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Sharks from the Middle–Late Devonian Aztec Siltstone, southern Victoria Land, Antarctica

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Abstract – Shark teeth representing three new taxa are described from the Middle-Late Devonian Aztec Siltstone of southern Victoria Land, Antarctica. *Portalodus bradshawae* gen. et sp. nov. is represented by large diplodont teeth which have a base with a well-produced labial platform. It occurs in the middle to upper sections of the Aztec Siltstone. *Aztecodus harmsenae* gen. et sp. nov. is represented by broad bicuspid teeth, wider than high, with numerous medial crenulations and twin nutritive foramina penetrating the rectangular base. It occurs in the middle sections of the Aztec Siltstone. The teeth of *Anareodus statei* gen. et sp. nov. are characterised by having a main cusp which is more than twice as high as the second cusp, a small cusplet developed on the outer cutting edge of the main cusp, sometimes with few crenulations developed in the middle of the two cusps, and the base is strongly concave. *Antarctilamna* cf. *prisca* Young, 1982 is also recorded from the middle and upper sections of the Aztec Siltstone above the thelodont horizons and occurring with phyllolepids and *Pambulaspis* in the Cook Mountains section south of Mt Hughes. The chondrichthyan fauna from the Aztec Siltstone now contains at least 5 species, being the most diverse assemblage of Middle Devonian chondrichthyans (based on teeth) from one stratigraphic unit.

INTRODUCTION

Fossil shark remains were first identified in the Devonian Aztec fish fauna of southern Victoria Land in the material collected from moraine at Granite Harbour, near the coast of McMurdo Sound, during the British Antarctic 'Terra Nova' Expedition of 1910–13. Among the fish scales observed in thin section were some which Woodward (1921: 57) described as 'typically Elasmobranch, each large cusp showing a trace of an original pulp cavity'. Many of these scales subsequently turned out to be thelodont scales, whose existence in a fish fauna of Late Devonian aspect was completely unsuspected by Woodward and other early workers. These were recently described as a new species of *Turinia* by Turner and Young (1992). White (1968), who studied the first *in situ* material, collected by B.M. Gunn and G. Warren during the Trans-Antarctic Expedition of 1958 (Gunn and Warren 1962), then found one definitive shark specimen, a single tooth which he described as a new form, *Mcmurdodus featherensis*, placed in a new family Mcmurdodontidae. This specimen came from Mt Feather, 18 km due east of the Lashly Range (Figure 1). Young (1982) described a second shark, *Antarctilamna prisca*, based on partially articulated remains which included teeth, scales and fin-spines also provided the first illustrations of the large diplodont teeth from Portal Mountain recorded by Ritchie (1971) as resembling those of *Xenacanthus* sp. These shark remains form part of a diverse fish fauna from the Aztec Siltstone, including arthrodires (Ritchie 1975; Long in press), antiarchs (Young 1988), acanthodians (Young 1989b), rhipidistians (Young *et al.* 1992), lungfish (Woolfe *et al.* 1990, Young 1991), and an undescribed actinopterygian (Young 1991). The faunal list now stands at 22 named genera and 31 species, including the new forms described here, of which all species and 18 genera are endemic to the region of East Gondwana (Table 1).

The material described herein comes mainly from a new collection of Aztec Siltstone fossils made by J. Long on the joint 1991/92 New Zealand Antarctic Research Program-Australian National Antarctic Research Expedition trip to the Cook Mountains and Skelton Névè regions, but also includes shark material previously collected by A. Ritchie and G.C. Young during the Victoria University of Wellington Antarctic Expedition VUWAE 15 (1970/71 season). The new material is sufficient to describe three new genera of Devonian sharks, based on teeth. In addition, information from the new localities in the Cook Mountains extends the known stratigraphic range of

Table 1 Vertebrate faunal list for the Aztec Siltstone, Antarctica.

AGNATHA	*Turinia antarctica* Turner and Young , 1992
PLACODERMI	
Antiarchi	*Bothriolepis antarctica* Woodward , 1921
	B. alexi Young, 1988
	B. askinae Young, 1988
	B. barretti Young, 1988
	B. karawaka Young, 1988
	B. kohni Young, 1988
	B. macphersoni Young, 1988
	B. mawsoni Young, 1988
	B. portalensis Young, 1988
	B. vuwae Young, 1988
	B. sp. indet 1–13.
	Pambulaspis antarctica Young, 1989
Arthrodira	*Antarctolepis gunni* White, 1968
	Groenlandaspis antarcticus Ritchie, 1975
	Groenlandaspis spp.
	Boomeraspis goujeti Long, 1995a
	phlyctaeniids spp.
Phyllolepida	?*Austrophyllolepis* sp.
	phyllolepid indet.
Incertae sedis	*Antarctaspis mcmurdoensis* White, 1968
CHONDRICHTHYES	
	Mcmurdodus featherensis White, 1968
	Antarctilamna prisca Young, 1982
	Anareodus statei gen. et sp. nov.
	Aztecodus harmsenae gen. et sp. nov.
	Portalodus bradshawae gen. et sp. nov.
ACANTHODII	*Gyracanthides warreni* White, 1968
	Antarctonchus glacialis White, 1968
	Byssacanthoides debenhami Woodward, 1921
	Culmacanthus antarctica Young, 1989
	Cheiracanthoides sp. (scales).
	Ischnacanthid gen. indet.
OSTEICHTHYES	
Actinopterygii	palaeoniscoid gen. nov.
	?palaeoniscoid indet.
Rhipidistia	*Gyroptychius? antarcticus* (Woodward)
	Koharalepis jarviki Young *et al.*, 1992
	Mahalalepis resima Young *et al.*, 1992
	Platyethmoidea antarctica Young *et al.*, 1992
	Vorobjevaia dolonodon Young *et al.*, 1992
	Notorhizodon mackelveyi Young *et al.*, 1992
	porolepiform indet.
Dipnoi	? *Eoctenodus* sp.
	Howidipterus sp.
	?ctendontid indet.

Antarctilamna prisca. Specimens are lodged in the Western Australian Museum, Perth (prefix WAM), the Australian Museum, Sydney (prefix AMF), and the Commonwealth Palaeontological Collection, Australian Geological Survey Organisation, Canberra (prefix CPC).

LOCALITY INFORMATION

Full details of all fossil fish localities known to that time from the Aztec Siltstone were provided by Young (1988). Information is given below for new localities and previous localities yielding described shark material. Numbers refer to localities 1–24 of Young (1988, figure 3). The regions are dealt with here from south to north.

Cook Mountains

Several new sites were discovered in the Cook Mountains during the 1991/92 field season (Figure 1, left). Shark teeth were recovered from "Gorgon's Head" near Mt Hughes, the same area from where fish were first recorded during the 1988/89 season (Woolfe *et al.* 1990). Other material came from the Fault Bluff sections and at Mt Gudmundson. Stratigraphic sections of the Aztec Siltstone and Beacon Heights Orthoquartzite from these localities were measured by M. Bradshaw and F. Harmsen and are currently being compiled. Figure 2 shows the provisional stratigraphic position of the fish faunas from the Cook Mountains referred to in the text, based on field measurement of stratigraphic sections.

Fault Bluff, "fish hotel" section

This stratigraphic section was measured along a low ridge running north-south outcropping immediately north of Fault Bluff (79°18'S, 157° 41'E). The stratigraphic sections were logged by M. Bradshaw and F. Harmsen. A continuous outcrop of Aztec Siltstone approximately 91 m thick is exposed here, although the base of the section is covered by scree. By comparison with the surrounding outcrops, the top of the Beacon Heights Orthoquartzite would sit within 20 m of the base of the section. Several fossil fish bearing horizons were located: site "A", about 45 m above the base, contained isolated impressions of fish plates in hard white orthoquartzite; site "B", about 67 m above the base, has rich accumulations of well-preserved fish remains in a medium-coarse to gritty quartzose sandstone; site "M", about 72 m above the base, is a fine, green siltstone with small fragments of well-sorted fish bone and scale debris; site "Y" about 85 m above the base, has occasional fish plates in quartz sandstone; and site "Z", at the top of the exposure about 88–90 m above the base, is a clean, indurated orthoquartzite rich in fish and plant remains. Lycopod stem axes are here

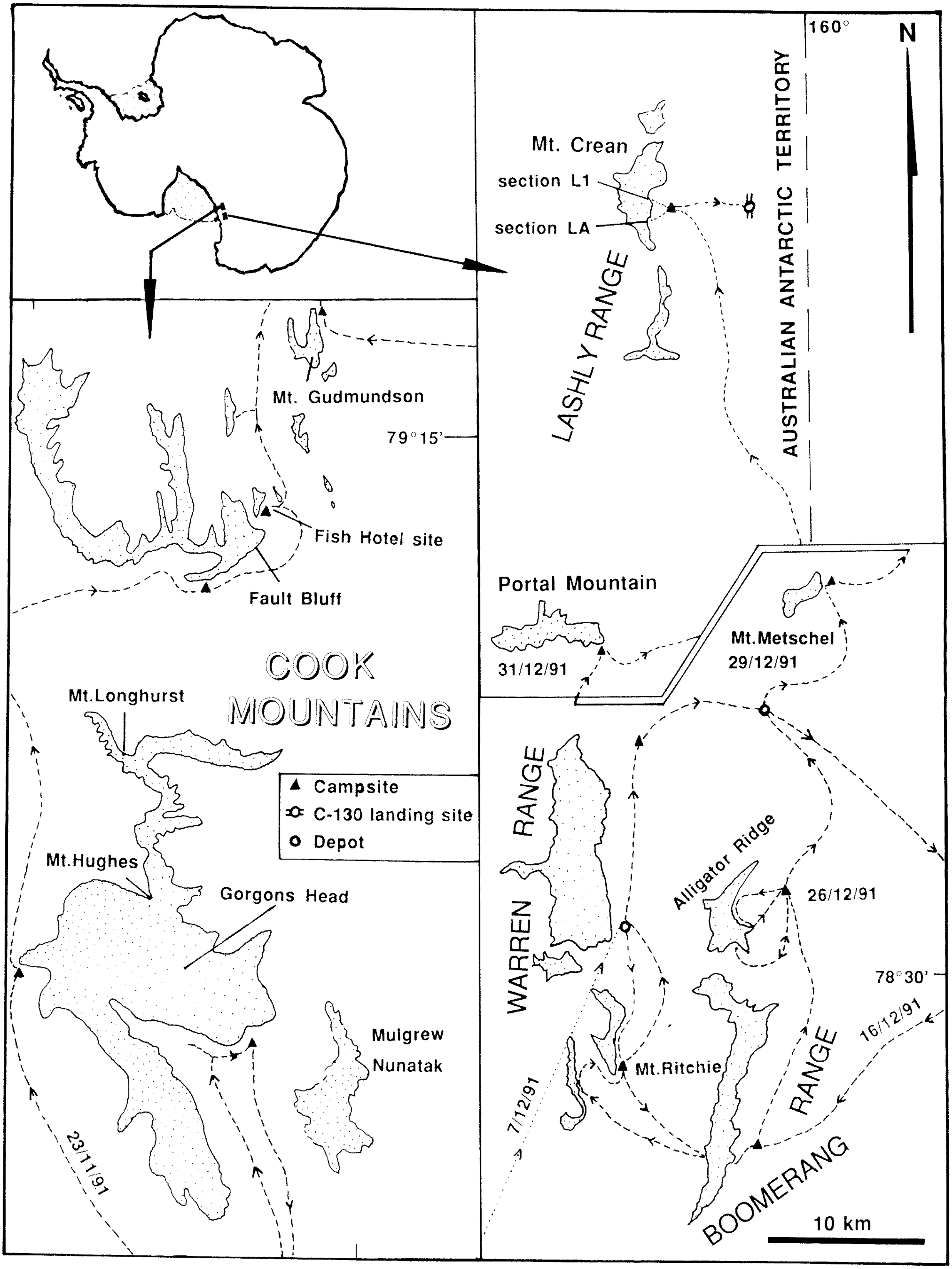

Figure 1 Locality map showing sites visited during the 1991/92 field expedition and localities mentioned in the text.

preserved as 3-D impressions (McLoughlin and Long 1994).

Mt Gudmundson

Approximately 93 m of Aztec Siltstone is exposed here in continuous outcrop, conformably resting upon a thick exposure of Beacon Heights Orthoquartzite and unconformably topped by Darwin Tillite. The stratigraphic section was measured and described by J. Long. At least six different fish bearing horizons identified: site "1", about 2.5 m above the base, with isolated fish plates preserved in black siltstones; site "2", a boulder scree resting on a table of quartzite, about 10 m from base, with rare isolated fish plates; site "3", contains fish fragments about 2 metres higher than previous site in similar lithology; site "4", about 21 m above the base, has isolated fish plates in clean, white medium-grained quartz arenite; site "5" about 54 m above the base, a rich bonebed of fish plates in a pebbly, gritty coarse sandstone-conglomerate, and site "6", about 90 m above the base in the highest exposure of flat-lying sandstones of the Aztec Siltstone, also a gritty layer with abundant fish bones. Some scree material containing fish fossils in a coarse sandstone was found in between sites 5 and 6 and labelled as site "5.5".

Southern Warren Range

Site 23 (Young 1988)

Section A5, west of Mount Ritchie (70/71). The shark tooth illustrated by Young (1982, plate 88, figure 4) came from the vicinity of section A5 of Askin *et al.* (1971). The precise horizon is uncertain, but was interpreted by Young (1988, text-figure 5) to lie within the range of "*Xenacanthus*" sp. (described herein as *Portalodus bradshawae* gen. et sp. nov.).

Site 24 (Young 1988)

Section A4, Mount Ritchie (70/71). Arthrodire,

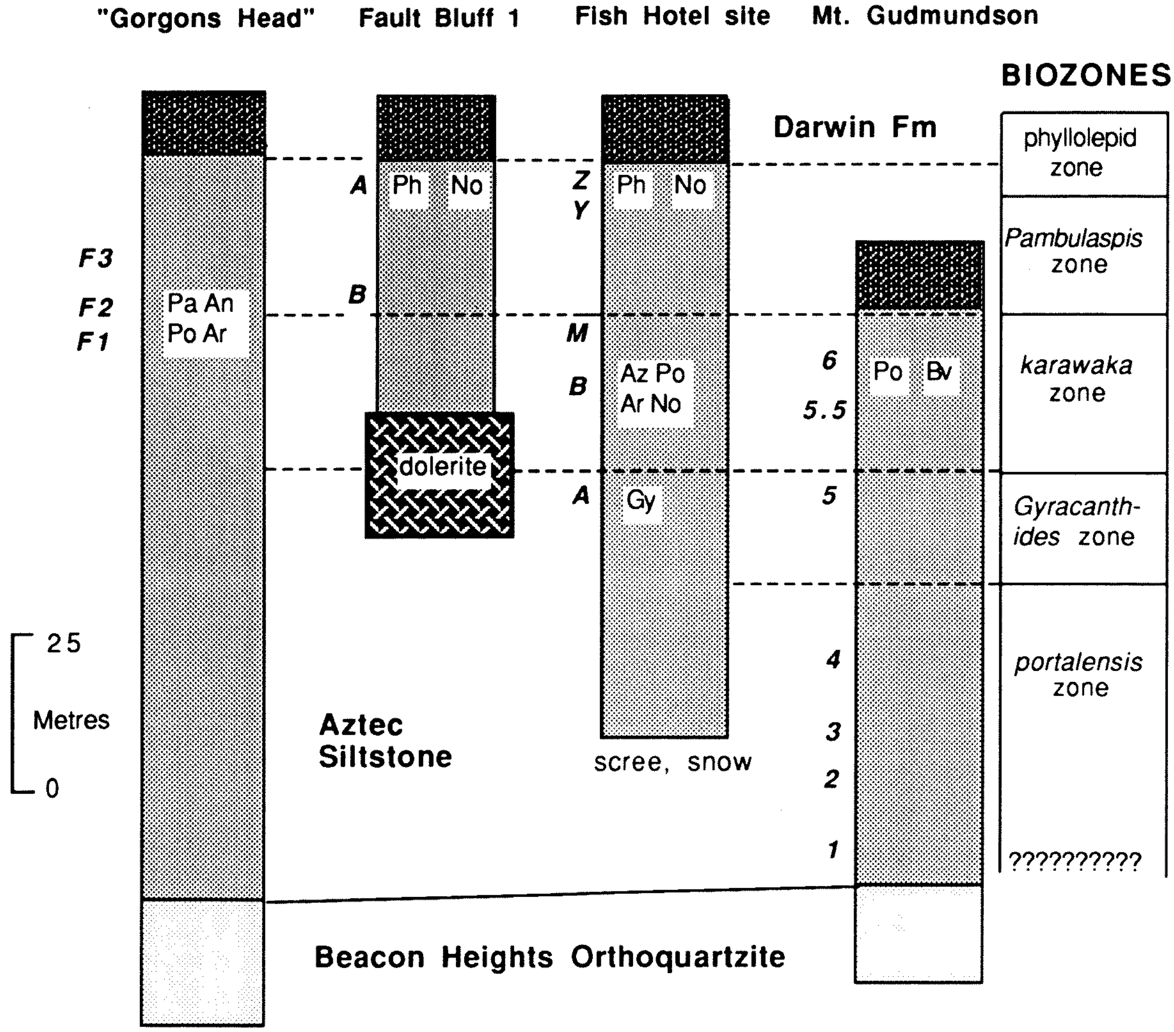

Figure 2 Comparisons of stratigraphic sections from four new localities of Aztec Siltstone fish fauna in the Cook Mountains. Biozonation modified from Young (1988). An, *Antarctilamna prisca*; Ar, *Anareodus* gen. nov., Az, *Aztecodus* gen. nov., Bv, *Bothriolepis vuwae*; Gy, *Gryracanthides warreni*; No, *Notorhizodon mackelveyi*; Pa, *Pambulaspis antarctica*; Ph, phyllolepids common; Po, *Portalodus bradshawae*. Other numbers and abbreviations refer to field localities of fish-bearing horizons.

antiarch and crossopterygian material from the upper fish horizons in this section (units 54 and 62, 187–212 m above base) were described by Ritchie (1975), Young (1988) and Young *et al.* (1992) respectively. Askin *et al.* (1971) also recorded fish remains in the A4 section from lower units 37 and 44 (137 m and 158 m above the underlying Beacon Heights Orthoquartzite), which were not collected in 1970/71. New material from this section collected in 1991/92 comes from a newly discovered site about 120 m above the base in a coarse pink-buff quartzose sandstone, labelled in the field as horizon "M".

Portal Mountain

Site 11 (Young 1988)

Portal Mountain, 68/69 locality. Fish remains were discovered here on the southern face near the end of the eastern ridge from the summit of Portal Mountain by VUWAE 13 in 1968–69. The small collection, including shark teeth, was briefly described by Ritchie (in McKelvey *et al.* 1972). This is section 10 of Barrett and Webb (1973), and the original teeth of *Portalodus bradshawae* gen. et sp. nov. came from unit 17, about 40 m above the lowest exposure of the Aztec Siltstone (base obscured by ice). A fin-spine recorded from here was provisionally referred to *Antarctilamna prisca*, as was another from a higher horizon in the same section (unit 26, 70.8 m above lowest exposure), where more 'xenacanth' (*Portalodus bradshawae* gen. et sp. nov.) teeth were found (Young 1982).

Site 12 (Young 1988)

Portal Mountain, 70/71 locality. The adjacent section P1 of Askin *et al.* (1971) was measured up the eastern face of this outcrop, and shark scales and teeth were referred to *Antarctilamna prisca* by Young (1982).

Portal Mountain, 91/92 locality

New material was collected from the eastern face about 200 m west of locality 11. The specimens came from about 70 m from the base of the Aztec Siltstone in a red mudstone which has lenses of fish bones and scales.

Lashly Range

Site 8 (Young 1988)

Mount Crean. The original *in situ* material from this locality (Gunn and Warren 1962) was described by White (1968). Section L2 of Askin *et al.* (1971; also McPherson 1978) was measured here, and stratigraphic levels for seven collecting sites at this locality (MC 1–7) were discussed by Young (1988: 12,13).

Site 9 (Young 1988)

Lashly Mountains, southeast of Mount Crean. The type locality and horizon for the holotype of *Antarctilamna prisca* Young, 1982, is from about 15 m above the base of the Aztec Siltstone, probably units 8–10 in section L1 of Askin *et al.* (1971).

New locality, third outcrop of Aztec Silstone southeast of locality 8

This is the type locality for *Aztecodus harmsenae* gen. et sp. nov. This section (field name "LA") is the second exposure of sediment south of the main L2 section (locality 8, text-figure 4 of Young 1988). Two horizons yielding fish remains were located during 1991/92. The lowest horizon (field name LA–1) occurs about 38 m from the base and is a medium-grained clean quartzo-feldspathic sandstone containing *Bothriolepis* cf. *askinae*, *Portalodus bradshawae* gen. et sp. nov., a low-crested, finely tuberculated species of *Groenlandaspis*, with the notable absence of thelodont scales. The holotype tooth of *Aztecodus harmsenae* gen. et sp. nov., along with several other specimens came from a slightly higher horizon about 68–70 m from the base of the Aztec Siltstone. The lithology exposed here is a buff-coloured pink medium-coarse quartzose sandstone with interspersed green silts. Fish remains occur as scattered debris consisting largely of isolated, and commonly fragmented placoderm plates (*Bothriolepis* sp.), acanthodian spines and scales, and shark teeth. In addition *Portalodus bradshawae* gen. et sp. nov. also occurs in this horizon, although teeth of *Aztecodus* gen. nov. are more abundant.

Mount Feather

10. Gunn and Warren locality (57/58)

This locality has not been recollected. The original material obtained by B.M. Gunn and G. Warren included a single shark tooth described by White (1968) as the holotype of *Mcmurdodus featherensis*. Its horizon within the Aztec Siltstone is unknown.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Antarctilamna Young, 1982

Antarctilamna cf. *prisca* Young, 1982

Figures 3, 4, 13

Material

Seven isolated teeth, mostly complete: WAM 90.2.37, 92.2.2 – 92.2.6, 92.3.68.

Localities and horizon

WAM 90.2.37, 92.3.68, 92.4.5: Cook Mountains, at "Gorgon's Head", near Mt Hughes, in the upper 20 m of the Aztec Siltstone, associated with a diverse fauna including phyllolepid placoderm remains, *Pambulaspis*, *Bothriolepis*, *Groenlandaspis*, osteolepiform scales, *Gyracanthides* spines, and a lungfish toothplate resembling *Eoctenodus* sp. (Woolfe *et al.*, 1990). WAM 92.4.3, 92.2.4, 92.4.6: Mt Ritchie, middle horizon, about 120 m from base of section 24 of Young, (1988); WAM 94.2.2: Lashly Range (LA 2 site, third outcrop of Aztec Siltstone south of L2, Mt Crean main section, lower horizon).

Remarks

These specimens resemble the type material in having large divergent main cusps ornamented with 4–6 sparse ridges, and 1 to 5 small median cusps. However some come from a much higher horizon than the type material (which occurs in the lowest Aztec biozones of Young1988). Until more material is found on which morphological differences might be demonstrated, we provisionally consider the specimens as close to the type species of *Antarctilamna*.

Description

These specimens vary in size as measured across the base, all falling within the range of 1–4 mm described in the holotype. As noted above they resemble the type material in having two divergent main cusps, ornamented with 3–6 sparse ridges which curve up from the base. WAM 90.2.37, preserved in labial view, shows an impression where a single median cusp was present. The labial surface is somewhat weathered but still shows evidence for 3–4 weak striae on the main cusps. WAM 92.3.68 (Figures 3B,4C) has a median cusp slightly larger than the two lateral cusplets, all of which sit between the two main divergent cusps. This specimen comes from the youngest horizon at the top of the Aztec Siltstone at Gorgon's Head (Mt Hughes) and shows the base being more subrectangular in form rather than having a rounded lingual margin as shown in Young's reconstructed specimen (1982, text-figure 3 C). The striations extend onto the intermediate cusps (Figure 3C, 4). Between the two main cusps on WAM 94.2.2 (Figure 3A) there are two pairs of small median cusps lateral to a slightly larger central cusp that has broken off at its base. Thus there would have been five median cusps between the two divergent main cusps. The striae on this specimen number up to 7 on each main cusp and even the median cusplets have striae developed. In cross-section the cusps and intermediate cusplets are weakly compressed, almost round at the base become flatter near the apex of each cusp. The lateral and mesial edges have a sharp cutting edge running half way down the sides of each main cusp.

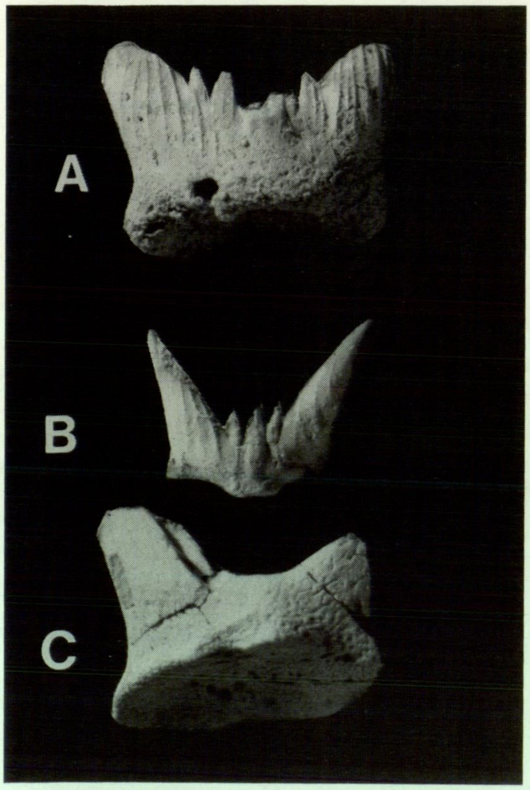

Figure 3 *Antarctilamna* teeth. A, WAM 94.2.2 from the Lashly Range (site LA–2) in labial view. B, WAM 92.3..68, from "Gorgons' Head", Cook Mountains, in labial view. C, WAM 2.3.62, from the top horizon at Mt. Ritchie, labial view. All x 8.

All the known *Antarctilamna* teeth have three or more small intermediate cusps, and of these the central cusp is slightly larger than the two or four lateral cusps, as was observed in the type material (Young 1982: 824, plate 87, figure 1; also see Appendix, Figure 13). In these specimens the number of intermediate cusps varied between two and three, but this was a much larger sample (about 65 teeth from the holotype). It is possible, however, that all *Antarctilamna* teeth from these higher horizons have three intermediate cusps, but this needs to be substantiated with a larger sample. Hampe (1993) indicated that a range of tooth abnormalities occurs in bicuspid xenacanth teeth, including the appearance of additional median cusplets. In the holotype of *Antarctilamna prisca* it was suggested that striations may be restricted to the outer surface of the crown (Young 1982: 824), and this observation is confirmed by the new specimens. WAM 92.3.62 (Figures 3C, 4A, B) shows a larger ventral foramen surrounded by some smaller foramina opening through the base, as in *Phoebodus* (e.g., *P. gothicus*; Gross 1973: plate 34, figure 15b; Ginter 1990), but not previously noted by Young (1982) in the type material. A slight protuberance on the labial margin (Figure 4A, B) is the basal tubercle corresponding to that developed

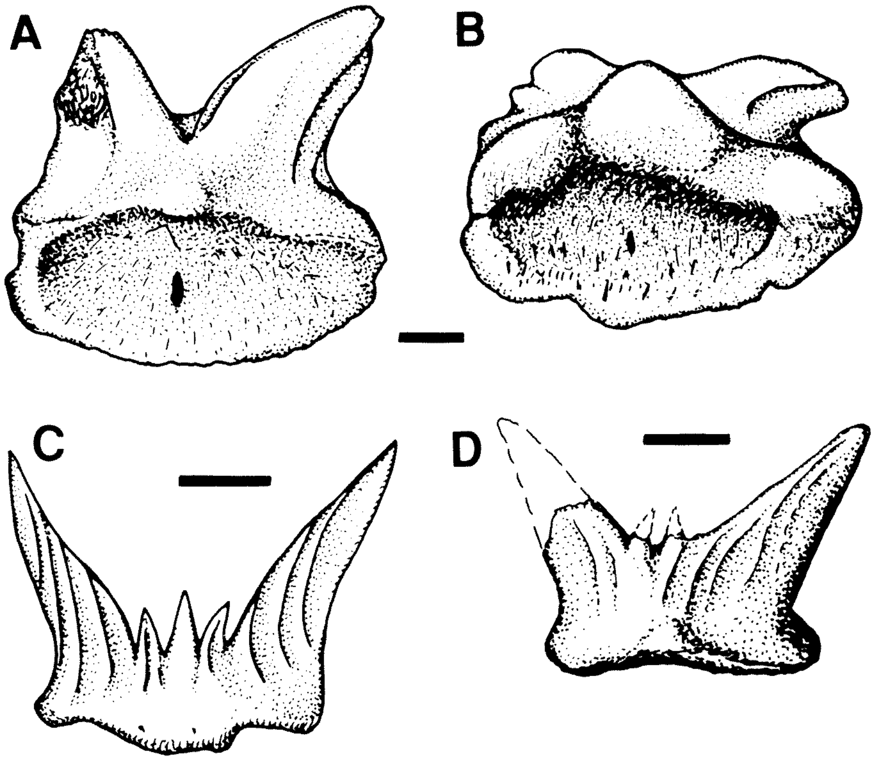

Figure 4 *Antarctilamna* teeth. A, B, WAM 92.3.62, in labial view. B, in basal view, from the top of Mt. Ritchie. C, WAM 92.3.68 from "Gorgon's Head", Cook Mountains, showing three intermediate cusps, labial view. D, a tooth from the holotype of *Antarctilamna prisca* (CPC 21187) previously illustrated by Young (1982, plate 89, figure 7), which shows two small intermediate cusps. Bar scales are all 1 mm.

in advanced xenacanth teeth (e.g., Hampe 1988a: figure 1). The corresponding region in *Phoebodus* teeth is the 'labio-basal thickening' of Ginter and Ivanov (1992, figure 2).

Stratigraphic occurrance

Antarctilamna teeth are now known from the base of the Aztec Siltstone (*A. prisca, askinae* zone, with thelodonts) through to the youngest biozones (occurring with phyllolepids and *Pambulaspis* at Gorgon's Head), although the latter specimens may possibly belong in a different species.

Portalodus gen. nov.

Portalodus bradshawae sp. nov.

Figures 5–7

'tooth [which] resembles .... the diplodont teeth found in *Xenacanthus*', Ritchie, in McKelvey *et al.*, 1972: 351.

Xenacantheus sp. Young 1982: 833, figure 3E–G, plate 89, figures 1–4.

Xenacantheus sp., Grande and Eastman 1986: 121.

'*Xenacanthus*' sp., xenacanth shark teeth, Young 1988: 13, 14, 16, figure 5.

'*Xenacanthus*' sp., Schneider 1988: 71–2, figure 2 A–C.

'xenacanth shark tooth', Young 1989a: figure 4D.

teeth of *Xenacanthus* sp.', Young 1991: figure 15.6c, d.

'xenacanthid gen. nov. 1', Young *et al.* 1993: 248.

'xenacanth shark tooth', Vickers-Rich and Rich 1993: 93, plate 82.

'teeth identified as... *Xenacanthus*', Capetta *et al.* 1993: 597.

'xenacanthid indet.', Davis 1994: 60.

'a new form of fossil shark's tooth...', Long 1995b: p.69 (photo).

Etymology

From the type locality, Portal Mountain; and in honour of K221 expedition leader Margaret Bradshaw.

Diagnosis

Shark with large diplodont teeth, base to cusp apex length up to 2 cm in largest specimens. Principal cusps divergent, one about a third larger than the other, and twisted in different planes in occlusal view. Few sparse external striae may be developed on lingual surface, but labial surface smooth. Cusps almost rounded in cross-section, slightly compressed with cutting edges developed along mesial and marginal edges. Base normally broader than the height of the shorter cusp, with a prominent labial platform, and lacking a projection on lingual face. Underside of base simple, without

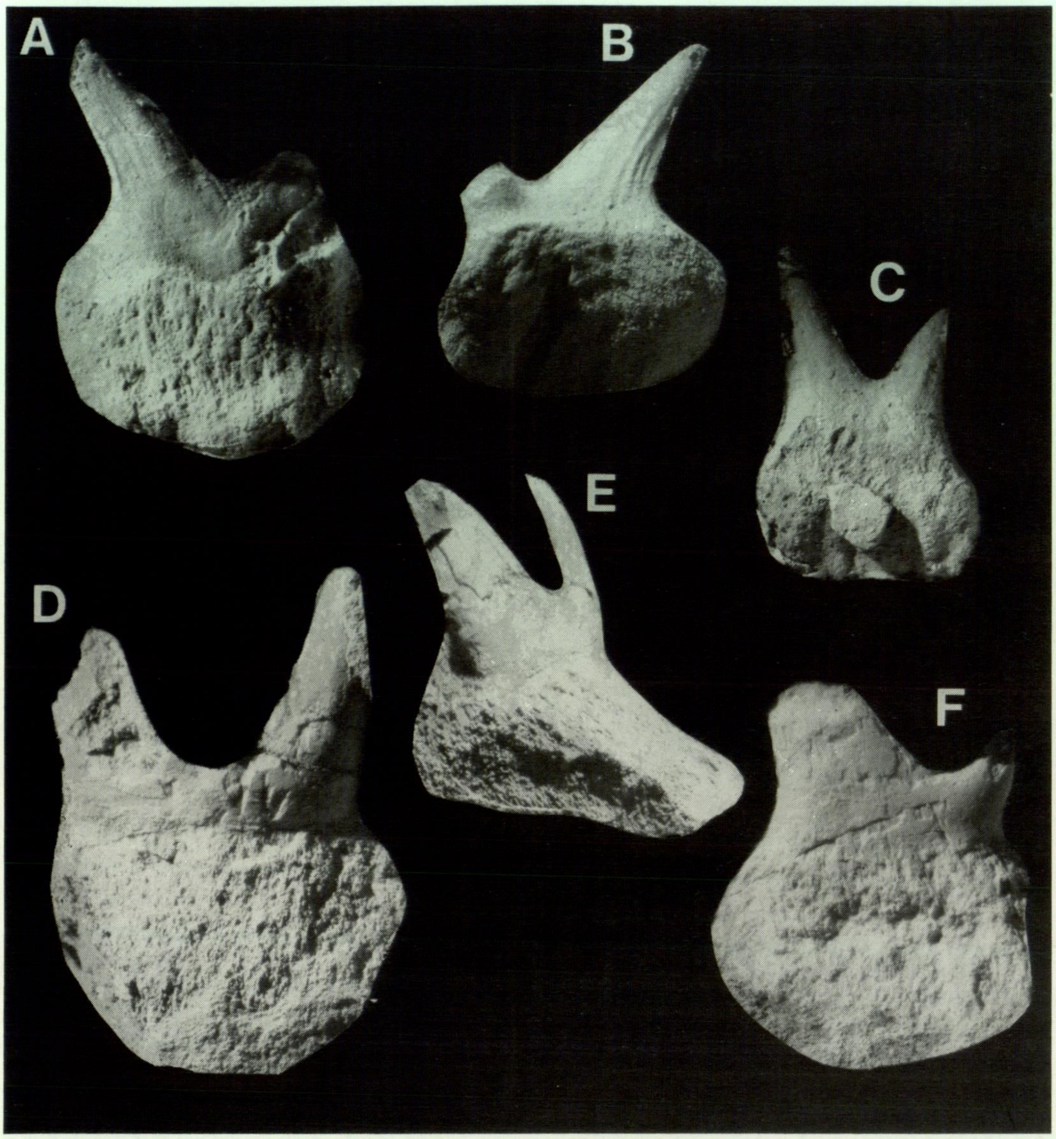

Figure 5 *Portalodus bradshawae* gen. et sp. nov. A, WAM 94.2.8., labial view, X 4 . B, WAM 94.2.10., lingual view, X 4 (both from Portal Mountain, type locality). C, WAM 94.2.12., lingual aspect, slightly flattened to show basal view also, X 2, from "Gorgon's Head", Cook Mountains. D, E, Holotype WAM 92.3.60. X 4, D, labial view, E, left lateral view (Portal Mountain, type locality). F, WAM 92.3.65, labial view, from Fault Bluff, "fish hotel" B horizon. A–C are latex casts whitened with ammonium chloride, D–F are actual specimens (whitened).

well-defined ridges or transverse groove. Single large nutritive foramen and rostrocaudal groove on ventral surface.

Remarks

Young (1982: 835) oriented these teeth with the 'expanded side of the base assumed for the purpose of description to correspond to the lingual torus of other forms'. However the curvature of the cusps (which should point into the mouth) indicates that this basal projection must be an extension of the labial, not the lingual surface, and in this respect *Portalodus* gen. nov. differs from *Xenacanthus*, and all other forms with diplodont teeth, in lacking a lingual torus, and instead having the opposite surface of the base developed as a labial projection. The only other shark tooth type known with this configuration is the genus *Omalodus* erected by Ginter and Ivanov (1992; earlier named as *Phoebodus bryanti* by Wells 1944), but this form is much smaller, and differs in having three principal cusps with smaller cusplets in between them.

Holotype

WAM 92.3.60 (Figures 5D, E; 6A), a large tooth from Portal Mountain, section 200 m west of section P1, collected by J. Long.

Other Material

Approximately 32 teeth. Portal Mountain (teeth): CPC 21214–227, 31614, AMF 54329–331, 555735,

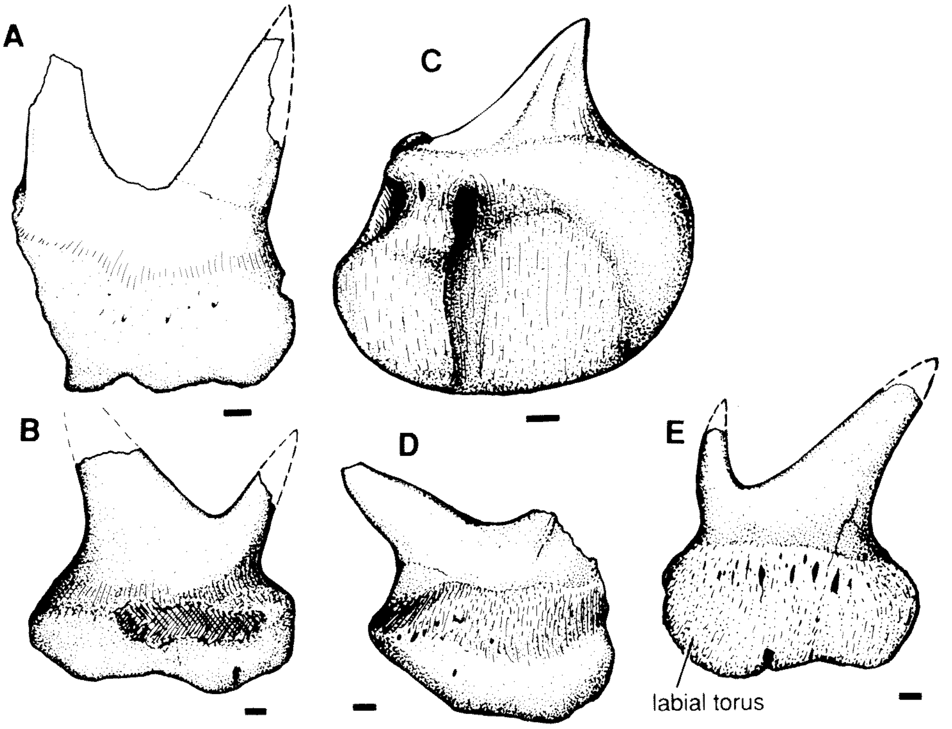

Figure 6 *Portalodus bradshawae* gen. et sp. nov. A, Holotype WAM 92.3.60, labial view. B, WAM 92.3.63, labial view. C, WAM 94.2.10 showing basal view; D,WAM 94.2.8, labial view. E, CPC 21224 (from Young, 1982 text-fig. 3F). Bar scales are all 1 mm.

from locality 11 of Young (1988), section 10 of Barrett and Webb (1973), all from unit 17 except CPC21214, 215 (from unit 26); WAM 92.3.60, 92.3.63, 94.2.1, 94.2.8, , section about 200 m west of locality 12 of Young (1988; section P1 of Askin *et al.* 1971), at approximately the same level as the upper vertebrate assemblage at locality 11 of Young (1988, figure 5; section 10 of Barrett and Webb, 1973). Portal Mountain (fin-spines): CPC 21192, AMF 55617 from units 26 and 17 may possibly belong to *Portalodus* gen. nov. (by association only). West of Mt Ritchie: CPC 21228, one tooth from locality 23 of Young (1988). WAM 92.3.65, 92.3.66., "fish hotel" site B (Fault Bluff, Cook Mountains, Figure 1). WAM 92.3.64, Mt Ritchie, middle horizon (new site 1991/92). WAM 94.2.12, "Gorgon's head" (near Mt Hughes), Cook Mountains. WAM 94.2.11, Mt Gudmundson (Cook Mountains), horizon 6. WAM 94.2.7, Mt Crean (section l2, site MC7, Young 1988).

Description

These are the largest teeth yet recorded in Devonian sharks, the biggest specimen measuring 2 cm in height from base of root to tip of crown (WAM 94.2.12; Figure 5C). Most specimens fall in the size range of 10–15 mm (maximum dimension). As originally described (Young 1982: 834, 835), these teeth were distinguished from *Antarctilamna* teeth by the unequal size of the cusps, the way the cusps were twisted in different planes in dorsal view, and in the opposite direction to the projection of the base, the absence of central cuspules, and the deeper, more bulbous base. Each cusp is rounded in section distally, but proximally the labial face is flattened, and separated from the more rounded lingual face by a fine ridge continuous between cusps. The labial face of the cusps is smooth (Figures 5A, D, F; 7A, C), but the lingual face (Figures 5B, C; 7D) normally carries two to four coarse striations (in contrast, a smooth lingual and striated labial surface is known in some other forms, e.g., *Antarctilamna*, *'Phoebodus' heslerorum*; Williams 1985: 127). The base is normally notched in about the middle of its basal margin, in which a large foramen is seen in labial view (WAM 94.2.10, Figures 5B, 6C). The ventral surface of the base is shown in WAM 94.2.10 (Figure 6C, also 7B, D). There is a large foramen placed near the lingual margin, and a well-defined ledge separating the lingual half of the base from the more concave labial half. The labially-projected division of the base has a weak outer ledge developed on the dorsal surface. The ventral surface is crossed by a shallow groove connected to the foramen on the labial surface (Figures 6 C, 7B, D).

Two fin-spines (CPC 21192, AMF 55617) associated with the teeth of *Portalodus* from the type locality were assigned to *Antarctilamna prisca* by Young (1982). However, it is possible that these belong to *Portalodus*, since *Antarctilamna* teeth have not been found at this locality and horizon (units

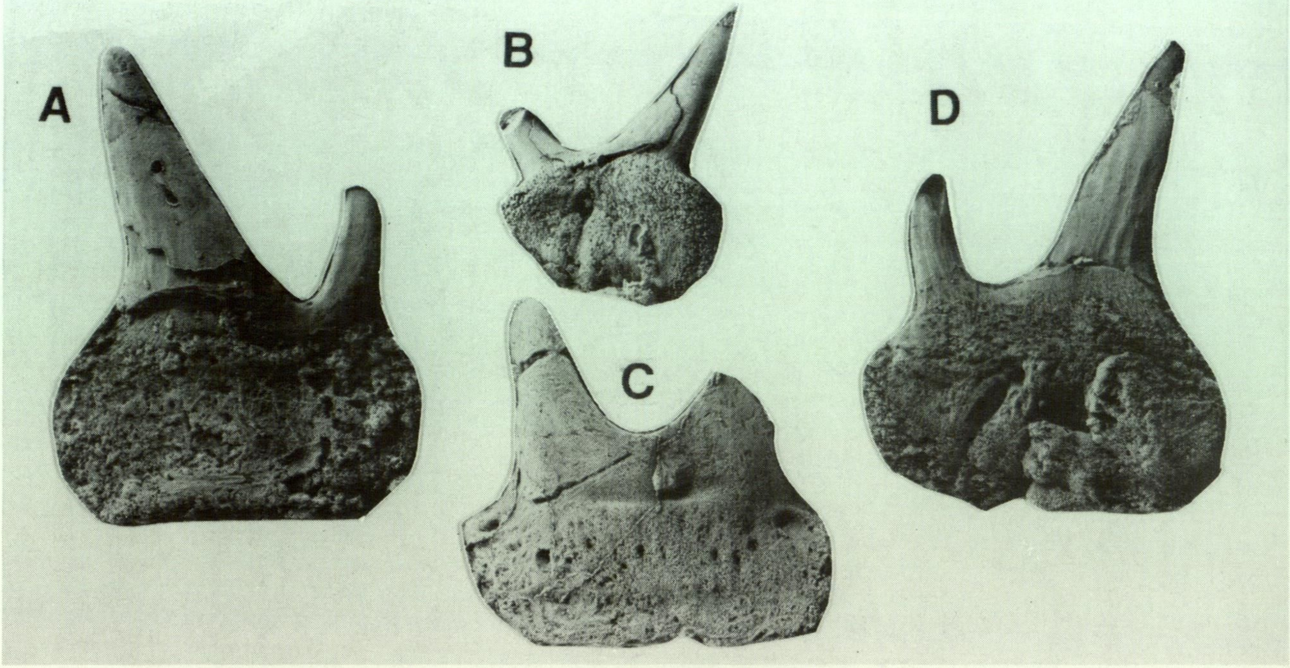

Figure 7 *Portalodus bradshawae* gen. et sp. nov., A, D, labial and lingual views of SN96a; B, lingual view of SN 96b, C, labial view of SN 93a. All x4. Latex casts whitened with ammonium chloride.

17 and 26). The figured specimen (Young 1982, plate 87, figure 2) was noted to differ somewhat in sculpture of the ridges from other spines assigned to *Antarctilamna*, and CPC 21192 has only 16 costae on one side, whereas other spines have a greater number. More material is needed to clarify whether these spines actually belong to *Portalodus*.

Stratigraphic occurrence

The type material comes from Portal Mountain;, but the species is also found at "Gorgon's Head" near Mt Hughes (top level), Cook Mountains; Mt Gudmonson (level 6, top horizon), Fault Bluff, Cook Mountains, ("fish hotel" B site); Mt Crean (site MC7, Young 1988), Lashly Ranges, section "LA" (second outcrop south of Mt Crean L2 section); Mt Ritchie, horizon "M". All occurrences of *Portalodus bradshawae* gen. et sp. nov. come from above the *Turinia antarctica* biozones (first appearance within the *portalenesis* zone) and range right through to the top of the biostratigraphic zonation scheme (occurring with phyllolepids and *Pambulaspis* at Gorgon's Head).

Aztecodus gen. nov.

Aztecodus harmsenae sp. nov.

Figures 8, 9.

Mcmurdodus? cf. *featherensis* Young 1982: text-figure 3H, plate 88, figure 4

'tooth ... tentatively referred to *Mcmurdodus*', Turner and Young 1987: 236.

Mcmurdodus? cf. *featherensis*, Davis 1994: 61.

Etymology

After the Aztec Siltstone, which has produced all the known specimens, and for Dr. Fraka Harmsen, California State University at Fresno, sedimentologist on K221–A136 Expedition.

Diagnosis

Shark with diplodont teeth up to 2cm wide, with a low base which is broader than the height of the cusps. Second principal cusp of nearly equal size to approximately three-quarters the height of the largest cusp, and both cusps are widely separated by a cutting ridge bearing approximately 12 small crenulations. Cusps are smooth both lingually and labially with strongly compressed cross-sections, and well-developed cutting edges. Small accessory cusplets usually developed at mesial and marginal ends of tooth adjacent to main cusps. Base low and broad in labial view, with two transverse canals. Ventral surface of base subrectangular with gently convex margins all round, and approximately 2.5 times as long as broad.

Remarks

This genus differs from *Portalodus bradshawae* gen. et sp. nov. because it is based on broad teeth with cusps widely separated by a crenulated cutting ridge, by the low height of the base, the presence of very small accessory cusplets, and the paired transverse canals penetrating the the base. It is also generally of smaller size, although the largest specimen (WAM 92.3.59, Figures 8H, 9C) in width approaches the maximum height of *Portalodus* gen. nov. The larger size, central crenulated cutting ridge, wide separation and

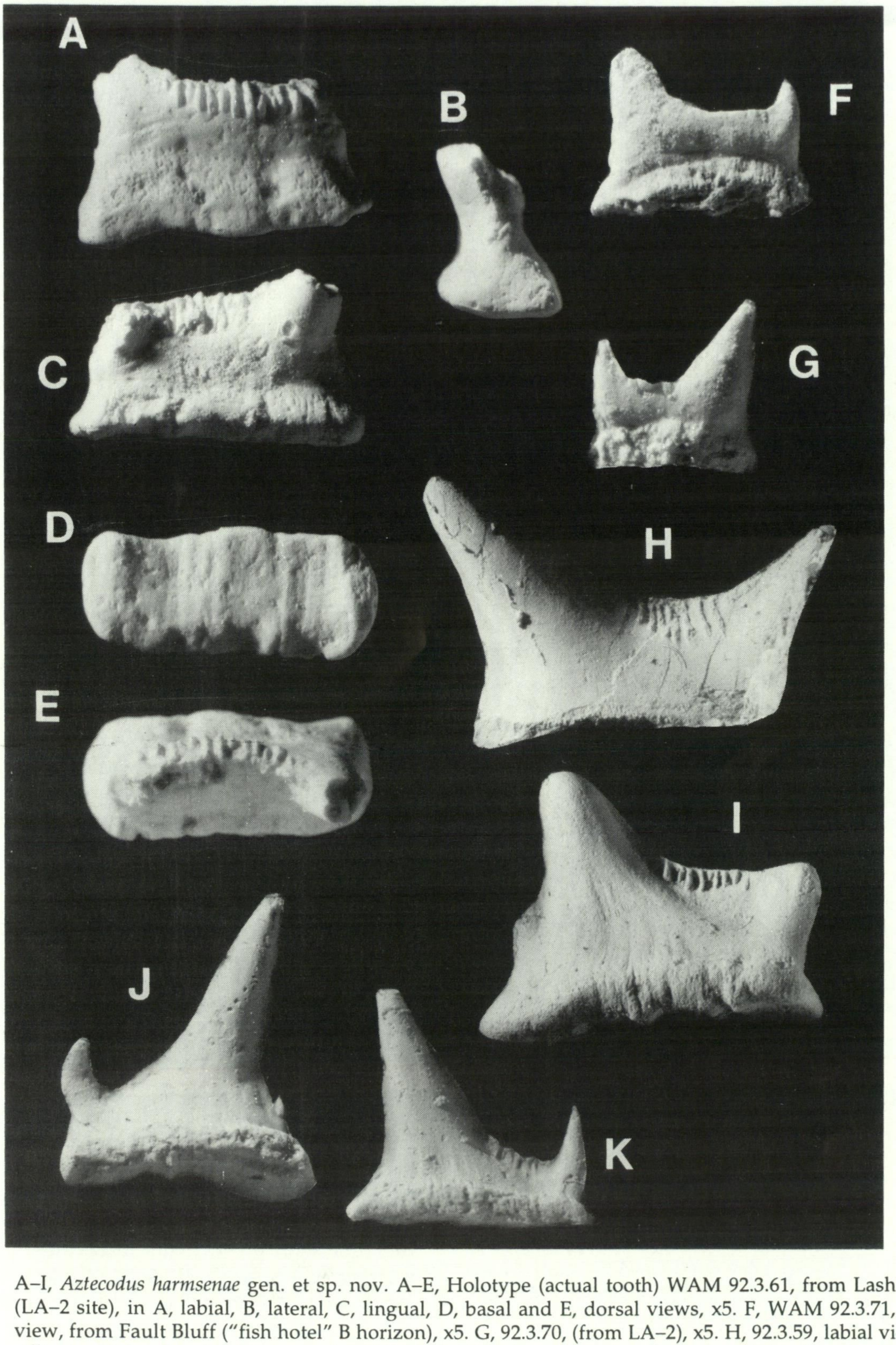

Figure 8 A–I, *Aztecodus harmsenae* gen. et sp. nov. A–E, Holotype (actual tooth) WAM 92.3.61, from Lashly Range (LA–2 site), in A, labial, B, lateral, C, lingual, D, basal and E, dorsal views, x5. F, WAM 92.3.71, in labial view, from Fault Bluff ("fish hotel" B horizon), x5. G, 92.3.70, (from LA–2), x5. H, 92.3.59, labial view, from Alligator Ridge (locality 20, top), x4. I, WAM 92.3.58, labial view, from Alligator Ridge (locality 21, top) x4. J, K, *Anareodus statei* gen. et sp. nov. J, WAM 94.2.9, labial view, x8. K, 94.2.13, Holotype, labial view, both from Fault Bluff ("fish hotel" B horizon), x 8. A–G are actual specimens, others are latex peels; all specimens whitened with ammonium chloride.

unequal size of cusps, and the lack of striae on cusps clearly distinguish this genus from the teeth of *Antarctilamna*. No other Palaeozoic shark has widely separated divergent cusps with a well-developed mesial crenulated region. As originally described (Young 1982: 835), this tooth type resembles *Mcmurdodus* in its elongate compressed form, with minor cusps at the margins of the tooth.

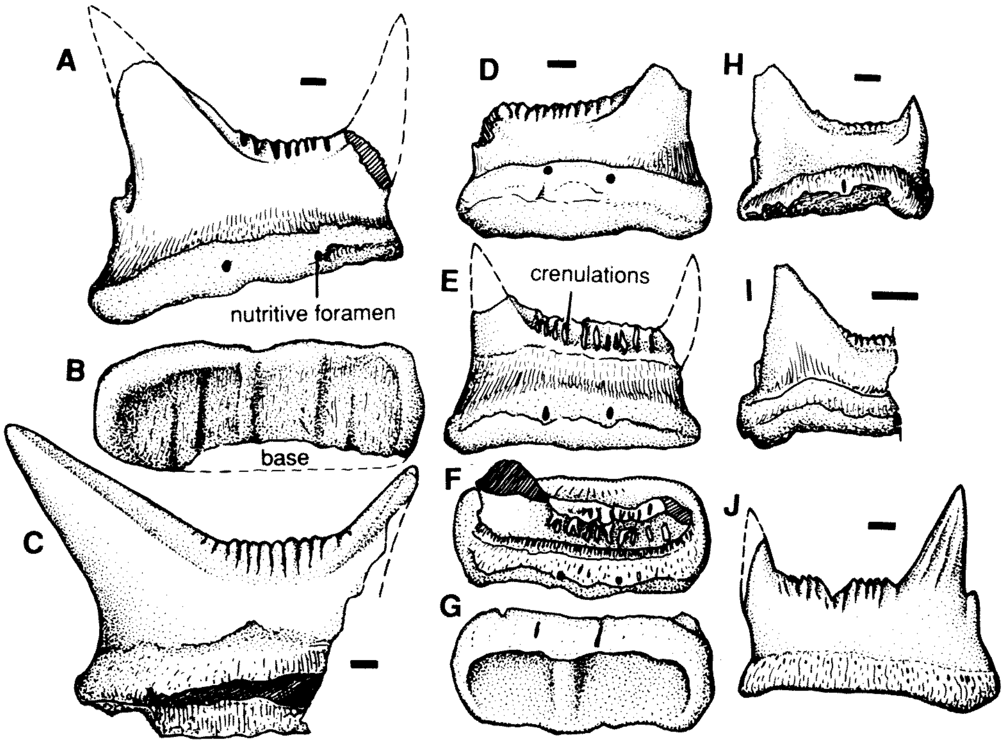

Figure 9 *Aztecodus harmsenae* gen. et sp. nov. A, B, WAM 92.3.58, labial and ventral views. C, WAM 92.3.59, labial view; D–G, holotype WAM 92.3.61, in D, lingual, E, labial, F, dorsal, and G, ventral views; H, WAM 92.3.71, labial view. I, WAM 92.3.69, from Fault Bluff, ("fish hotel" B horizon) x4. J, CPC 21229, labial view (previously illustrated by Young, 1982, figure 3H, plate 88, figure 4). All bar scales are 1 mm.

There is also a resemblance to *Mcmurdodus* in the shape of the base in ventral view, as subsequently described by Turner and Young (1987: figure 4B). However, the main differences lie in the larger number of cusps and absence of a lower crenulated cutting ridge in the central part of the *Mcmurdodus* tooth, where instead the largest cusps are situated, the lack of the ventral groove on the base, and the fact that the minor cusps at either end are directed almost horizontally in that form.

Holotype

WAM 92.3.61 (Figures 8A–E, 9D–G), from the section LA, site LA–2, Lashly Mountains, about 200 metres south of Mt Crean, from the second fish horizon (LA2) about 70–80 m above the base of the section.

Material

Six other teeth. CPC 21229, from Mt Ritchie, section A4 near units 61, 62 (figured Young 1982, text-figure 3H, plate 88, figure 4); WAM 94.2.17, from LA–2 (type locality); WAM 92.3.58, from site 20 (scree); 92.3.59, from Alligator Peak, locality 20 (top horizon); WAM 92.3.70, 92.3.71, from Fish Hotel site B, Cook Mountains.

Description

These teeth range in size from about 5 mm (92.3.70) to 16 mm across the cusps (WAM 92.3.59, Figures 8H, 8C), being considerably wider than high, and with a distinctive almost rectangular base when viewed dorsally or ventrally (Figures 8D, E, 9B, F G). The holotype (WAM 92.3.61, Figures 8 A–E, 9D–G) was extracted from *in situ*, and although the main cusps are damaged it shows the distinctive crenulated mesial edge, a feature not seen on any other Devonian sharks tooth. In this specimen there are approximately twelve small ridges forming the crenulated mesial edge which is gently curved, being weakly convex when viewed labially. The enameloid-root boundary is well defined and gently curved on the labial face. The two prominent main cusps have a strong lingual curvature and are relatively broad and flat, tapering mesially to form a sharp cutting edge before the crenulations develop (e.g., Figures 8H, I, 9 A–C). The basal view (Figures 8D, 9 B, G) shows the root with an anterior thickening and a few rostrocaudal ridges and weak grooves, but lacking any foramina. Two well defined nutritive foramina pass through the tooth from labial to lingual side at the level of the ventral margin of the base (e.g., Figure 9A, D, E, H). Other specimens show the same proportions as the holotype (Young 1982, text-figure 3H; Figures 8F, 9H).

Two specimens have slightly different morphologies, and come from the top of the Aztec Silstone at site 20 in Alligator Ridge, within the phyllolepid biozone of Young (1988). WAM 92.3.59 and 92.3.58 are slightly larger than the other specimens, and have more widely splayed main cusps and, relative to the holotype, they show a more curved, and distictly shorter, mesial crenulated area when viewed in labial or lingual aspect. WAM 92.3.58 shows the presence of a small accessory cuspule on the external edge of the main cusp, a feature seen on nearly all specimens with that edge well-preserved (e.g., Figure 9J), although absent on 92.3.59 (Figure 8H, 9C). It is possible that these two teeth could represent a different, younger species of *Aztecodus*, although as only two specimens are known, and they show only slight differences from the other specimens, we prefer to place them in the same species until more material can substantiate or refute these morphological differences.

Stratigraphic occurrence

The type material comes from the Lashly Ranges, (section "LA"); other specimens are from Mt Ritchie, section A4 near units 61, 62; from Alligator Peak, locality 20 (top horizon) and from Fault Bluff, "fish hotel" site B, Cook Mountains. The teeth all come from above the thelodont biozones, with first appearance high in the section at "fish hotel" (at least 65 m from base of unit covered by scree, occurring with phyllolepids, *Groenlandaspis antarcticus*, *Portalodus bradshawae* gen. et sp. nov., and ranging right through to about 20 m from the top of the Aztec Siltstone at Alligator Ridge, site 20 (possibly uppermost *portalensis* or *karawaka* biozones).

Anareodus gen. nov.

Anareodus statei sp. nov.

Figures 8J–K, 10

Etymology

After ANARE (Australian National Antarctic Research Expeditions) who funded J. Long's field work, and for Brian Staite, survival leader on K221/A136 Expedition.

Diagnosis

A diplodont shark tooth with main cusps of very unequal size, separated by a mesial-marginal ridge sometimes bearing small crenulations, and a small accessory cusplet normally present on the mesial side of the main cusp. Main cusp quite flat and sigmoidally curved in lateral/mesial view. Base low, strongly concave, and rectangular in outline in basal view.

Remarks

This genus resembles *Aztecodus harmsenae* gen. et sp. nov. in sometimes showing crenulations on the central cutting ridge, in the presence of a small

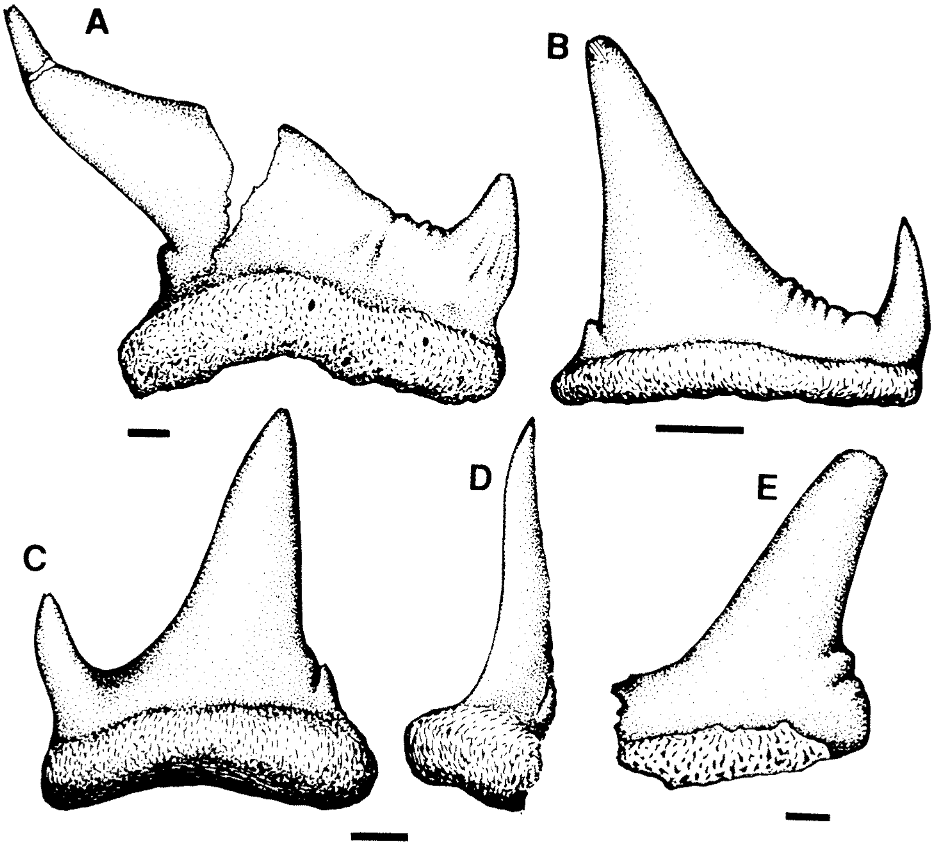

Figure 10 *Anareodus statei* gen. et sp. nov. All specimens, except D, shown in labial view; D, in lateral view. A, WAM 90.2.38, from "Gorgon's Head" (Cook Mountains). B, WAM 94.2.13. C, WAM 94.2.9 (both from Fault Bluff, "fish hotel" B horizon). E, WAM 90.2.39 (Gorgon's Head). All bar scales are 1 mm.

accessory cuspule on the lateral edge of the main cusp, and in the shape of the base in ventral view. However it differs from *Aztecodus* in having a much larger, flatter main cusp, in the more concave shape of the base, with sigmoid curvature along its length, and the absence of the two nutritive foramina.

Holotype

WAM 94.2.13, from the Fish Hotel site B, Cook Mountains (Figures 8K, 10B).

Material

WAM 90.2.38, 90.2.39 ("Gorgon's Head", near Mt Hughes, Cook Mountains); also 94.2.9 from Fault Bluff, "fish hotel" (site B), Cook Mountains.

Description

These teeth are all of small size (less than 1 cm in width or height) but nonetheless overlap in size range with both *Portalodus* gen. nov. and *Aztecodus* gen. nov., indicating that they are not likely to be juvenile or extreme posterior teeth of one of the other Antarctic genera occurring in the same horizons. The main cusp of *Anareodus* gen. nov. is relatively flat and broad quite unlike that of the previous genera, with a well-defined thin cutting edge, and lacking any external ornamentation on the enameloid. In mesial view this cusp shows a weak sigmoidal curvature (WAM 94.2.9, Figure 10D). Incipient crenulations of the type described above in *Aztecodus* are seen in two specimens (e.g., WAM 94.2.13, Figures 8K, 10B; WAM 90.2.38, Figure 10A). The base is weakly concave to almost straight. In the largest specimen, WAM 90.2.38 (base 8.5 mm width, Figure 10A) the main cusp is approximately three times larger than the other cusp and diverges from it at a right angle. There is a weak development of median crenulations on this specimen. The root is coarsely textured with three small nutritive foramina present on the largest specimen (90.2.38) but not seen on any other specimen. None of the specimens shows the basal view of the root.

DISCUSSION

Heterodonty

One of the difficulties in dealing with small samples of isolated shark teeth is the possibility of variation in tooth morphology within the species, a problem in Palaeozoic shark systematics in general (e.g., Williams 1985: 85). Many modern sharks of the Neoselachii have a heterodont dentition, for example the largest family (Carcharinidae) in which upper and lower dentitions are markedly different, and the symphysial teeth have their own morphology (e.g., Reif 1985). Heterodont dentition has been suggested for various Palaeozoic sharks, and demonstrated in some, for example the Pennsylvanian *Cobelodus*, with single cusped teeth in the upper jaw, and tricusped teeth in the lower (Zangerl and Case 1976: figure 16). However, recent work on forms with diplodont teeth (Hampe 1988a, b, 1989) suggests that undetected heterodonty is not a problem for this group. Thus, in *Xenacanthus* (Hampe 1988a: figure 2) the largest teeth are located in the middle region of the jaw, and small posterior teeth lack the central cusp, but otherwise there is little variation in tooth morphology, and no known differences between teeth of upper and lower jaws. This is also the case in the modern *Chlamydoselachus* (e.g., Pfeil 1983; J. Long pers. observ.), and for the present seems a reasonable inference for the chondrichthyans under consideration here.

Is *Antarctilamna* a xenacanth?

Antarctilamna prisca was placed cladistically by Young (1982: figure 9) as the sister-group to the late Palaeozoic form *Xenacanthus*, and subsequently referred to (e.g., Maisey 1984; Young 1989a) as the most primitive known member of the Order Xenacanthida Glikman 1964, a major group of late Palaeozoic elasmobranchs characterised by 'diplodont' teeth, but also by many other derived features. The original analysis of *Antarctilamna* was carried out without access to Zangerl's (1981) article, nor the description by Dick (1981) of another early xenacanth, *Diplodoselache*, from the Early Carboniferous of Scotland. Since then, the teeth named *Leonodus* from the Early Devonian of Spain have also been referred to the Family Xenacanthidae by Mader (1986).

The proposed xenacanthid relationship of *Antarctilamna* was followed by Maisey (1984) and Lund (1985), but not by other authors (e.g., Williams 1985; Mader 1986). Zidek (1990) has argued that both tooth types described by Young (1982) (*Antarctilamna*, and *Portalodus* gen. nov. as described above) belonged to the phoebodontid ctenacanth sharks, and any affinity with xenacanths was considered to be exceedingly doubtful. In the original cladogram (Young 1982, figure 9), previous practice was followed (e.g., Schaeffer 1981: figure 26) in using one genus, *Xenacanthus*, to represent a higher taxon (the Family Xenacanthidae of Zangerl 1981). However, there are other genera normally placed in this family which clearly have a closer relationship to *Xenacanthus*, and this has caused some confusion. The question of whether *Antarctilamna* is a xenacanth must therefore distinguish 'crown-group' xenacanths (family Xenacanthidae) from a more inclusive higher taxon (e.g., order Xenacanthida of Zangerl 1981). Whether *Antarctilamna* is a xenacanth in this latter sense depends partly on whether the Xenacanthida is defined as a 'stem-based' or 'apomorphy-based' clade in the sense of de Queiroz and Gauthier (1990; also Doyle and Donoghue 1993). More important, however, is the issue of whether *Antarctilamna* is better placed within the Phoebodontidae, as Zidek (1990) has suggested. This decision must be based on synapomorphies, and there is a need to clarify the characters on which the various families are based, using a cladistic framework which distinguishes symplesiomorphy, synapomorphy, and autapomorphy. From this perspective we may consider 'crown-group' and 'stem-group' xenacanths separately, before examining the validity of the family Phoebodontidae.

Regarding 'crown group' xenacanths, Zangerl (1981) recognised two xenacanth families: Diplodoselachidae and Xenacanthidae Fritsch, 1889, the latter including three genera: *Orthacanthus*, with a straight spine of circular cross-section attached to the shoulder girdle, and *Xenacanthus* and *Pleuracanthus* with a cranial spine transversely elliptical in cross-section, but which differed in dentition and pectoral fin structure (lepidotrichia present in *Xenacanthus*). Zidek (1990, in press) provided new information on the spine of *Orthacanthus*, which is cephalic in the type (*O. cylindricus* Agassiz, 1843), but positioned above the shoulder girdle in the species *'O.' senkenbergianus* Fritsch, which perhaps may be closely related to *Diplodoselache*. Zidek otherwise recognised four valid xenacanth genera: *Expleurocanthus*, *Orthacanthus*, *Xenacanthus*, and *Triodus*. Details of tooth morphology for some of these was reported by Hampe (1988a) (*Xenacanthus*; 1988b, 1991; *Orthacanthus*; 1989, *Triodus*). These genera are distinguished by such dental characters as the height of the central cusp, the presence or absence of striations and serrated edges on the cusps, and the number of nutritive foramina on the base, as well as by numerous histological features (Hampe 1991). These are similar features to those used to differentiate phoebodont teeth from xenacanth teeth in the Devonian, so there is little point in including these late Palaeozoic forms in comparisons of stem group taxa. However, these studies are instructive in giving an indication of variability in tooth morphology. Thus, in *Xenacanthus* there are about 16 teeth in each jaw ramus, with the largest teeth located in the middle region of the jaw, and small posterior teeth lacking the central cusp (Hampe 1988a: figure 2). Apart from this 'gradient' heterodonty (Duffin and Ward 1983), there is little variation in tooth morphology.

Regarding stem-group xenacanths, *Antarctilamna* was considered by Zidek (1990) to be of phoebodontid (ctenacanthoid) affinity because its teeth have bilobed bases. The Family Phoebodontidae was placed within the Superfamily Ctenacanthoidea by Zangerl (1981), and the latter was united with hybodonts and neoselachians on the possession of two dorsal fin spines of neoselachian morphology. However, as noted by Ginter and Ivanov (1992), the tooth character (outer pair of cusps as high or higher than main cusp) by which the family was diagnosed by Williams (1985) does not occur in the articulated specimen *'Phoebodus' heslerorum*. Ginter and Ivanov (1992) considered this family to contain three genera: *Phoebodus*, *Omalodus*, and *Thrinacodus*, but the last genus was earlier interpreted as a xenacanth (Johnson 1984), although subsequently included with *Phoebodus* by Turner (1982). Long (1990: 62) included *Thrinacodus* within the Phoebodontidae and noted similarities between the expanded root of *Thrinacodus* with that of *Phoebodus gothicus* (Ginter 1990).

Omalodus Ginter and Ivanov, 1992 resembles *Portalodus* in the labial projection of the base, and the absence of a lingual torus. If this is the important taxonomic character, then the diplodont condition of *Portalodus* must have evolved separately from that in other forms (e.g., *Antarctilamna*, crown xenacanths), implying that the family Phoebodontidae containing their three genera is a paraphyletic grouping. It is clear that phoebodontid monophyly is not well established, and there is a need to assess the polarity for a range of characters concerned with fin-spines and teeth, as analysed below.

Analysis of Morphology

Fin-spines

Zangerl (1981: figure 51) used a branching diagram ('cladogram') to place Desmiodontida, Xenacanthida, Symmoriida and some other groups together with a basal node representing the absence of spines of neoselachian morphology, which he regarded as the primitive condition for Elasmobranchii. However, outgroup comparison to holocephalans, placoderms, acanthodians and osteichthyans would indicate that at least one dorsal fin-spine could be primitive, as previously argued by Young (1982) and followed by Maisey (1984) and Lund (1985). The single dorsal spine of crown-group xenacanths, which attached to the shoulder girdle or the back of the cranium, is an autapomorphy, with the more posterior position of the spine supporting the dorsal fin in *Diplodoselache* (Dick 1981), and a specimen ascribed to *Orthacanthus* (see above), showing that this specialisation evolved within the group. Together with the unique combination of diplodont teeth and a ctenacanth-like spine, as demonstrated in *Antarctilamna*, Zangerl's hypothesis is difficult to sustain on the grounds of parsimony. Furthermore,

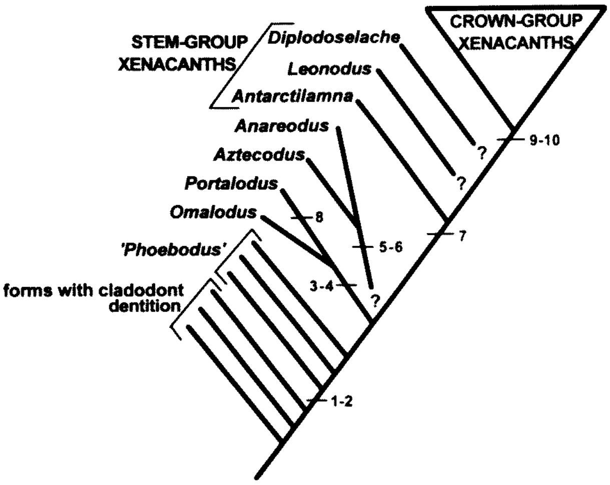

Figure 11 Cladogram summarising relationships between taxa discussed in the text, including the new forms *Portalodus*, *Aztecodus*, and *Anareodus* described here. Synapomorphies (as discussed in the text) are: 1, phoebodont tooth crown (having three main cusps, central cusp slightly smaller). 2, single button on lingual torus. 3, base with labial extension. 4, lingual torus lost. 5, crenulated mesial cutting ridge. 6, accessory lateral cusps. 7, diplodont tooth crown (central cusps much reduced or absent, two main lateral cusps). 8, diplodont tooth crown (inferred parrallelism). 9, spine detached from dorsal fin, with pectoral or occipital attachment. 10, squamation lost.

that a ctenacanth-like spine is primitive for xenacanths is not inconsistent with Zangerl's suggestion that their dentition is derived from a cladodont tooth type (see below). We therefore conclude that objections to xenacanth affinity for *Antarctilamna* based on its 'ctenacanth-like' spines are concerned with symplesiomorphy, and have no foundation.

Teeth

Teeth presumably originated as modified dermal denticles, and primitively can be assumed to have resembled scales in both size and morphology (e.g., Williams 1985: 141). However, faced with the morphological range of known Devonian shark teeth (from diplodont to cladodont), either one condition must be interpreted as primitive and the others derived, or special arguments may be invoked to justify a less parsimonious hypothesis of an unknown primitive morphological type. Zangerl (1981: 7) proposed that the simplest cladodont tooth form was a single elongate crown and a small base, which could then be 'enhanced', first by expansion of the base and addition of cusps, and then by modifications in cusp size. Thus he regarded xenacanth teeth as of 'modified cladodont design' (1981: 63), thereby implying that the cladodont condition was primitive. Lund (1985: 15) agreed that a single simple cone was the primitive tooth crown condition, using outgroup comparison with osteichthyans, but noted that the 'simplest condition known among mandibular teeth of chondrichthyans was the coronodont state: a distal-proximal series of subequal cusps fused into a 'multicuspid unit'. Lund suggested that this is plesiomorphic for elasmobranchs, and that protacrodont (low, subequal cusps), diplodont, and cladodont types are alternate derived conditions of the tooth crown developed on a 'synapomorphic' base. These alternative hypotheses of Zangerl and Lund were both apparently accepted by Williams (1985), who noted a tendency to fusion in typical anacanth branchial denticles, which could then be modified into a typical cladodont dentition by enhancement of the central cusp, and development of a lingual torus. Williams regarded these two features as advanced for all anacanthous sharks except *Cobelodus*, which he suggested exhibited the primitive condition for anacanthous sharks (where most teeth are small simple cones, with poorly developed bases, resembling the small *Petrodus*), like scales on the head of *Stethacanthus* and other form. However this interpretation has the unparsimonious consequence of requiring the evolution of multicuspid teeth in anacanth sharks independently of that in other elasmobranch groups.

Support for Lund's hypothesis is provided by the multicuspid branchial denticles observed in many forms, including *Antarctilamna* (Young, 1982: plate 87, figures 9, 10). However to interpret diplodont, cladodont and other types as alternate derived conditions of the tooth crown requires the same interpretation for the 'phoebodontid' tooth type as well, or any other combination. For heuristic reasons therefore, we provisionally follow Zangerl's interpretation that the cladodont tooth type (seen in a diversity of Palaeozoic sharks) is plesiomorphic relative to the diplodont type. We note, however, that the known fossil record (*Leonodus* of Mader 1986) suggests the opposite. The differences in tooth morphology and histology within the Family Xenacanthidae (e.g., Johnson 1980: 930; Zangerl 1981: figure 69; Hampe 1991) may be seen as variations on the diplodont theme. However the fact that the crown in xenacanthids always comprises three cusps with an orthodentine histology, which emerge separately from the base, may be derived features characterising the family (Hampe 1991), by which they are distinguished from more primitive tooth types of *Antarctilamna* and phoebodontids (but histology is not yet known in these).

Under this interpretation, the phoebodont tooth type would represent an intermediate stage of cusp reduction. Phoebodontid teeth are characterised by

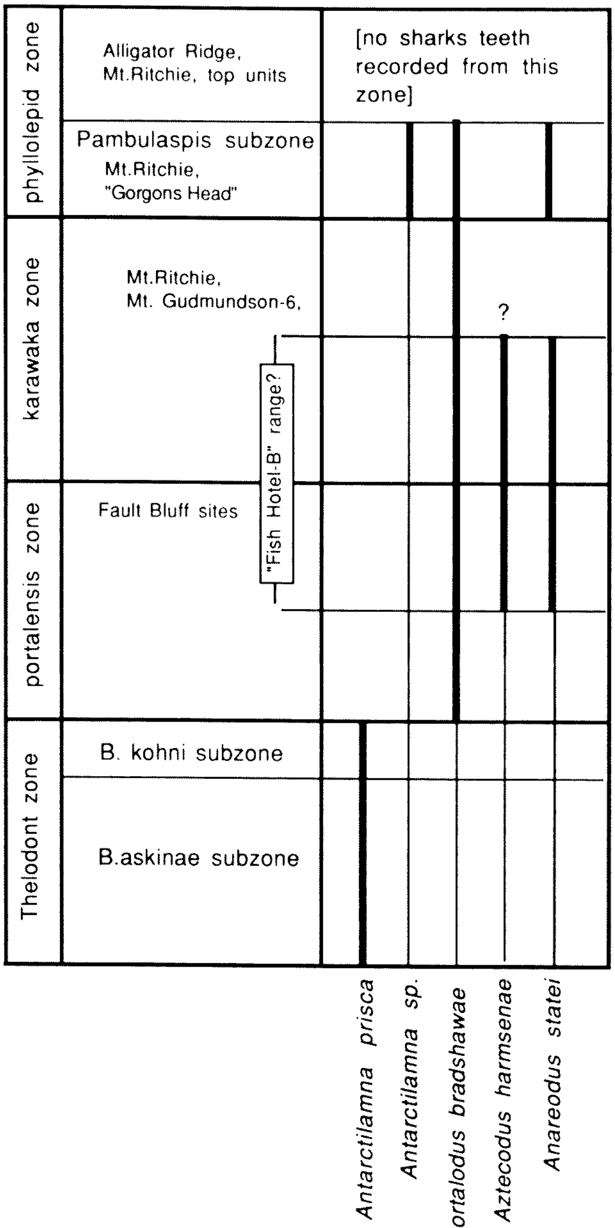

Figure 12 Summary of biostratigraphic occurrence of shark remains from the Aztec Siltstone, using overall faunal list data from new sites in Cook Mountains.

having three main cusps in the crown, with the central cusp slightly smaller; and primitively there is a bilobed base. Including smaller intermediates there may be five cusps, but specimens with four cusps are uncommon, and with six or seven extremely rare (Ginter and Ivanov 1992). Apart from reduction of the central cusp, the only other tooth character possibly uniting the group is the 30–40° inclination of the lateral cusps away from the central cusp mentioned by Zangerl (1981), but this is seen in other forms (e.g., *Mcmurdodus*) and is not a clear-cut character. Thus on the evidence of coronal morphology the phoebodontids would be a paraphyletic grouping.

Regarding the structure of the base, the bilobed condition in some phoebodont teeth was considered primitive for the family by Ginter and Ivanov (1992), presumably by outgroup comparison with forms like stethacanthids (e.g., Lund 1985). However, in the latter, two tubercles are developed on the dorsal surface, whereas in phoebodont teeth, including those with a bilobed base, and in all xenacanth teeth, a single 'button' is developed on the dorsal surface of the lingual torus. In *Antarctilamna*, re-examination of the tooth figured by Young (1982: figure 3C) suggests that it may be incomplete, with the base possibly larger and bilobed (M. Ginter, pers. comm.). One example of a tooth from the holotype was reported to show a 'button', but some others which apparently lacked it (Young 1982: 827) may be abraded (M. Ginter, pers. comm.), so the state of this character needs confirmation.

The lingual torus is regarded as a derived character by most authors, and is one of a variety of mechanisms evolved within the Chondrichthyes to maintain proper spacing between successive teeth in a tooth family (Zangerl 1981: 8) until they move up into a functional position (e.g., Hampe 1988a: figure 3). Thus the 'button' on the dorsal surface of the lingual torus in *Phoebodus* fits into a depression in the base of the overlying tooth (Ginter and Ivanov 1992: figure 2), with teeth presumably held together by inter-dental ligaments (Lund 1985). In various cladodont teeth the lingual torus may have two buttons developed, but the single button in phoebodont and diplodont teeth seems to be a consistent feature, and may be interpreted as a synapomorphy uniting 'phoebodontids' as a paraphyletic stem-group to xenacanths in the broad sense (see Figure 12). A differentiated 'basal tubercle', developed from a general 'labio-basal thickening' of some phoebodonts (Ginter and Ivanov 1992: figure 2), which in certain species (e.g., *P. australiensis*, Long 1990: figure 4D) is developed as a distinct 'ventro-labial boss', may define a less inclusive group (some *Phoebodus* species, and stem and crown-group xenacanths; Figure 12). It should be noted that Zidek (in Cappetta *et al.* 1993) has suggested that in the Early Devonian form *Leonodus* 'the basolabial boss and basolingual margin show a tendency toward splitting', on which evidence he suggests a possible ctenacanthoid affinity. But this resemblance, if confirmed, may be a symplesiomorphy, in which case it would indicate only that reduction of the central cusps preceded the development of a single basal tubercle in the *Leonodus* lineage. On the other hand, phoebodontid teeth, as just discussed, demonstrate the opposite situation, so there is clearly some homoplasy involved in these detailed tooth characters.

In *Omalodus* and *Portalodus*, which have a labial extension instead of a lingual torus, the base must have been held in the tooth row in a different way. However it is not clear from its orientation whether the labial projection functioned as a spacing device.

The arrangement of foramina and canals for vascular supply to the tooth is another feature of the base which may be different in closely related forms. Hampe (1988b: figure 3a) described the system in *Orthacanthus* as two parallel, labio-lingually arranged canals connected to a cavity below the crown, with a separate supply to the small intermediate cusp. In contrast, in *Triodus* there is a ramifying system to all three cusps (Hampe 1989: figure 2). In *Phoebodus gothicus* there is a single canal traversing the base (Gross 1973: 34, figure 13b), and a similar foramen is observed on the ventral face of the base in *Antarctilamna* (Figure 3A). However a different arrangement is seen in *Phoebodus australiensis*, which has two large transverse canals passing through the base (Long 1990: figure 4E). Although internal structure has not been studied, *Portalodus* (Figure 6C) and probably *Mcmurdodus* (Turner and Young 1987: figure 3B) show labial and lingually placed foramina on the base, with the intervening canal partly or wholly enclosed, or expressed as a groove across the ventral surface – a combination of the supposedly distinctive types of vascularisation pattern illustrated by Duffin and Ward (1983: figure 4A–C). It is not clear at present that these different patterns have any phylogenetic significance.

Relationships of the new taxa

Based on the foregoing discussion, the three new taxa described above may be placed in a provisional cladistic framework (Figure 11). All the new taxa are variants on the diplodont pattern, with largest cusps placed at the lateral margins rather than centrally, as in cladodont teeth. However *Aztecodus* and *Anareodus* share features not seen in *Portalodus* (crenulated cutting ridge, small accessory cusps at lateral margins of crown), which we assume to indicate a close relationship. On the other hand, *Portalodus* resembles the genus *Omalodus* erected by Ginter and Ivanov (1992: 62) in the absence of a lingual torus, and development of a labial extension to the base, which forms an obtuse angle with the crown. By outgroup comparison (e.g., *Antarctilamna*, *'Phoebodus'*, *'Cladodus'* tooth types), the labial extension is interpreted as a unique derived feature, whereas the absence of a lingual torus must be a secondary loss. On available evidence therefore we consider *Portalodus* and *Omalodus* immediately related, and *Aztecodus* and *Anareodus* immediately related as two sister-group pairs. This implies that the diplodont condition evolved independently in *Portalodus*, and as discussed above there may be other evidence based on character distribution which indicates further homoplasy in this feature. However, for the present we suggest that the diplodont condition of *Antarctilamna*, *Diplodoselache*, and crown group xenacanths is a synapomorphy by which those taxa are grouped together. Lacking information on other features (e.g., fin-spine morphology), the *Aztecodus*-*Anareodus* clade does not have a clear position either within or outside the Xenacanthida on available evidence.

Biostratigraphy

The use of Devonian shark teeth in biostratigraphy is becoming increasingly important. Many new species have been recently identified and their age ranges tied into well-dated sections, some intercalated with marine sections containing conodonts or spore zonations (Turner 1982, 1990, 1991, 1992, 1993; Turner and Young 1987; Long 1990; Ginter 1990; Ginter and Ivanov 1992). Ginter and Ivanov (1992: figure 9) summarise the biostratigraphic distribution of *Phoebodus* teeth through the Late Devonian of eastern Europe in relation to the standard conodont zonation. They note their absence thus far from the early Frasnian, and rarity in the latest Frasnian *linguiformis* Zone level in sequences in Moravia (Hladil *et al.* in press) which may be due to the Kellwasser extinction event. Phoebodont maximum diversity apparently corresponds with that of palmatolepid conodonts in the Famennian, and their widespread distribution is indicated by occurrences in Australia (Turner 1982), Thailand (Long 1990), and Morocco (Derycke 1992).

Ginter and Ivanov (1992) give the earliest occurrence of *Phoebodus* teeth as the Givetian of North America (Paul Frank Quarry bone beds), and they also record Givetian occurrences from Poland, Australia, and the Kutsnetz Basin. Stritzke (1986) figured a phoebodont tooth from the *hermanni-cristatus* conodont zone of the Rhenish Schiefergebirge, Germany. The new Antarctic taxa are of similar age (see discussion in Young 1988: 16–19). The biostratigraphic distribution of the new taxa in Antarctic sections is summarised in Figure 12, and corresponds to zones 6a–e in the scheme of Young (1993), which are provisionally equated with varcus to *hermanni-cristatus* Zone conodonts (Givetian).

An older *'Phoebodus'* tooth from the Jauf Formation of Saudi Arabia (Forey *et al.* 1992) is a considerably large tooth that has very small central cusps. It has been studied by one of us (JAL) and is not regarded here as properly referred to the genus. Zidek (in Cappetta *et al.* 1993) considered the earliest *Phoebodus* to be of Eifelian age (*P. floweri*, a form synonymised with *P. fastigatus* by Ginter and Ivanov 1992), but his evidence of age is

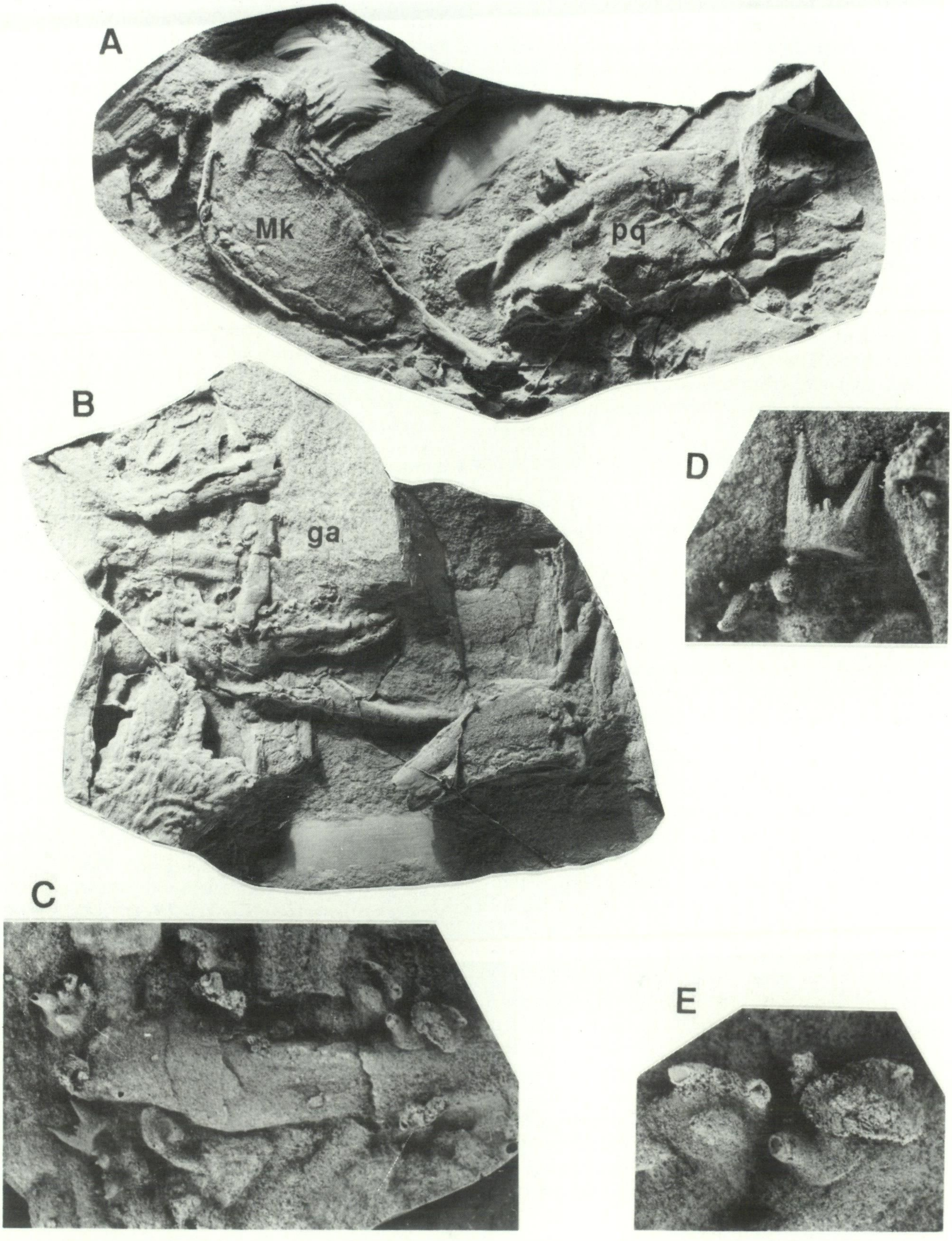

Figure 13 *Antarctilamna prisca* Young 1982. CPC 21213, Bunga Beds, south coast of New South Wales. A, latex cast showing impressions of the palatoquadrate (pq) previously illustrated by Young (1982, fig. 8C) and associated meckelian cartilage (Mk, x1). B, latex cast of counterpart to A, showing associated gill-arch elements (ga) and teeth (x1). C, detail of gill arch element shown in B, with associated teeth (x 4)., D, teeth from lower left of C showing striations on labial side of cusps (upper tooth) and small cusplets lateral to major cusps (lower tooth, base obscure; x 4). E, teeth from top right corner of C showing the button on the lingual torus (x4).

not provided. *Omalodus bryanti* Ginter and Ivanov 1992, is recorded from the late Givetian of the Kuznetsk Basin, but the original material of Wells (1944) came from the same locality as *Ph. floweri* (Kiddeville bone-bed, lower part of Boyle Limestone), and this was also regarded by Wells (1944) as Givetian in age.

Biogeography

The diversity of middle Palaeozoic chondrichthyans from the Gondwana continents resulting from new discoveries over the last 15 years indicates that a substantial part of their fossil record is not represented in the well-studied Palaeozoic successions of the Northern Hemisphere. The only possible chondrichthyans (based on teeth) from the Early Devonian of the Euramerican or Asian terranes is material of *Doliodus problematicus* from the Emsian of Campbelltown, New Brunswick, Canada. This material, now housed in the Natural History Museum, London, was originally described by Woodward (1892) as acanthodian teeth, and has been re-examined by one of us (JAL). Some teeth (e.g., BMNH 7076) show a well-developed root system with vascular canals present, a characteristic of chondrichthyan teeth. Despite this, most of the record of Early Devonian sharks is from Gondwanan or neighbouring Gondwanan terranes, suggestive of a Gondwana origin for the chondrichthyans (exclusive of identifications based on scales alone).

Apart from the diplodont teeth of several taxa in the Aztec fauna dealt with above, similar teeth are also known from southern Africa (Bokkeveld Formation, upper Middle Devonian, Oelofson 1981), and South America and various parts of the Middle East have yielded similar fin-spines (but apart from Saudi Arabia, no teeth as yet). All of these areas are thought to have been part of Palaeozoic Gondwana, and a synthesis of these occurrences is given in Lelievre *et al.* (1993). Previous biostratigraphic and biogeographic assessment of the Antarctic Aztec assemblage led to the hypothesis of Gondwana origin for the xenacanth clade, and subsequent dispersal into the northern hemisphere (Young 1989a, 1990). This was in accord with evidence from a range of taxa, both invertebrate and vertebrate, indicating a biotic dispersal episode, perhaps related to changes in global palaeogeography (e.g., Young 1981, 1987).

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