| | |
|---|---|
| L | lateral plate |
| lcg | main lateral line sensory groove |
| Ml2-5 | lateral marginal plates 2-5 of pectoral fin |
| Mm1 | mesial marginal plate 1 |
| Mm2 | mesial marginal plate 2 |
| MV | median ventral plate |
| MxL | mixilateral plate |
| m1-3 | anterior, middle and posterior divisions of mesial margin of AVL plate |
| mc | lateral corner of Nu |
| mp | middle pit-line groove |
| Nu | nuchal plate |
| nm | obtected nuchal area of headshield |
| nPP | postpineal notch of Nu |
| nprl | prelateral notch of head-shield |
| oa.ADL | area overlapped by ADL |
| oa.AVL | area overlapped by AVL |
| om | orbital margin |
| orb | orbit |
| PM | postmarginal plate |
| PMD | posterior median dorsal plate |
| PNu | paranuchal plate |
| PP | postpineal plate |
| PrL | prelateral plate |
| PrM | premedian plate |
| PVL | posterior ventrolateral plate |
| pbr | processus brachialis |
| pc | posterolateral corner of Nu |
| prc | prepectoral corner |
| pr.dep | preorbital depression |
| prdm | dorsomesial process |
| pt1 | anterior ventral pit of dorsal wall of trunk armour |
| ptoc | postobstantic corner |
| r.dm | dorsomesial ridge on Cv1 |
| r.sg | ridge along inner edge of sensory groove |
| ri | ridge |
| Sm | semilunar plate |
| sap | lateral subanal process of PVL plate |
| sg | sensory groove |
| soa | subobstantic area |
| soc | anterior section of supraorbital sensory line on PrM |
| sop | supraoccipital pit of head-shield |
| T | terminal plate |