

## Devonian fish remains from Billiluna, eastern Canning Basin, Western Australia

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Fragmentary remains of Devonian fishes are described from the Knobby Sandstone, a thick non-marine clastic formation in the eastern Canning Basin, which is a potential petroleum reservoir in subsurface fault-bounded sequences overlain by marine carbonates. The fauna includes a new species of the antiarch *Bothriolepis*, a few dermal plates of an asterolepidoid antiarch, various coarsely ornamented placoderm fragments probably belonging to a much larger antiarch, and some isolated rhipidistian teeth and scales. The

fragmentary preservation suggests a high-energy depositional environment. Associated are plant remains, including *Leptophloeum australe* (M'Coy). All fossils are preserved as moulds in a coarse sandstone. The fauna is probably Late Devonian (Famennian) in age, but better material is required for detailed correlation with other Late Devonian vertebrate assemblages in the Canning Basin and elsewhere.

### Introduction

The existence of Upper Devonian or Lower Carboniferous sediments of probable non-marine origin in the eastern part of the Canning Basin was first noted by Casey & Wells (1964), who collected lycopod remains (*Leptophloeum australe*) from sandstone in the Knobby Hills, about 20 km northeast of Billiluna Homestead. Fish plates were reported by Veevers & others (1967) from the same unit (referred to by them as the Knobby Sandstone) and from rocks of similar lithology in the nearby Falconer Hills, which had previously been mapped as Grant Formation of Permian age. During 1972, further fish and plant remains were collected by the author, A.T. Wells, A.N. Yeates, and V.L. Passmore (Bureau of Mineral Resources), and geologists from Mines Administration Ltd, from the Knobby and Falconer Hills and other isolated outcrops in the vicinity (Fig. 1).

The fish-bearing Knobby Sandstone (Yeates & others, 1975) occurs on the surface as isolated outcrops over an area about 50 km long and 25 km wide (Fig. 1), but its relation to older rocks is not exposed. The nearest older strata are the Ordovician Carranya Beds, which have been mapped about 25 km to the northwest of the Knobby Hills and 50 km to the southeast. Blake & others (1977) noted seismic data indicating Knobby Sandstone equivalents in the subsurface, apparently underlain unconformably by younger Ordovician to Devonian sediments. More recent seismic and drillhole information over the Billiluna Shelf indicates that the Knobby Sandstone is underlain disconformably by carbonates of early Late Devonian age, which are probable equivalents of the Pillara or Sadler Limestones farther to the west (Botten, 1984; Smith, 1984).

Because of the nature of the outcrop (variable subhorizontal dips in sandstone outliers), field mapping gave little idea of the thickness of the Knobby Sandstone. An early drillhole indicated a thickness of at least 162 m in the Falconer Hills (Blake & others, 1977). More recent drilling increased this to at least 300 m in the Billiluna area (Botten, 1984), and seismic data across the Billiluna Shelf and Balgo Terrace suggest much greater thicknesses, in excess of 1 km (e.g. Jacobson, 1984; Purcell & Poll, 1984).

The most common lithology in surface exposures of the Knobby Sandstone is medium to coarse-grained sandstone with abundant shale clasts. There are minor red siltstone and conglomeratic interbeds at some levels. The sandstones are commonly cross-bedded, and point bars up to 15 m wide are abundant (Botten, 1984) together with extensive distributional channel-fill systems. Botten (1984) interpreted the depositional environment as a major progradational delta sequence of Mississippi type, with dominant flow towards

the southwest, and various sedimentary features indicating a reasonable water depth. Derivation of the Knobby Sandstone from the eastern edge of the basin is consistent with the notion that this was an active fault-bound margin during the Late Devonian (Smith, 1984). The fish remains from the Knobby Sandstone studied by the author, although mainly small fragments, came from individuals of moderate to large size, suggesting permanent bodies of water.

Other sandstones of similar lithology occur in the region, but are probably of younger (Early Carboniferous) age. The sandstone at Red Bluffs reported by Veevers & others (1967) to contain *Leptophloeum australe* was also examined by the author, but appears to be devoid of vertebrate remains, although plant material (including *Leptophloeum*) is quite abundant. Veevers & Wells (1961, p.56) noted the occurrence of *Leptophloeum* in a sandstone outlier about 80 km to the south, near Balgo Mission, but more recent mapping in this region failed to produce further fossil material (A.N. Yeates, BMR, personal communication).

The Knobby Sandstone has some economic potential. It has been investigated as part of a geological mapping and drilling program for possible uranium mineralisation, although results of this study indicate low potential for economic accumulations of this mineral (Botten, 1984). Thick sequences of Knobby Sandstone overlain by shallow-marine carbonates have been identified in fault-bounded blocks on the Balgo Terrace by seismic exploration. The Knobby Sandstone shows fair to good reservoir characteristics, and is a main objective for petroleum exploration in the region (Jacobson, 1984).

The vertebrate remains from the Knobby Sandstone dealt with here were all collected from its surface exposures in the Knobby Hills and Falconer Hills areas. Other isolated outcrops about 20 km to the northeast near Overlander Waterhole were not visited. The specimens are generally poorly preserved as moulds in the coarse sandstone, but with better material the fishes could have potential for biostratigraphic studies. Most of the samples available for study are indeterminate fragments of dermal bone, but it is evident from the coarseness of the ornament that they came from fairly large bones belonging to several placoderm taxa. The fragmentary condition of what would have been fairly thick and robust bones indicates a high-energy depositional environment for this part of the Knobby Sandstone. The presence of rhipidistian (crossopterygian) fishes in the fauna is indicated by three moulds of isolated lanian teeth, and five other specimens are referred to the antiarchs, a group of placoderm fishes widespread in Middle and Late Devonian continental deposits, and therefore of some biostratigraphic interest. Two of these are described as a new species of the cosmopolitan genus *Bothriolepis*, and the other three belong to an asterolepid antiarch, although its generic assignment is uncertain.

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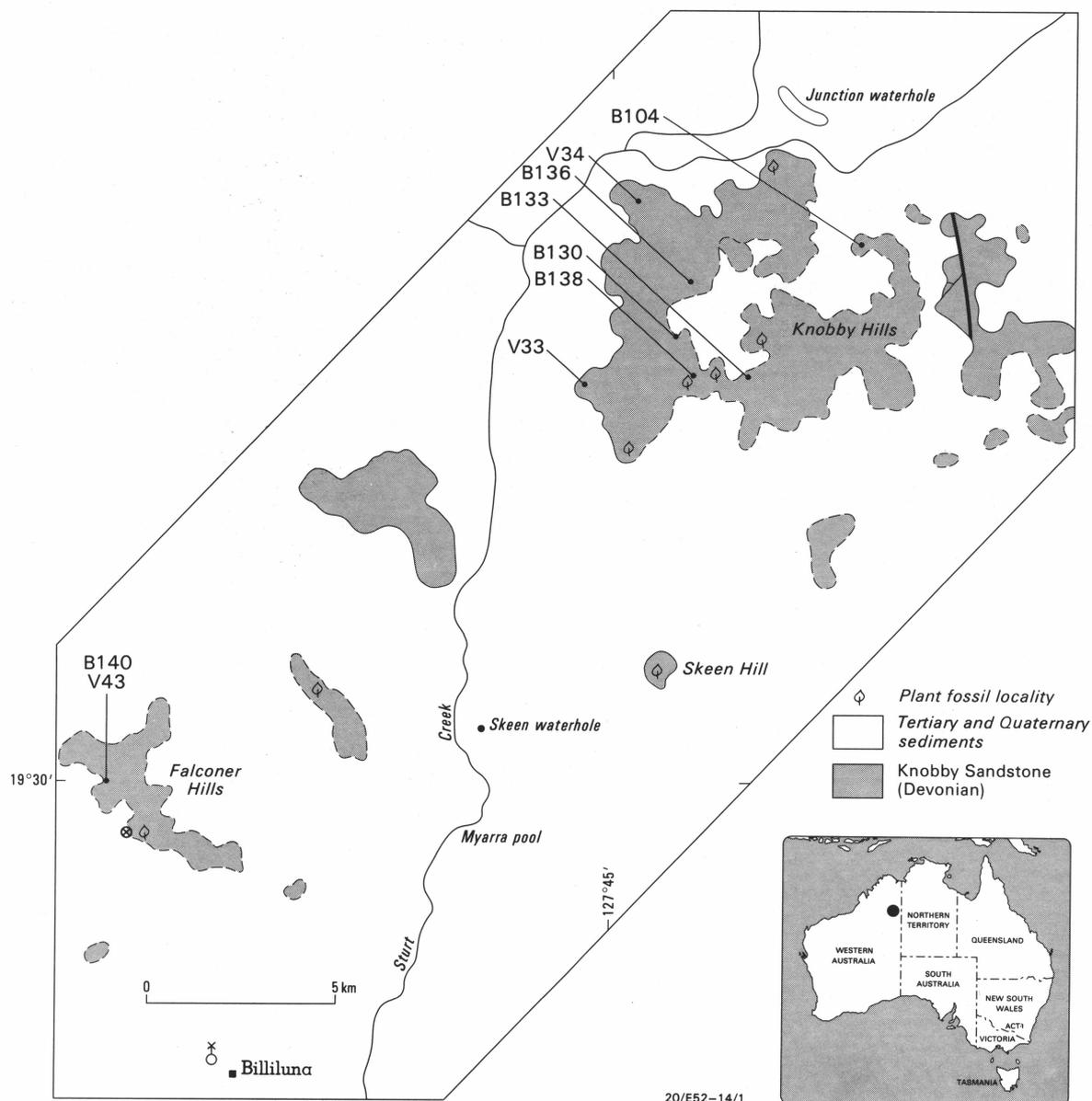


Figure 1. Geology of the Knobby Hills–Falconer Hills area (Billiluna 1:250 000 Geological Sheet), showing fossil localities for material described in this paper.

In Australia, *Bothriolepis* has been reported from many localities in Victoria, New South Wales, central, and northwestern Australia (Gilbert-Tomlinson, 1968; Gardiner & Miles, 1975; Long, 1983; Young, 1985), and is the most widely known of Australian Devonian fishes, although only a few species have been formally described (Hills, 1929; Young & Gorter, 1981; Long, 1983). Asterolepid antiarchs are apparently somewhat less common. The Upper Devonian form *Remigolepis* occurs at several localities in New South Wales (e.g. Young, 1974; Campbell & Bell, 1977), and other forms from central and southeastern Australia have been described by Young & Gorter (1981) and Young (1983, 1984a).

### Age of the fauna

This is a small and poorly preserved fauna, and both the placoderms and crossopterygians are at present too incompletely known to be of much biostratigraphic use. The stratigraphic range of antiarchs in the Middle and Late Devonian was reviewed by Young (1974); more recent contributions have been made by Young & Gorter (1981) and

Long (1983). The earliest species of *Bothriolepis* (known from China and Australia) may be as old as Eifelian, although most of the occurrences in southeastern and central Australia are probably Late Devonian in age (Long, 1983; Young, 1985). *Bothriolepis* from the Gogo Formation in the Canning Basin is dated by a variety of invertebrate fossils, including conodonts, as early Frasnian (e.g. Gardiner & Miles, 1975). The asterolepidoid antiarch *Remigolepis* occurs in probable Famennian strata (the Worange Point Formation) on the south coast of New South Wales, where it characterises the highest vertebrate faunal zone in the sequence (Fergusson & others, 1979; Young, 1983), and a species of *Asterolepis* (*A. sinensis*) defines the highest (late Famennian) vertebrate zone in China (Pan, 1981). The presence of an asterolepidoid antiarch in the Knobby Sandstone is therefore consistent with a Late Devonian (Famennian) age, although the fragmentary nature of the material, and the fact that this is the first record of this group from the Canning Basin, means this evidence must be regarded as provisional.

Other evidence on the age of the Knobby Sandstone fishes

comes from the associated plants, palynology, and fossiliferous carbonates above and below the formation inferred from seismic and drillhole data. The lycopod plant *Leptophloeum australe* (M'Coy) is generally considered to have a Late Devonian/Early Carboniferous range, but may be as old as Late Emsian in eastern Australia (e.g. Gould, 1975, p. 455). The *Leptophloeum*-bearing beds at Red Bluffs, about 150 km to the northwest, overlie late Famennian limestones (Veevers & others, 1967) and are probably Early Carboniferous. *Leptophloeum* also occasionally occurs in the marine Gumhole Formation of the Fairfield Group (Druce & Radke, 1979, p. 38, fig. 8C), which is dated as late Famennian, but similar remains have not been found in younger or older limestones in the region (E.C. Druce, personal communication). This suggests that in this region *Leptophloeum* may have been more abundant during the Famennian-Tournaisian, but of course was not necessarily restricted stratigraphically to this interval. Botten (1984) also records *Leptophloeum* in sandstones of presumed late Famennian age in the Van Emmerick Range on the Lennard Shelf. However, an Early Carboniferous age for the Knobby Sandstone fish fauna can be discounted on the presence of placoderms, since there are no confirmed reports of this group extending into the Carboniferous (e.g. Young, 1974; Westoll, 1979; Pan, 1981). This is consistent with seismic evidence that Knobby Sandstone equivalents in the subsurface are overlain by carbonates of the Tournaisian Laurel Formation (Jacobson, 1984; Botten, 1984). Botten also cites palynological evidence from the Knobby Sandstone for a late Famennian age, but details of horizon and locality are not given. It is assumed here that the palynological data and the fish and plant remains collected in surface outcrops refer to the upper 300 m of section, relative to the much thicker sequences of Knobby Sandstone identified by seismic methods (e.g. Jacobson, 1984).

More detailed comparisons with other fish faunas known from elsewhere in the Canning Basin are of limited value because of the fragmentary nature of this material, but some general points can be made. Fishes are fairly well represented at various levels within the Late Devonian–Early Carboniferous sequence in the Canning Basin, but apart from the diverse fauna of the Gogo Formation (Miles, 1971, 1977; Gardiner & Miles, 1975; Dennis & Miles, 1979–1982; Young, 1984b) they are very poorly known. As noted above, a species of *Bothriolepis* also occurs in the early Frasnian Gogo fauna, but the *Bothriolepis* material described below clearly represents a different species. Fish remains are also known from the Late Famennian Gumhole Formation at Red Bluffs (locality WCB 014; see Druce & Radke, 1979, p.15). These consist mainly of large coarsely ornamented bones of a brachytracoid arthrodire reminiscent of the genus *Aspidichthys*, which is known from the Frasnian and Famennian of North America, Europe, and the Middle East (Denison, 1978). Also present are a few fragments of lungfish toothplates, but apparently no antiarchs. This faunal difference could be attributed to the different environments of deposition of the two formations. A few fish remains from another locality in the Gumhole Formation (WCB 005, near Oscar Hill) again have dipnoan tooth fragments and also a small piece with possible antiarch ornament. From the lower part of the overlying Yellow Drum Sandstone at the same locality are fragmentary antiarchs and acanthodian and dipnoan remains. A microfauna from the Yellow Drum Sandstone includes elasmobranch remains (J. A. Long, personal communication). According to Druce & Radke's (1979) stratigraphy, the Yellow Drum Sandstone crosses the Devonian–Carboniferous boundary. The fish fauna from the overlying Laurel Formation is of typical Early Carboniferous aspect, dominated by elasmobranchs (Thomas, 1957, fig. 1;

1959, fig. 4; Druce & Radke, 1979, p.29). Thus, on the limited evidence available, the Knobby Sandstone fauna may be compared with the Gumhole Formation–lower Yellow Drum Sandstone interval, which contains the only other antiarchs of Famennian age so far known from the Canning Basin.

The only positively identified form in the Knobby Sandstone fauna is a new species of the antiarch *Bothriolepis*. Elsewhere in the world, *Bothriolepis* is widely distributed in Famennian strata in Europe (e.g. Denison, 1978), but in the uppermost vertebrate succession in East Greenland its highest occurrence is *B. nielseni* in the lower part of the *Remigolepis* Series (e.g. Jarvik, 1961). The higher assemblages in this sequence (the upper *Remigolepis*, and the *Groenlandaspis* Series) may broadly correlate with the uppermost vertebrate-bearing strata on the New South Wales south coast where *Remigolepis* and *Groenlandaspis* are associated. According to Pan (1981), *Bothriolepis* also extends to the top of the Late Devonian vertebrate succession in China. However, according to Sandberg & others (1983), in the western United States *Bothriolepis* does not extend above the *Polygnathus styriacus* Zone in the late Famennian, which is older than either the Gumhole Formation or Yellow Drum Sandstone in the Canning Basin (P.J. Jones, personal communication). Relevant here is a new fauna from Turkey recently described by Janvier & others (1984), which contains a mixture of latest Devonian and earliest Carboniferous fishes and ostracods, and is dated as post-Famennian (Strunian, Tn 1a) in age, but also lacks antiarchs. The only placoderm in this fauna is *Groenlandaspis*, and the presence of typical Carboniferous osteichthyans and chondrichthyans have led Janvier & others (1984) to suggest that their new fauna may represent a level between the uppermost faunas of East Greenland, and the Early Carboniferous faunas of Glencartholm in Scotland and Bear Gulch in Montana. One of the Devonian elements in this fauna is a new species of lungfish tentatively referred to by Janvier & others (1984) to *Chirodipterus*. This genus is represented by two older species from the Frasnian Gogo Formation in the Canning Basin (Miles, 1977). However, the illustrated toothplates from Turkey differ in various respects from the corresponding elements in the Gogo species. A preliminary examination of the fragmentary dipnoan toothplates from the Gumhole Formation, mentioned above, showed strong development of columnar dentine, and an extensive pulp cavity between the dentine of the toothplates and the underlying bone (K.S.W. Campbell, personal communication). These are relatively advanced features, not seen in *Chirodipterus* from Gogo, but present, for example, in the Carboniferous form *Sagenodus* (e.g. Smith, 1979). Such differences may prove of biostratigraphic use when this group is investigated in more detail.

This discussion may be summarised as follows. Various lines of evidence noted above point to a Famennian age for the Knobby Sandstone fish fauna. The presence of a *Bothriolepis* species might indicate an older age than the upper vertebrate assemblages in East Greenland or the upper *Polygnathus styriacus* conodont Zone in the western United States. Alternatively, the asterolepid antiarch in the fish fauna permits a tentative correlation either with the *Remigolepis* series in East Greenland, or the zone of *Asterolepis sinensis* in China. Fragmentary fish from the Gumhole Formation and lower Yellow Drum Sandstone apparently include antiarchs, and, apart from the Frasnian Gogo Formation, this is the only other occurrence of the group known so far from the Canning Basin. Facies differences may account for other differences in the fish faunas. A *Groenlandaspis* fauna, which elsewhere apparently represents the youngest known Devonian vertebrate assemblage, has not yet been identified from Western Australia.

### Systematic descriptions

All fossils described below are housed in the Commonwealth Palaeontological collection, Bureau of Mineral Resources, Canberra, A.C.T. The classification adopted is that used in Young & Gorter (1981) and antiarch bone terminology follows Stensiö (1948) and Miles (1968).

#### Subclass Placodermi

#### Order Antiarcha

#### Suborder Bothriolepidoidei, Miles, 1968

#### Family Bothriolepididae Cope

#### Genus *Bothriolepis* Eichwald

#### *Bothriolepis billilunensis* sp. nov.

(Fig. 2; Pl. 1, figs 1-3)

1974 *Bothriolepis* Young, pp. 252, 254

1975 *Bothriolepis* Yeates & others, p. 50

1977 *Bothriolepis* Blake & others, p. 19

1983 *Bothriolepis* Towner & Gibson, p. 26

**Material.** A detached, incomplete left mixilateral plate (CPC13853) preserved as an internal and external mould, and a detached incomplete right posterior ventrolateral plate (CPC13854) preserved as an external mould.

**Holotype.** CPC13853, a left mixilateral plate.

**Occurrence.** Locality B130 in the Knobby Sandstone, Knobby Hills, eastern Canning Basin, Western Australia (see Fig. 1).

**Diagnosis.** A *Bothriolepis* with a mixilateral plate only slightly less broad than long, the dorsal lamina about 1.3 times as long as broad and the lateral lamina twice as long as deep. Dorsal and lateral laminae enclosing an angle of about  $100^\circ$  at the dorsolateral ridge. The posterior ventrolateral plate with a length/breadth index of about 2, the lateral lamina about 2.8 times as long as deep and the ventral lamina about 3.7 times as long as broad. Subanal division of ventral lamina about 10 per cent of the total length of the plate. Angle between lateral and ventral laminae about  $130^\circ$ .

**Remarks.** The mixilateral and posterior ventrolateral plates in *Bothriolepis* are contiguous overlapping bones, but the ventral margin of the external cast in the holotype is not preserved, so there is no good morphological evidence that the two specimens are conspecific, although this is assumed for the purpose of description. Ornament is coarser on the posterior ventrolateral, which comes from a larger individual, but in other respects is similar to that of the holotype.

**Description.** The internal surface of the mixilateral plate is complete except for portions of the dorsal and posteroventral

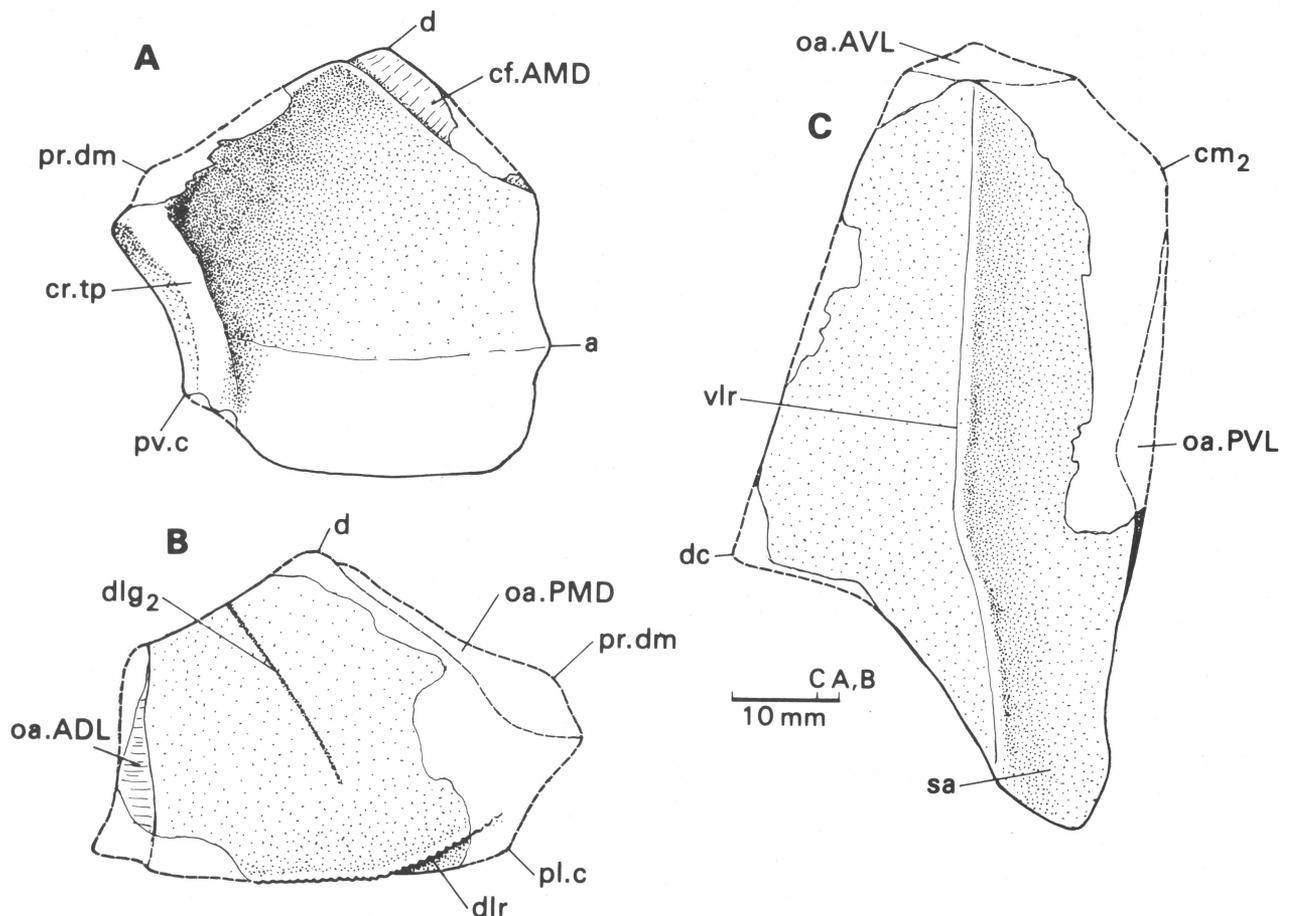


Figure 2. *Bothriolepis billilunensis* sp. nov.

A, left mixilateral plate in visceral view (holotype, CPC13853). B, reconstruction of the dorsal lamina of the left mixilateral plate in dorsolateral view (after CPC 13853). C, reconstruction of the right posterior ventrolateral plate in ventrolateral view (after CPC13854).

a, anterior corner of mixilateral;  $cm_2$ , anteromesial corner of ventral lamina of posterior ventrolateral; cf.AMD, area that overlapped anterior median dorsal plate; cr.tp, crista transversalis interna posterior; d, dorsal corner of mixilateral; dc, dorsal corner of lateral lamina of posterior ventrolateral;  $dlgs_2$ , posterior oblique abdominal pitline groove; dlr, dorsolateral ridge; oa.ADL, area overlapped by anterior dorsolateral plate; oa.AVL, area overlapped by anterior ventrolateral plate; oa.PMD, area overlapped by posterior median dorsal plate; oa.PVL, area overlapped by left posterior ventrolateral plate; plc, posterolateral corner of trunk armour; pr.dum, dorsomesial process of mixilateral; pv.c, posteroventral corner of mixilateral; sa, subanal division of ventral lamina of posterior ventrolateral; vlr, ventrolateral ridge.

margins and posteroventral corner (*pv.c.*, Fig. 2A). Of the external surface, the anterior two-thirds of the dorsal lamina and the dorsal part of the lateral lamina are preserved and show parts of the anterodorsal margin, the posterior oblique abdominal pit-line groove, and the dorsolateral ridge. As reconstructed, the plate is unusually short and broad with a total length of 39 mm and total breadth of 38 mm. The posterodorsal margin is 1.5 times as long as the anterodorsal, and the angle enclosed at the dorsal corner is about  $114^\circ$ . The anterior margin is 1.3 times as long as the posterior. The ornament is typical of *Bothriolepis*, with anastomosing ridges and occasional tubercles. A ventrolaterally directed keel is developed along the dorsolateral ridge. An unusual feature is the very short posterior margin.

The posterior ventrolateral plate is preserved as an impression of its external surface (Pl. 1, fig. 3). It is deficient along the anterior and anteromesial margins, and lacks the dorsal corner of the lateral lamina.

As preserved, it is 87 mm long, but the restored overlap area for the right anterior ventrolateral (*oa.AVL*, Fig. 2C) indicates an original length of about 95 mm. On the mesial edge of the ventral lamina the posterior end of the overlap area for the left posterior ventrolateral is preserved (*oa.PVL*). On the lateral lamina the dorsal corner was apparently abraded or broken off before embedding. Total breadth of the restored plate between the dorsal corner and the mesial margin of the ventral lamina is estimated at 45–50 mm.

The breadth of the incomplete ventral lamina can be estimated on the assumption that the lamina was broader at the anteromesial corner (*cm*<sub>2</sub>, Fig. 2C) than across the subanal division, as it is in other species of the genus. This gives a minimum breadth of about 200 mm. As restored in Figure 2C the ventral lamina has a breadth of 25 mm, giving a length/breadth index of 3.7. This is an unusually high value, but is considered reasonable in view of the constant narrow width of the posterior portion of the lamina, where the mesial margin is almost parallel to the ventrolateral ridge. In most other species of *Bothriolepis* the subanal division differs in being more or less triangular in shape, with the lamina itself correspondingly more or less broad behind the middle mesial corner.

The preserved length of the lateral lamina is 77 mm, and is estimated to have been about 83 mm originally. The subanal division of the ventral lamina is very short, comprising just over 10 per cent of the total length of the plate. The height of the lateral lamina as restored at about 30 mm, giving a length/height index of 2.8. The margins and overlap areas of the plate as far as preserved appear normally developed. There is no indication of a posterodorsal corner, and the plate was overlapped mesially by the left posterior ventrolateral, as is normal for *Bothriolepis*.

The ventrolateral ridge is distinct, but there is only slight development of a keel. Ornament is similar to, but slightly coarser than that of the mixilateral plate.

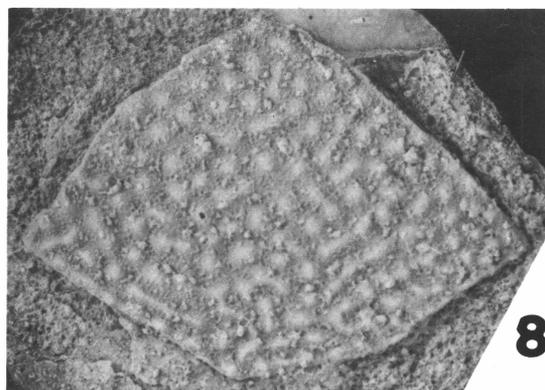
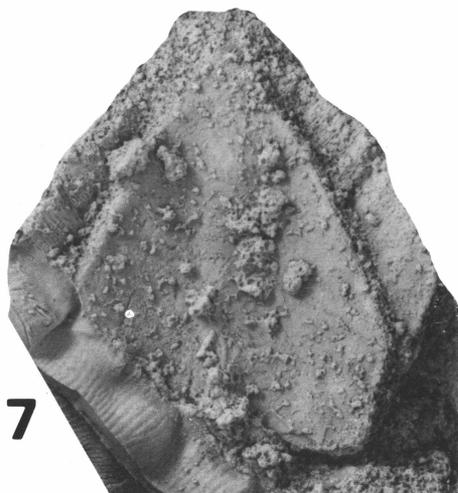
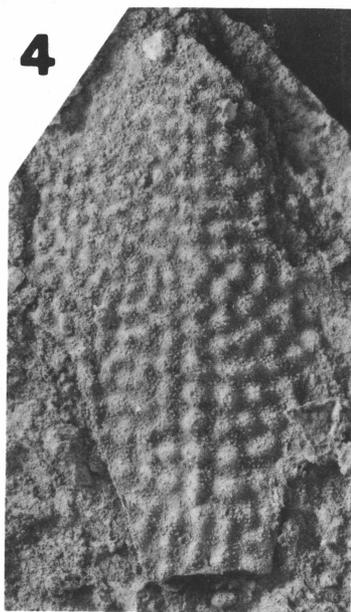
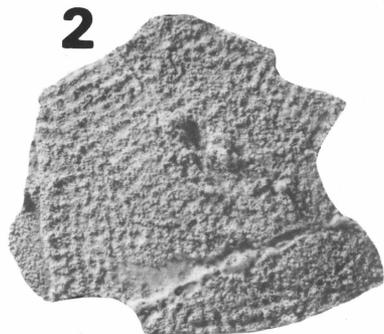
**Discussion.** The features of the mixilateral plate show that this material is referable to *Bothriolepis*. The mixilateral is represented by separate posterior dorsolateral and posterior lateral plates in *Remigolepis*, *Byssacanthus*, *Gerdalepis*, *Stegolepis*, *Pambulaspis*, and *Yunnanolepis*, and in the asterolepidoids *Asterolepis*, *Pterichthyodes*, and *Sherbonaspis* the so-called mixilateral is differently developed, with an external anteroventral overlap area for the anterior ventrolateral. Janvier & Pan (1982) have suggested that this plate is not homologous to the mixilateral of bothriolepids. *Bothriolepis* is the only member of this group so far recorded

in Australia, and there is every reason to believe, therefore, that the specimens described here belong to a species of this genus.

In its proportions the mixilateral of *B. billilunensis* sp. nov. is quite distinctive, with a broad dorsal and unusually deep lateral lamina, combined with the acute angle enclosed at the dorsolateral ridge. The plate may be compared with that of *B. canadensis* and *B. cellulosa*, in which, however, the length/breadth indices are always greater than 1.5 and 2.25 for the dorsal and lateral laminae respectively (Gross, 1941b; Stensiö, 1948). *B. laverocklochensis* is also similar in the proportion of the dorsal lamina and the acute angle between laminae, but differs in having a long, low lateral lamina, and apparently lacking a distinct dorsolateral ridge (Miles, 1968, p. 53; pl. 5, fig. 5). *B. cristata* may be distinguished by the more obtuse angle between laminae (Miles, 1968, p. 57).

Of species recently described from Australia, the mixilateral of *B. verrucosa* is much more elongate in both dorsal and lateral laminae (Young & Gorter, 1981). Species recently described from Victoria (Long, 1983) include *B. bindareei*, which has a mixilateral broader than long, and *B. warreni*, which is said to have a breadth/length index for the dorsal lamina of 36. Material from the Amadeus Basin in central Australia described by Gilbert-Tomlinson (1968) did not include a mixilateral, but new material from here shows that at least two species are represented (Young, 1985). Mixilateral plates in this collection can be distinguished on various characters from the specimen described here. The left mixilateral figured by Young (1985, fig. 8A) has a more obtuse angle between laminae, a lower dorsal and deeper lateral lamina, and a less-marked dorsolateral ridge. Other plates, with the dorsolateral ridge similarly developed to *B. billilunensis* sp. nov., are readily distinguished as a separate species by their more elongate overall proportions. Unnamed species are probably represented by an isolated mixilateral from Mount Canoblas, New South Wales figured by Hills (1932, pl. 6, fig. 8), but this is much more elongate, with a dorsal lamina about twice as long as broad, and a lateral lamina twice as long as deep. Finally, undescribed mixilateral plates of a *Bothriolepis* species from the Gogo Formation in the Canning Basin of Western Australia have finer ornamentation, no dorsolateral keel, and a more obtuse angle of about  $125^\circ$  between the laminae (personal observation on BMR material).

The referred posterior ventrolateral plate is also readily distinguished from other *Bothriolepis* species by the unusually short subanal division of its ventral lamina. The subanal division in other species is generally at least one third as long as the total length of the plate, and only in *B. wilsoni* does its relative length decrease to 20 per cent (Miles, 1968, pp. 85, 88), but this is still proportionately longer than in *B. billilunensis* sp. nov. The other characteristic feature of the plate is the high length/breadth index of the ventral lamina. The Canadian antiarch *Bothriolepis ? traquairi* Bryant is comparable in this regard (Stensiö, 1948, p. 398), but is readily distinguished by the more uniform width of the subanal division, and the posterior concavity in the ventrolateral ridge. The Chinese species *B. kwangtungensis* from the Mangzixia Series of northern Kwangtung as described by P'an (1964) probably also had a long and narrow ventral wall of the trunk armour although the posterior ventrolateral is unknown. The anterior ventrolateral in this species varies from 3.4 to 4 times as long as broad, a value not attained by any other species. In other species the ventral laminae of both anterior and posterior ventrolaterals have similar proportions, but with the length/breadth index for the latter plate increased somewhat by the subanal division. It is probable therefore that the posterior ventrolateral of *B. kwangtungensis* had



similar proportions to the corresponding plate of *B. billilunensis* sp. nov.

Considering Australian species, the description given by Hills (1931, p. 221) of the posterior ventrolateral of *B. gippslandiensis* suggests an unusual 'square cut and not rounded' configuration of the posterior margin. However, according to Long (1983), the posterior ventrolateral in this and other Victorian species is typically developed for the genus, with normal proportions. Another incomplete posterior ventrolateral from the Dulcie Range, Northern Territory, was briefly described by Hills (1959). It bears little similarity to the specimen described above, with lateral and ventral laminae meeting at about 100°, and a conspicuous keel of fused tubercles along the ventrolateral ridge. Posterior ventrolateral plates have also been figured from the Amadeus Basin by Young (1985), but again are readily distinguished in shape and proportions from *B. billilunensis* sp. nov.

Comparisons with some other species of *Bothriolepis* in the proportions of both plates considered together are summarised in Table 1. The length/breadth index for the ventral lamina of the posterior ventrolateral varies between 2 and 3, whilst the length/breadth index for the dorsal lamina of the mixilateral is generally lower, ranging between 1.4 and 2. Two exceptions are *B. jarviki* (Stensiö, 1948) and *B. alvesiensis* (Miles, 1968), in which both indices have about the same value. This would suggest that *B. billilunensis* sp. nov. as described above is unusual in combining a very elongate ventral lamina with a short broad dorsal lamina. In the lateral wall of the trunk armour, length/breadth indices

**Table 1. Approximate length/breadth values for laminae of the mixilateral and posterior ventrolateral plates in some *Bothriolepis* species.**

<i>Bothriolepis</i> species	Mixilateral plate		Posterior ventrolateral plate	
	dorsal lamina	lateral lamina	lateral lamina	ventral lamina
<i>gigantea</i>	—	4	1.5	2
<i>alvesiensis</i>	2	4	3	2
<i>cristata</i>	1.4-2	2	3	2.5
<i>leptocheira</i>	2	3	3	2.8
<i>obesa</i>	1.5	2.5	1.3	2
<i>wilsoni</i>	2	2.5	2.5	2.5
<i>hayi</i>	2	3	1.5-1.7	2.5
<i>canadensis</i>	1.5-2	2.25-2.33	2-2.5	2-2.3
<i>cellulosa</i>	1.5-2	2.5-3	2.5	2.5-2.75
<i>jarviki</i>	2	2	—	2
<i>tungseni</i>	1.7-1.8	2.5-2.7	2.4	2.8
<i>billilunensis</i>	1.3	2	2.8	3.7

Data from Stensiö (1948), Chang (1965), and Miles (1968).

are about the same for the lateral laminae of both plates in several species, including *B. leptocheira* and *B. wilsoni* (Miles, 1968), *B. cellulosa* and *B. canadensis* (Stensiö, 1948) and *B. tungseni* (Chang, 1965). The mixilateral lamina is proportionately much longer than that of the posterior ventrolateral in *B. alvesiensis*, *B. hayi*, *B. gigantea* and *B. obesa* (Stensiö, 1948), and is proportionately shorter only in *B. cristata* (Miles, 1968) and *B. billilunensis* sp. nov. (Table 1). In two respects, therefore, the trunk armour of this new species is unusual: it resembles *B. cristata* in the anomalous proportions of the lateral wall, and shows a difference in

indices for the dorsal and ventral walls comparable to that in lateral lamina proportions in *B. gigantea*, which is also much greater than in other known species (Table 1). However, the inferred trunk armour proportions in *B. billilunensis* sp. nov., although unusual, are not considered to lie outside the expected range of variation for species of the genus, and, for this reason, both plates are provisionally treated here as one species.

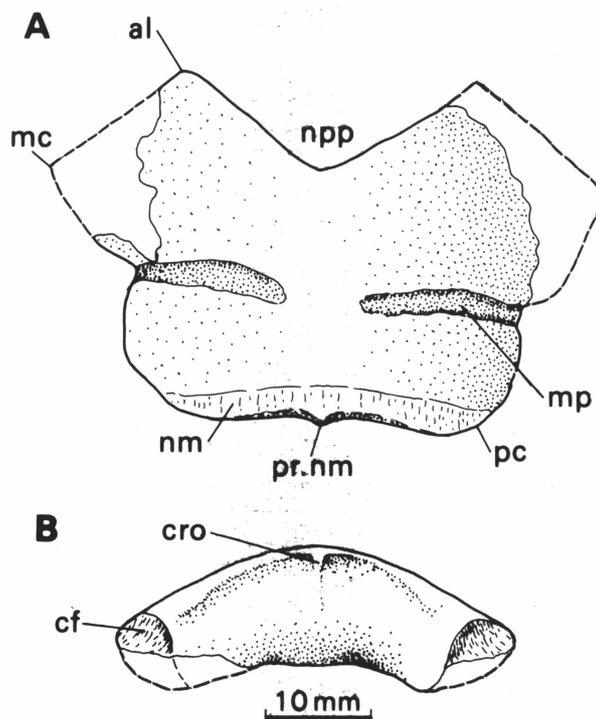
**Suborder Asterolepidoidei Miles, 1968**

asterolepidoid indet.

(Figs 3, 4; Pl. 1, figs 5-7)

- 1967 'fish plates' (*pars*) Veevers & others, p. 331
- 1968 'arthrodian plates' (*pars*) Gilbert-Tomlinson, p. 210
- 1974 *Asterolepis* Young, p. 252
- 1975 *Asterolepis* Yeates & others, p. 50
- 1977 *Asterolepis* ? Blake & others, p. 19
- 1978 *Asterolepis* sp. Denison, p. 113
- 1983 *Asterolepis* or *Remigolepis* Young, p. 71
- 1983 *Asterolepis* Towner & Gibson, p. 26

**Material.** A detached incomplete nuchal plate (CPC13855) preserved as an external mould, and two detached incomplete anterior median dorsal plates (CPC 13856, 13857), both preserved as internal impressions of parts of their anterior divisions.



**Figure 3. Asterolepidoid indet.**

Reconstruction of the nuchal plate in dorsal (A) and posterior views (B). After CPC13855.

al, anterolateral corner; cf, contact face for paranuchal plate; cro, median occipital crista; mc, lateral corner; nm, obtect nuchal area; npp, postpineal notch; pc, posterolateral corner; pr.nm, posterior median process, mp, middle pitline sensory groove.

**Plate 1. *Bothriolepis billilunensis* sp. nov.**

**Figs. 1, 2.** Holotype (CPC13853), an incomplete left mixilateral plate in visceral and lateral views respectively (x1.5). **Fig. 3.** Incomplete right posterior ventrolateral plate (CPC13854) in external view (x1.5).

**asterolepidoid indet.**

**Fig. 5.** Incomplete nuchal plate (CPC13855) in dorsal view (x2). **Figs. 6, 7.** Incomplete anterior median dorsal plates (CPC13856, 13857) in visceral view (both x1.5).

**antiarch indet.**

**Fig. 4.** Undetermined plate (CPC13939) in external view (x1.5). **Fig. 8.** Undetermined plate (CPC13940) in external view (x1.5).

(all photographs of latex rubber casts whitened with ammonium chloride).

**Occurrence.** Localities V33 (CPC13856) and V34 (CPC13857) in the Knobby Hills, and locality V43 (CPC13855) in the Falconer Hills, in the Knobby Sandstone, eastern Canning Basin, Western Australia (see Fig. 1).

**Remarks.** The three specimens included here are clearly asterolepidoids and are described together on the assumption that they are conspecific.

**Description.** The nuchal plate is preserved as an impression of its dorsal and posterior surfaces (Pl. 1, fig. 5). It shows the posterior margin and posterolateral corners (*pc*, Fig. 3), left anterolateral corner (*al*), most of the postpineal notch (*npp*), and well-developed transverse sensory grooves (*mp*). The lateral margin is only preserved posterior to the sensory grooves and on the left side for a short distance anterior to the groove, and the position of the lateral corners (*mc*, Fig. 3A) is, therefore, uncertain. The postpineal notch clearly lacked orbital facets, which shows that the postpineal plate excluded the nuchal plate from the orbital margin, as in non-bothriolepid antiarchs.

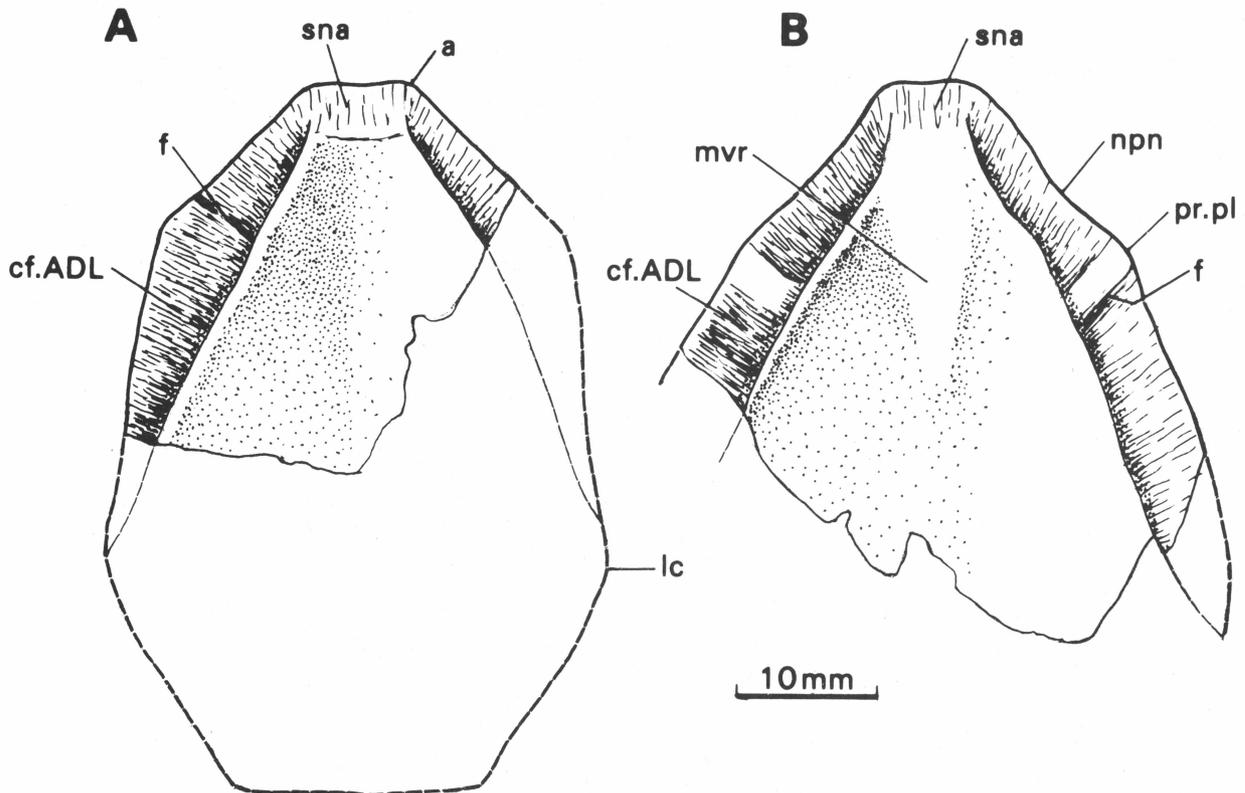
The plate has a total length of 30.5 mm, and a median length (excluding the postpineal notch) of 23.5 mm. Width at the posterior margin is 32.5 mm and, as restored in Figure 3A, the anterolateral corners are 25 mm apart. The breadth across the lateral corners was probably at least 40 mm.

The ornament consists of low irregular anastomosing ridges and occasional tubercles, with an unornamented strip, the obtected nuchal area (*nm*), extending along the posterior margin. This margin is slightly concave with a small posterior median process (*pr.nm*). Posterolateral processes are not developed.

Several features of the nuchal plate as developed in other antiarchs are absent. The external openings for the endolymphatic ducts are not preserved, and other sensory grooves or pit-lines are apparently not developed. Significant is the absence of a central sensory line, which is typically well developed on the nuchal plate in *Bothriolepis* and related genera.

In posterior view (Fig. 3B) the specimen exhibits a fairly deep occipital surface with a strongly developed transverse nuchal crista. The median occipital crista (*cro*) is present, but not pronounced, and there are no clearly defined fossae for the insertion of the levator muscles of the head, as are known in *Asterolepis ornata* (Stensiö, 1931, fig. 15). At each side a contact face is developed for the adjacent paranuchal plate (*cf*).

The anterior median dorsal plate is represented by two incomplete specimens showing part of the ventral surface of the anterior division (Pl. 1, figs. 6, 7). CPC13856 (Fig. 4A) shows most of the contact face that overlapped the right anterior dorsolateral (*cf. ADL*), and the anterior end of the contact face for the left plate. The anterior margin and supra-nuchal area (*sna*) are completely preserved. Total preserved midline length is 27.5 mm and the width between the anterolateral angles (*a*) is 6 mm. The plate is slightly arched to enclose an angle of about 150° at the midline. As restored in Figure 4A, the breadth between lateral corners (*lc*) is estimated at about 35 mm, giving a midline length for the anterior division of the plate of about 30 mm. The contact faces are deeply impressed into the visceral surface and reach a maximum width of about 6 mm approximately halfway between the anterior and lateral corners. Somewhat in front of this maximum width the contact face is crossed by a shallow groove (*f*).



**Figure 4.** Asterolepidoid indet.

Two anterior median dorsal plates in visceral view: **A**, CPC13856; **B**, CPC13857.

*a*, anterolateral angle; *cf.ADL*, area that overlapped anterior dorsolateral plate; *f*, groove crossing contact faces for anterior dorsolaterals; *lc*, lateral corner; *mvr*, median elevation on the visceral surface; *npp*, postnuchal notch; *pr.pl*, postlevator process; *sna*, supra-nuchal area.

CPC13857 (Fig. 4B) is a similar portion of another anterior median dorsal plate, with a preserved midline length of 36 mm. The anterior margin is more rounded than in the previous specimen and anterolateral angles are indistinct. It is also flatter anteriorly, with a slight broad elevation on the ventral surface in the midline (*mvr*). Again a groove (*f*) crosses the contact face for the anterior dorsolateral plate, in front of which the margins of the plate are slightly concave (*npn*). As in the previous specimen, the contact faces are deeply impressed into the visceral surface of the plate.

**Discussion.** The absence of orbital facets on the nuchal plate and the narrow anterior margin of the anterior median dorsal plate, are features found in only two antiarch groups—the yunnanolepids and the asterolepidoidei. Since members of the first group are not known to occur outside south China, and display a variety of primitive features not seen in other antiarchs, including an oblong nuchal plate (see Zhang, 1978), I assume that the specimens dealt with here belong to an asterolepidoidei antiarch. Within the Asterolepidoidei, the anterior margin of the anterior median dorsal plate is fairly broad and truncated in *Pambulaspis* (Young, 1983), *Pterichthyodes* (Hemmings, 1978), *Sherbonaspis* (Young & Gorter, 1981), *Gerdalepis* (Gross, 1941a), *Byssacanthus* (Gross, 1940, fig. 10B; Karatajute-Talimaa, 1960, fig. 2), and probably *Lepadolepis* (Gross, 1933, pl. 3), whilst in *Grossaspis* it is broad and somewhat rounded (Gross, 1937, fig. 10). Only in *Asterolepis* and *Remigolepis* is the anterior margin as narrow as in the material described above, but the three available specimens provide too few characters for confident assignment to either form. In addition to published accounts, I have made a preliminary examination of well-preserved *Remigolepis* collected by the Geology Department, Australian National University, from near Forbes, New South Wales (Campbell & Bell, 1977), and this has been used in the following discussion to supplement Stensiö's account with data on Australian species.

The main characters by which *Remigolepis* differs from *Asterolepis* are the absence of a distal joint in the pectoral appendage, the separate posterior dorsolateral and posterior lateral plates, and the overlap relationship between the anterior median dorsal and posterior dorsolateral. Species in both genera vary considerably in size, and the specimens from Billiluna suggest a moderately large form comparable with *Asterolepis scabra* (Nilsson, 1941) or *Remigolepis acuta* (Stensiö, 1931).

In both genera the nuchal plate and the anterior division of the anterior median dorsal are closely similar. In *Asterolepis* the breadth/length index of the nuchal ranges from 132 in

*A. savesoderberghi* (Stensiö & Säve-Söderbergh, 1938, fig. 1) to 210 in *A. scabra* (Nilsson, 1941, pl. VI). In *Remigolepis* it may also be low, as in *R. cristata* (130) and *R. acuta* (125) (Stensiö, 1931), whilst the *Remigolepis* sp. figured by Stensiö (1948), fig. 16) has an index of over 200. In CPC13855 the index was at least 130, placing it within the range of several species in both genera (Table 2).

Regarding the size and shape of the postpineal notch (*npp*, Fig. 3A), the Greenland species *R. cristata* and *R. kochi* have the midline length of the plate over five times the midline length of the notch, which is much more shallow and broad in relation to total length and breadth than is normal in *Asterolepis* (Table 2). Similar proportions occur in *Remigolepis* from New South Wales, although nuchal plates ascribed to *R. incisa* and *R. acuta* by Stensiö (1931, pl. 3, figs 2, 3) have somewhat deeper notches, and this feature may vary within a single species (e.g. Stensiö, 1931, figs 13B, G). In general, however, the notch tends to be broader and shallower in *Remigolepis*, and in this regard CPC 13855 shows closer affinity to *Asterolepis* in having a notch about 3.5 times as broad as deep.

In *Asterolepis* the notch normally extends back to a position near or behind the level of the lateral corners; in *A. maxima* (Traquair, 1894) and *A. sinensis* (P'an, 1964) it extends well behind this level. An exception is *A. estonica* (Gross, 1940, fig. 8) in which the lateral corners have a more posterior position. By comparison, the various nuchal plates described for *Remigolepis*, including the species recently described from China (Pan & others, 1980), and the undescribed material from New South Wales, always show the level of the lateral corners to lie well behind the postpineal notch. Furthermore, the posterolateral margin has a simpler configuration than the nuchal plate of *Asterolepis*, which always shows a constriction in its breadth behind the lateral processes. The nuchal plate from the Knobby Sandstone resembles that of *Asterolepis* in both these features.

Regarding the anterior median dorsal plate, CPC13856, as reconstructed above, has a median breadth about 1.2 times the length of the anterior division, which compares closely with many species of *Asterolepis* and *Remigolepis*. Only *A. orcadensis* (Watson, 1932), *R. kochi*, and *R. cristata* (Stensiö, 1931) are appreciably broader in proportion to length (Table 2). The relative length of the anterior margin varies intraspecifically in both *Asterolepis* (Gross, 1940, p.33; Karatajute-Talimaa, 1963, p. 159), and *Remigolepis* (Stensiö, 1931). One Greenland species, *R. acuta*, has been defined on the extreme narrowness of this margin, and a similar development is evident in *Remigolepis* material from Forbes,

**Table 2. Nuchal and anterior median dorsal plate measurements in different species of *Asterolepis* and *Remigolepis* compared with specimens described here.**

Species of <i>Asterolepis</i> or <i>Remigolepis</i>	Nuchal plate		Anterior median dorsal plate	
	Breadth/ length index	Total length/ length post- pineal notch	median breadth/ length anterior division	median breadth/ length anterior margin
<i>A. savesoderberghi</i>	132	2.9	1.14	2.6-4.3
<i>A. radiata</i>	150	3.4-4.4	1.2	9.4-16
<i>A. ornata</i>	159	3.3-4.6	1.2	4.3-8.2
<i>A. orcadensis</i>	188	2.7	1.55	3.4
<i>A. scabra</i>	210	3.1	1.25	6.8
<i>R. acuta</i>	125	4	1.14	24
<i>R. cristata</i>	130	5.5	1.36	3.5
<i>R. kochi</i>	175	5.7	1.45	4.3
CPC13855	> 130	3.5	—	—
CPC13856	—	—	1.2	4.9

Data from Stensiö (1931), Watson (1931), Gross (1931, 1940), Nilsson (1941), and Karatajute-Talimaa (1963).

New South Wales (M.W. Bell, personal communication). Stensiö (1948, footnote, p. 188) noted the tendency towards development of a postnuchal notch and external postlevator process in the anterior median dorsal of *Asterolepis scabra*, and similar structures have been figured for *A. ornata* and *A. estonica* (Gross, 1931, 1940; Karatajute-Talimaa, 1963, fig. 33). In *A. estonica* there is a distinct groove crossing the contact face for the anterior dorsolateral (Gross, 1940, p. 34; Karatajute-Talimaa, 1963, fig. 14), as described above. In CPC13857 this groove is associated with a distinct postlevator process (*pr. pl*) and slight postnuchal notch (*npn*, Fig. 4B). CPC13856 has a less pronounced groove situated in front of the maximum width of the contact face. In *Remigolepis*, however, these features are generally absent or only very slightly developed.

To summarise, in the configuration and structure of the anterolateral margins of the anterior median dorsal, the form of the postpineal notch, and the shape of the posterior part of the lateral margin of the nuchal, this material shows closer similarity to *Asterolepis* than to *Remigolepis*. However, these are only minor distinctions, and until further material becomes available the three specimens described here are left in open nomenclature.

*Asterolepis* has been reported from the Australian Devonian on two previous occasions. McCoy (1876) named placoderm plates from Buchan, Victoria as *Asterolepis ornata* var. *australis*, but these belong to an arthrodire (see Young, 1979, p. 347). Hills (1958, p. 89) referred to *Asterolepis* an antiarch posterior median dorsal plate previously figured by him (Hills, 1936, fig. 3; see also Hill & others, 1967, pl. DXV, fig. 1). The lateral margins in this specimen appear to be slightly convex, and Stensiö (1931, p. 77) suggested that in this feature *Asterolepis* could be distinguished from *Bothriolepis*, in which the margin is normally slightly concave. However, this distinction is not reliable (e.g. Miles, 1968) and Hills' original conclusion that 'generic determination of this specimen is not possible' (1936, p. 163) still applies, although there are no good reasons to indicate that the plate does not belong to a species of *Bothriolepis* (Young & Gorter, 1981, p. 90; Turner, 1982).

antiarch indet.

(Fig. 5; Pl. 1, figs. 4, 8; Pl. 2, figs. 1,2,9,10)

1967 'fish plates' (*pars*) Veevers & others, p. 331

1968 'arthrodiran plates' (*pars*) Gilbert-Tomlinson, p. 210

**Material.** An incomplete median dorsal plate (CPC13937), preserved as an internal mould; a large incomplete plate, (CPC13943), and various ornamented fragments (CPC13938-42), all preserved as external moulds.

**Occurrence.** Localities B104 (CPC13938), B130 (CPC13939, 41, 42), B133 (CPC13943), B138 (CPC13937, 940) in the Knobby Sandstone, Knobby Hills, eastern Canning Basin, Western Australia (see Fig. 1).

**Remarks.** The most common vertebrate fossils in the Knobby Sandstone are moulds of fragmentary plates with a coarse ornamentation of low rounded tubercles. These may be arranged in even rows (Pl. 1, fig. 4), or are widely spaced and irregular (Pl. 2, fig. 10), but in general show some degree

of fusion into an anastomosing arrangement of nodose ridges (Pl. 2, figs. 1, 9). Determination of such remains is difficult in the absence of plate margins or any preserved bone. Hills (1932, pl. 56, fig. 7) previously figured a similar coarsely ornamented fragment from Jemalong Gap near Forbes, New South Wales, which he subsequently compared (1936, p. 168) with the ornament of the holonematid arthrodire *Gyroplacosteus panderi* Obruchev (see Obruchev, 1932, pl. 6, fig. 3; 1964, pl. 2 fig. 3). However, I consider it much more likely that such remains belong to a large antiarch, and this is borne out by what is now known of the Jemalong Gap fauna (Ritchie, 1975), where the only arthrodire so far recorded (*Groenlandaspis* sp.) has a much finer pustulose ornament. On the other hand, some of the *Remigolepis* specimens from here attained a large size with coarsely ornamented dermal bones.

The Knobby Sandstone remains evidently came from an even larger fish, as indicated by one incomplete dermal plate, the largest in the collection (Pl. 2, fig. 2), with a maximum preserved dimension of 167 mm. Otherwise, the specimens are generally less than 40 mm across, and show no features other than ornament. Position in the skeleton can be positively determined for only one specimen, and there are no distinguishing features to show whether this large antiarch is a bothriolepidoid or asterolepidoid.

**Description.** The only specimen in this material identified with any reliability is an antiarch median dorsal plate exposed in visceral view (Fig. 5), showing the diagnostic median ridge (*mvr*) and pit (*pt*) on its inner surface. The external surface and ornament are not preserved, but the specimen is assumed to belong to the same form as the ornamented fragments.

None of the margins is complete, but one appears to have broken along the edge of the contact face for overlapping the adjacent bone (cf. *MxL*, Fig. 5). The orientation of this margin suggests that this fragment is part of a posterior median dorsal plate, probably with an original length of 70-80 mm. The median ridge is strongly developed for a posterior median dorsal, and there is no clear development of a ventral tuberosity. The posterior thickening of the transverse crista is missing, and was probably broken off. No other significant structures are shown by the specimen.

It is clear that this plate does not belong to the asterolepidoid *Remigolepis*, in which a posterior ventral pit and process are not developed. On the other hand, in *Asterolepis* the process may be separately developed behind the pit (e.g. Stensiö, 1948, p. 114), but this region is not fully preserved in CPC13937.

In *Bothriolepis* the pit is developed essentially as displayed here, but a more complete example is required to determine to which taxon the specimen belongs.

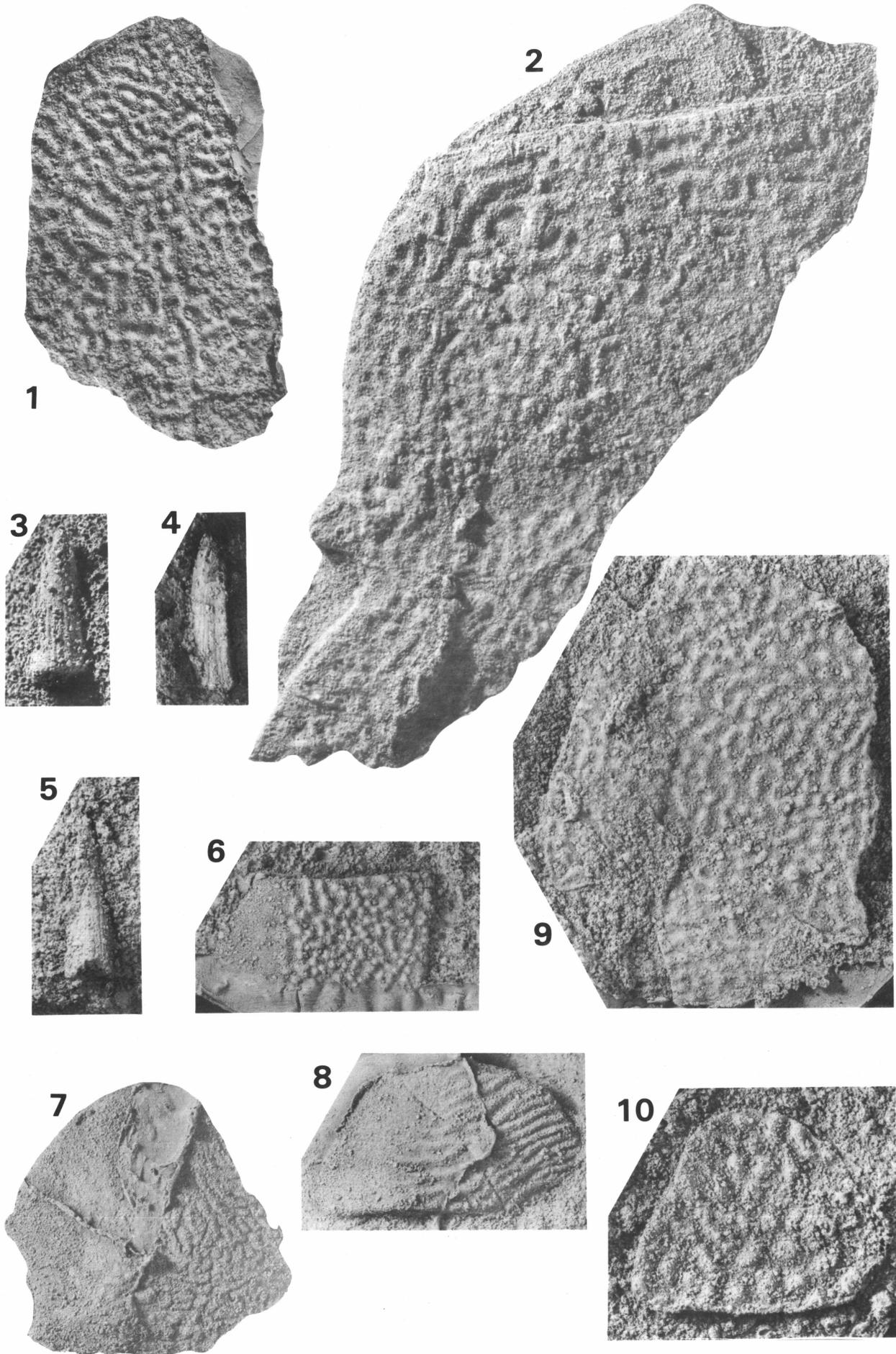
The largest specimen in the collection (Pl. 2, fig. 2) is preserved as an external mould of a somewhat triangular fragment with two natural margins, both truncated by a long broken edge. The surface is ornamented with coarse anastomosing ridges, which tend to align along the margins of the ornamented area. The shorter of these margins carries a well-developed overlap area, and along the longer margin are two shorter overlap areas separated by a distinct process and notch. The plate may be slightly arched about an axis

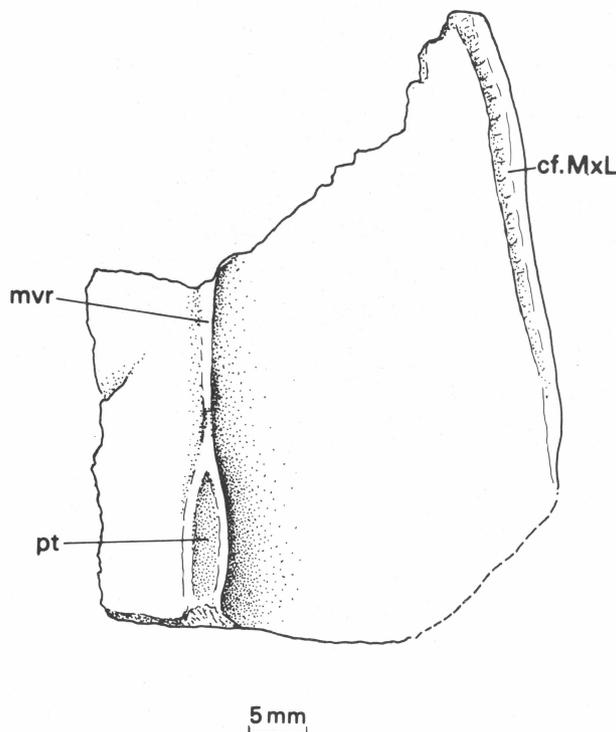
#### Plate 2. antiarch indet.

Fig. 1. Undetermined plate (CPC13938) in external view (x1). Fig. 2. Undetermined plate (CPC13943) in external view (x1.3). Fig. 9. Undetermined plate (CPC13942) in external view (x1.3). Fig. 10. Undetermined plate (CPC13941) in external view (x1.3).

#### rhpidistian indet.

Fig. 3. Isolated tooth (CPC13949) (x2). Figs. 4, 5. Isolated teeth (CPC13947, 13946) (x 1.3) Figs. 6-8. Incomplete scales (CPC13945, 13946, 13944) in external view (x1). (all photographs of latex casts whitened with ammonium chloride).





**Figure 5.** *Antiarch* indet.

Incomplete plate in visceral view, interpreted as a posterior median dorsal (CPC13937).

*cf. MxL*, remnant of the contact face for overlapping the left mixilateral plate, *mvr*, median ventral ridge; *pt*, posterior ventral pit.

passing through the notch, but this could be a post-mortem feature.

This specimen shows that the antiarch in question attained a very large size, comparable to that of *Bothriolepis maxima* or *B. gigantea*, and *Asterolepis maxima* or *A. scabra*. However, the specimen is still too incomplete for its position in the skeleton to be determined, except for the fact that it is almost certainly a bone from the trunk armour. It may be an anterodorsal portion of the dorsal lamina of a left mixilateral plate, or an anterior part of the ventral lamina of a right posterior ventrolateral, both of which are overlapped on adjacent margins by contiguous bones.

The other illustrated fragments (Pl. 1, figs 4, 8; Pl. 2, figs 1, 9, 10) seem to have at least one natural bone margin, but apart from ornament show no features facilitating their identification.

Subclass **Osteichthyes**  
Superorder **Rhipidistia**  
rhipidistian indet.  
(Pl. 2, figs. 3-8)

1975 'crossopterygian remains' Yeates & others, p. 50

**Material.** Three grooved teeth (CPC13947-49) and three ornamented scales (CPC13944-46) preserved as external moulds.

**Occurrence.** Localities B130 (CPC13947, 48), B136 (CPC13944, 46), B140 (CPC13949), and V34 (CPC13945) in the Knobby Sandstone, Knobby and Falconer Hills, eastern Canning Basin, Western Australia (see Fig. 1).

**Description.** The presence of rhipidistians in the Knobby Hills fauna is demonstrated by the three isolated teeth (Pl. 2, figs. 3-5).

CPC13949 is 15 mm long, with a diameter of 65 mm at the base of the preserved portion. It is oval in cross section and slightly curved, smooth at the tip, and grooved towards the base. The total number of grooves was probably about 25.

CPC13947 is 21 mm long, laterally compressed in cross section, and has a width of 6 mm. It is slightly curved, with a posterior cutting edge, and is ornamented with fine longitudinal grooves over most of its preserved length.

CPC13948 is also 21 mm long, but is subcircular in cross section, with a diameter of about 6 mm. It is slightly curved and more slender and pointed than the previous two specimens, with a posterior cutting edge. It is similarly ornamented with thin longitudinal grooves.

These specimens are only preserved as moulds, so there is no information on the degree of infolding of dentine walls and other histological details that may be distinctive amongst the major rhipidistian subgroups (e.g. Schultze, 1970). Otherwise, there is no way of identifying such isolated teeth on external morphology, which can be highly variable even in a single individual. Jarvik (1937, p. 67) noted that in material of the osteolepiform species *Eusthenopteron foordi* from Scaumenac Bay, Canada, all combinations of round, compressed, straight, blunt, pointed, striated, and smooth teeth may occur, often with several different morphological types and a large size range in one individual. Clearly the poor preservation here, and the few available specimens, preclude any positive identifications being made.

The three specimens identified as probable rhipidistian scales differ in shape and ornament, and several taxa may have been present. In each there is a smooth anterior region, which, presumably, was overlapped by the preceding scale. The boundary between the unornamented and ornamented parts is not marked by any groove or step in the bone surface. Such features are usual in rhipidistian scales that lack cosmine. CPC13945 (Pl. 2, fig. 6) is very incomplete, and only short sections of the anterior and posterior margins are preserved undamaged. The broken dorsal and ventral margins are extensive, suggesting that significant parts of the scale are missing. This specimen may be interpreted as the central part of a cycloid scale about 30 mm across, with about the anterior third of the scale being the smooth overlapped part. The exposed portion of the scale is ornamented with crowded tubercles aligned in short irregular rows. CPC13944 (Pl. 2, fig. 8) appears to be fairly complete. Again, the anterior unornamented area is a little over one third the total length (50 mm) of the specimen. The exposed surface is ornamented with subparallel ridges. A third scale (CPC13946) has a sub-circular shape, and about half the external surface is unornamented (Pl. 2, fig. 7). Its maximum width is about 50 mm, and the anteroventral and posterodorsal margins are incomplete. This scale is ornamented with vermicular grooves.

Little can be concluded from these specimens, except that they probably belonged to one or more large rhipidistian fish, which were advanced in possessing cycloid rather than rhomboid scales. Cycloid scales in Late Devonian deposits may belong either to porolepiform or osteolepiform rhipidistians, which can be readily distinguished by the presence or absence of a boss on the inner scale surface. This detail is not preserved for the examples dealt with here, and like the isolated teeth, they must remain indeterminate for the present.

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## References

- Blake, D.H., Passmore, V.L., & Muhling, P.C., 1977—Billiluna, Western Australia—1 250 000 Geological Series, Second Edition. *Bureau of Mineral Resources, Australia, Explanatory Notes SE/52-14*.
- Botten, P., 1984—Uranium exploration in the Canning Basin: a case study. In Purcell, P.G., (editor). The Canning Basin, W.A. Proceedings of Perth symposium, 1984. *Geological Society of Australia and Petroleum Exploration Society of Australia*, 485–501.
- Campbell, K.S.W., & Bell, M.W., 1977—A primitive amphibian from the Late Devonian of New South Wales. *Alcheringa*, 1, 369–381.
- Casey, J.N., & Wells, A.T., 1964—The geology of the north east Canning Basin, Western Australia. *Bureau of Mineral Resources, Australia, Report* 49, 1–61.
- Chang Kuo-Jui, 1965—New antiarchs from the Middle Devonian of Yunnan. *Vertebrata palasiatica* 9, 1–14, pl. 1–3 (in Chinese and English).
- Denison, R.H., 1978—Placodermi. Handbook of paleoichthyology, Volume 2 (H.-P. SCHULTZE, editor). *Gustav Fischer Verlag, Stuttgart*.
- Dennis, K. & Miles, R., 1979a—A second eubranchyothoracid arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society of London*, 67, 1–29.
- Dennis, K. & Miles, R., 1979b—Eubranchyothoracid arthrodires with tubular rostral plates from Gogo, Western Australia. *Zoological Journal of the Linnean Society of London*, 67, 297–328.
- Dennis, K. & Miles, R.S., 1980—New duronophagous arthrodires from Gogo, Western Australia. *Zoological Journal of the Linnean Society of London*, 69, 43–85.
- Dennis, K., & Miles, R.S., 1981—A pachyosteoromorph arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society of London*, 73, 213–258.
- Dennis, K., & Miles, R.S., 1982—A eubranchyothoracid arthrodire with a snubnose from Gogo, Western Australia. *Zoological Journal of the Linnean Society of London*, 75, 153–166.
- Druce, E.C., & Radke, B.M., 1979—The geology of the Fairfield Group, Canning Basin, Western Australia. *Bureau of Mineral Resources, Australia, Bulletin* 200, 1–62.
- Fergusson, C.L., Cas, R.A.F., Collins, W.J., Craig, G.Y., Crook, K.A.W., Powell, C.McA., Scott, P.A., & Young, G.C., 1979—The Late Devonian Boyd Volcanic Complex, Eden, N.S.W. *Journal of the Geological Society of Australia*, 26, 87–105.
- Gardiner, B.G., & Miles, R.S., 1975—Devonian fishes of the Gogo Formation, Western Australia. *Colloques internationaux du Centre National de la Recherche Scientifique*, 218, 73–79.
- Gilbert-Tomlinson, J., 1968—A new record of *Bothriolepis* in the Northern Territory of Australia. *Bureau of Mineral Resources, Australia, Bulletin*, 80, 189–224.
- Gould, R.E., 1975—The succession of Australian pre-Tertiary megafossil floras. *Botanical Reviews*, 41, 453–83.
- Gross, W., 1931—*Asterolepis ornata*. Eichw. und das Antiarchi-Problem. *Palaeontographica*, 75A, 1–62.
- Gross, W., 1933—Die Wirbeltiere des rheinischen Devons. *Abhandlungen der Preussischen geologischen Landesanstalt*, 154, 1–83.
- Gross, W., 1937—Die Wirbeltiere des rheinischen Devons. Teil II. *Abhandlungen der Preussischen geologischen Landesanstalt*, 176, 1–83.
- Gross, W., 1940—Acanthodier und Placodermen aus *Heterostius*-Schichten Estlands und Lettlands. *Annales Societatis rebus naturae investigandis in universitate Tartuensi constitutae*, 46, 1–88.
- Gross, W., 1941a—Neue Beobachtungen an *Gerdalepis rhenana* (Beyrich) *Palaeontographica*, 93A, 193–212.
- Gross, W., 1941b—Die *Bothriolepis*-arten der *Cellulosa*—Mergel Lettlands. *Kungliga Svenska Vetenskapsakademiens Handlingar* (3) 19, 1–79.
- Hemmings, S.K., 1978—The Old Red Sandstone antiarchs of Scotland: *Pterichthyodes* and *Microbrachius*. *Palaeontographical Society (Monograph)*, 131, 1–64.
- Hill, D., Playford, G., & Woods, J.T., (editors), 1967—Devonian Fossils of Queensland. *Queensland Palaeontographical Society, Brisbane*.
- Hills, E.S., 1929—The geology and palaeontology of the Cathedral Range and Blue Hills in north-western Gippsland. *Proceedings of the Royal Society of Victoria*, 41, 176–201.
- Hills, E.S., 1931—The Upper Devonian fishes of Victoria, Australia, and their bearing on the stratigraphy of the state. *Geological Magazine*, 68, 206–231.
- Hills, E.S., 1932—Upper Devonian fishes from New South Wales. *Quarterly Journal of the Geological Society of London*, 88, 850–858.
- Hills, E.S., 1936—Records and descriptions of some Australian Devonian fishes. *Proceedings of the Royal Society of Victoria*, 48 (N.S.), 161–171.
- Hills, E.S., 1958—A brief review of Australian fossil vertebrates. In Westoll, T.S., (editor), *Studies on fossil vertebrates*, 86–107. *Athlone Press, London*.
- Hills, E.S., 1959—Record of *Bothriolepis* and *Phyllolepis* (Upper Devonian) from the Northern Territory of Australia. *Journal of the Royal Society of New South Wales*, 92, 174–175.
- Jacobson, T., 1984—The role of seismic in play type and prospect development: eastern Canning Basin. In Purcell, P.G., (editor), The Canning Basin, W.A. Proceedings of Perth symposium, 1984. *Geological Society of Australia and Petroleum Exploration Society of Australia*, 121–134.
- Janvier, P., & Pan Jiang, 1982—*Hyrceanaspis bliecki* n.g. n.sp., a new primitive euantiarch (Antiarcha, Placodermi) from the Middle Devonian of northeastern Iran, with a discussion on antiarch phylogeny. *Neue Jahrbuch für Geologie und Paläontologie Abhandlungen*, 164, 364–392.
- Janvier, P., Lethiers, F., Monod, O., & Balkas, O., 1984—Discovery of vertebrate fauna at the Devonian–Carboniferous boundary in SE Turkey (Hakkari Province). *Journal of Petroleum Geology*, 7, 147–168.
- Jarvik, E., 1937—On the species of *Eusthenopteron* found in Russia and the Baltic States. *Bulletin of the Geological Institute of the University of Uppsala*, 27, 63–127.
- Jarvik, E., 1961—Devonian vertebrates. In Raasch, G.O., (editor), *Geology of the Arctic*. *University of Toronto Press*, 197–204.
- Karatajute-Talimaa, V., 1960—*Byssacanthus dilatatus* (Eichw.) from the Middle Devonian of the U.S.S.R. *Collectanea Acta Geologica Lithuanica*, (1960), 293–305. (in Russian and English).
- Karatajute-Talimaa, V., 1963—Genus *Asterolepis* from the Devonian of the Russian platform. In Grigelis, A., & Karatajute-Talimaa, V., (editors), *The data of geology of the Lithuania*. 85–223, pl. 1–27. Vilnius (in Russian with Lithuanian and English summaries).
- Long, J.A., 1983—New bothriolepids (placoderm fishes) from the Late Devonian of Victoria, Australia. *Palaeontology*, 26, 295–320.
- McCoy, F., 1876—*Asterolepis ornata* (Eichwald) var. *australis* (McCoy). *Geological Survey of Victoria. Prodrum of the Palaeontology of Victoria*, 4, 19–20.
- Miles, R.S., 1968—The Old Red Sandstone antiarchs of Scotland. Family Bothriolepididae. *Palaeontographical Society (Monograph)*, 122, 1–130.
- Miles, R.S., 1971—The Holonematidae (placoderm fishes), a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Philosophical Transactions of the Royal Society of London (B)* 263, 101–234.
- Miles, R.S., 1977—Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *Zoological Journal of the Linnean Society of London*, 61, 1–328.
- Nilsson, T., 1941—The Downtonian and Devonian vertebrates of Spitzbergen. Order Antiarchi. *Skrifter om Svalbard og Ishavet*, 82, 1–54.
- Obruchev, D.V., 1932—Holonemidae des Russischen Devons. *Travaux de l'Institut paleozoologique de l'Academie des Sciences de l'U.R.S.S.*, 2, 97–115 (in German with Russian summary).
- P'an Kiang, 1964—Some Devonian and Carboniferous fishes from south China. *Acta palaeontologica Sinica*, 12, 139–83, pl. 1–8 (in Chinese with English Summary).
- Pan Jiang, 1981—Devonian antiarch biostratigraphy of China. *Geological Magazine*, 118, 69–75.
- Pan Jiang, Wang Shitao, Liu Shiyu, Gu Qichang, & Jia Hang,

- 1980—Discovery of Devonian *Bothriolepis* and *Remigolepis* in Ningxia. *Acta Geological Sinica*, 54, 176–186 (Chinese with English summary)
- Purcell, P.G., & Poll, J., 1984—The seismic definition of the main structural elements of the Canning Basin. In Purcell, P.G. (editor). The Canning Basin, W.A. Proceedings of Perth symposium 1984. *Geological Society of Australia and Petroleum Exploration Society of Australia*, 73–84.
- Ritchie, A., 1975—*Groenlandaspis* in Antarctica, Australia and Europe. *Nature*, 254, 569–573.
- Sandberg, C.A., Gutschick, R.C., Johnson, J.G., Poole, F.G., & Sando, W.J., 1983—Middle Devonian to Late Mississippian geological history of the overthrust belt region, western United States. *Rocky Mountain Association of Geologists, Geological Studies of the Cordilleran Thrust Belt*, 2, 691–719.
- Schultze, H.-P., 1970—Folded teeth and the monophyletic origin of tetrapods. *American Museum Novitates*, 2408, 1–10.
- Smith, G., 1984—The tectonic development of the Gregory Sub-Basin and adjacent areas, northeastern Canning Basin. In Purcell, P.G., (editor). The Canning Basin, W.A. Proceedings of Perth symposium, 1984. *Geological Society of Australia and Petroleum Exploration Society of Australia*, 109–120.
- Smith, M.M., 1979—Structure and histogenesis of tooth plates in *Sagenodus inaequalis* Owen considered in relation to the phylogeny of post-Devonian dipnoans. *Proceedings of the Royal Society of London*, (B), 204, 15–39.
- Stensiö, E.A., 1931—Upper Devonian vertebrates from East Greenland collected by the Danish Greenland expeditions in 1929 and 1930. *Meddelelser om Grønland*, 86, 1–213.
- Stensiö, E.A., 1948—On the Placodermi of the Upper Devonian of East Greenland 2. Antiarchi: Subfamily Bothriolepinae. *Meddelelser om Grønland*, 139, 1–622.
- Stensiö, E.A., & Säve-Söderbergh, G., 1938—Middle Devonian vertebrates from Canning Land and Wegener Peninsula (east Greenland), part 1: Placodermi, ichthyodorulithes. *Meddelelser om Grønland*, 96, 1–38, pl. 1–14.
- Thomas, G.A., 1957—Lower Carboniferous deposits in the Fitzroy Basin, Western Australia. *Australian Journal of Science*, 19, 160–161.
- Thomas, G.A., 1959—The Lower Carboniferous Laurel Formation of the Fitzroy Basin. *Bureau of Mineral Resources, Australia, Report* 38, 31–36.
- Traquair, R.H., 1894—A monograph of the fishes of the old red sandstone of Britain. Pt. 2—The Asterolepidae. *Palaeontographical Society (Monograph)*, 48, 63–90.
- Towner, R.R., & Gibson, D.L., 1983—Geology of the onshore Canning Basin, Western Australia. *Bureau of Mineral Resources, Australia, Bulletin*, 215, 1–51.
- Turner, S., 1982—A catalogue of fossil fish in Queensland. *Memoirs of the Queensland Museum*, 20, 599–611.
- Veevers, J.J., Roberts, J., White M.E., & Gemuts, I., 1967—Sandstone of probable Lower Carboniferous age in the north-eastern Canning Basin, W.A. *Australian Journal of Science*, 29, 330–331.
- Veevers, J.J., & Wells, A.T., 1961—The geology of the Canning Basin, Western Australia. *Bureau of Mineral Resources, Australia, Bulletin* 60, 1–321.
- Watson, D.M.S., 1932—On three new species of fish from the Old Red Sandstone of Orkney and Shetland. *Great Britain Geological Survey Memoir. Summary of progress*, 1931 (2), 157–63.
- Westoll, T.S., 1979—Devonian fish biostratigraphy. In House, M.R., Scrutton, C.T., & Bassett, M.G. (editors), The Devonian System. *Special Papers in Palaeontology*, 23, 341–353.
- Yeates, A.N., Crowe, R.W.A., Passmore, V.L., Towner, R.R., & Wyborn, L.I.A., 1975—New and revised stratigraphic nomenclature, northeast Canning Basin. *Geological Survey of Western Australia, Annual Report*, 1974, 49–51.
- Young, G.C., 1974—The stratigraphic occurrence of some placoderm fishes in the Middle and Late Devonian. *Newsletters on Stratigraphy*, 3, 243–261.
- Young, G.C., 1983—A new antiarchan fish (Placodermi) from the Late Devonian of southeastern Australia. *BMR Journal of Australian Geology & Geophysics*, 8, 71–81.
- Young, G.C., 1984a—An asterolepidoid antiarch (placoderm fish) from the Late Devonian of the Georgina Basin, central Australia. *Alcheringa*, 8, 65–80.
- Young, G.C., 1984b—Reconstruction of the jaws and braincase in the Devonian placoderm fish *Bothriolepis*. *Palaeontology*, 27, 635–660.
- Young, G.C., 1985—New discoveries of Devonian vertebrates from the Amadeus Basin, Central Australia. *BMR Journal of Australian Geology & Geophysics*, 9, 239–254.
- Young, G.C., & Gorter, J.D., 1981—A new fish fauna of Middle Devonian age from the Taemas/Wee Jasper region of New South Wales. *Bureau of Mineral Resources, Australia, Bulletin*, 209, 83–147.
- Zhang Guorui, 1978—The antiarchs from the Early Devonian of Yunnan. *Vertebrata Palasiatica*, 16, 147–86. (Chinese with English summary).