# DEVONIAN SHARKS FROM SOUTH-EASTERN AUSTRALIA AND ANTARCTICA

*by* G. C. YOUNG

ABSTRACT. Devonian shark remains from the Aztec Siltstone in south Victoria Land, Antarctica, are described as *Antarctilamna prisca* gen. et sp. nov., *Xenacanthus* sp., and *Mcmurdodus*? cf. *featherensis* White. Similar spines, teeth, and associated endocranial and jaw remains from the Bunga Beds on the far south coast of New South Wales are also referred to *A. prisca*. In this genus the teeth are diplodont, the fin-spines ctenacanthiform, and the braincase had a long otic region, prominent subocular shelves, and probably a persistent lateral occipital fissure. The double mandibular joint on the palatoquadrate resembles that of acanthodians. The other taxa are known only from isolated teeth. Both are freshwater occurrences of late Givetian to early Frasnian age. In a new hypothesis of interrelationships for early elasmobranchs, diplodont teeth are regarded as a synapomorphy of *Antarctilamna* and *Xenacanthus*, with the fin-spines of the former interpreted as a primitive feature. A ctenacanth origin for euselachians is rejected, and hybodonts and euselachians are considered to be closely related. A single dorsal fin and spine are interpreted as the primitive elasmobranch condition, shared with holocephalans, and the absence of spines in some Palaeozoic sharks is regarded as secondary.

FOSSIL shark remains from the Palaeozoic rocks of Australia have so far received little attention in the literature. The main references are Teichert's (1940, 1943) accounts of Permian bradyodont and *Helicoprion* teeth from Western Australia, the illustration of some Lower Carboniferous cladodont and bradyodont teeth from the Canning Basin by Thomas (1959), and Ørvig's (1969) brief mention of the occurrence of *Ohiolepis* scales in the Lower Devonian limestones from the Taemas/Wee Jasper region of New South Wales. These few reports give some hint of the diversity of early elasmobranchs awaiting discovery in the Australian region, and to these may be added the new material from south-eastern Australia and Antarctica described below. These new occurrences are in freshwater deposits of approximately the same age (late Middle/early Upper Devonian), and represent early records of another major group of elasmobranchs (the xenacanth sharks), which flourished in Carboniferous and Permian times. It is of interest that shark remains of similar age have recently been reported also from South America (Janvier 1978*a*) and Iran (Blieck *et al.* 1980).

## SHARK REMAINS FROM THE AZTEC SILTSTONE, SOUTH VICTORIA LAND, ANTARCTICA

Woodward (1921) first described Devonian fish remains from moraine material derived from the 'Beacon Sandstone' of south Victoria Land, and the first *in situ* deposits were reported by Gunn and Warren (1962), and their material described by White (1968). Further localities in the same region of the Transantarctic Mountains were discovered in the summer field season of 1968–1969 by a geological expedition from the Victoria University of Wellington (McKelvey *et al.* 1972), and large collections were made by another Victoria University expedition in 1970–1971. These collections are currently being studied at the Australian Museum, Sydney, and the Bureau of Mineral Resources, Canberra (Ritchie 1971*a*, *b*, 1974, 1975; Young *in prep.*).

Woodward (1921, p. 56) tentatively referred various small dermal denticles in his material 'either to primitive Ostracoderms or to Elasmobranchs'. White (1968) identified a single small elasmobranch tooth for which he erected a new genus and species, *Mcmurdodus featherensis* White. Subsequently, Ritchie (in McKelvey *et al.* 1972) identified an elasmobranch tooth of completely different form, which he compared with *Xenacanthus*, in material from an important vertebrate locality in the Aztec

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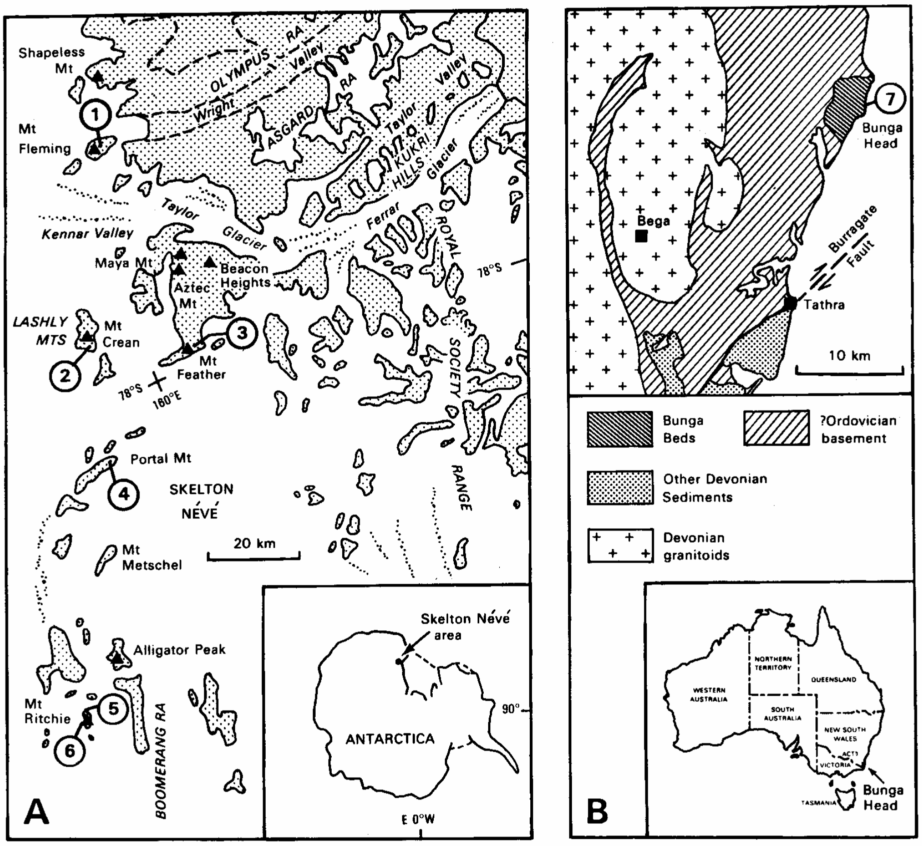

TEXT-FIG. 1. Localities (1–7) for the fossil shark remains described in this paper. A, outcrop map of the Skelton Névé region in the Transantarctic Mountains, south Victoria Land, Antarctica: B, generalized geology of the region around Bunga Head on the far south coast of New South Wales, Australia. Details of the numbered localities are given in the text.

Siltstone at Portal Mountain (text-fig. 1A). Further collecting in 1970–1971 yielded additional teeth from this locality, and teeth, spines, and scales from other localities including an incomplete, partly articulated specimen from the Lashly Mountains. With one exception, all this material comes from the Aztec Siltstone, the uppermost formation in the Devonian Taylor Group of the Beacon Supergroup (McKelvey *et al.* 1970, 1972, 1977; McPherson 1978). One elasmobranch spine (AMF 55550) comes from the underlying Beacon Heights Orthoquartzite at Mount Fleming.

Locality information for this material is as follows (numbers refer to text-fig. 1A). Horizons within the Aztec Siltstone are based on detailed sections reported in Askin *et al.* (1971) and Barrett and Webb (1973; see also McKelvey *et al.* 1977; McPherson 1978). Antarctic specimens described here which are housed in the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra have been allocated numbers CPC 21187–21192 and 21214–21229. Other material is held in the Australian Museum, Sydney (prefix AMF), and the British Museum (Natural History), London (prefix P).

1. Mount Fleming. Beacon Heights Orthoquartzite exposed in the floor of the cirque east of Mount Fleming, 77° 32′ 43″ S., 160° 21′ E. (locality MS228 of McKelvey *et al.* 1972, 1977). One fin-spine referred to *Antarctilamna prisca* gen. et sp. nov. (AMF 55550) from near the top of the formation (Section 26, Barrett and Webb 1973).

2. Lashly Mountains. Section L1, Unit 8 of Askin *et al.* (1971). Southern end of low ridge extending south-east from Mount Crean, 77° 54·5′ S., 159° 34·5′ E. One specimen, the holotype of *A. prisca* (CPC 21187), from about 15 m above the base of the Aztec Siltstone.

3. Mount Feather. '300 ft above base of east ridge of Mount Feather, at junction of Ferrar and Skelton Glaciers, 77° 59′ S., 160° 30′ E.' (White 1968, p. 8). Locality MS7 of Gunn and Warren (1962). Holotype (P.49157) of *M. featherensis* White.

4. Portal Mountain. Section P1 of Askin *et al.* (1971), measured up the steep east-facing slope of the easternmost rock spur, 78° 7·2′ S., 159° 24′ E. Isolated scales and teeth (CPC 21188, 21189, 21191) from Unit 4, 7·1 to 15·9 m above the base of the Aztec Siltstone. One scale (CPC 21190) from Unit 14, 44·3 to 53·1 m above the base of the Aztec Siltstone. These specimens are referred to *A. prisca*.

Section 10 of Barrett and Webb (1973), measured up the south-facing slope of the easternmost rock spur, 78° 7·2′ S., 159° 23·5′ E. Fin-spine of *A. prisca* (AMF 55617) and various teeth of *Xenacanthus* sp. (CPC 21216–21227; AMF 54329–54331, 55573) from locality MS232 of McKelvey *et al.* (1972), which is Unit 17 of the measured section, 40·2 m above the lowest exposure of Aztec Siltstone. Fin-spine of *A. prisca* (CPC 21192) and teeth of *Xenacanthus* sp. (CPC 21214, 21215) from Unit 26, 70 m above the lowest exposure of Aztec Siltstone.

5. Near Mt. Ritchie. Lower part of Section A5 of Askin *et al.* (1971), measured up a rocky knoll at the northern end of a ridge running north from Mt. Kohn, 78° 31·7′ S., 158° 19·5′ E. One tooth of *Xenacanthus* sp. (CPC 21228) in greenish-grey siltstone.

6. Mt. Ritchie. Section A4 of Askin *et al.* (1971), measured up the east face from the edge of the Deception Glacier, 78° 32·2′ S., 158° 26′ E. One tooth (CPC 21229) in a loose piece of greenish-grey siltstone, probably from near Units 61 and 62. Described below as *M.*? cf. *featherensis* White.

## SHARK REMAINS FROM THE SOUTH COAST OF NEW SOUTH WALES

These shark remains occur in the Bunga Beds, a circumscribed outcrop of Devonian sediments in the region of Bunga Head (text-fig. 1B), sitting unconformably on metaquartzites and slates of the (?) Ordovician Mallacoota Beds. This deposit has been interpreted as part of a complex system of Devonian volcanics and sediments which are widespread in the Eden–Pambula area (the 'Boyd Volcanic Complex' of Fergusson *et al.* 1979), and it is regarded as a lacustrine flysch deposit which accumulated in a rift-valley lake ponded against the nearby Burragate Fault (Fergusson *et al.* 1979, p. 93).

Fish remains in the Bunga Beds were first collected by Scott (1972) from a fossil plant locality at Bunga Beach (GR 2364E 59486N Murrah 1:25 000 Sheet; loc. 7, text-fig. 1B). These and a few subsequently collected specimens were briefly described in Fergusson *et al.* (1979, p. 102). At that time the characteristic diplodont teeth had not been identified in the material and the elasmobranch nature of these remains was not recognized. The locality was revisited in October 1979 and more elasmobranch fin-spines, many teeth, and a few other remains were collected. The associated fauna includes acanthodians and a holoptychoid rhipidistian, which also occur at two other localities higher in the Bunga Beds sequence. However, the shark remains are known only from the Bunga Beach locality, which is near the base of the sequence. At this locality they are the most common element in the fish fauna. Associated are abundant lycopod plants referred to the genera *Protolepidodendron* or *Lepidosigillaria* (see Gould 1975).

All the elasmobranch material from this locality is referred below to *A. prisca*. Specimens are housed in the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra (CPC 16994, 16995, 21193–21213), and the Geology Department collections at the Australian National University, Canberra (ANU 35333, 35334).

## AGE AND CORRELATION

Since material referred to *A. prisca* comes from both the Antarctic and New South Wales localities, a tentative correlation may be proposed between the lower part of the Aztec Siltstone of south Victoria

Land, and the Bunga Beds of the New South Wales south coast. The age of the Bunga Beds has previously been assessed as 'no younger than early Frasnian, and probably Givetian' (Young *in* Fergusson *et al.* 1979, p. 103). The fish fauna in the Aztec Siltstone was initially regarded as Upper Devonian in age (Woodward 1921), but with better material White (1968, p. 6) favoured an age 'nearer the top of the Middle Devonian than the base of the upper . . .'. Subsequent work on the 1969–1971 collections now indicates some variation in the vertebrate assemblages through the Aztec sequence. Ritchie (1975, p. 571) has reported evidence of more than one species of the arthrodire *Groenlandaspis*, and there are several species of *Bothriolepis* (Young *in prep.*). Both genera occur right through the sequence, but some others (e.g. the placoderm *Phyllolepis* and the acanthodian *Gyracanthides*) appear to be restricted to upper levels. However, the elasmobranch material referred below to *Antarctilamna* comes mainly from the lower fossiliferous part of the sequence, being recorded from the upper beds of the Beacon Heights Orthoquartzite at Mt. Fleming, from 15 m above the base of the overlying Aztec Siltstone in the Lashlys, up to 53 m above the base in Section P1 (Askin *et al.* 1971) at Portal Mountain (a single scale), and probably at similar levels (two spines) in the adjacent Section 10 (Barrett and Webb 1973) at Portal. (Detailed correlation between the two Portal sections is uncertain, since in Section 10 the Aztec is some 40% thinner than in the nearby Section P1, the lower contact is not exposed, and the upper contact poorly exposed and probably disconformable.) The precise horizon of the holotype of *M. featherensis* is not known, but Helby and McElroy (1969, p. 379) imply that the Mt. Feather collections of Gunn and Warren (1962) came from near the top of the Aztec Siltstone. A single tooth tentatively referred below to *Mcmurdodus* sp. also comes from a high Aztec horizon in Section A4. The teeth described as *Xenacanthus* sp. are associated with *Antarctilamna* spines in Portal Section 10, and there is one tooth from the upper part of the Aztec Siltstone in Section A5.

To summarize, remains of *A. prisca* occur predominantly in the lower part of the Aztec Siltstone, and the other elasmobranchs appear to be restricted to the middle and upper parts, but whether this represents a faunal change through time or is facies controlled cannot be decided. It should be noted that the relevant lower beds of the Aztec at both the Portal and Lashlys localities are predominantly finely laminated lacustrine beds, this lithology being less common elsewhere.

In addition to the fish remains, a microflora from about 3 m below the top of the Aztec Siltstone at Aztec Mountain was described by Helby and McElroy (1969) as strongly reminiscent of assemblages from the Gneudna Formation of the Carnarvon Basin, Western Australia. They suggested a Frasnian age for the Aztec assemblage, although Seddon (1969) concluded on conodont evidence that the Gneudna Formation was slightly older than previously proposed, being of latest Givetian and/or earliest Frasnian age (see also Turner and Dring 1981). A less reliable maximum age for the Aztec is provided by lycopod remains from the underlying Beacon Heights Orthoquartzite, which have been dated as Lower–Middle Devonian (McKelvey *et al.* 1972, p. 348; see also Kyle 1977; Grindley, Mildenhall and Schopf 1980).

Taken together the evidence is thus consistent with a late Givetian/early Frasnian age for the Aztec fauna, which accords well with evidence from other early elasmobranch occurrences.

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EXPLANATION OF PLATE 87

Figs. 1–10. *Antarctilamna prisca* gen. et sp. nov. 1, three teeth from piece *c* of the holotype, CPC 21187, ×6. 2, portion of ornamented fin-spine, AMF 55617 (latex rubber cast), ×6. 3, fin-spine, dorsal view, CPC 21205 (latex rubber cast), ×3. 4, fin-spine, dorsolateral view, CPC 21206 (latex rubber cast), ×3. 5, portion of fin-spine showing ornament, left lateral view, CPC 21204 (latex rubber cast), ×3. 6, 7, two scales in dorsal view from piece *j* of the holotype, CPC 21187, ×36. 8, scale in anterior view, with base preserved as an impression, piece *b* of the holotype, CPC 21187, ×24. 9, 10, dermal denticles from the branchial region, piece *d* of the holotype, CPC 21187, ×24. Figs. 1, 2, 6–10 from Aztec Siltstone, Lashly Mountains, south Victoria Land, Antarctica. Figs. 3–5 from Bunga Beds, Bunga Beach, south coast of New South Wales.

All specimens whitened with ammonium chloride.

PLATE 87


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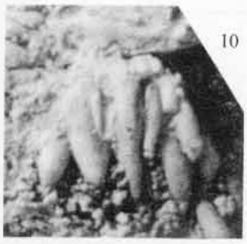
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YOUNG, *Antarctilamna*

Diplodont teeth referred to xenacanth sharks are first recorded elsewhere from the 'Genesee conodont bed' in New York State (Patterson *in* Andrews *et al.* 1967, p. 667), which lies at the base of the Genesee Group (Hussakof and Bryant 1918, p. 12). Rickard (1975) assessed these horizons as basal Frasnian, although evidence regarding the precise position of the Givetian/Frasnian boundary in this sequence is equivocal. The earliest ctenacanth spines noted by Patterson (*in* Andrews *et al.* 1967) occur in the underlying Hamilton Group in New York State, which is probably Givetian (Rickard 1975). These spines differ in various respects from those described below, but spines closely similar to this new material have recently been described from the Middle Devonian (?Eifelian) of Iran (Blieck *et al.* 1980; Janvier 1980). I conclude, therefore, that the lower part of the Aztec Siltstone may be late Givetian, and the upper part early Frasnian in age, and that available evidence strongly suggests a correlation with part or all of the Bunga Beds on the New South Wales south coast (the 'Flyschoid facies' of the Boyd Volcanic Complex—see Fergusson *et al.* 1979).

## SYSTEMATIC PALAEONTOLOGY

### Subclass CHONDRICHTHYES
### Infraclass ELASMOBRANCHII
### Genus *ANTARCTILAMNA* gen. nov.
### *Antarctilamna prisca* sp. nov.

Plate 87, figs. 1-10; Plate 88, figs. 1-3, 5; Plate 89, figs. 5-8; text-figs. 2, 3A-D, 4-8.

| | |
|---|---|
| 1971*a* | *Gyracanthides* Ritchie, p. 16. |
| 1971*b* | *Gyracanthides* Ritchie, p. 70. |
| 1978 | *Ctenacanthus* McPherson, p. 667. |
| 1979 | 'endocranial casts . . . of a small placoderm . . .', 'large acanthodian spine with . . . tuberculate longitudinal ridges . . .'; Young *in* Fergusson *et al.*, p. 102. |
| 1981 | 'elasmobranchs . . . with diplodont teeth and ctenacanth-like spines'; Young and Gorter, p. 90. |

*Etymology.* From the Greek *antarktikos* (southern) and *lamna* (a kind of shark), and the Latin *priscus* (ancient).

*Holotype.* CPC 21187, a partly articulated incomplete specimen from the Lashly Mountains, south Victoria Land, Antarctica.

*Other material.* Isolated scales (CPC 21188-21190), teeth (CPC 21191), and spines (AMF 55550, 55555, 55617; CPC 21192) from Antarctica, and isolated teeth (CPC 21193-21202), spines (CPC 16995, 21203-21209; ANU 35334), endocrania (CPC 16994, 21210, 21211; ANU 35333, 35334) and jaw remains (CPC 21212, 21213) from the Bunga Beds, south coast of New South Wales, Australia. (For locality details see above.)

*Definition.* Elasmobranchs with probably five gill openings; braincase with a long otico-occipital division, small postorbital and larger lateral otic processes, extensive subocular shelf and probably a persistent lateral occipital fissure; teeth diplodont with up to three mesial cusps and a lingual torus; lateral cusps curved in a single plane and directed lingually. Palatoquadrate with both pre- and postarticular processes for the mandibular joint, the former with an articular depression on its lateral

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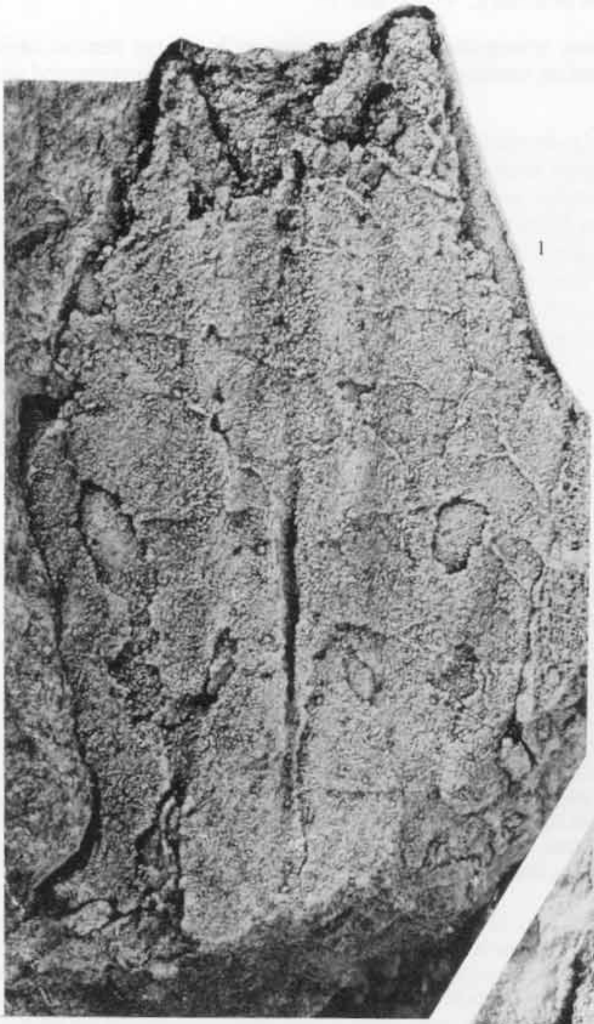
EXPLANATION OF PLATE 88

Figs. 1-3, 5. *Antarctilamna prisca* gen. et sp. nov. 1, 5, endocranial casts (ANU 35333, CPC 16994) in ventral view, Bunga Beds, Bunga Beach, south coast of New South Wales, × 3. 2, 3, incomplete left palatoquadrate in lateral and mesial views, CPC 21212 (latex rubber cast), locality and horizon as for figs. 1, 5, × 1.

Fig. 4. *Mcmurdodus*? cf. *featherensis* White. Isolated tooth (CPC 21229), with base preserved mainly as an impression, Aztec Siltstone, Mt. Ritchie, south Victoria Land, Antarctica, × 4.

All specimens whitened with ammonium chloride.

PLATE 88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YOUNG, *Antarctilamna* and *Mcmurdodus?*

face. Probably two dorsal costate fin-spines, triangular in cross-section with a large central cavity posteriorly placed, and a small inserted portion; scales compound, with a flat crown ornamented with concentric ridges, and a cup-shaped base.

*Remarks.* The single elasmobranch tooth previously described from the Aztec Siltstone by White (1968) as *Mcmurdodus featherensis* shows no resemblance to the teeth of this new form. As far as could be observed in the holotype and in other specimens, the teeth of *Antarctilamna prisca*, apart from size, show little variation, a common feature of Devonian elasmobranchs, even though some degree of heterodonty has recently been described in the Lower Carboniferous form *Tristychius* (Dick 1978). It is surprising that several freshwater sharks with such distinctive dentition should coexist in the Aztec Siltstone, and that no definite further remains of *M. featherensis* have yet been identified. Since, however, there is no evidence of variation in tooth morphology in the articulated specimen described below, and as far as is known heterodonty is not a feature of other Devonian elasmobranchs, this specimen has been designated the holotype of a new species in a new genus, to which a few isolated scales, teeth, and incomplete spines from Portal Mountain and Mt. Fleming may be referred. The elasmobranch material from the Bunga Beds is regarded as conspecific on the evidence of associated teeth and spines which cannot be distinguished in any significant details from corresponding elements in the Antarctic material.

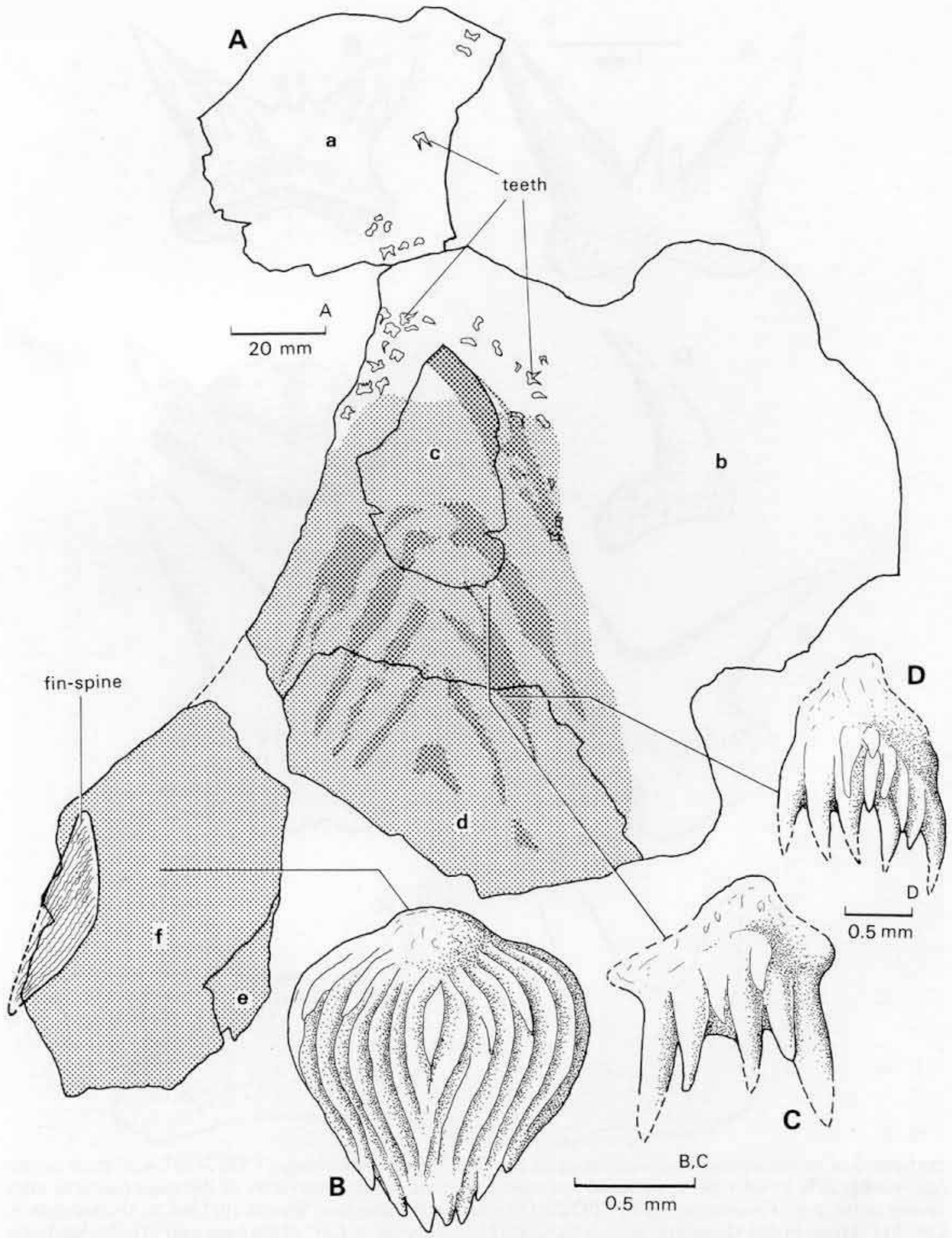
*Description.* The holotype is preserved in six main pieces of a flat nodule of fine calcareous siltstone which was incomplete and separated when collected. The largest piece (*b*, text-fig. 2) has two smaller pieces as counterparts (*c*, *d*), and pieces *e* and *f* are also part and counterpart, but their relationship to the other pieces is uncertain. The bedding plane containing the fish is partly enclosed in piece *a*, with broken teeth and scales exposed around its convex margin. In addition, there are three smaller pieces (labelled *g*, *h*, *j*) associated with *e* and *f*, and various small flakes displaying fragments of teeth or shagreen patches.

Despite its incompleteness, a general orientation for the specimen has been determined. Teeth are scattered around the anterior end of piece *b* (as oriented in text-fig. 2), and around the margins of piece *a*, indicating proximity to the head region and mouth. Most of the area of shagreen on piece *b* displays a pattern of irregular but apparently symmetrical undulations converging anteriorly, which I interpret as ventral extensions of the gill openings. Some of these elongate depressions contain patches of a granular material, possibly remains of the ceratobranchials, and it is assumed therefore that the area of shagreen on piece *b* represents a visceral view of the ventral surface of the branchial region. Consistent with this interpretation is the imbrication of surrounding denticles, each overlapping the one behind. In the branchial region these are aligned parallel to the branchial arches.

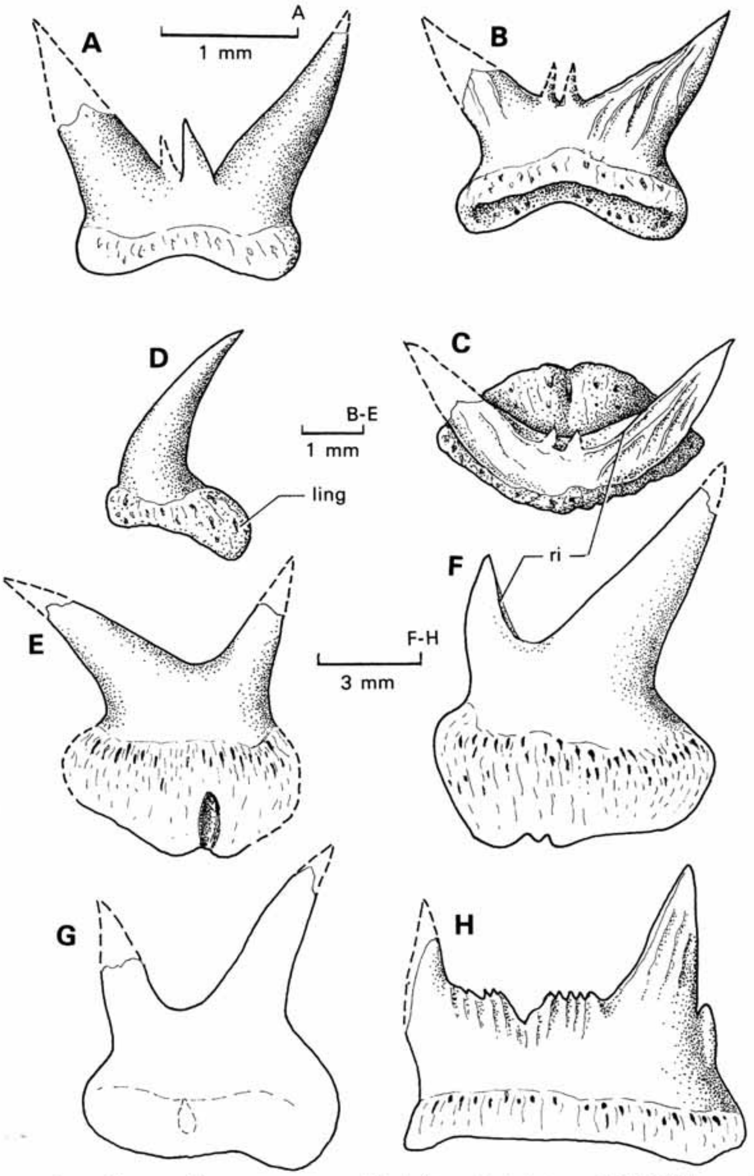
The texture of the outer surface of piece *e* shows that it is also from the ventral side of the nodule. A fin-spine is partly preserved at the edge between pieces *e* and *f* and presumably represents the dorsal midline of the fish. The orientation of the spine and the alignment and imbrication of surrounding denticles suggest an approximate position for pieces *e* and *f* relative to pieces *a* and *b* as shown in text-fig. 2, the fish having been compressed in the nodule with the dorsal spine folded over to the left side. Thus interpreted, a considerable portion of the specimen is missing, and little can be deduced of general body form and fin shape. The specimen is of major significance, however, in demonstrating scale, fin-spine, and tooth morphology within a single species.

*Teeth.* About sixty-five teeth or parts thereof are visible on the articulated specimen, and isolated teeth are common in the Bunga material. The teeth in CPC 21187 vary in size, a large tooth (text-fig. 3A) being about 4 mm across the root, with cusps about 2·5 mm long. One of the smallest visible teeth (on piece *b*) is slightly under 1 mm wide across the root. For most of the teeth this measurement is about 3 mm.

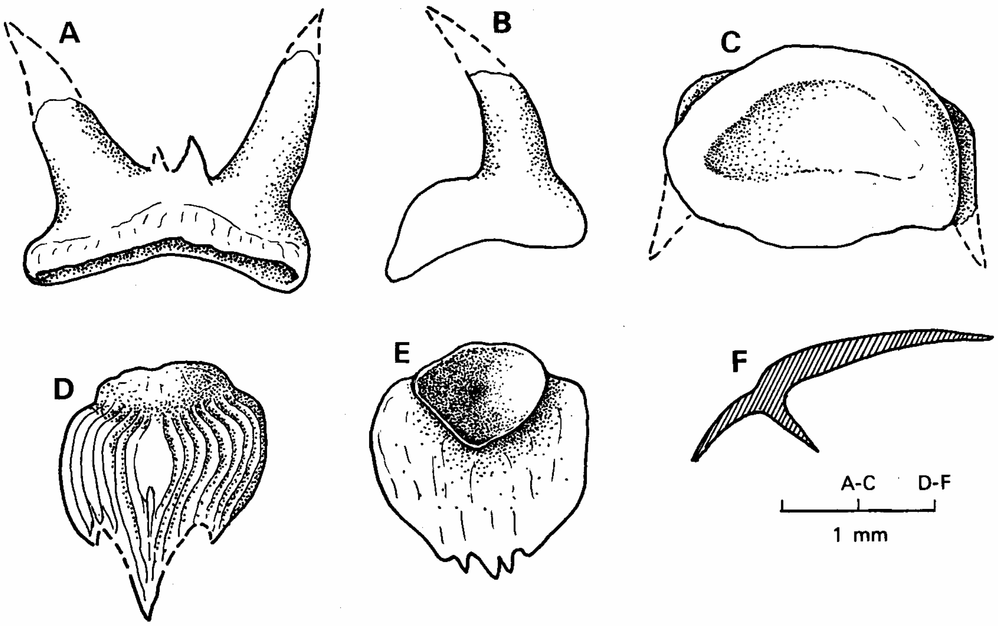
All teeth are of diplodont type, with two prominent, curved lateral cusps separated by two or three much smaller mesial cusps. Where there are three subsidiary cusps the central one may be slightly larger (Pl. 87, fig. 1), but it does not approach the size of the lateral cusps, and in this respect this species differs from teeth previously described by Hussakof and Bryant (1918, fig. 51B, C) as *Dittodus priscus* (Eastman), or those named by Wells (1944) as *Phoebodus* (e.g. Gross 1973, pl. 34, fig. 15). The crown and its cusps have a shiny enameloid-like surface. The cusps may be smooth (text-fig. 3A), or more commonly striated (text-fig. 3B, C), the striations tending to spiral slightly towards the tip. The number of striations varies but typically about six are exposed on the labial surface. They are not as strongly developed as the striations on *D. priscus* (see Hussakof and Bryant 1918, pl. 44, fig. 3). The only tooth with the lingual surface of the cusps clearly exposed (on the edge of piece *c*) is smooth here, so the striations may have been restricted to the outer surface, as these authors have described (Hussakof and Bryant 1918, p. 145). The striation lying in the plane of the mesial cusps may be slightly



TEXT-FIG. 2. *Antarctilamna prisca* gen. et sp. nov. Holotype (CPC 21187), a partly articulated specimen from the Lashly Mountains, showing (A) the six main pieces from the nodule (labelled *a–f*), and illustrating some variation in the size and morphology of denticles from different regions of the specimen (B–D). Extent of shagreen shown by stippling. Granular material, possibly representing remains of ceratobranchials, densely stippled.



TEXT-FIG. 3. A–D, *Antarctilamna prisca* gen. et sp. nov. Teeth from the holotype, CPC 21187. A, B, from piece *a* (see text-fig. 2) in labial view. C, D, dorsal and posterior views showing curvature of the cusps (restored after several teeth). E–G, *Xenacanthus* sp. E, CPC 21215 from Portal Mountain, Section 10, Unit 26, lingual view. F, CPC 21224 from Portal Mountain, Section 10, Unit 17, lingual view. G, CPC 21228 from near Mt. Ritchie, lower part of Section A5. Outline shape only of this tooth, which is abraded, and preserved partly as an impression in labial view. Position of the pore on the lingual surface indicated by a dashed line. H, *Mcmurdodus*? cf. *featherensis* White. CPC 21229 from Mt. Ritchie, Section A4, near Units 61 and 62. *ling*, lingual torus; *ri*, ridge on cusps forming a cutting edge.



TEXT-FIG. 4. *Antarctilamna prisca* gen. et sp. nov. A–C, restoration of a tooth from the Bunga Beds (CPC 21198) in labial, posterior, and ventral views. D, an isolated trunk scale from Portal Mountain, Section P1, Unit 14 (CPC 21190). E, sketch restoration of a scale in basal view, after various broken scales on pieces *c*, *e*, *h*, and *j* of the holotype (cf. Pl. 89, fig. 6). F, vertical midline section through a scale, restored after various scales on piece *e* of the holotype.

accentuated as a thin cutting-edge on the adjacent basal parts of the lateral cusps (*ri*, text-fig. 3C). Otherwise the cusps are circular in cross-section.

The root of the tooth is always clearly delineated from the crown, being composed of the cancellous bone-like tissue typically seen in elasmobranch teeth. Its basal surface is distinctly concave, and there is a lingual torus (*ling*, text-fig. 3D), which in one broken tooth removed from the matrix has a slight swelling on its dorsal surface corresponding to the 'button' structure figured by Hussakof and Bryant (1918, pl. 44, fig. 3A, B). Two other examples (from near the left margin of the anterior end of piece *b*) have a slight depression here, and an elongate opening slightly larger than surrounding pores in the basal tissue (text-fig. 3C). A corresponding large pore is seen in examples of *Phoebodus politus* Newberry figured by Gross (1973, pl. 34, figs. 13*a*, 14, 16, 21). In most instances the curvature of the cusps on these teeth in relation to the morphology of the root could not be determined because of incomplete preservation. However, in the examples illustrated in text-fig. 3B and Pl. 87, fig. 1, there is no doubt that the cusps curved to the lingual side. The opposite curvature is indicated for other teeth referred below to *Xenacanthus* sp.

None of these teeth has been sectioned, but several broken examples show the cancellous basal tissue occupying the core of the lower part of the cusp, and surrounded by a compact lamellar tissue, presumably dentine. Above this a thin pulp cavity extends to the tip of the cusp.

Teeth in the Bunga Beds material (text-fig. 4) are all of similar size and form, but less well preserved. Invariably the original tissue has disappeared and they have been studied using latex rubber moulds. Of the ten teeth studied, CPC 21195 and 21200 show clearly at least one small intermediate cusp, possibly flanked by additional, more diminutive cusps. In CPC 21198 the concave ventral surface of the base, the curvature of the cusps, and the extent of the lingual torus are all well shown (text-fig. 4A, B, C). The concave base is also seen in CPC 21196, and CPC 21201 shows a swelling on the dorsal surface of the torus similar to that described above. Only one tooth (CPC 21195) shows striations on the cusps, but their absence may be attributed to the inferior preservation, and no other significant differences from the teeth in the Antarctic material are apparent.

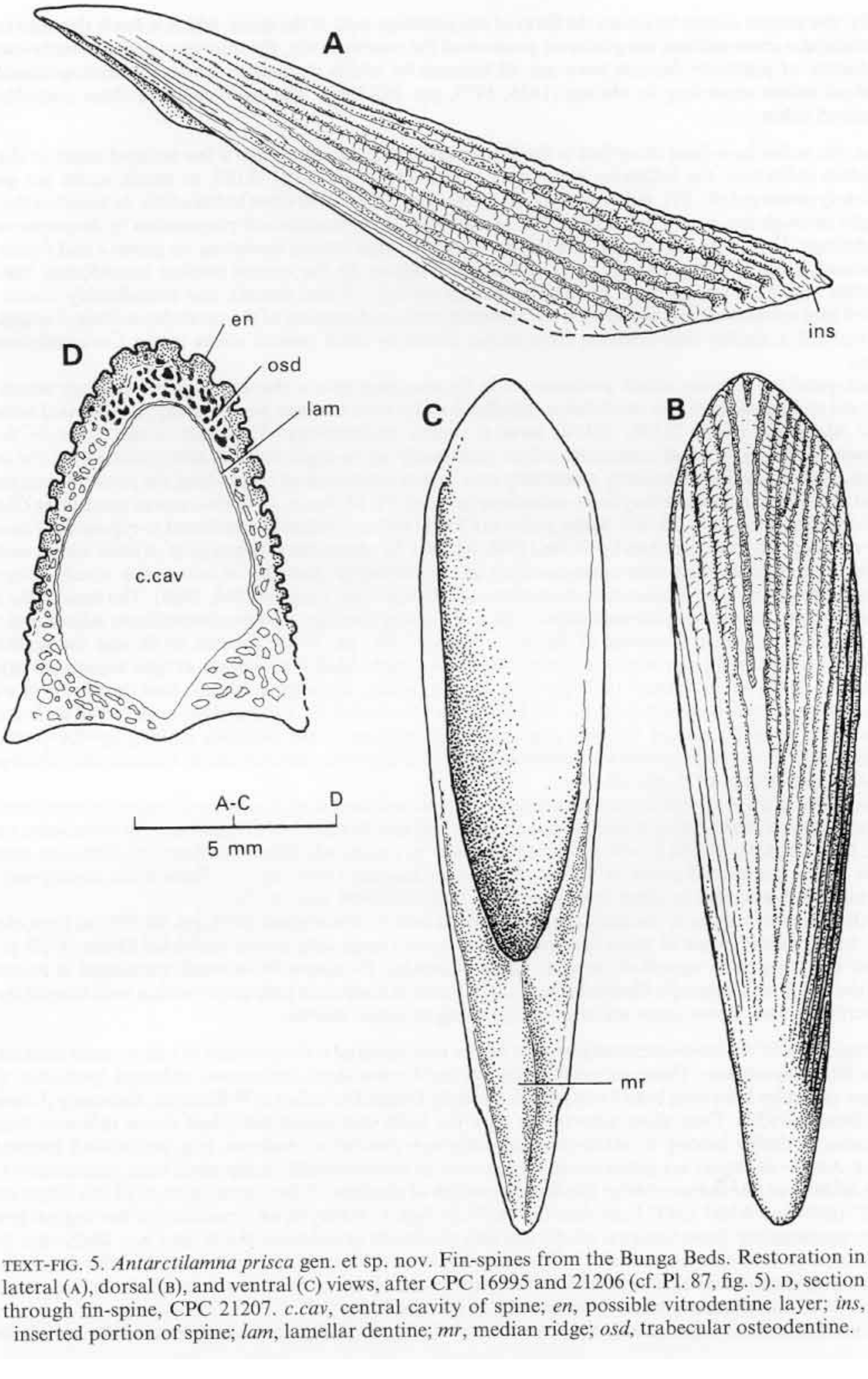
*Fin-spines*. Teeth of the diplodont form just described have long been recognized to belong to a shark bearing a single, barbed cephalic spine of the type named *Xenacanthus* by Beyrich (see Woodward 1889, p. 2). These spines are elongate, straight, subcircular to subelliptical in cross-section, and bear two rows of denticles (e.g. Davis 1880). Similar spines, but lacking the denticle rows, were named *Anodontacanthus* by Davis (1881), although Traquair (1888) pointed out that the absence of denticles in this case could be attributed to wear. The earliest recorded xenacanth spine, also named *Anodontacanthus*, came from the Middle-Upper Devonian 'Genesee conodont bed' (Andrews *et al.* 1967, p. 667), and Hussakof and Bryant (1918, p. 157) commented that the occurrence with *Dittodus* teeth from the same horizon was to be expected, such teeth also being recognized as belonging to xenacanth sharks.

It is of some interest therefore that the spines described below are of completely different form, resembling in several respects those of another group of early sharks, the ctenacanths. That the teeth and spines described here belong to one species is established by the spine in CPC 21187 (text-fig. 2), which, although somewhat flattened, has the same short, broad form as disarticulated spines in the Bunga Beds material. The latter are well represented in the collection, and provide the basis for a fairly complete description of fin-spine morphology. All are relatively short and broad, with little curvature (text-fig. 5; Pl. 87, figs. 3, 4). They are readily distinguished from early North American examples of ctenacanth spines, which are more slender (e.g. *Ctenacanthus wrighti* Newberry, 1889, pl. 26, fig. 4), or slender and curved (e.g. *C. nodocostatus* Hussakof and Bryant 1918, pl. 51, fig. 1). However, a similar overall form is shown by a recently figured spine with ctenacanth ornament from the Eifelian of Iran (Blieck *et al.* 1980, pl. 1, fig. 20).

All spines bear strong longitudinal costae, which when well preserved and unworn exhibit the cone-in-cone type ornament characteristic of ctenacanths. In detail the ornament shows some variation, with the separation of nodes along each costa approximating their width in the holotype and CPC 21192, but being more widely spaced in another spine fragment from Antarctica (Pl. 87, fig. 2). The Bunga spines show less variation, but are generally more poorly preserved. However, in CPC 21204 the ornament is well shown (Pl. 87, fig. 5), and appears identical to that on the spine of the holotype. In many specimens the costae are worn down to a smooth area on the anterior margin near the tip of the spine (text-fig. 5B). The number of costae varies considerably; in 11 spines from Bunga there may be as few as about 15 or as many as 26 costae per side, reducing to between 6–10 near the tip of the spine. Costae near the posterolateral borders of the ornamented area become much finer and more closely spaced. Similar variation is indicated in the Antarctic material, with about 16 costae on one side of CPC 21192 but at least 25 on the spine of CPC 21187. There is some coalescence of costae along the anterior margin (e.g. CPC 21192, 21206), but they are otherwise fairly continuous. Typically there is a very narrow zone of insertion along the spine base (*ins*, text-fig. 5A), again a point of resemblance to the figured specimen from Iran, and clearly different in this respect from other ctenacanthiform spines. The spine must have been only loosely attached in the skin, as in *Cladoselache* (see Harris 1938). This was probably the primitive condition. However, in two Bunga specimens (CPC 21205, 21208) the inserted portion of the spine is more extensive (Pl. 87, fig. 3), and it is likely therefore that there were spines anterior to both dorsal fins, the posterior being more deeply inserted into the body musculature. In all spines examined the edge of the inserted portion makes a fairly constant angle (about 35°) with the anterior border of the spine.

The posterior surface of the spine is well displayed in CPC 16995, and is partly visible in CPC 21206. It is slightly concave, with elevated lateral rims (text-fig. 5C), and a low median ridge extending from near the tip to the distal end of the basal opening. In CPC 21206 the ridge is sufficiently prominent to be visible in lateral view. The basal opening occupies about 50% of the length of the spine in CPC 16995, and slightly more (about 60%) in CPC 21206. There is no sign of posterior denticle rows, said to be typical of ctenacanth and sphenacanth spines by Woodward (1889, p. 241; but cf. Maisey 1978, p. 658).

A section through a spine associated with CPC 21206 was exposed in trimming this specimen with a saw (text-fig. 5D). It may be an oblique section, passing through the spine probably just above the basal opening, but nevertheless indicates the triangular form seen in some (but not all) ctenacanth spines (Maisey 1977, p. 265; cf. Newberry 1889, pl. 26, fig. 1). Blieck *et al.* (1980, p. 146) have commented that the elasmobranch spines from Iran are atypical in their 'rounded anterior edge', and this could also be said of the spines described here. The hard tissue of the sectioned spine is partly weathered, but some significant features can be made out. Lining the large central cavity (*c.cav*) is a thin compact layer (*lam*), presumably the lamellar inner layer of dentine reported by Maisey (1977, p. 263) to occur distally in ctenacanth spines. Surrounding this is a zone of trabecular osteodentine traversed by numerous canals, many of which have a thin lining of compact tissue similar in appearance and its whitish colour to the lamellar lining of the central cavity. The trabecular structure extends into the costae, although these are differently stained (indicated by stippling in text-fig. 5D). Whether this differential staining indicates outer and inner osteodentine zones is uncertain, and needs confirmation on better material. A thin dark outer layer (*en*) is interpreted as vitrodentine investing the surface of the costae and the intercostal furrows.



TEXT-FIG. 5. *Antarctilamna prisca* gen. et sp. nov. Fin-spines from the Bunga Beds. Restoration in lateral (A), dorsal (B), and ventral (C) views, after CPC 16995 and 21206 (cf. Pl. 87, fig. 5). D, section through fin-spine, CPC 21207. *c.cav*, central cavity of spine; *en*, possible vitrodentine layer; *ins*, inserted portion of spine; *lam*, lamellar dentine; *mr*, median ridge; *osd*, trabecular osteodentine.

Finally, the section clearly indicates the form of the posterior wall of the spine, which is fairly thin and concave. The triangular cross-section, the posterior position of the central cavity, the thinner concave posterior wall, and the absence of posterior denticle rows are all features by which ctenacanth spines are distinguishable from hybodont spines according to Maisey (1975, 1977, pp. 263–265). The significance of these resemblances is considered below.

*Scales.* No scales have been identified in the Bunga material, and apart from a few isolated scales in the Portal Mountain collection, the following account is based entirely on CPC 21187, in which scales are generally excellently preserved (Pl. 87), although detail is often obscured by their close imbrication. In addition the nodule has split through the interior of most scales, necessitating some mechanical preparation to determine external morphology. The scales vary in size, the largest (about 1·5 mm across) occurring on pieces *e* and *f* (text-fig. 2), presumably from the dorsolateral parts of the trunk region. In the ventral midline immediately behind the branchial region on piece *b* they are slightly smaller (about 1·3 mm across), and considerably smaller scales (0·5–0·9 mm across) are associated with the scattered teeth and remains of the ceratobranchials. Zangerl (1968) has recorded a similar size-variation from larger dorsal to small ventral scales in the Carboniferous shark *Orodus*.

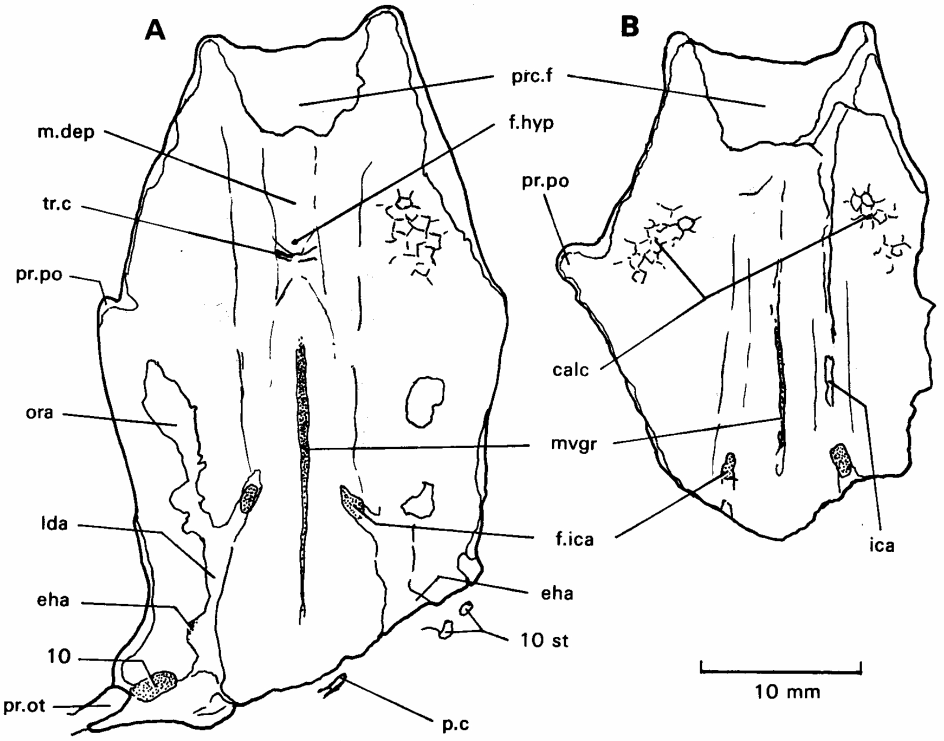
The typical trunk scales which predominate in the specimen have a characteristic morphology which is well displayed on both sides of two small flakes (labelled *h* and *j*) from between pieces *e* and *f*. The isolated scales from Portal Mountain (CPC 21188, 21190) have a similar morphology. The scale crown is fairly flat, and ornamented with a series of concentric ridges (commonly six to eight on each side) arising near the anterior margin, and converging posteriorly where they may be extended as short cusps along the posterior margin (text-fig. 2B). Anteriorly the ridges may carry subsidiary grooves (Pl. 87, figs. 6, 7), in this respect resembling *Cladolepis* scales (see Gross 1973, pls. 31–33). Many scales in CPC 21187 are broken or weathered to expose their concentric inner structure, as first described by Gross (1938, fig. 5M). In others the separate pulp cavities within each ridge are clearly seen, the ridges thus corresponding to the individual denticles or odontodes which make up the composite scales of other Palaeozoic elasmobranchs (Ørvig 1966; Zangerl 1966, 1968). The base of the scale is not well shown, but sections through imbricated scales along the edge of piece *e* immediately adjacent to the fin-spine (text-fig. 4F) are reminiscent of Zangerl's figure (1968, fig. 2) for *Orodus*. In *Orodus* the scale base is described as comprising two bony projections which were embedded in the dermis at right angles and parallel to the surface of the skin (Zangerl 1968, p. 401). In these scales, however, it is clear that the base was a deeply concave, cup-shaped structure (text-fig. 4E; Pl. 89, fig. 6) attached by a constricted neck to the scale crown. A central pore possibly opened into the coalesced pulp cavities of the denticles making up the crown. This morphology is in marked contrast to the thickened cushion-like base seen in scales of *Protacrodus*, *Ohiolepis*, and *Cladolepis* (e.g. Gross 1973, pls. 30–32).

In addition to these typical trunk scales there are a small number of other scales with more discrete denticles on the crown, which seem to be restricted to the gill-arch and mouth region of the specimen. In these scales (text-fig. 2C, D; Pl. 87, figs. 9, 10) the crown comprises a cluster of posteriorly directed, finger-like denticles, somewhat similar to the compound scales of *Orodus* figured by Zangerl (1968, fig. 1). These must correspond to the branchial teeth described in other xenacanths (e.g. Glikman 1964, figs. 21, 22).

Nothing exactly similar to the dermal tubercles described by Woodward (1921, pp. 56–57) has been identified in the new material. Some of these were reported to have a large pulp cavity, which led Gross (1950, p. 72) to suggest that they were agnathan remains (psammosteids). In others Woodward mentioned a microscopic structure which was 'typically Elasmobranch', with traces of a separate pulp cavity within each cusp of the scale, as described above. These latter scales possibly belong to *Antarctilamna*.

*Braincase.* One of the more interesting aspects of this new material is the presence of endocranial remains in the Bunga Beach specimens. These are perhaps the earliest known shark braincases, although (probably) slightly younger examples have long been known from the early Upper Devonian of Wildungen, Germany (Gross 1937, 1938; Stensiö 1937). Their close association with the teeth and spines described above indicates that these braincases probably belong to *Antarctilamna*, although conclusive evidence (e.g. articulated specimens) is lacking. All five examples are preserved in ventral view as dorsoventrally compressed casts, presumably formed by the infilling of fine sediment after the decomposition of cartilage. A hexagonal pattern of fine ridges on parts of CPC 16994 and ANU 35333 (*calc*, text-fig. 6B; Pl. 88, figs. 1, 5) may be an impression of the original prismatic surface calcification. Some internal canals are also preserved as sediment infills, and it is likely that detailed information on internal structure will be forthcoming when additional specimens are available for study. Such detailed preparation and examination is beyond the scope of this preliminary account, but some attempt has been made to interpret canals and foramina visible externally.

The most informative specimen is ANU 35333 (text-fig. 6A; Pl. 88, fig. 1), in which all the endocranial processes

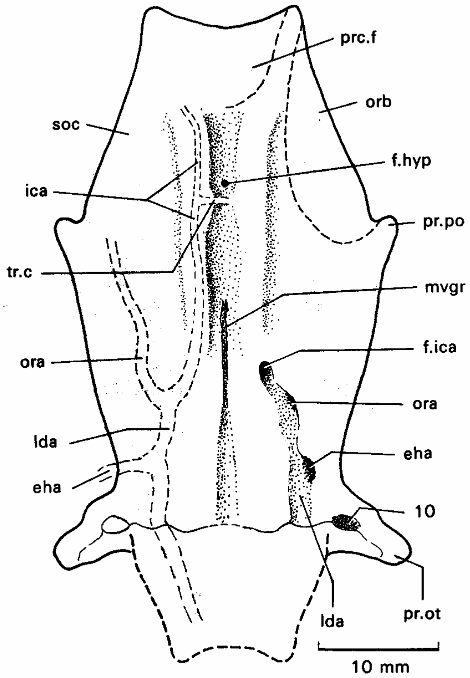


TEXT-FIG. 6. *Antarctilamna prisca* gen. et sp. nov. Braincases from the Bunga Beds in ventral view. A, ANU 35333 (cf. Pl. 88, fig. 1); B, CPC 16994 (cf. Pl. 88, fig. 5). *calc*, impressions of prismatic calcified cartilage; *eha*, canal for efferent hyoidean artery; *f.hyp*, possible buccohypophysial foramen; *f.ica*, foramen or canal for internal carotid artery; *ica*, canal for internal carotid artery; *lda*, canal or groove for lateral dorsal aorta; *m.dep*, median depression; *mvgr*, median ventral groove; *ora*, canal for orbital artery; *p.c*, canal, possibly for a spino-occipital nerve, or for the occipital artery; *prc.f*, precerebral fontanelle; *pr.ot*, lateral otic process; *pr.po*, postorbital process; *tr.c*, canal possibly connecting the internal carotid canals of each side; *10*, foramen, possibly for vagus nerve; *10 st*, foramina, possibly for the supratemporal branch of the vagus nerve.

of one side are preserved. In this and another specimen (Pl. 88, fig. 5) an anterior notch is assumed to represent the precerebral fontanelle (*prc.f*, text-figs. 6, 7), its floor having broken away. The right postorbital process is clearly preserved in both specimens (*pr.po*, text-fig. 6), and in ANU 35333 there is also the remnant of a prominent lateral otic process (*pr.ot*). The ventral midline of the braincase is marked by a deep groove (*mvgr*) separating conspicuous paired foramina near the posterior end (*f.ica*). Each foramen lies at the anterior end of a shallow groove extending from the posterior preserved margin (the nature of the preservation suggests that this groove may in part have been a canal which has lost its thin ventral wall). A pair of low ridges extend anteriorly from these foramina, separated by a shallow median depression in which a possible buccohypophysial foramen has been identified in ANU 35333 (*f.hyp*, text-fig. 6A). That these ridges contain paired canals extending almost to the precerebral fontanelle is shown by CPC 16994 and 21211 (text-fig. 6B; Pl. 88, fig. 5; Pl. 89, fig. 5), where the canal floor has broken away. CPC 21211 shows a large lateral branch behind the main foramen, also seen on the right side of ANU 35333 (left side of Pl. 88, fig. 1), whilst on the left side of ANU 35333 a more posterior lateral branch is indicated (*eha*, text-fig. 6A).

This canal system can only be for the paired lateral dorsal aorta and its various branches. The partial enclosure of these arteries in the braincase floor is probably a primitive gnathostome feature (e.g. Gardiner 1973, p. 111), and the condition has been noted in many Palaeozoic elasmobranchs (Romer 1964; Schaeffer 1967). In such forms, however, the main arteries derived from the lateral dorsal aorta (the efferent hyoidean and orbital arteries) normally emanate from the anterior end of a fairly long aortic canal, and a considerable distance in front of the occiput (e.g. Schaeffer 1981, fig. 12). In contrast, ANU 35333, which is the only specimen with an apparently natural posterior margin partly preserved, has these branches located near the posterior end of the main length of aortic canal. This condition could be due to the relatively long otic and almost completely reduced occipital segment of the braincase in this form. Nevertheless, these branches are similarly placed, relative to the postorbital and otic processes, to those figured for *Xenacanthus* by Schaeffer (1981, fig. 12A), and since even in early elasmobranchs with the otico-occipital region reduced (e.g. *Cladoselache*) the occipital segment projects out behind the otic processes, I suggest that the occipital segment has been lost from this specimen. In *Tamiobatis*, Romer (1964, p. 97) noted a break in surface calcification at the base of the otic process, and a similar condition may have obtained in *Antarctilamna*. An occipital segment has been restored in text-fig. 7. The reconstruction is generally comparable in overall proportions to that for *Xenacanthus*, but with a broader otic region behind the postorbital processes (which are less prominent), and with more pronounced subocular shelves, of similar extent to those illustrated for *Tristychius* by Dick (1978, fig. 9). *Antarctilamna*, *Xenacanthus*, *Tamiobatis*, and '*Cladodus*' *wildungensis* resemble each other in the relatively elongate otic region, a resemblance which has been interpreted as phylogenetically significant by Schaeffer and Williams (1977).

A few other canals and foramina have been noted in the material. ANU 35333 shows a trace of a narrow transverse canal (*tr.c*) passing behind the assumed buccohypophysial foramen. A swelling in this region connecting the paired longitudinal ridges suggests a median confluence of canals, perhaps to give an arrangement for the internal carotids like that figured by Schaeffer (1981, fig. 12). A fairly large ventral foramen in the base of the otic process may be for the vagus nerve (*10*, text-figs. 6A, 7), and surrounding cracks may be remnants of a ventral otic notch (cf. Schaeffer 1981, fig. 6). A canal on the broken posterior edge of ANU 35333 (*p.c*, text-fig. 6A) may have carried a spino-occipital nerve, or perhaps the occipital artery,



TEXT-FIG. 7. *Antarctilamna prisca* gen. et sp. nov. Partial reconstruction of the braincase in ventral view. Dashed lines on the right side indicate the probable extent of the precerebral fontanelle and left orbital cavity. A groove is restored for the left lateral dorsal aorta, as preserved in all available specimens, but this artery may have been contained in a canal in the braincase floor. Assumed course of major arteries indicated by dashed lines on the left side of the figure: *orb*, orbital cavity; *soc*, subocular shelf; for other abbreviations see text-fig. 6.

and two smaller canals (*10 st*) passing dorsally through the otic process are in the appropriate position for the supratemporal branch of the vagus nerve.

The material provides little information on the structure of the dorsal surface of the braincase. As noted above, the extent of the precerebral fontanelle is well shown (text-fig. 6), whilst the anterior extremity of the left orbital cavity is partly indicated as an impression in CPC 16994. The probable configuration of these structures is shown by dashed lines in text-fig. 7 (right side). A final point is that the extensive subocular shelf indicated in ventral view for *Antarctilamna* suggests an interorbital region which was narrower dorsally than ventrally, as in *Tristychius* (see Dick 1978, fig. 9), and unlike *Xenacanthus*, *Tamiobatis*, and '*Cladodus*' as figured by Schaeffer (1981).

*Jaws and visceral arches*. Apart from the traces of ceratobranchials in CPC 21187 (text-fig. 2), no other remains of jaws or visceral arches have been identified in the Antarctic material. In the Bunga collection, however, there are impressions of various shapes and sizes which lack dermal ornament, and therefore may be elasmobranch remains. Many are fragmentary, and no positive branchial arch elements have been identified, but two specimens are tentatively determined as remains of the palatoquadrate. CPC 21212, preserved in part and counterpart, provides information on the morphology of the postorbital ramus and mandibular joint (text-fig. 8A, B, D; Pl. 88, figs. 2, 3), although the suborbital ramus is unfortunately missing. The configuration of the ventral margin on the preserved portion, concave posteriorly with a blunt protuberance (*v.pr*) towards the palatine region, corresponds well with the form of the palatoquadrate in *Xenacanthus* (Hotton 1952, pl. 58). The second specimen (CPC 21213) is less clearly preserved, being intimately associated with other undeterminable remains (possibly elasmobranch), and also badly fractured. As interpreted here (text-fig. 8C) it shows a fairly long postorbital, and short suborbital ramus, in total proportions being more elongate than previously figured xenacanth palatoquadrates (e.g. Hotton 1952; Moy-Thomas and Miles 1971, fig. 9.12). Better preservation is required for these apparent differences in palatoquadrate shape to be assessed properly, and for the present both examples are assumed to be conspecific with the other elasmobranch material from this locality.

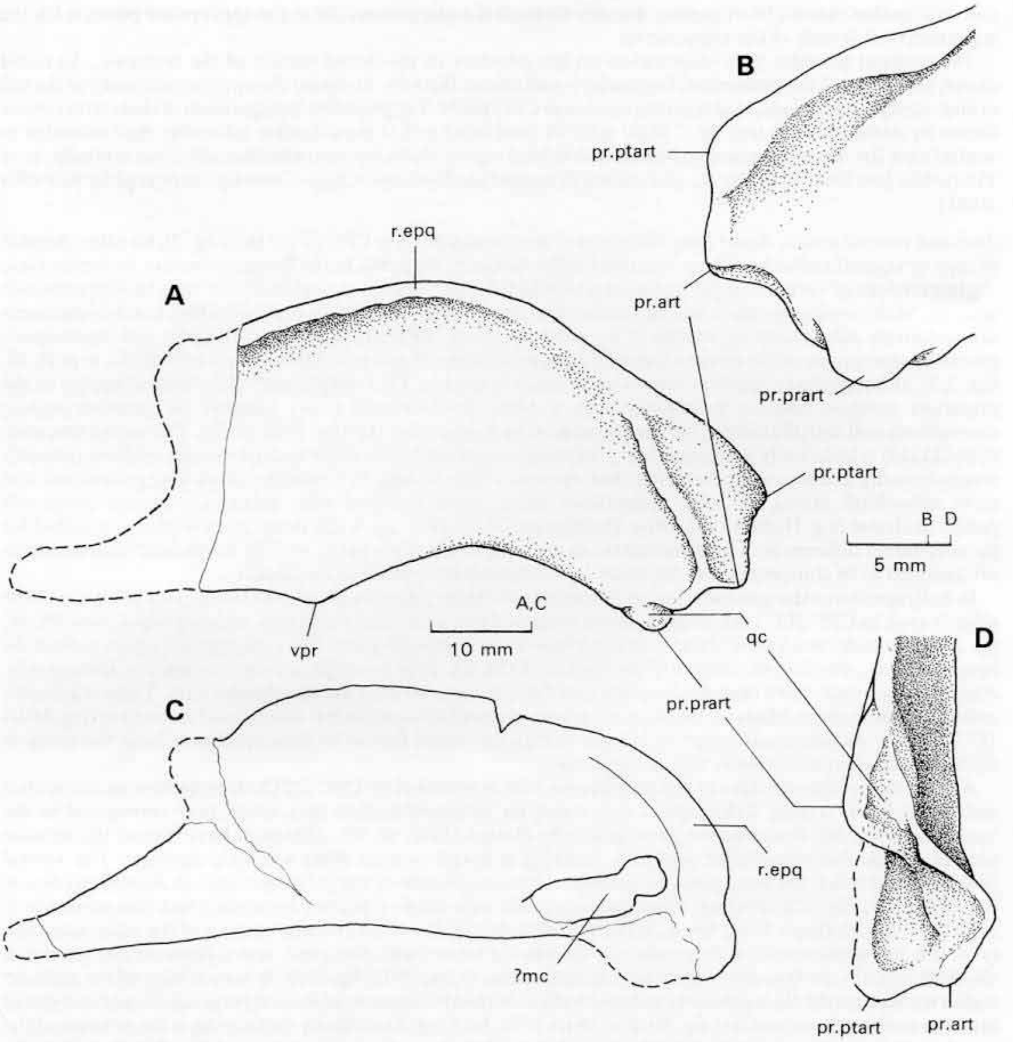
In both specimens the quadrate part of the cartilage is heavily developed, with a strong extra-palatoquadrate ridge (*r.epq*). In CPC 21212 this ridge is carried posteriorly on a rounded expansion, which in mesial view (Pl. 88, fig. 3) is seen to form a distinct concavity just above the mandibular joint. This concavity may have carried the hyomandibula, which is reconstructed by Hotton (1952, fig. 1) in a corresponding position for *Xenacanthus*. Alternatively, it may have been the insertion area for ligaments binding the mandibular joint. There is a similar groove for the hyomandibula on the palatoquadrate of acanthodians, but it is more dorsal in position (e.g. Miles 1973, fig. 12). As previously noted by Hotton (1952), the dental furrow in these specimens lacks the series of shallow vertical grooves seen in '*C.*' *wildungensis*.

A good idea of the structure of the mandibular joint is provided by CPC 21212. A projection on the ventral margin (*pr.prart*, text-fig. 8A) carries a depression on its lateral surface (*qc*), which may correspond to the 'quadrate concavity' described for *Xenacanthus* by Hotton (1952, pl. 58). This must have formed the anterior part of the double mandibular joint, by receiving a dorsal process from Meckel's cartilage. The ventral projection has much the same position as the prearticular process of the palatoquadrate in *Acanthodes bronni* (see Miles 1973, fig. 12), although other elasmobranchs with the double joint apparently lack this process (e.g. Allis 1923, fig. 29; Gross 1938, figs. 1, 3; Hotton 1952, fig. 1). The main articular process of the palatoquadrate (*pr.art*) is less pronounced in *Antarctilamna* than in the other forms just cited, and a postarticular process is visible in mesial view (*pr.ptart*), again as in acanthodians (Miles 1973, fig. 12B). A ventral view of the articular region emphasizes the close similarity to acanthodians in the arrangement of these three processes and associated articular surfaces (compare text-fig. 8D, and Miles 1973, fig. 13B). Particularly noteworthy is the position of the anterior articular depression (*qc*) on the lateral face of the prearticular process, as Miles has described. By contrast, this articulation in other elasmobranchs (Allis 1923; Gross 1938; Hotton 1952) lies on the mesial face of the palatoquadrate. Since the palatoquadrate of *Antarctilamna* is probably the oldest known example of this element in elasmobranchs, such a resemblance could be regarded as having phylogenetic significance (see Jarvik 1977; cf. Miles 1973, p. 72). This is considered further below. The corresponding region in CPC 21213 is obscured by a superimposed impression, possibly the posterior end of Meckel's cartilage (*?mc*, text-fig. 8B).

## Genus XENACANTHUS Beyrich
## *Xenacanthus* sp.

Plate 89, figs. 1–4; text-fig. 3E–G

1972 'tooth (which)... resembles the diplodont... teeth found in *Xenacanthus*'; Ritchie *in* McKelvey *et al.*, p. 351.



TEXT-FIG. 8. *Antarctilamna prisca* gen. et sp. nov. A, lateral view of left palatoquadrate, CPC 21212 (cf. Pl. 88, fig. 2). B, D, mesial and ventral views of the articular region of the palatoquadrate showing the mandibular joint, after CPC 21212. C, lateral view of possible left palatoquadrate, CPC 21213. ?*mc*, superimposed impression, possibly part of Meckel's cartilage; *pr.art*, articular process; *pr.prart*, prearticular process; *pr.ptart*, postarticular process; *qc*, quadrate concavity; *r.epq*, extra-palatoquadrate ridge; *v.pr*, ventral protuberance.

*Material*. Eighteen isolated teeth from Portal Mountain (CPC 21214–21217; AMF 54329–54331, 55573), and one (CPC 21228) from near Mt. Ritchie, south Victoria Land, Antarctica.

*Remarks*. These teeth may be distinguished from the smaller diplodont teeth described above on the following characters: the equal size of cusps, their curvature in different planes, and in a labial rather than a lingual direction, the absence of central cuspules, and the deeper, more bulbous base. There are no large ctenacanthiform spines at the Portal locality, where most of these teeth were found, and it is assumed for the present that two genera with diplodont teeth were represented in the Antarctic fauna. By their combination of characters these teeth may also be distinguished from previously described species of *Xenacanthus*, but in the absence of other remains (e.g. barbed cephalic spines) they are left for the present in open nomenclature.

*Description.* These teeth are known only from Portal (two horizons) and near Mt. Ritchie (Section A5). They are most common from the lower horizon in the Portal section, from where they were first recognized by Ritchie (in McKelvey *et al.* 1972). They differ in several respects from the teeth in CPC 21187. They are larger (between 3·5 and 8·0 mm across the base), the height of the biggest example (CPC 21218) being estimated at 11 mm. In addition the base is noticeably more extensive and bulbous relative to the length of cusps, the cusps are less slender and slightly shorter, and instead of being of similar proportion one cusp is considerably longer and larger than the other. However, according to Hotton (1952, p. 496) at least two of these features (proportionately larger base and less slender cusps) may vary with size within a species.

Each cusp is rounded in section distally, but proximally the (assumed) lingual face is flattened, and separated from the more rounded side of the cusp by a fine ridge continuous between cusps (*ri*, text-fig. 3F). This probably formed a cutting edge, as in the teeth of *Antarctilamna* described above. In two examples with the surface of the cusps well preserved, the flattened side is smooth (Pl. 89, fig. 1) but the opposite side carries several vertical striations (Pl. 89, fig. 4). By comparison with *Antarctilamna* it may be assumed for the purpose of description that the smooth side is lingual and the striated side labial. Thus oriented, however, the teeth differ from those of *Antarctilamna* in that the cusps apparently curve towards the opposite (labial) side (Pl. 89, fig. 2; cf. text-fig. 3D). In addition, each cusp is curved in a slightly different plane, giving them a twisted appearance in dorsal view (Pl. 89, fig. 3). As first noted by Ritchie (*in* McKelvey *et al.* 1972), there is consistently no small middle cuspule in these teeth, although this is reported to be variable in other species (e.g. *X. texensis* and *X. compressus*; see Hotton 1952, p. 497). The morphology of the base in both lingual and labial views is well shown in two specimens. CPC 21219 and several other specimens exhibit a notch in the basal margin (text-fig. 3E, F) similar to that figured by Hotton (1952, fig. 2B) for *X. depressus*. This expanded side of the base is assumed for the purpose of description to correspond to the lingual torus of other forms, although in an antero-posterior view (Pl. 89, fig. 2) the cusps are not clearly situated closer to the labial margin (cf. Hotton 1952, p. 495 n.). In CPC 21215 there is a large pore above the notch corresponding to the similar pore on the lingual torus in *Antarctilamna*. On the (assumed) labial side the basal margin is concave (Pl. 89, fig. 4), with no sign of the basal tubercle figured by Hotton (1952). Nor is there any sign of an apical button on the lingual torus.

### Genus MCMURDODUS White

### *Mcmurdodus*? cf. *featherensis* White

Plate 88, fig. 4; text-fig. 3H

*Material.* One tooth (CPC 21229) from Mt. Ritchie, south Victoria Land, Antarctica.

*Remarks.* This tooth is twice the size of the holotype of *M. featherensis*, and is generally dissimilar (White 1968, fig. 1; pl. 1, fig. 6). However, both teeth are of elongate compressed form, with the larger lateral cusps separated by a long cutting edge, and minor cusps at one or both ends of the tooth. The main difference is the almost horizontal direction of the cusps in White's specimen, and its thin root, but the latter feature may be an artefact since the exposed root surface is abraded. White tentatively referred his tooth to the notidanoids, which are otherwise unknown in Palaeozoic rocks (although an early differentiation of this group has been suggested; see Patterson *in* Andrews *et al.* 1967). However, the tooth referred here to the genus shows no resemblance to other hexanthid teeth, so one or other assignment is probably incorrect. It may be significant that both teeth come from near the top of the Aztec Siltstone, and for the purpose of description this tooth is tentatively compared with the type species of *Mcmurdodus* on the basis of the resemblances listed above.

*Description.* CPC 21229 is 10 mm across the base, which is partly broken away but preserved as a clear impression. The smaller of the two main cusps is incomplete and its original size and shape uncertain. Noteworthy features of the tooth are the wide separation of the major cusps, the prominent striations, the development of a serrated irregular cutting-edge between the lateral cusps, and the minor cusp developed at one end (right side of text-fig. 3H).

## DISCUSSION

This new material shows that several elasmobranchs were established in freshwater environments of East Gondwana towards the end of Middle Devonian time, and at least one of these (*Antarctilamna prisca*) possessed both diplodont teeth and ornamented dorsal fin-spines. Teeth of this type are characteristic of the xenacanth sharks, which are well known especially from Carboniferous and Permian freshwater deposits, but do not bear fin-spines. It has been suggested, however (e.g. Glikman 1964; Schaeffer and Williams 1977), that the characteristic cephalic spine of xenacanthids may be a modified and transposed fin-spine, and this would appear to be confirmed by this new material. I suggest that *Antarctilamna* is immediately related to *Xenacanthus*, on the basis that diplodont teeth are a synapomorphy, and that dorsal fin-spines are plesiomorphic. The proper assignment of the other teeth referred above to the genus *Xenacanthus* will depend on the discovery of associated material exhibiting other specializations of the genus (e.g. a cephalic spine, biserial pectoral fins, diphycercal tail, elongate dorsal and double anal fins, etc.).

Fin-spines also occur in several other groups of early elasmobranchs, and they have variously been regarded as a primitive feature for the whole group (e.g. Patterson 1965, p. 197; Schaeffer 1967, p. 13), for chondrichthyans generally, or possibly for all gnathostomes except placoderms (Schaeffer and Williams 1977, p. 294). Patterson (1965) commented that the spines of elasmobranchs and holocephalans are similar structures which have arisen and evolved in the same way, whilst Schaeffer and Williams (1977) have implied that the primitive condition for both holocephalans and elasmobranchs was probably a single spinose dorsal fin (cf. Patterson 1965, p. 197). However, most early elasmobranchs known to have a single dorsal fin lack fin-spines, and those with fin-spines, where known, generally have two spinose dorsal fins. The relevance to this problem of the new information provided by *Antarctilamna* can only be considered within the context of a hypothesis of its relationships to other early elasmobranchs.

As just noted, the teeth of *Antarctilamna* may be taken to indicate an immediate relationship to *Xenacanthus*. However, the origin and relationships of the xenacanthids themselves are obscure, and under the grade concept of elasmobranch evolution elaborated by Schaeffer (1967; also Zangerl 1973) they have been regarded as a highly specialized offshoot of the basal elasmobranch stock. Because of their poor fossil record (mainly isolated teeth and spines), the early history of elasmobranchs generally has been viewed only in terms of evolutionary grade. Recently, however, attempts have been made to move towards a more phylogenetic approach to their early diversification. Maisey (1975, p. 558) suggested that 'phalacanthous sharks belong to a single phyletic unit within the elasmobranchs', and he proposed a subdivision of this unit into three groups (Euselachiformes, Hybodontiformes, and Ctenacanthiformes). He further argued (Maisey 1975, 1977, 1978; cf. Schaeffer 1967; Moy-Thomas and Miles 1971), mainly on the basis of fin-spine structure, that the euselachians are more closely related to ctenacanthiform than to hybodont sharks (see also Schaeffer and Williams 1977). This has since been challenged by Dick (1978, p. 107), on the grounds that resemblances in fin-spine structure are no more than shared primitive features. A more explicit

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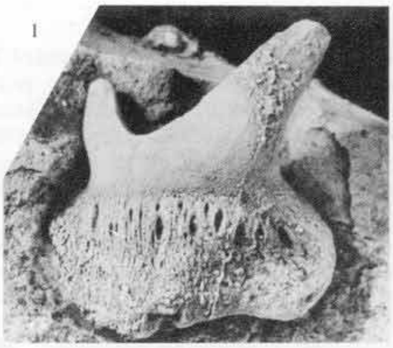
### EXPLANATION OF PLATE 89

Figs. 1–4. *Xenacanthus* sp. 1, 2, 3, isolated tooth (CPC 21219) in (assumed) lingual, antero-posterior and dorsal views (latex rubber cast), × 6. 4, isolated tooth (CPC 21218) in (assumed) labial view (latex rubber cast), × 6; all from Aztec Siltstone, Portal Mountain, south Victoria Land, Antarctica.

Figs. 5–8. *Antarctilamna prisca* gen. et sp. nov. 5, endocranial cast (CPC 21211) in ventral view, × 2. 6, portion of shagreen from piece *j* of the holotype (CPC 21187). Abraded scales are shown in the lower right corner; in the upper left corner scale crowns have broken off, to show impressions of the cup-shaped scale bases, × 16. 7, tooth in labial view from piece *a* of the holotype (CPC 21187), × 12. 8, isolated tooth (CPC 21198) in labial view (latex rubber cast), × 12. Figs. 5, 8 from Bunga Beds, Bunga Beach, south coast of New South Wales. Figs. 6, 7 from Aztec Siltstone, Lashly Mountains, south Victoria Land, Antarctica.

PLATE 89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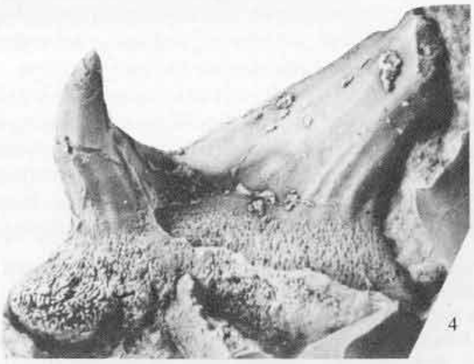
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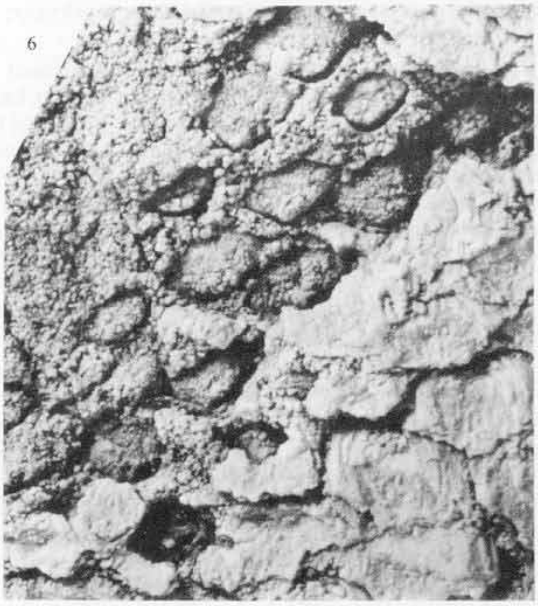
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7


8

YOUNG, *Xenacanthus* and *Antarctilamna* scheme of relationships for early elasmobranchs in the form of a cladogram was presented by Schaeffer and Williams (1977). They regarded xenacanthids (as represented by the genus *Xenacanthus*) to be the pleisomorph sister-group of other representative genera of early elasmobranchs (*Denaea*, *Cladoselache*, *Hybodus*, *Ctenacanthus*, *Palaeospinax*), which they united on the basis that the triangular basal portion of the pectoral fin is a derived feature. Schaeffer and Williams also followed Maisey in placing *Ctenacanthus* in closer relationship to *Palaeospinax* than is *Hybodus* (but cf. Schaeffer 1981).

Schaeffer and Williams (1977) acknowledged that their preliminary scheme of relationships would be subject to testing and emendment as new information became available, and on the new evidence of *Antarctilamna* an alternative scheme can be proposed. [Schaeffer (1981) has also put forward a modified scheme of relationships for some of the genera considered below, based mainly on braincase structure. This has not been considered in detail, but is generally compatible with conclusions reached here using other characters.] As previously noted, the fin-spine morphology of *Antarctilamna* is ctenacanthiform according to Maisey's criteria (see above), and using Schaeffer and Williams's (1977) cladogram, but with *Antarctilamna* and *Xenacanthus* as sister-groups, these resemblances would have to be independently acquired. Alternatively, one may accept Dick's (1978) arguments that the fin-spine resemblances between ctenacanths and euselachians are symplesiomorphies, and that the latter are more closely related to hybodonts, which has long been the traditional view. The two alternative schemes of interrelationship, incorporating the new evidence of *Antarctilamna*, are given in cladogram form in text-fig. 9. The following may be listed as unparsimonious consequences of Schaeffer and Williams's (1977) scheme (letters refer to text-fig. 9A):

(*a*) Independent acquisition of the ctenacanthiform type of fin-spine and teeth with an expanded lingual torus (Maisey 1975) in *Antarctilamna* and the common ancestor of *Ctenacanthus* and *Palaeospinax*.

(*b*) Independent loss of the metapterygial axis of the pectoral fin in *Hybodus* and *Palaeospinax*.

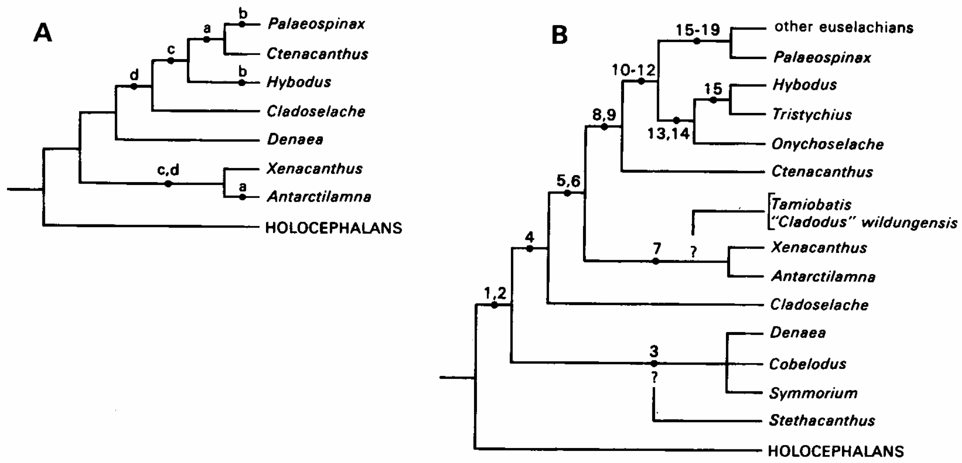
(*c*) Independent acquisition of an anal fin in *Xenacanthus* and the common ancestor of *Hybodus*, *Ctenacanthus*, and *Palaeospinax* (but Schaeffer and Williams 1977 suggest that its double structure in xenacanthids indicates separate derivation).

(*d*) Independent closure of the hyoidean gill slit in xenacanthids and the common ancestors of *Cladoselache*, *Hybodus*, *Ctenacanthus*, and *Palaeospinax* (assuming the condition described for *Cobelodus* is primitive; see below).

Unique specializations (autapomorphies) of the taxa shown on this cladogram are listed by Schaeffer and Williams (1977). They apparently regard the postaxial radials in the pectoral fin of *Xenacanthus* as a specialized feature, but this raises a difficulty because they elsewhere propose the long pectoral metapterygial axis as an elasmobranch autapomorphy, with this axis presumably lacking postaxial radials. It is thus not clear in what respect the pectoral fin shape given as a synapomorphy of all taxa above *Xenacanthus* in their cladogram differs significantly from the postulated primitive condition of the fin, and some other character is needed to unite these forms.

Under the new scheme of relationships proposed here (text-fig. 9B) these unparsimonious consequences are eliminated. It will be noted that this also applies to the cladogram based on braincase structure proposed by Schaeffer (1981), which, except in its treatment of '*Ctenacanthus*', generally conforms to that put forward here. Further to Schaeffer's new scheme, the genera *Tristychius*, *Onychoselache*, and *Cobelodus* have been included here on the basis of recent detailed description (Zangerl and Case 1976; Dick 1978; Dick and Maisey 1980). In addition, *Cobelodus*, *Symmorium*, and possibly *Stethacanthus* are shown as closely related to *Denaea* (Zangerl 1973; Schaeffer and Williams 1977), and *Tamiobatis* and '*Cladodus*' *wildungensis* are tentatively grouped with xenacanthids, on the assumption that the long otic region of the braincase is specialized. The synapomorphies supporting the scheme of relationships put forward here are as follows (numbers refer to text-fig. 9B):

1. Prominent metapterygial axis in the pectoral fin; palatoquadrates with palatine processes and symphysial connection.
2. Loss of pharyngohyal, and development of an articulation between the hyomandibula and the braincase (assuming the unmodified hyoid arch of holocephalans is primitive).



TEXT-FIG. 9. A, cladogram of elasmobranch interrelationships proposed by Schaeffer and Williams (1977), but with *Antarctilamna* included as the sister group of *Xenacanthus*. B, alternative scheme of interrelationships for certain elasmobranchs. For explanation of letters and numbers see text.

3. Loss of dorsal fin-spine, and development of a short deep neurocranium, and large orbits.
4. Two dorsal fins, each with an unornamented spine lacking an outer orthodentine coat.
5. Ctenacanthiform type of fin-spine, consisting mainly of osteodentine with little or no lamellar tissue, and an ornamented outer coat of orthodentine. Spine cross-section is triangular with a posteriorly placed central cavity, a thinner, flat-to-concave posterior wall, and no posterior ornament or denticles.
6. Evolution of an anal fin.
7. Braincase with elongated otic region, and large semicircular canals.
8. Fin-spines deeply embedded between the myotomes.
9. Tribasal pectoral fin.
10. Caudal fin not lunate.
11. Calcified ribs.
12. Pectoral metapterygial axis reduced or lost.
13. Hybodontiform type of fin-spine, oval in cross-section, with a centrally placed cavity and posterior denticle rows.
14. Teeth lacking a lingual torus.
15. Aplesodic pectoral fin.
16. Calcified centra.
17. Jaws sub-terminal and hyostylic.
18. Right and left halves of pectoral and pelvic girdles fused ventrally.
19. Smooth fin-spines, with clearly defined mantle and trunk components, the latter made up largely or completely of lamellar tissue.

Some remarks are required to elaborate on this list of characters. As noted by Schaeffer and Williams (1977), unique derived characters for the elasmobranchs as a whole are difficult to find, and the pectoral metapterygial axis is at present the only one they mention which has not been disputed. Miles (1973, p. 71) has suggested, however, that the symphysial connection between palatoquadrates, and their palatine processes, may also be elasmobranch specializations. With regard to character 2, the presence of an unmodified hyoid arch in ancestral elasmobranchs is implied both by the putative pharyngohyal in holocephalans, and by the different relationship of the hyomandibula to the lateral head vein and hyomandibular nerve in modern elasmobranchs and osteichthyans. However, both points are of disputed significance (e.g. Patterson 1965, p. 103 n.; Gardiner 1973, p. 109). Furthermore, Zangerl and Williams (1975) have suggested that in *Cobelodus* the hyoid gill-slit was still complete, even though the epihyal had developed an articulation with the braincase. Thus, it can be hypothesized on this evidence that all elasmobranchs lack a pharyngohyal, but whether this is a primitive gnathostome character, or an independently acquired specialization in elasmobranchs (or elasmobranchs plus another gnathostome group), is an unresolved question (see also Stahl 1980). Character 3 as used above was similarly treated by Schaeffer and Williams (1977), although Maisey (1975) previously suggested that the spine(s) of *Cladoselache* were acquired independently of other spinose forms (see also Zangerl 1973). The absence of a deeply inserted portion is here interpreted as a primitive feature shared with *Antarctilamna*, which, like *Cladoselache*, is assumed to have two dorsal fins and spines, although the evidence is not conclusive. As noted above, typical phalacanthous sharks have two dorsal fin-spines, although comparison with holocephalans suggests that a single spinose dorsal fin might be the primitive elasmobranch condition. Of relevance here is the inadequately known *Stethacanthus*, which is reported to have a single unornamented dorsal spine (Zangerl 1973; Lund 1974), and is tentatively suggested by Schaeffer and Williams (1977, p. 299) to be a sister taxon to the *Denaea* complex. If confirmed, this would indicate that the absence of a dorsal spine in *Denaea* and its close relatives is secondary, and would obviate the difficulty otherwise implied by the cladogram of text-fig. 9B, that the dorsal spines of elasmobranchs and holocephalans were independently acquired. The tribasal pectoral fin is shown as present in *Ctenacanthus* (character 9), although this is not so in Maisey's reconstruction (1975, fig. 5; cf. Zangerl 1973, p. 9). Finally, two anomalies are raised by the recent paper of Dick and Maisey (1980). First, they suggest (p. 372) that the reduced postorbital part of the palatoquadrate is a shared derived character of *Onychoselache*, *Tristychius*, Mesozoic hybodontids, *Palaeospinax*, and other neoselachians, but some Recent forms (e.g. Compagno 1977, fig. 2) show this to be invalid. Secondly, they describe the pectoral fins of *Onychoselache* as plesodic. But if the previous suggestion of Dick (1978, p. 107) is accepted, that the similar fin-spine of ctenacanths and early euselachians is a symplesiomorphy, it follows that the hybodontiform spine morphology must be specialized. This is unsatisfactory as it implies (text-fig. 9B) that the aplesodic fin must have evolved independently in the common ancestor of *Tristychius* and *Hybodus*, and in the common ancestor of *Palaeospinax* and higher euselachians. Using a similar type of argument, it is clear that the close resemblance mentioned above in the structure of the mandibular joint between *Antarctilamna* and acanthodians cannot be regarded as phylogenetically significant, since under either hypothesis of relationships this must have been acquired independently in the two groups.

Notwithstanding the above anomalies, and conditional upon confirmation that *Stethacanthus* both retains a single spinose dorsal fin and exhibits synapomorphies with *Denaea* and *Cobelodus*, I suggest that the cladogram of text-fig. 9B depicts a more parsimonious interpretation of early elasmobranch interrelationships than has previously been put forward. This interpretation incorporates the new information provided by *Antarctilamna*, and it implies that one of the three orders proposed by Maisey (1975), the Ctenacanthiformes, is paraphyletic. On the other hand, a close hybodontid/euselachian relationship is supported, and, as noted by Dick (1978), this suggests that euselachians had already differentiated by early Carboniferous time.

To conclude this discussion a brief comment should be made concerning some biogeographic aspects of the new elasmobranch occurrences dealt with here. There have recently been suggestions that early tetrapods (Panchen 1977; Janvier 1978*b*), and certain osteolepid fishes (Janvier, Termier and Termier 1979) and placoderms (Young 1981) had a Gondwanan origin. The new elasmobranch occurrences described here might indicate that xenacanths can be added to this list. There is little doubt that both the Bunga Beds and Aztec Siltstone sediments are non-marine, this being consistent with the accepted habitat of xenacanths, which are widely known from Carboniferous and Permian freshwater deposits. It could be suggested, therefore, that their early dispersal was limited by marine barriers, and that changed continental configuration permitted their geographic expansion during the Carboniferous and Permian. But the early North American occurrences of isolated diplodont teeth are in marine deposits, as are some of the elasmobranch remains from Iran and South America (Janvier 1978*a*, 1980), so such a simple hypothesis regarding their distributional history is unsatisfactory. Nevertheless, the Antarctic and south-east Australian occurrences, considered with reported 'ctenacanth' spines from several different localities and horizons in Iran, and other elasmobranch remains from South America (otherwise devoid of authenticated Devonian fish occurrences), certainly suggest that an important part of early elasmobranch evolution took place on the Gondwana continents. This has potential biogeographic significance, and when these new faunas have been studied in more detail they are likely to further modify current ideas regarding the early differentiation of major elasmobranch taxa. Such ideas have previously been based almost entirely on Northern Hemisphere occurrences.

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