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Disarticulated acanthodian and chondrichthyan remains from the upper Middle Devonian Aztec Siltstone, southern Victoria Land, Antarctica

CAROLE J. BURROW[1,*], JOHN A. LONG[2] and KATE TRINAJSTIC[3]

[1]*Geosciences Annex, Queensland Museum, 122 Gerler Rd, Hendra, Brisbane, QLD 4011, Australia*
[2]*Museum Victoria, PO Box 666E, Melbourne, VIC 3001, Australia*
[3]*School of Earth and Geographical Sciences, University of Western Australia, Crawley, Perth, WA 6009, Australia*
**carole.burrow@gmail.com*

Abstract: Well-preserved vertebrate microremains are abundant in the residues from a calcareous grey siltstone in the *karawaka* biozone (?late Givetian) of the Aztec Siltstone at Mount Crean, Lashly Mountains, Antarctica. Acanthodians are represented by scales of acritolepid *Pechoralepis juozasi* sp. nov., climatiid *Nostolepis* sp. cf. *N. gaujensis* Valiukevičius, diplacanthid *Milesacanthus antarctica* Young & Burrow, and an undetermined acanthodiform. The acanthodian assemblage resembles those from early Frasnian carbonates of central Iran. Chondrichthyan elements in the fauna include rare teeth of *Aztecodus harmsenae* Long & Young and *Antarctilamna prisca* Young, ctenacanthoid-type scales and branchial denticles which are possibly from *Antarctilamna*, and scales of an indeterminate chondrichthyan. An isolated set of acanthodid acanthodiform jaws from the uppermost 'phyllolepid' biozone of the Aztec Siltstone at Mount Ritchie, Warren Range, Antarctica is also described.

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Key words: Acanthodidae, *Anareodus*, *Antarctilamna*, *Aztecodus*, *Milesacanthus*, *Nostolepis*, *Pechoralepis*

Introduction

The history of fossil fish research on the Antarctic continent extends back for nearly a century, with Devonian fossils first being discovered by the British Antarctic "*Terra Nova*" expedition in 1910–13. Woodward (1921) described this material, identifying specimens from six major groups of Devonian fishes. However, the extreme conditions experienced during field work in Antarctica limited further collecting until the 1950s. The first *in situ* fossil fish material, described by White (1968), was collected from the Aztec Siltstone during the Trans-Antarctic Expedition of 1955–58. Later expeditions between 1968 and 1992, as summarized by Long *et al.* (2008), yielded an abundant collection of fossil fish, and many detailed systematic studies of Devonian vertebrate faunas were published over the last quarter of a century. These publications described thelodonts, placoderms, chondrichthyans, acanthodians, sarcopterygians, and most recently, an actinopterygian (Long *et al.* 2008). Young & Long (2005, table 1) listed 45 taxa from the Aztec Siltstone, making it one of the most diverse vertebrate assemblages known from Middle–Late Devonian strata. Until now, much of the microvertebrate fauna remained undescribed.

In this paper we describe acanthodian microremains from collecting site MC7 at Mount Crean, Lashly Mountains, Australian Antarctic Territory (see Young 1988, fig. 3 and Young & Long 2005, fig. 1 for locality details) and a single isolated set of acanthodian jaws from Mount Ritchie, southern Warren Range, collected by JAL on the joint 1991–92 New Zealand Antarctic Research Program–Australian National Antarctic Research Expedition. Vertebrate fossils previously reported from site MC7 include dermal plates of placoderms *Bothriolepis barretti* Young, 1988 and *Groenlandaspis* sp., a sarcopterygian jaw (Young *et al.* 1992), and teeth from the elasmobranch *Portalodus bradshawae* Long & Young, 1995. The faunal assemblage from the highest site at Mount Ritchie includes placoderms *Bothriolepis macphersoni* Young, 1988, *Pambulaspis antarctica* Young, 1988, and acanthodian *Gyracanthides*?, indicative of the 'phyllolepid' zone of Young (1988), above the '*Pambulaspis*' subzone (Long & Young 1995, fig. 12). To date, no shark teeth have been found at this site. Young & Long (2005, fig. 12) dated the entire Aztec Siltstone assemblage as within the *varcus* conodont zone (middle Givetian), however evidence is lacking for a lower age limit (Long *et al.* 2008).

The microremains from site MC7 comprise abundant scales of the thelodont agnathan *Turinia antarctica* Turner & Young, 1992, rare scales of an undetermined actinopterygian, placoderm, porolepiform and dipnoan fragmentary remains, as well as the acanthodian scales and spine fragments and chondrichthyan scales and teeth which we describe here.

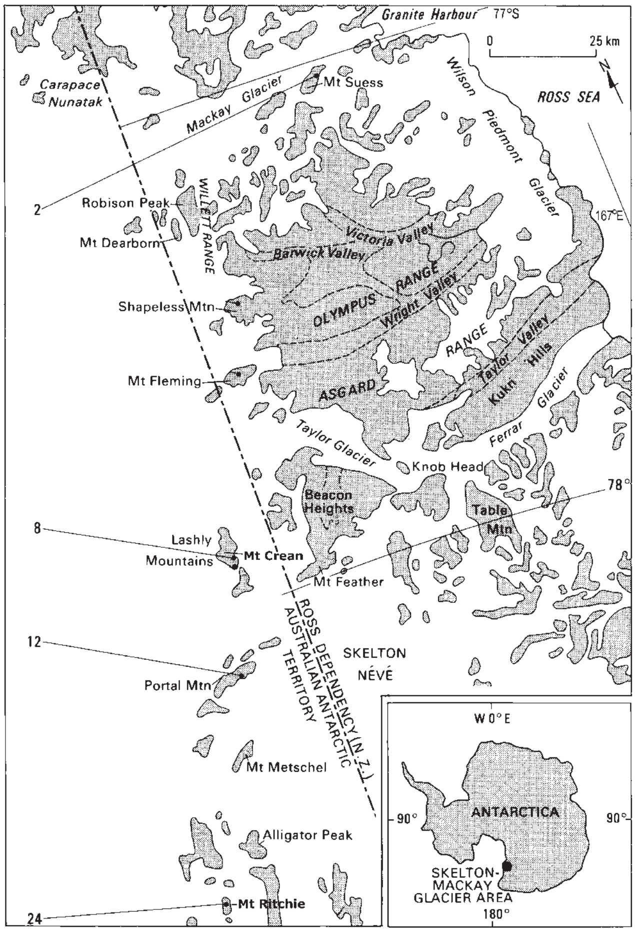

Fig. 1. Locality map after Young (1988, fig. 3), pinpointing Mount Suess (Young's locality 2), the site from which the first fossil fish discovered in Antarctica originated; microvertebrate assemblage site MC7 at Mount Crean (loc. 8); acanthodid jaw site at Mount Ritchie (loc. 24); and the type locality for *Milesacanthus antarctica* Young & Burrow, 2004 at Portal Mountain (loc. 12).

Material and methods

All of the Mount Crean specimens described here are from a calcareous grey siltstone block collected by JAL at site MC7 of Young (1988), the highest fossiliferous horizon of the outcrop at locality 8 (Young 1988, p. 12–13, fig. 3; Fig. 1) on the eastern side of the mountain. The horizon is about 140 m above the base of the Aztec Siltstone. The calcareous matrix was dissolved in dilute (10%) acetic acid, and the residues picked for vertebrate microremains. The specimen comprising articulated acanthodid jaws was collected by JAL from the top layers of the Aztec Silstone, 212 m above base, at Mount Ritchie, locality 24 of Young (1988, fig. 3; Fig. 1). The jaws were prepared by mechanical removal of bone remnants, followed by latex casting of the cleaned mold. Most Mount Crean specimens are housed in Museum Victoria (NMV P); several thin sections and the articulated jaws are housed in the Western Australian Museum (WAM); *Milesacanthus antarctica* type material is housed in the Research School of Earth Science, Australian National University (ANU V).

The isolated scales, teeth and fin spine fragments were digitally imaged using a Jeol JSM-6300F Scanning Electron Microscope, and ground thin sections were imaged using an Olympus BX-50 transmission microscope and DP-12 imaging system. Latex casts of the Mount Ritchie specimen were whitened with ammonium chloride and photographed with a Panasonic Lumix DMC-FZ20, as were the *Aztecodus* teeth. Figures were compiled using Adobe Photoshop®. Abbreviations used in the figures are: Aup = autopalatine, bcl = bone cell lacuna, br = branchiostegal ray, c = pulp canal, cc = circular canal, co = canal opening, cr.epq = extrapalatoquadrate ridge, dc = dentine canal, dd = durodentine, dt = dentine tubules, en = enameloid, f.add = adductor muscle fossa, for = foramina, gl = growth lamina, gr = gill raker, Hb = hyoid bar ossification, Hm.v = ventral ossification of hyomandibula, lb = lingual boss, Mk.a = anterior ossification of Meckel's cartilage, Mk.p = posterior ossificaton of Meckel's cartilage, oc = odontocyte, o.i = indeterminate ossification, o.md = mandibular ossification, pc = pulp cavity, Pq = palatoquadrate, pr.ptart = posterior process of quadrate articulation, rvc = radial vascular canal, scl = sclerotic ring plate, Sg = Stranggewebe, slo = sensory line ossification, smd = simple mesodentine, tse = edges of thin section, vc = vascular canal.

Systematic palaeontology

ACANTHODII
Family ACRITOLEPIDAE Valiukevičius & Burrow, 2005
Genus *Pechoralepis* Valiukevičius & Burrow, 2005

Type species. Pechoralepis zinaidae (Valiukevičius, 2003a)

Included species. Pechoralepis zinaidae, *P. adzvensis* (Valiukevičius, 2003a), *P. valentinae* (Valiukevičius, 2003a), *P. juozasi* sp. nov.

Pechoralepis juozasi sp. nov.
Fig. 2a–m

Etymology. For Lithuanian scientist Dr Juozas Valiukevičius, the world's premier worker on acanthodian microremains over the last thirty years.

Holotype. Scale NMV P228897 (Fig. 2a & b); paratypes are the other material figured here.

Other material. Twenty scales including NMV P228898 (Fig. 2c & d), NMV P228899 (Fig. 2e & f), NMV P228900 (Fig. 2g & h), NMV P228901 (Fig. 2i & j), and thin sections NMV P228941 (Fig. 2k & l) and NMV P228942 (Fig. 2m).

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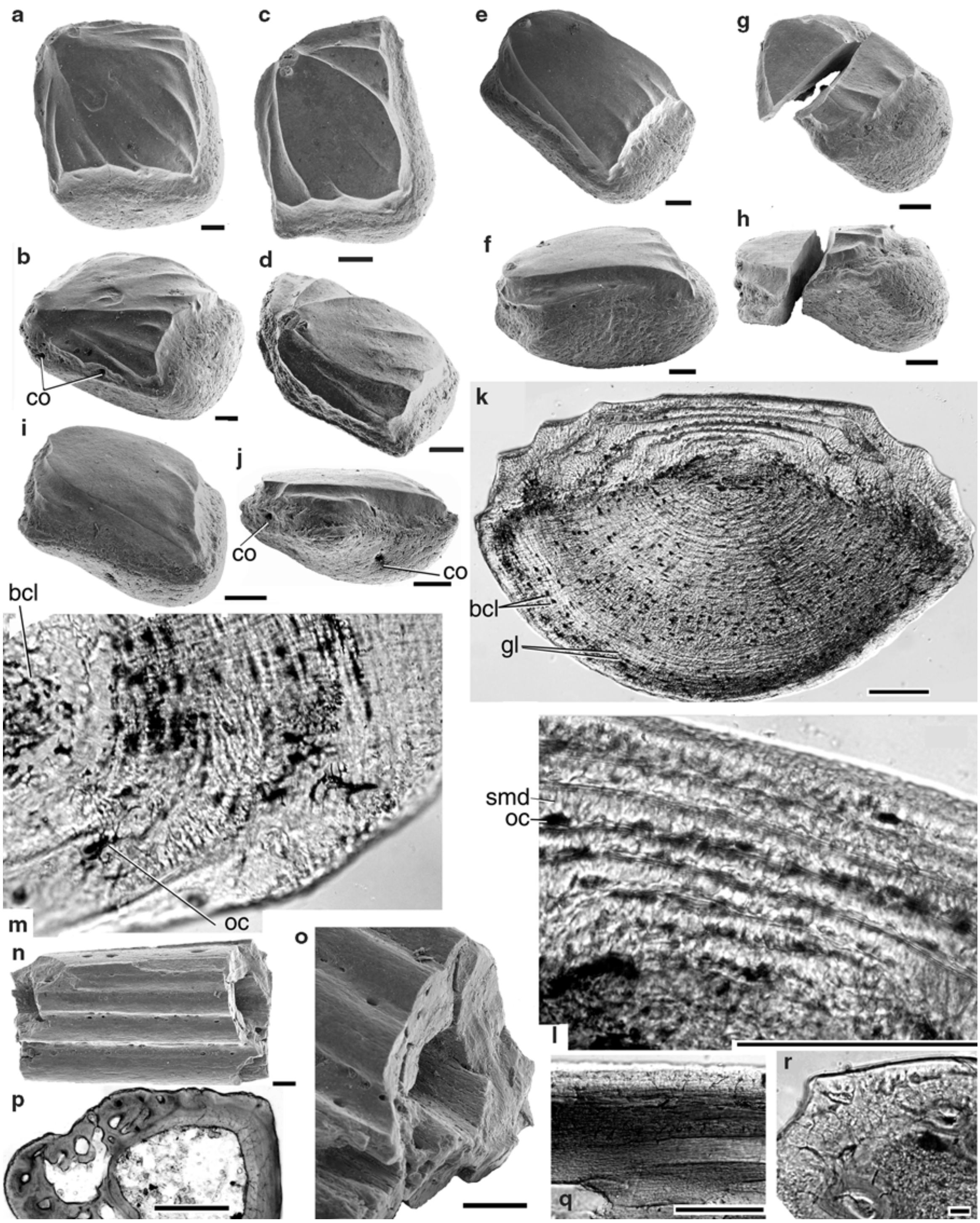

Fig. 2. Scales and possible fin spine fragments of acritolepid acanthodian *Pechoralepis juozasi* sp. nov. from the Aztec Siltstone, locality MC7, Mount Crean, Antarctica. **a. & b.** Holotype NMV P228897 in crown and lateral views, **c. & d.** NMV P228898 in lateral and basal views, **e. & f.** NMV P228899 in crown and lateral views, **g. & h.** NMV P228900 in crown and lateral views, **i. & j.** NMV P228901 in crown and lateral views, **k. & l.** vertical transverse section NMV P228941, showing whole section and closeup of central crown, **m.** horizontal section through apex of base and lower crown NMV P228942, showing area at lateral corner with bone cell lacunae of upper base and odontocytes and Stranggewebe of lower crown. **n.–r.** Fin spine fragments possibly from *P. juozasi*. **n. & o.** fragment NMV P228920. **p.** Transverse thin section of spine tip fragment NMV P228955 (leading edge to left). **q. & r.** Longitudinal and transverse thin sections through one side of spine fragment NMV P228954. Scale bar is 0.1 mm in a–q, 0.01 mm in r; anterior of scales is to the right.

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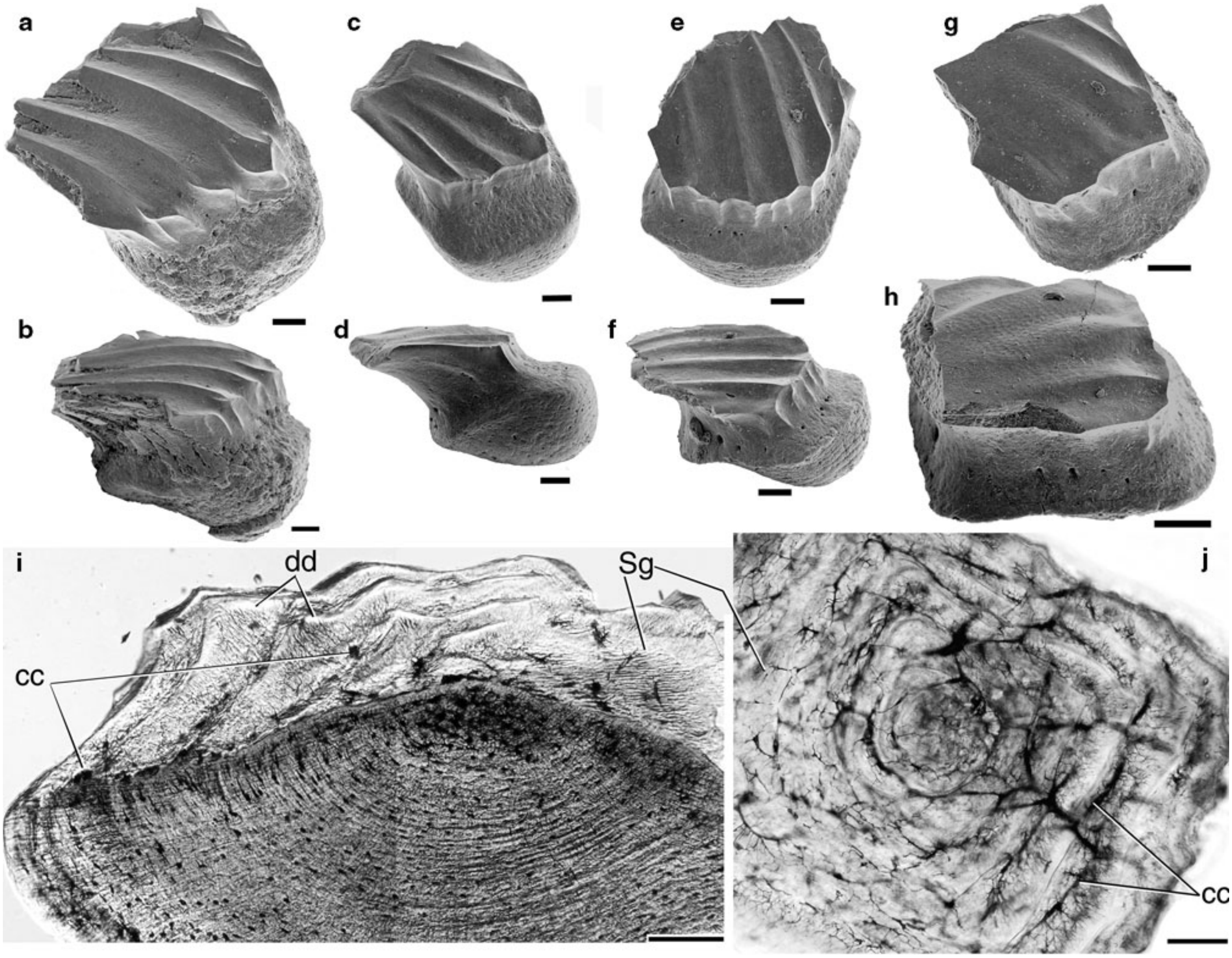

Fig. 3. Scales of climatiid acanthodian *Nostolepis* sp. cf. *N. gaujensis* Valiukevičius, 1998 from the Aztec Siltstone, locality MC7, Mount Crean, Antarctica. **a. & b.** NMV P228902 in laterocrown and lateral views, **c. & d.** NMV P228903 in laterocrown and lateral views, **e. & f.** NMV P228904 in anterocrown and lateral views, **g. & h.** NMV P228905 in laterocrown and posterocrown views, **i.** vertical transverse section NMV P228943, **j.** horizontal section of crown NMV P228944. Scale bar is 0.1 mm; anterior of scales is to the right unless indicated by arrows.

Diagnosis. *Pechoralepis* with diamond- or square-shaped scales in which the base is wider and longer than the crown; posterolateral ridges along edges of high central crown plate are curved, converging to form a blunt posterior corner; 1–3 subradial ridges on anterior central crown plate fade out by midcrown; the scale neck rarely has vascular canal openings, as radial canals are only rarely developed in the crown; ascending vascular canals are lacking and circular canals are developed at two levels, just above the base and in the angle between the upper and lateral crown areas; the crown has 4–7 superposed growth zones; odontocytes fill the lowest level of the central part in each growth zone; Stranggewebe is only developed low in the posterior crown.

Description. Scales are medium-sized, *c.* 0.5–1.0 mm long and wide. Scale crowns are usually diamond- or square-shaped with a raised medial area bordered by curved sharp edges from lower lateral areas; the outermost crown perimeter is sharp all round. The crown is relatively flat, and usually pinched in and sloping down slightly at the anterior corner, widening gradually towards the centre and then narrowing to form the posterior point (Fig. 2a, c & i). Rare scales have a straight anterior edge (Fig. 2e). The medial crown area has 1–3 short, evenly-spaced ridges running back from the anterior edge(s) towards the side edges, but fading out before mid-crown; lateral crown areas have one or two (Fig. 2i) ledges with (Fig. 2a) or without (Fig. 2e) shorter ridges. The neck is short or absent. Rarely, large pores are present along the neck-base junction (Fig. 2b & j), and more rarely canals pierce the base (Fig. 2j). Scales bases have a square or rhombic outline, and are usually slightly wider and longer than the crowns; the base is rounded convex and deepest slightly forward of centre.

Histological investigations show that the scale crowns have 4–7 superposed growth zones, which are relatively thin centrally (Fig. 2k & l). Growth zones are filled with odontocytic mesodentine (*sensu* Valiukevičius & Burrow 2005: lacunae often present where dentine tubules branch) plus a small area of Stranggewebe (i.e. mesodentine comprising parallel elongated lacunae and processes) low in the posterior crown, but not in the primordium (i.e. the first formed, central growth zone). The elongated lacunae are very fine and densely packed (Fig. 2m). Odontocytes interconnected by short processes are abundant in the lowest level of all growth zones, across the whole width of the central plate (Fig. 2l). The scales appear to have circular vascular canals at two levels, just above the base and in the angle between the upper and lateral crown areas; other vascular canals are rare. Polygonal or rounded osteocytes are abundant throughout the base, which is formed of very thin bone lamellae. The osteocytes are interconnected by winding processes, forming a particularly dense network in the apex of the base, which is the primordial growth zone (Fig. 2m).

Comparison. The scales are assigned to *Pechoralepis* because of their distinctive histological structure (fourth structural group *sensu* Valiukevičius & Burrow 2005); morphologically they most closely resemble scales of *P. valentinae* (Valiukevičius 2003a) from the Lochkovian Toravey Formation of Timan-Pechora, Russia. Histologically, scales of *P. juozasi* sp. nov. mainly differ from those of *P. valentinae* (Valiukevičius 2003a, fig. 21) in having more crown growth zones (4–7 vs. 2–4) and only rare vascular canals in the crown. *Pechoralepis juozasi* also shows some similarites to *Iranolepis ginteri* Hairapetian, Valiukevičius & Burrow, 2006 from early Frasnian shallow water carbonates in the Chahriseh profile, Kaftari Mountain, central Iran. The main differences between the two taxa are that *Iranolepis* scales have a pronounced anteromedian sulcus on the crown, lack the sharp perimeter along the anterior crown edge, and have sparser odontocytes in the crown. Both taxa appear to have circular vascular canals at two levels in the crown (Hairapetian *et al.* 2006, fig. 4D). The overall scale shape resembles that of some of the new undetermined shark scales described below, but scales of *P. juozasi* are distinguished by having lateral crown ledges rather than lateral odontodes, a symmetrical base rim outline, relatively smooth bases, superpositional crown growth zones, and lacking an anteromedian sulcus on the crown. The distinctive shape of the crown in *P. juozasi*, with a medial crown area bearing short ridges edged by lower lateral ledges and short oblique neck ridges, is mirrored in many other taxa, including the Early Devonian acanthodians *Nobilesquama minilonga* (Valiukevičius, 2003a), *Nostolepis kozhymica* Valiukevičius, 2003a, *Nostolepis terraborea* Valiukevičius, 2003a, *Nostovicina laticristata* (Valiukevičius, 1994), *Pechoralepis valentinae* and *P. adzvensis*, as well as the modern, deep water Gulper shark, *Centrophorus granulosus* (Reif 1985, pl. 5, text-fig. 21G).

ACRITOLEPIDAE?
Fig. 2n–r

Material. Ten short mid-distal fin spine fragments including NMV P228920 (Fig. 2n & o), transverse section near spine tip NMV P228955 (Fig. 2p), and vertical longitudinal and transverse sections of a mid-distal spine fragment NMV P228954 (Fig. 2q & r).

Description. Fragments have up to three longitudinal ribs per side and a wider leading edge rib, with a wide central cavity. Lateral ridge crests are slightly convex in transverse section, with an angular lower edge (Fig. 2r). Shallow grooves separating ribs have irregularly-spaced pore openings. The largest fragment is the slender tip of a spine, 3 mm long, with a relatively broad flat trailing face. NMV P228955, the transverse section of this spine tip (Fig. 2p), shows a wide central cavity and numerous longitudinal canals in the upper half (leading edge) of the spine, and a finely lamellar acellular bone forming a thick layer surrounding the central cavity (Fig. 2q). Transverse sections show denteons formed around the longitudinal canals. All sections show mesodentine without lacunal widenings forming a network in the ridges, and an outer durodentine or enameloid layer on the ridges (Fig. 2r).

Comparison. Unfortunately no fragments with an insertion area were found in the residues: a group of Gondwanan diplacanthid genera, including *Milesacanthus*, are distinguished from other acanthodians with longitudinal ridges on fin spines by having very thin parallel ridges forming the surface of the insertion area. The sections described here show no evidence of the radiating canals and deep inter-ridge grooves with a subcircular cross-section which characterize the Antarctic diplacanthid acanthodians in which spine histology is known (e.g. Young & Burrow 2004, fig. 6H, J, M, O, P). Acritolepids are one of the non-diplacanthiform acanthodians with spines having a morphology similar to the Mount Crean fragments: unpaired and pectoral fin spines of Lochkovian taxa *Pechoralepis zinaidae* (Valiukevičius, 2003a) and *Acritolepis* spp. (Valiukevičius 2003b, figs 1, 2, 6B, 13A, 13B, 15A) have equal-width lateral longitudinal ridges with a sharp-edged 'corner' in transverse section, and a histological structure (Valiukevičius 2003b, figs 8, 14) similar to the Mount Crean fragments, differing mainly in cellularity and lack of an outer enameloid layer. The Antarctic spines are much younger (Givetian) than the Arctic acritolepids (Lochkovian). Loss of bone cell lacunae in dentinous tissues from older to younger species of the

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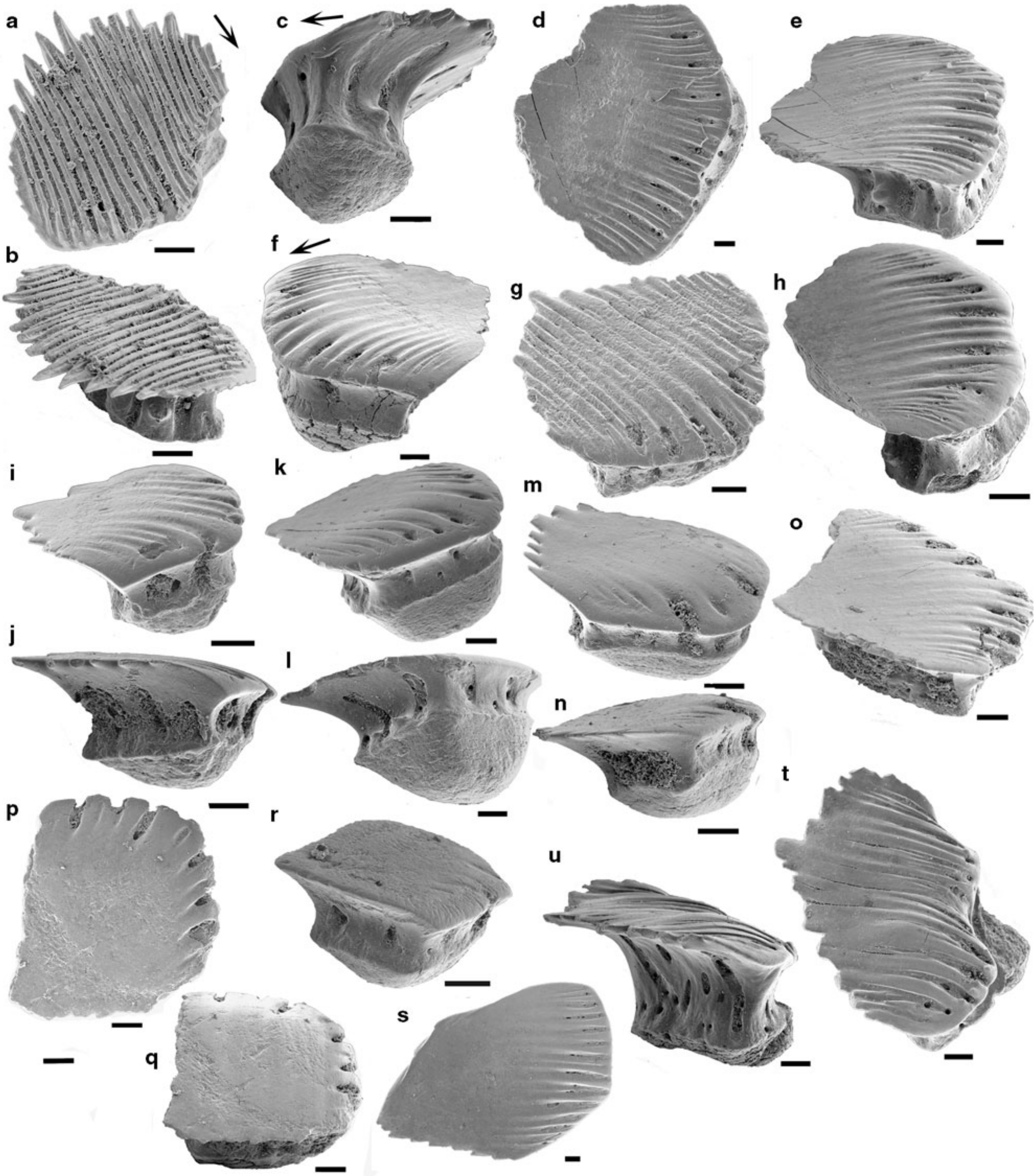

Fig. 4. Scales of *Milesacanthus antarctica* Young & Burrow, 2004 from the Aztec Siltstone, collecting site MC7, locality 8 of Young (1988), Mount Crean, Antarctica. **a. & b.** NMV P228906, in crown and posterolateral views, **c.** NMV P228907, in laterobasal view, **d & e.** NMV P228908, in crown and laterocrown views, **f.** NMV P228909, in anterocrown view, **g.** NMV P228910, in crown view, **h.** NMV P228911, in laterocrown view, **i. & j.** NMV P228912, in laterocrown view, **k. & l.** NMV P228913, in laterocrown and lateral views, **m. & n.** NMV P228914, in anterocrown and lateral views, **o.** NMV P228915, in laterocrown view, **p. & q.** NMV P228916, in crown and laterocrown views, **r.** NMV P228917, in posterocrown view, **s.** NMV P228918, in crown view, **t. & u.** NMV P228919, in crown and posterolateral views. Scale bar is 0.1 mm; anterior of scales is to right unless indicated by arrows.

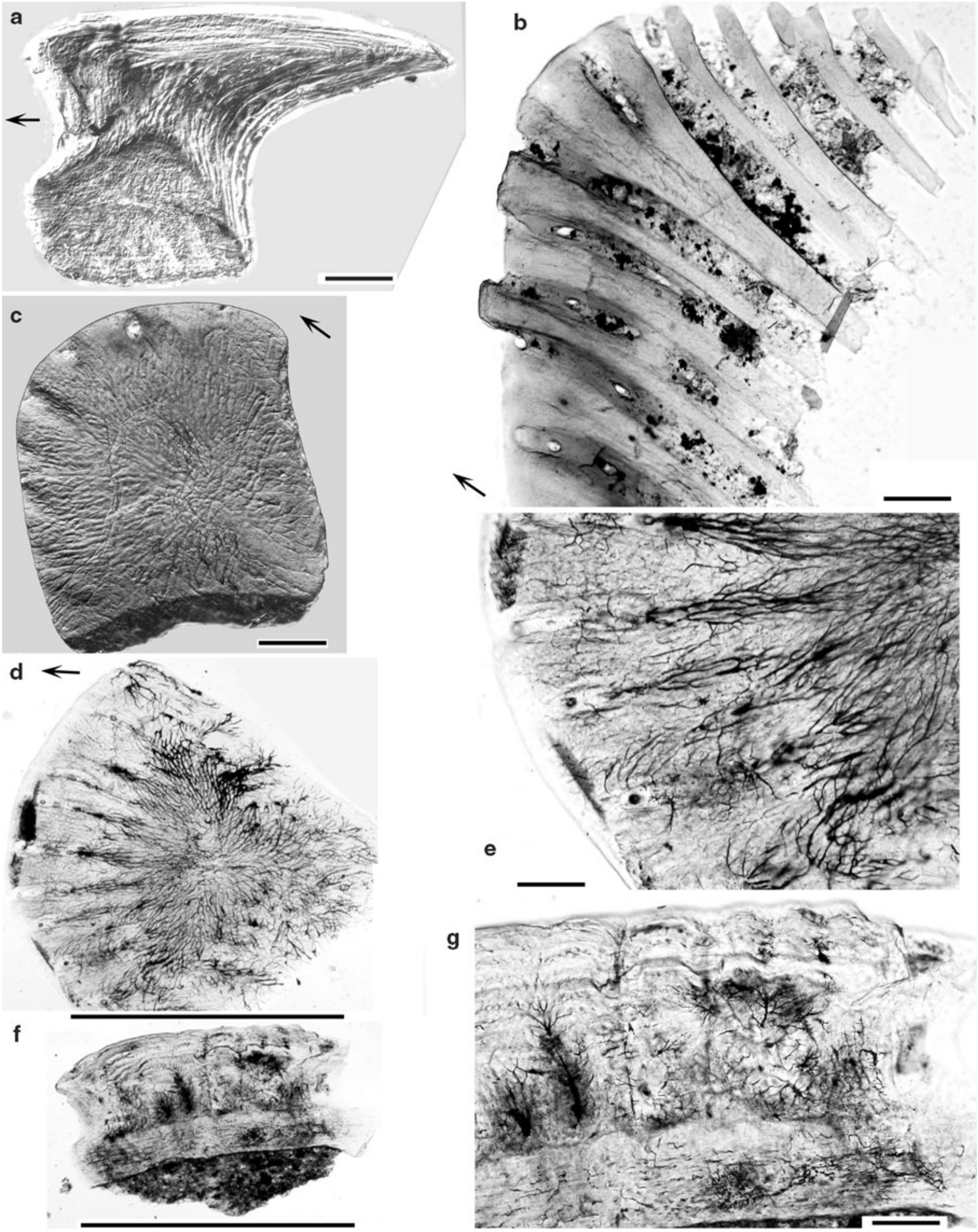

Fig. 5. Ground thin sections of scales of *Milesacanthus antarctica* from the Aztec Siltstone, locality MC7, Mount Crean, Antarctica. **a.** WAM 03.1.2, vertical longitudinal section of scale with unworn ornament ridges, deep neck, shallow base, light polarized under Nomarski optics, **b.** WAM 03.1.1, horizontal section of crown of scale with unworn ornament ridges, deep neck, shallow base, **c.** NMV P228945, horizontal section of crown of scale with worn ornament ridges, short neck, medium base, viewed under Nomarski optics, **d. & e.** NMV P228946, horizontal section of crown of scale with slightly worn crown and smooth anterior edge, **f. & g.** NMV P228947, vertical transverse section of scale, worn crown with only short grooves behind smooth anterior rim; matrix stuck to broken base of scale. Scale bar is 0.1 mm in a–c, e, g, and 1.0 mm in d and f; anterior of scales is indicated by arrows.

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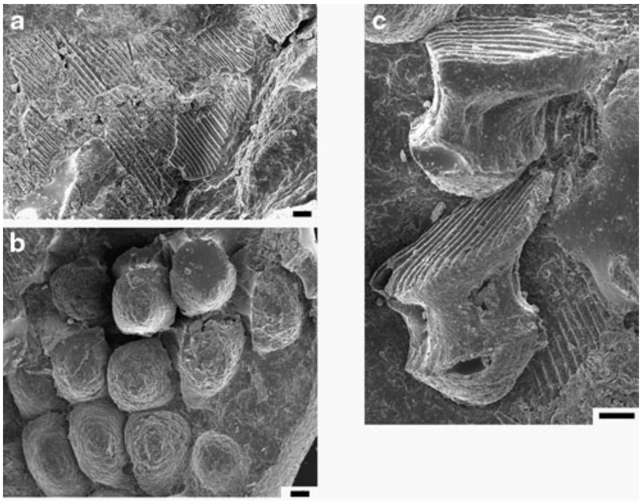

Fig. 6. Casts of impressions of squamation patches which had flaked off *Milesacanthus antarctica* holotype or associated specimens on block ANU V773 from Portal Mountain, Antarctica. **a.** scale crowns, **b.** scale bases, **c.** laterally exposed scales. Scale bar is 0.1 mm.

same genus has been noted relatively commonly in Devonian acanthodians and actinopterygians (Valiukevičius & Burrow 2005), supporting the possibility that the spines could be from *Pechoralepis juozasi* n. sp.

Family CLIMATIIDAE Berg, 1940
Genus *Nostolepis* Pander, 1856

Diagnosis. See Valiukevičius & Burrow (2005) for a revised diagnosis.

Type species. Nostolepis striata Pander, 1856

Nostolepis sp. cf. *N. gaujensis* Valiukevičius, 1998
Fig. 3

Material. Thirty-seven scales including figured specimens NMV P228902 (Fig. 3a & b), NMV P228903 (Fig. 3c & d), NMV P228904 (Fig. 3e & f), NMV P228905 (Fig. 3g & h), and thin sections NMV P228943 (Fig. 3i) and NMV P228944 (Fig. 3j).

Description. Scales are relatively large, up to 1.0 mm wide and 1.5 mm long. The horizontal crown bears 4–6 sharp and robust parallel ridges running back from a sharply defined anterior edge; vertical ridges extend down the anterior face of the crown on better-preserved scales. Crown ridges decrease in height posteriorly, extending two-thirds or more of the length of the crown and fading out in the posterior third. Some pores are visible at the crown/neck junction laterally and anteriorly. The base is moderately convex, usually subrhombic in outline, and protrudes in front of the crown; the posterior part of the crown extends beyond the base. A fine honeycomb-like network of polygonal depressions, each *c.* 15 μm diameter, forms ultrasculpture on well-preserved scale crowns (e.g. Fig. 3h).

Histological study shows that the crown has up to six growth zones, penetrated by circular and interconnecting radial canals (Fig. 3j), with Stranggewebe low in the posterior part of the crown including the primordium, and mesodentine filling the rest of the crown (Fig. 3i). This tissue is odontocytic in the lowest level of each growth zone and syncitial (non-lacunal: *sensu* Valiukevičius & Burrow 2005) in the outer level, where it is orthodentine-like with fine tubules oriented perpendicular to the outer surface; a very thin, birefringent durodentine layer overlies the mesodentine in the central part of the crown. The base is formed of thin bone lamellae, with osteocytes abundant throughout, and a dense network of interconnected processes and large polygonal osteocytes in the primordial growth zone.

Comparison. The type scales of *N. gaujensis* are from the Frasnian of the Baltic Upper Old Red Sandstone (Valiukevičius 1998). Similar scales, assigned to *Nostolepis* sp. cf. *N. gaujensis*, have also been described from ?Frasnian siltstones of the Cuche Formation, Colombia (Burrow *et al.* 2003), carbonates of the Chahriseh profile (Turner *et al.* 2002, Hairapetian *et al.* 2006) and perhaps the Bidou 1 locality, central Iran (Janvier 1974, pl. 6, figs 2 & 3: see Turner *et al.* 2002). Scales from the ?late Givetian Campo Chico Formation of Venezuela, assigned to Acanthodii indet. by Young & Moody (2002, fig. 16A–C), are possibly conspecific. The main distinguishing features of the Antarctic scales is the sharpness of the ridges and crown edges and the 'honeycomb' ultrasculpture. Undoubtedly these features are correlated, with the microornament almost certainly being the imprint of epidermal cells, by comparison with the identical pattern formed on scales of modern sharks (Reif 1985). The lack of abrasion and wear on the scale crowns suggests that the scales had not erupted through the skin. Amongst acanthodians, ultrasculpture has previously only been observed on acanthodiform scales (e.g. Trinajstic 2001, Beznosov 2005). The most similar pattern in acanthodians is seen on Upper Carboniferous *Acanthodes*-type scales from the Moscow district (Beznosov 2005, pl. 12.4, 8, 10), which have rounded depressions of similar dimensions to the polygonal depressions in the *Nostolepis* sp. cf. *N. gaujensis* scale crowns. Amongst other vertebrates, the ultrasculpture is identical to that on tubercles of *Psammosteus* sp. 2 from the Givetian Abava Beds of Estonia (Märss 2006, fig. 4L). Like *Nostolepis* sp. cf. *N. gaujensis*, taxa with comparable imprints have an outer birefringent durodentine or enameloid layer.

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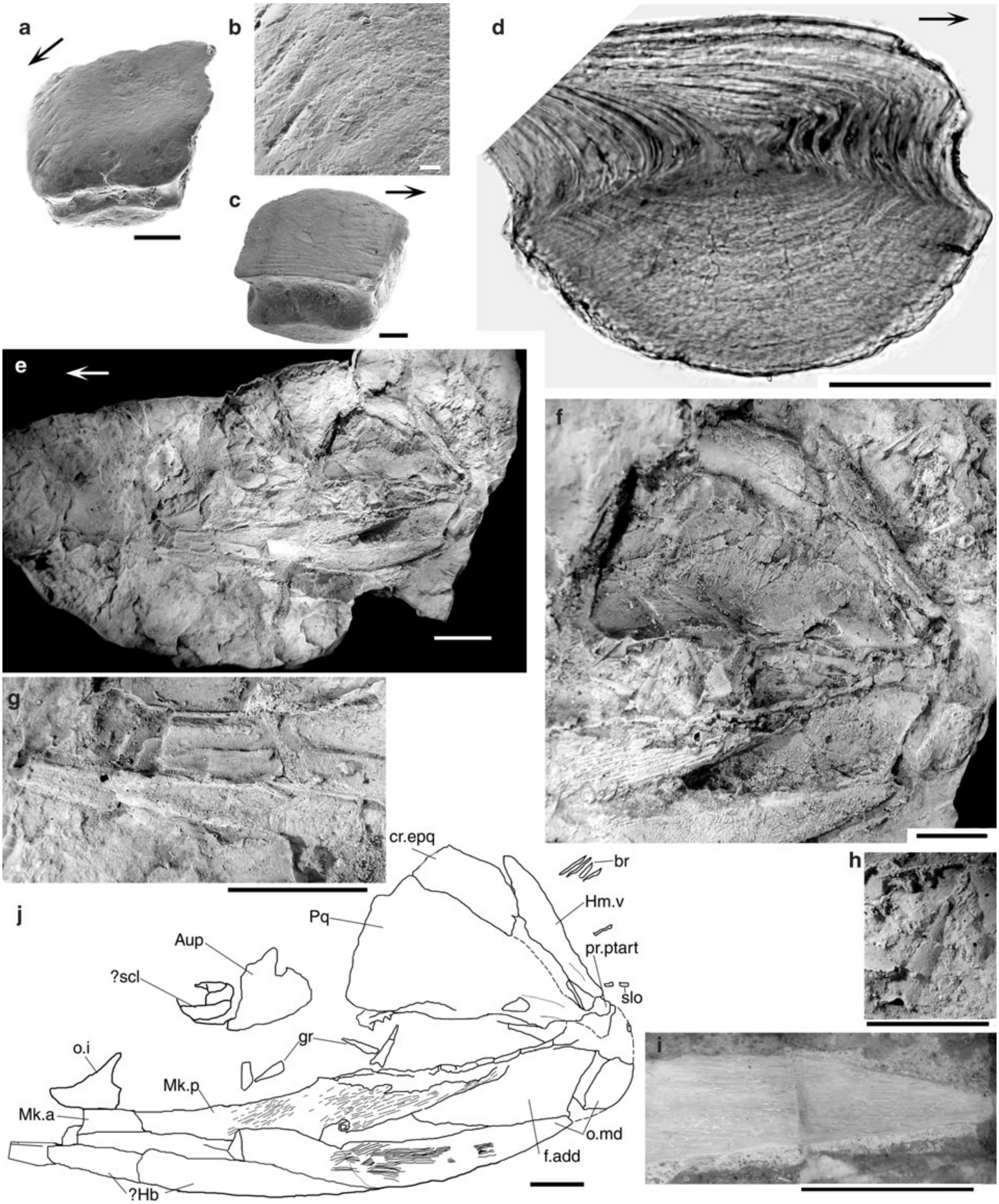

Fig. 7. Acanthodidae gen. et sp. indet. **a.–d.** Scales from the Aztec Siltstone, locality MC7, Mount Crean, Antarctica. **a. & b.** NMV P228921 in anterocrown view and closeup of ?abraded grooves on the crown, **c.** NMV P228922 in posterocrown view, **d.** NMV P228923, vertical longitudinal section of scale. **e.–j.** Cast of impression of articulated left upper and lower jaws WAM 92.3.7 from the Aztec Siltstone, Mount Ritchie, Antarctica. **e.** cast of whole specimen, **f.** Palatoquadrate, jaw articulation area, and posterior end of lower jaw. **g.** Anterior ossification of Meckel's cartilage, mandibular ossification, and hyoid bar. **h.** Robust conical gill raker. **i.** Mandibular ossification of lower jaw preserved on counterpart. **j.** Labelled sketch of the whole specimen. Scale bar is 0.01 mm in b, 0.1 mm in a, c, d, 5 mm in i, 1 cm in e–h, j; anterior indicated by arrows.

Order DIPLACANTHIFORMES Berg, 1940
Family DIPLACANTHIDAE Woodward, 1891

Remarks. See Young & Burrow (2004, p. 26) for a revised diagnosis

Genus *Milesacanthus* Young & Burrow, 2004

Type species. Milesacanthus antarctica Young & Burrow, 2004

Milesacanthus antarctica
Figs 4–6

Material. More than 500 scales including NMV P228906 (Fig. 4a & b), NMV P228907 (Fig. 4c), NMV P228908 (Fig. 4d & e), NMV P228909 (Fig. 4f), NMV P228910 (Fig. 4g), NMV P228911 (Fig. 4h), NMV P228912 (Fig. 4i & j), NMV P228913 (Fig. 4k & l), NMV P228914 (Fig. 4m & n), NMV P228915 (Fig. 4o), NMV P228916 (Fig. 4p & q), NMV P228917 (Fig. 4r), NMV P228918 (Fig. 4s), NMV P228919 (Fig. 4t & u), and thin sections WAM 03.1.2 (Fig. 5a; Young & Burrow 2004, fig. 3D), WAM 03.1.1 (Fig. 5b; Young & Burrow 2004, fig. 4C), NMV P228945 (Fig. 5c), NMV P228946 (Fig. 5d & e), NMV P228947 (Fig. 5f & g).

Description. Scales are medium to large-sized, from 0.5–1.5 mm wide, 0.3–0.5 mm deep, and 0.5–1.7 mm long. Crown ornament comprises 14 to 24 sub-parallel or slightly fanned ridges and grooves extending to at least midcrown, with denticulated posterolateral crown edges. On scales with unabraded crowns bearing full-length ridges and grooves (Fig. 4a, b & g), the scale neck is deep and strongly concave, and the base is shallow and convex, with a marked base-neck rim. Other scales have worn crowns which are smooth except for 6–12 short grooves on the anterior part (Fig. 4k–n, p–r); these scales have relatively shorter necks and more tumid bases, and a less pronounced base-neck rim. Both scale types sometimes have 'warts' low on the posterior neck, between deep vertical grooves (Fig. 4b, c, e & l). Some scales show ornamentation intermediate between these two extremes. Most scale crowns are symmetrical and the anterior edges converge at *c.* 100°. Rare scales are asymmetrical (Fig. 4r–u).

Histological study shows that the scales have up to 12 crown growth zones. Thin, distally branching dentine tubules and canals (Fig. 5a) rise up through the neck and curve over to converge in the upper central parts of the growth zones of the crown (Fig. 5c–e), with the main canals running up to and under the crown grooves (Fig. 5g). Dentine is mostly syncitial mesodentine, forming a spongelike network in the lower crown (Fig. 5f & g). Scales also have a pore canal system penetrating the anterior part of the crown, with canals rising up from large pores in the lower neck and opening out through pores in the grooves between the ribs on the anterior half of the crown (Fig. 5b–e). Branches of this system probably also extend back through the scale crown to the posterior neck, where they possibly ran up grooves on the external surface of the scales (Fig. 4c, l, u). No bone cell lacunae are present in the crown or base; the latter is penetrated by Sharpey's fibre bundles and short, thin, irregularly branching canaliculi (Fig. 5a & g).

Comparison. Many of the scales on the holotype and associated articulated specimens of *M. antarctica* from Portal Mountain (Fig. 1, locality 12) have well-preserved ridges and grooves. However, most of the scales on those specimens have been split through the middle and the crown ornamentation is mainly known from casts of loose fragments on which scale patches were cleared with 10% hydrochloric acid (Young & Burrow 2004, fig. 4A; Fig. 6a–c). The isolated scales from Mount Crean show a greater range in preservation of ornamentation, from unabraded to almost smooth crowns (Fig. 4a–l). A similar range is seen in the older species *M. ancestralis* from the Emsian Jawf Formation of Saudi Arabia (Burrow *et al.* 2006, figs 7 & 8). The main difference between the species is in the numerical range of crown ridges and grooves, with 14–24 in *M. antarctica* and 6–18 in *M. ancestralis*. Burrow *et al.* (2006, p. 547) described the crown ornament of the latter as usually formed of grooves rather than ridges: in well-preserved scales with deep long grooves, the round-bottomed grooves cut into the flat surface of the crown (e.g. Burrow *et al.* 2006, fig. 8A). The distinction between grooves and ridges is not so clear-cut in the Mount Crean examples. *Milesacanthus ancestralis* scales were also distinguished by having wart-like bumps on the posterior part of the neck, but some *M. antarctica* scales, both in the microremains (Fig. 4b, c, e, h, l–o, q, r & u) and on the type material (Fig. 6c), also show this feature. Hairapetian *et al.* (2006) assigned similar scales from the early Frasnian of the Chahriseh profile in central Iran to *Milesacanthus* sp. aff. *M. antarctica*. They noted that *M. ancestralis* scales "differ from the Iranian ones in having a complicated syncitial mesodentinal network in the lower crown (neck area) filling the growth zones between the main branches of the ascending vascular canals . . . and also lacunal widenings of dentine canals, particularly dense in the lower neck; and the horizontal canals running under the grooves of the crown plate are the longest and widest of the species compared, and supplied by numerous winding canaliculi. . .". Scales of *M. antarctica*, like those of *M. ancestralis*, have a complex mesodentinal network in the lower crown (Fig. 5f & g). *M. antarctica* is distinguished by the density of dentine tubules converging in the centre of the upper scale crown (Fig. 5c–e).

ACANTHODIFORMES Berg, 1940
Family ACANTHODIDAE Huxley, 1861
Acanthodidae? gen. et sp. indet.
Fig. 7

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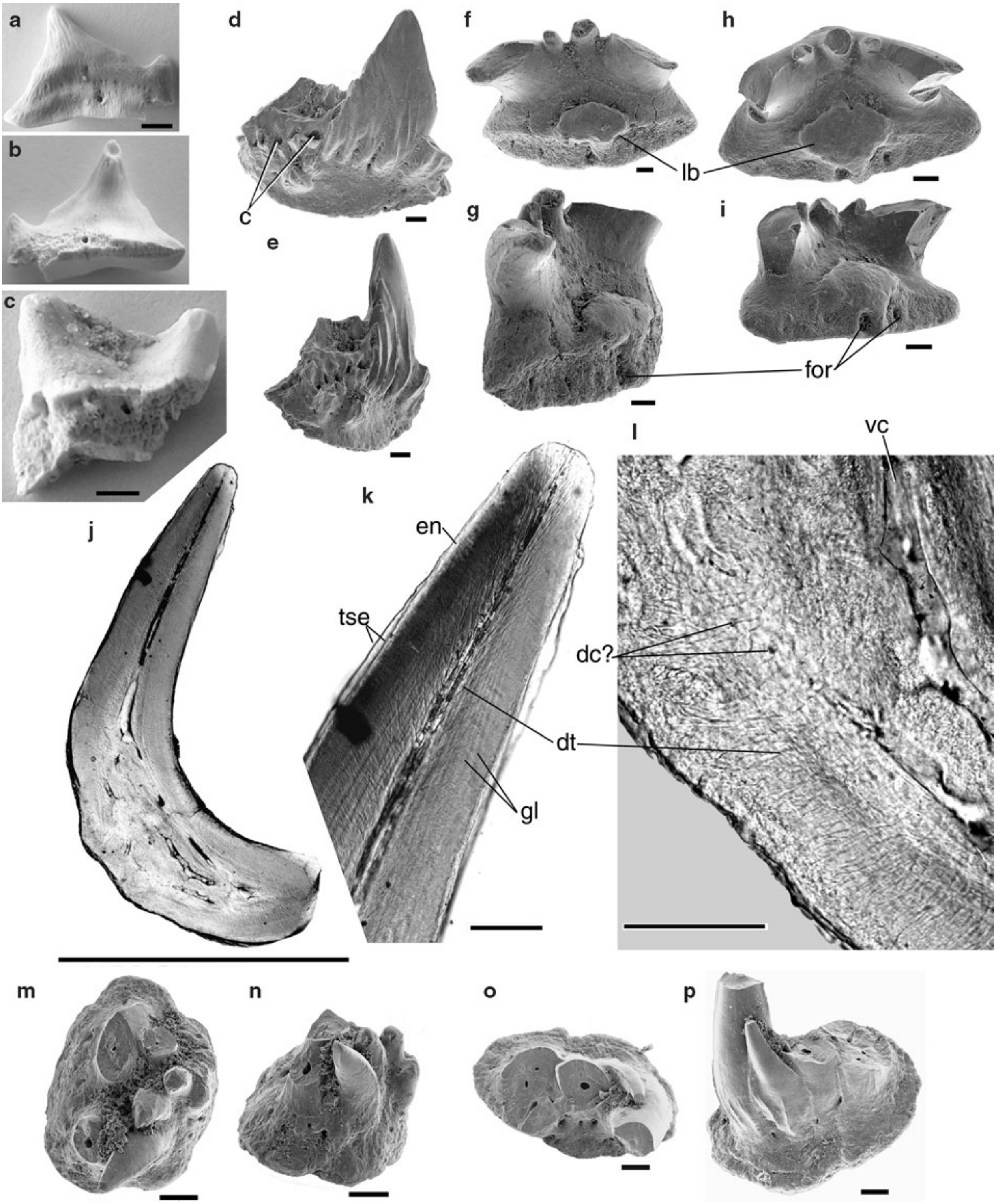

Fig. 8. Chondrichthyan teeth and denticles from the Aztec Siltstone, locality MC7, Mount Crean, Antarctica. **a–c.** Teeth of *Aztecodus harmsenae* Long & Young, 1995. **a. & b.** NMV P228829, in labial and lingual views. **c.** NMV P228830, in lingual view. **d.–l.** Teeth of *Antarctilamna prisca* Young, 1982. **d. & e.** NMV P228923, multiridged variant with one of two main cusps broken off, in labial and lateral views, **f. & g.** NMV P228924, in occlusal and lateral views, **h. & i.** NMV P228925, in occlusal and laterolingual views, **j.–l.** NMV P228949, transverse section along pulp canal of main preserved cusp of smooth tooth variant (other cusp has broken off), in whole section, and closeups of cusp tip (Nomarski optics) and labial centre of base. **m.–p.** Elasmobranchii indet. fam., gen. et sp. A. branchial denticles. **m. & n.** NMV P228926, in crown and posterior views, **o. & p.** NMV P228927, in crown and lateral views. Scale bar is 0.1 mm in a–i, k–p, 1.0 mm in j.

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Material. More than 50 scales including NMV P228921 (Fig. 7a & b), NMV P228922 (Fig. 7c), and thin section NMV P228948 (Fig. 7d) from Mount Crean site MC7; set of articulated jaws WAM 92.3.7 (Fig. 7e–j) from Mount Ritchie.

Description. Most scales are small, *c.* 0.3 mm wide and long, with some larger scales up to 0.5 mm long. The crown surface is flat, smooth and kite-shaped, with a shallow sulcus towards the anteromedian corner. The posterior crown point extends slightly beyond the base. The neck and base are of equal depth; the base is rounded convex and deepest centrally.

Histological study (Fig. 7d) shows that scale crowns have *c.* 10 thin growth zones. Scales appear to have two or three circular canals in the neck which are intersected by ascending canals in the lower half of neck. Dentine tubules show minimal branching, and lack the network of fine tubules which characterize *Acanthodes* Agassiz, 1833 (Denison 1979, fig. 9G). A very thin layer of birefringent durodentine forms the upper part in each crown growth zone. The upper surface of the base is relatively flat; canals of Williamson are distributed throughout the base.

Jaws (Fig. 7e–j). WAM 92.3.7 is a slab showing the impression of a pair of left jaws preserved in lateral view. The general size, shape and structure of the jaws is comparable with that of *Acanthodes bronni* Agassiz, 1833 (e.g. Miles 1973, fig. 12) from the Lower Permian of Europe, with separately ossified palatoquadrate and autopalatine cartilages forming the upper jaw (the metapterygoid is missing), and anterior and posterior ossifications of the lower jaw Meckel's cartilage. Short parallel striations of the superficial bone layer are obliquely oriented on the posterior ossification, which has a markedly thickened occlusal edge opposing the ventral edge of the palatoquadrate. Remnants of the hyomandibular cartilages appear stuck to the outer surface of the palatoquadrate. The mandibular ossification is relatively thick and deep compared with that of *A. bronni*, with a rugose surface ornament. The elongate, concave surfaced element underlying the mandibular bone is probably the hyoid bar. Several conical gill rakers *c.* 1 cm long are scattered between the upper and lower jaws. Small curved elements preserved in a circular formation in front of the autopalatine are interpreted as sclerotic ring plates. Short thin closely-spaced elements behind the palatoquadrate are branchiostegal rays, and several small tubular elements behind the jaw articulation are sensory line ossicles.

Comparison. All acanthodids have smooth-crowned scales with 10 or more crown growth zones in which birefringent durodentine forms the central upper layer. They also have perichondrally ossified jaws and branchial cartilages; the upper jaw has three ossification centres, the lower jaw has two ossification centres and is supported by a robust ventral mandibular bone. The rugose surface on this bone on the WAM 92.3.7 jaws resembles that of *A. sulcatus* Agassiz, 1835 (Denison 1979, fig. 2A) from the Lower Carboniferous of Scotland. The Mount Ritchie jaws are distinguished from those of other acanthodids by having the thickened perichondrally ossified occlusal shelf on the posterior Meckel's cartilage.

CHONDRICHTHYES
Subclass ELASMOBRANCHII
Order OMALODONTIFORMES Turner, 1997
Family AZTECODONTIDAE Hairapetian, Ginter & Yazdi, 2008
Genus *Aztecodus* Long & Young, 1995

Type species. Aztecodus harmsenae Long & Young, 1995

Aztecodus harmsenae
Fig. 8a–c

Revised diagnosis. Aztecondontid omalodontiform with teeth up to 2 cm wide with a low base that is broader than the height of the cusps. Second principal cusp is one-quarter to three-quarters the height of the largest cusp. Both cusps have smooth lingual and labial surfaces and are strongly compressed labio-lingually; the cusps are broad-based and widely separated by a sharp crenulated ridge. Small accessory cusplets are sometimes present laterally. The tooth base is approximately 2.5 times as long as broad.

Remarks. Based on the similarity of forms, and the minor differences between teeth of the two taxa, we follow the recommendation of Hairapetian *et al.* (2008) and regard *Anareodus statei* Long & Young, 1995 as a junior synonym of *Aztecodus harmsenae*.

Material. Teeth NMV P228829 (Fig. 8a & b) and NMV P228830 (Fig. 8c) from Mount Crean locality MC7.

Description. Tooth NMV P228829 closely resembles the holotype of *Anareodus statei*, although it is much smaller at *c.* 3.5 mm wide and lacks a small accessory cusplet on the main cusp. The basal surface of the tooth is narrow and flat, forming a horizontal plane to the vertically-directed base, and lacking labial or lingual extensions, directly comparable to the base of the type material of *Aztecodus*. The two main crown cusps are sharply pointed and markedly asymmetrical, with the large cusp curving lingually and having crenulated lateral cristae. The labial surface of the cusp is scored by random apically-directed grooves, recalling the pleromin composition of cusps of *Aztecodus harmsenae* (Hampe & Long 1999, fig. 5B). One large foramen penetrates the base below the main cusp, and smaller foramina open along the labial base-crown junction.

The second tooth (Fig. 8c) is *c.* 3 mm wide and relatively poorly preserved, with slightly asymmetrical worn lateral cusps and a smooth-crested narrow ridge between them. Although only half the base is present, it shows the

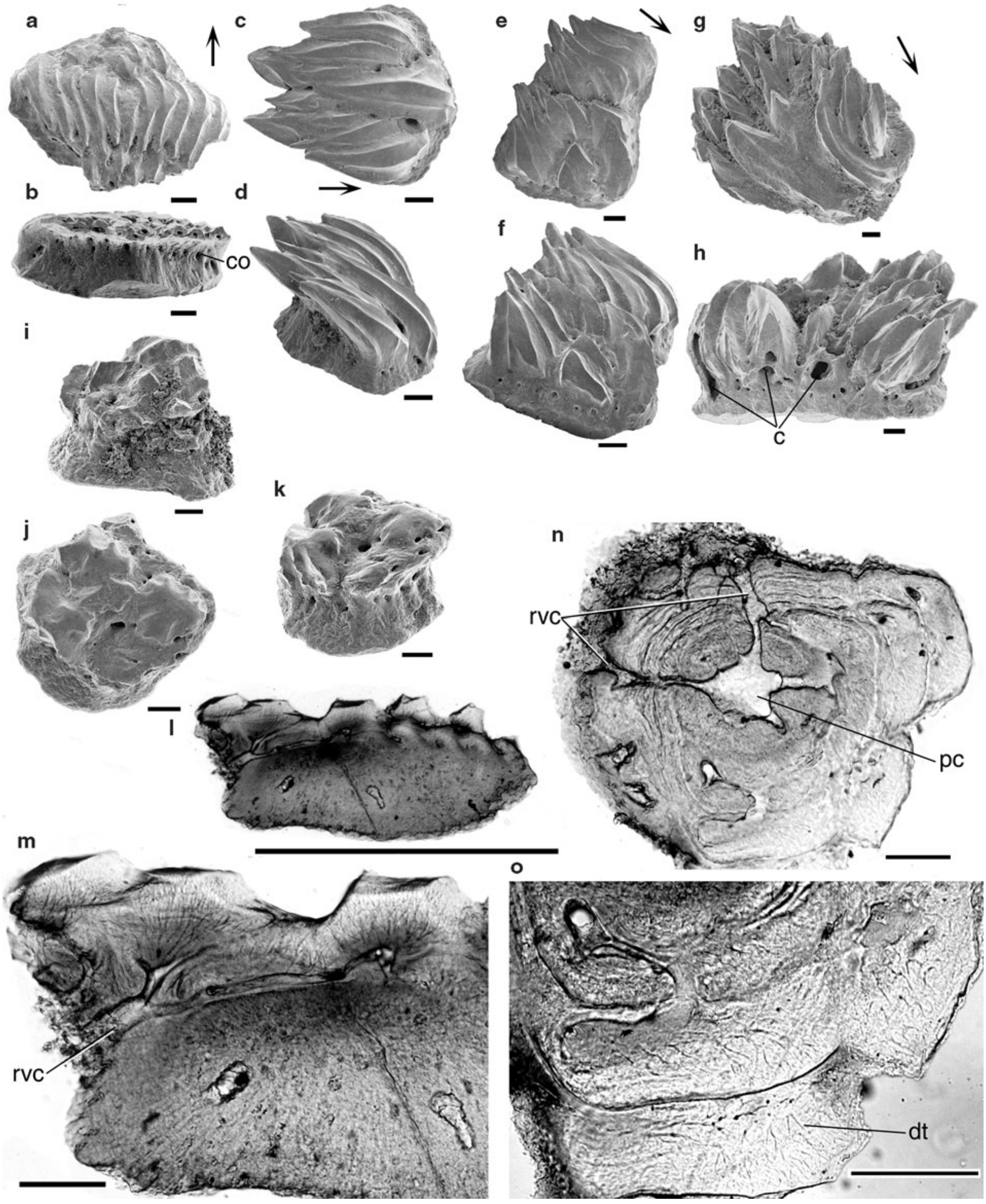

Fig. 9. Scales of Elasmobranchii indet. fam. gen. et sp. A from the Aztec Siltstone, locality MC7, Mount Crean, Antarctica. **a. & b.** NMV P228928 in crown and posterior views, **c. & d.** NMV P228929 in crown and lateral views, **e. & f.** NMV P228930 in crown and anterocrown views, **g.** NMV P228931 in crown view, **h.** ?transitional scale NMV P228932 in anterior view, **i.** possible head scale NMV P228933 in lateral view, **j. & k.** umbellate scale NMV P228934 in crown and ?anterior views, **l. & m.** NMV P228950, transverse section of flank scale, **n. & o.** NMV P228951, horizontal section through crown. Scale bar is 0.1 mm in a–k, m–o, and 1.0 mm in l; anterior of scales is to right unless indicated by arrows.

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laterally concave basal surface which characterizes the type specimen of *Aztecodus* (Long & Young 1995, fig. 8A), and labio-lingual canals penetrating the base below the base-crown margin. The labial and lingual faces of the base are vertical, without extensions.

Comparison. These two teeth support the assessment of Hairapetian *et al.* (2008) that *Anareodus statei* and *Aztecodus harmsenae* are conspecific, with the '*Anareodus*'-like tooth (Fig. 8a & b) having a large nutrient foramen in the base and lacking an accessory cusplet on the main cusp, and thus fitting in the gap between the two original diagnoses. If, as proposed above, *Anareodus* teeth are composed of pleromin, then this further supports *Anareodus* being a junior synonym of *Aztecodus*.

Order ANTARCTILAMNIFORMES Ginter, Liao & Valenzuela-Rios, 2008
Family ANTARCTILAMNIDAE Ginter, Liao & Valenzuela-Rios, 2008
Genus *Antarctilamna* Young, 1982

Revised diagnosis (teeth and scales). Antarctilamnid teeth with 4–7 cusps aligned in a single plane with main lateral cusps directed lingually, a basal projection on the mid-labial margin, and one or more large foramina between the button and the edge of the base; two tooth morphotypes, one with wavy vertical cristae and the other relatively smooth with weak lateral cristae on the main cusps. Ridged teeth have an osteodentine (= trabecular dentine) core and base, orthodentine extending up to half the radius of the cusps, and an outer layer of pallial dentine; smooth teeth have a central canal and orthodentine forming the lateral cusps, an osteodentine base, and a thin outer enameloid layer. Scales are compound, with a flat crown ornamented with semiconcentric odontodes, and a cup-shaped base.

Type species. Antarctilamna prisca Young, 1982

Antarctilamna prisca
Fig. 8d–p

Material. Seven teeth including NMV P228923 (Fig. 8d & e), NMV P228924 (Fig. 8f & g), NMV P228925 (Fig. 8h & i), and thin section NMV P228949 (Fig. 8j–l).

Description. Both the ridged and smooth diplodont tooth variants which were figured in the original description of type species *A. prisca* are represented in the Mount Crean sample; teeth are 1–2 mm wide. Only one example of the most distinctive teeth (Fig. 8d & e), which is commonly figured as the typical *Antarctilamna* form, was found. It shows strongly developed vertical ridges on the labial face, comparable to those figured by Young (1982, text-fig. 3A–D, pl. 89.7) on the *A. prisca* holotype. The ridges meet weaker ridges on the lingual face, appearing as a row of chevrons in lateral view on NMV P228923 (Fig. 8e). One of the main cusps has broken off this tooth (Fig. 8d & e), showing that each of the labial ridges has a large central pulp canal. Unfortunately the base is also broken, with the lingual extension missing. The tooth is possibly a pathological variant, as it has accessory cusplets labial to the main cusps.

The tooth form occurring more commonly in the residues has laterolingually-pointing main cusps separated by two or three smaller medial cusps (Fig. 8f–i); where three medial cusps are developed, the central cusp is larger than the other two. All medial cusps are smooth with a subcircular cross-section; the lateral cusps are labio-lingually flattened with weak carinae running up the lateral and medial edges. The lingual edge of the base is slightly convex, with one large foramen opening out below an oval-shaped lingual button on the central upper surface, and one or more smaller foraminae lateral to the large one. The lower surface of the base is concave, and the base outline is subdiamond/trapezoidal. A vertical ground thin section of one of these smooth tooth variants (Fig. 8j–l) shows a single central pulp canal in the lateral cusp joining a network of canals in the tooth base. Fine branching orthodentine tubules radiate up and out from the central canal in the main cusp, overlain by a very thin enameloid layer which merges with the underlying dentinous tissue. Incremental growth lines in the dentine layer run slightly obliquely to, or parallel with, the outer surface (Fig. 8k). Fine branching dentine tubules are also visible in the upper level of the base (Fig. 8l), at a level which probably represents the base of the medial cusps. A few dark spots in this area of the section could be bone cell lacunae, but are more likely to be crosscut dentine canals.

Comparison. Both Turner (1997) and Ginter (2004) noted the close similarity between teeth of *Antarctilamna* and *Wellerodus* Turner, 1997. Hampe & Long (1999, fig. 3) studied the histological structure of the strongly ridged tooth form. These differ from the smoother tooth form in having cusps with a trabecular core and purportedly lacking an enameloid layer, although the latter seems visible on the left in their figure 3A & B. Hampe & Long (1999) excluded *Antarctilamna* from the xenacanthoids based on the lack of a lingual button and a labial basal tubercle on the teeth, but these structures are present on the two *Antarctilamna* tooth forms (Long & Young 1995, fig. 4B; Fig. 8f–i). The antarctilamniforms are, however, differentiated from the xenacanthiforms by their vastly different fin spines (Ginter *et al.* 2008).

Antarctilamna teeth have been recorded from many levels of the Aztec Siltstone, from the base to the '*Pambulaspis*' zone (Long & Young 1995). While previously only known from the Antarctic, south-eastern Australia, South Africa (Anderson *et al.* 1999), and possibly Saudi Arabia (Ginter 2004), and South America (Maisey & Melo 2005),

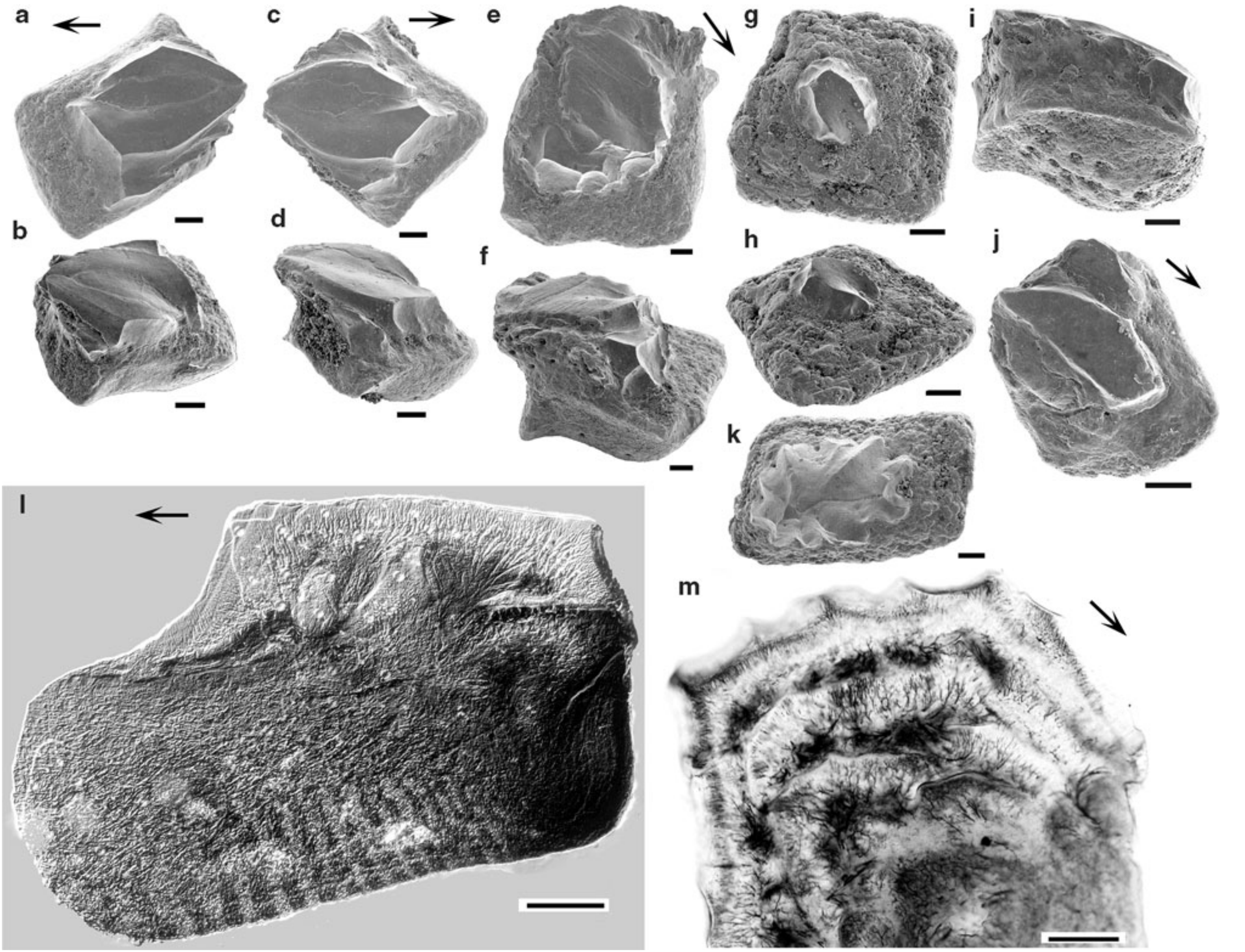

Fig. 10. Scales of Elasmobranchii indet. fam., gen. et sp. B from the Aztec Siltstone, locality MC7, Mount Crean, Antarctica. **a. & b.** NMV P228935 in crown and laterocrown views, **c. & d.** NMV P228936 in crown and lateral views, **e. & f.** NMV P228937 in crown and lateral views, **g. & h.** NMV P228938 in crown and laterocrown views, **i.** NMV P228939 in posterobasal view, **j.** NMV P228940 in crown view, **k.** possible head scale NMV P228941 in crown view, **l.** vertical longitudinal section NMV P228952, Nomarski optics polarization showing Sharpey's fibre bundles in base and branching orthodentine-like tissue in crown, **m.** horizontal section of crown NMV P228953 showing unoriented network of dentine tubules of inner parts of crown growth zones. Scale bar is 0.1 mm; anterior of scales indicated by arrows.

Antarctilamna, and also *Portalodus*, have now been recorded from the late Givetian-early Frasnian of western New York (Ginter *et al.* 2006; see also Turner 2004).

ELASMOBRANCHII indet. fam., gen. et sp. A
Figs 8m–p, 9

Material. Two branchial denticles NMV P228926 (Fig. 8m & n) and NMV P228927 (Fig. 8o & p), >150 scales including NMV P228928 (Fig. 9a & b), NMV P228929 (Fig. 9c & d), NMV P228930 (Fig. 9e & f), MC7b-17 (Fig. 9g), NMV P228931 (Fig. 9h), and thin sections NMV P228950 (Fig. 9l & m) and NMV P228951 (Fig. 9n & o), four head tesserae including NMV P228933 (Fig. 9i & j), and one umbellate scale NMV P228934 (Fig. 9k).

Description. Several elements with irregularly dispersed 'teeth' on an oval base are interpreted as branchial denticles, by comparison with similar elements from articulated Devonian–Carboniferous sharks (e.g. *Antarctilamna prisca* in Young 1982, text-fig. 2C & D). NMV P228926 has eight denticles, with the two larger ones broken off to show that each had a central pulp canal. NMV P228927 has four denticles, with the three largest broken off to show a single central pulp canal in two and multiple canals in the largest, which has broken right at the base presumably at the level of the vascular canal network below where the central canal would have branched off.

Presumed flank scales are of typical ctenacanthoid structure, with the crown formed of bunched, overlapping finger-like odontodes. Many scales (e.g. Fig. 9a & b) show a regular arrangement of odontodes, while others show a

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less ordered pattern (Fig. 9e–h). Each odontode has a central pulp canal (Fig. 9b, i & j), and the upper posterior area of the scale neck has a row of canal openings (Fig. 9b). Some scales have a large anteromedian odontode (Fig. 9c & d). The upper surface of each odontode is flat or slightly concave (Fig. 9i & j). Other scale forms include presumed head tesserae with areal-growth odontodes (Fig. 9i) and umbellate scales (Fig. 9j & k). The scales usually have a large pulp cavity piercing the base, from which relatively wide canals radiate just above the base (Fig. 9n & o). Branching, fine-calibre orthodentine-like tubules form the odontodes, although dentine in the innermost parts of each growth zone resembles the syncitial mesodentine in some 'young' climatiid acanthodians.

Comparison. Many Middle–Late Devonian chondrichthyans have scale variants and branchial denticles with very similar morphologies, as best shown by Williams (1998) for *Tamiobatus vetustus* Eastman, 1897. The branchial denticles are of the "double row coxcomb or "*Stemmatias bicristatus*" type" of Williams (1985, p. 156). The flank scales with regular rows of odontodes resemble *A. prisca* scales (Young 1982, text-fig. 4D). Scale crown histology is comparable with that of *Ohiolepis newberryi* Wells, 1944 from the Middle Devonian of the eastern United States of America.

ELASMOBRANCHII family, genus and species indet. B
Fig. 10

Material. More than 150 scales including scales NMV P228935 (Fig. 10a & b), NMV P228936 (Fig. 10c & d), NMV P228937 (Fig. 10e & f), NMV P228938 (Fig. 10g & h), NMV P228939 (Fig. 10i), NMV P228940 (Fig. 10j), and ground thin sections NMV P228952 (Fig. 10l) and NMV P228953 (Fig. 10m); possible head scale NMV P228940 (Fig. 10k).

Description. The scales show superficial resemblance to those of *P. juozasi* sp. nov., with a sharply delineated central crown flanked by lower crown areas. However, in the chondrichthyan scales these lateral areas are separate dentinous growth zones with upper surfaces that slope down medially. The central crown area has a deep anteromedian sulcus extending back towards the posterior corner (Fig. 10b & d). Anterolateral crown edges are sharp and straight, posterolateral edges are longer and slightly curved, converging to a single point just posterior to the base. All side faces of the central crown are deep and vertical; anterolateral faces sometimes bear vertical ridges (Fig. 10f). A few small canal openings are visible on some scales along the anterior crown-neck margin (Fig. 10c & f), with larger openings scattered over the upper posterior part of the neck (Fig. 10b, d & f). The scale base is quite distinctive, with one, or occasionally both, lateral corners strongly pinched out. The lower surface of the base is very lumpy and pustulose (Fig. 10i), distinguishing scales of this species from those of the acanthodian taxa in the assemblage. NMV P228940 (Fig. 10k) is possibly a head scale from this species, as it has similar pustulose upper and lower basal surfaces as on the small-crowned variant NMV P228938 (Fig. 10g & h). On normal flank scales, the base protrudes in front of the crown and is deepest below the anterior edge of the crown (Fig. 10k). The crown is formed of semicircular growth zones with syncitial mesodentine close to the pulp canals, becoming more orthodentine-like towards the outer surface of each growth zone (Fig. 10k).

Comparison. The scales resemble those of the older climatiid acanthodian *Canadalepis* Vieth, 1980, which have a blunt tongue-shaped crown. At least one of the scales from the Emsian Jawf Formation of Saudi Arabia, which Burrow *et al.* (2006, figs. 4.1, 2) assigned to *Canadalepis*? sp. closely resembles the new scale form, but its histological structure is not known. The structure of indet. sp. B scales resembles that of *Protacrodus wellsi* (Gross 1973, figs 25–27) from the Late Devonian of eastern USA. No scales have been associated with *Aztecodus* and *Portalodus*, which are known only from isolated teeth, thus it is not possible to assign the scales to any known species, even though it seems highly likely that they derive from one of these taxa.

Discussion

The Middle Devonian Aztec Siltstone macrovertebrate assemblages, while including several endemic genera and more than twenty endemic species, show strong biogeographic affinity with south-eastern Australian assemblages. Continuing work on microvertebrate faunas worldwide has led to new discoveries which reveal biogeographical and biostratigraphic relationships of the Aztec Siltstone acanthodians and chondrichthyans with those from other Gondwanan as well as Laurussian localities. Closest resemblance is with the early Frasnian assemblages in shallow water carbonates of the Chahriseh section in central Iran, which also comprise thelodont, actinopterygian, acanthodian, chondrichthyan, placoderm, and sarcopterygian microremains (Hairapetian *et al.* 2006). Early age estimates for the Aztec Siltstone assemblages were influenced by the presence of a diverse group of fish known only from younger, Late Devonian horizons in the Northern Hemisphere. The fauna is now considered to be Givetian at the youngest, indicating a delayed radiation of taxa from southeastern Gondwana to Laurussia. This argument is supported by the acanthodian assemblage, with *Nostolepis* sp. cf. *N. gaujensis* and *Milesacanthus* sp. aff. *antarctica* recorded from the early Frasnian of central Iran (Turner *et al.* 2002, Hairapetian *et al.* 2006) on the northern Gondwana margin, and Colombia (Burrow *et al.* 2003). However, much earlier occurrences of the Antarctic acanthodian genera are also known. Burrow *et al.* (2006) described a new species *Milesacanthus ancestralis* from the Early Devonian (Emsian) of Saudi Arabia, considered a precursor to the type species. The other known occurrences of *Pechoralepis* are even older, in the Lochkovian of Severnaya Zemlya and Timan-Pechora (Valiukevičius 2003a), and *Nostolepis* spp. range from the Ludlow to the Frasnian. Unfortunately the pre-Givetian fossil fish record from Antarctica is very poor, comprising a few *Machaeracanthus* spines (elements which have not yet been found in Australia) and arthrodire placoderm plates (Young 1992).

Recent discoveries of teeth from *Antarctilamna* show that it was widely distributed in Gondwana, and also present in Laurussia (now western New York). In Australia, Antarctica, South Africa, and possibly Saudi Arabia, *Antarctilamna* is restricted to middle Devonian (Givetian) sediments. Identifications of the genus from other strata are also not certain, as the general form of *Antarctilamna* teeth, spines and scales appears to represent the stem chondrichthyan bauplan. Maisey & Melo (2005) compared a tooth and spine from the late Eifelian–early Givetian of Brazil with *Antarctilamna*. Ctenacanthid-like scales resembling those of *Antarctilamna* are found throughout the Devonian, on articulated fish (e.g. Williams 1998, Miller *et al.* 2003, Soler-Gijón & Hampe 2003) as well as in microvertebrate assemblages. Mader (1986, pl. 7, fig. 6) figured and described ctenacanthiform spines from the upper Lochkovian of northern Spain; similar spines have since been found in the same region, associated with ctenacanthid-type scales and teeth of *Leonodus* Mader, 1986 (Soler-Gijón & Hampe 2003). As well as *Antarctilamna*, teeth of *Aztecodus* and *Portalodus* are found in the Givetian of South Africa (Anderson *et al.* 1999). Gess (2007) reported the presence of *Antarctilamna* in the Famennian of South Africa, making this the youngest occurrence of the taxon.

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