Acta Geologica Polonica, Vol. 58 (2008), No. 2, pp. 155-163

New information on the Devonian shark *Mcmurdodus*, based on material from western Queensland, Australia

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ABSTRACT:

BURROW, C.J., HOVESTADT, D.C., HOVESTADT-EULER, M., TURNER, S. & YOUNG, G.C. 2008. New information on the Devonian shark *Mcmurdodus*, based on material from western Queensland, Australia. *Acta Geologica Polonica*, **58** (2), 155-163. Warszawa.

Histological structure of the type and newly collected teeth of the shark *Mcmurdodus whitei* TURNER & YOUNG, 1987, from a Devonian (?late Emsian-early Eifelian) limestone outcrop in the Cravens Peak Beds of western Queensland, was determined by immersion in anise oil, thin sectioning, and acid etching of fractured surfaces. The morphology and vascularization of the teeth are comparable to those of modern hexanchiform and echinorhinid squaliform sharks, being most similar to those of *Echinorhinus*. A multilayered enameloid layer is not discernible in *Mcmurdodus* teeth, but a parallel-fibred layer is possibly present. Prismatic calcified cartilage, presumed to be from *M. whitei*, appears identical to that of all elasmobranchs. Scales and spines and distinctive ring-like elements occur in the same horizon, the latter comparable with elements that encircle the lateral line in *Echinorhinus*, and which are found in no other Recent elasmobranchs.

Key words: *Mcmurdodus*, Devonian, Hexanchiformes, *Echinorhinus*, Prismatic calcified cartilage, Tooth vascularization, Enameloid, Neoselachii.

INTRODUCTION

The genus *Mcmurdodus* WHITE, 1968 was erected for a ?late Middle-early Late Devonian tooth from Antarctica, type species *M. featherensis*. TURNER & YOUNG (1987) described a second and older species *Mcmurdodus whitei* based on teeth from the ?late Emsian-early Eifelian Cravens Peak Beds of the Georgina Basin, western Queensland. Following WHITE (1968), the hexanchid-like tooth characters of the genus were noted and the family McMurdodontidae WHITE, 1968 was tentatively assigned to the Hexanchiformes. TURNER & YOUNG (1987) also described prismatic calcified cartilage and scales possibly from *M. whitei*. *Mcmurdodus* is the only putative hexanchiform genus from the Palaeozoic, with until recently the only other record being a single tooth from the Late Permian of Japan, which GOTO (1994, 2002) assigned to Hexanchidae gen. sp. indet.

According to COMPAGNO (1984), the Hexanchidae comprises three living genera: *Heptranchias*, *Hexanchus* and *Notorhynchus*. Tooth morphology of extant hexanchid taxa was described and illustrated by Bass & *al.* (1975), Herman & *al.* (1987, 1994), Hovestadt-Euler & Hovestadt (1993) and Kemp (1978). Their unique tooth vascularization distinguishes the clade from all other modern sharks except for the genus *Echinorhinus*, which shares a significant number of tooth morphology and vascularization characters (Herman & *al.* 2003). Pfeil (1983) resurrected the monofamilial Order Echinorhiniformes, whereas Compagno (1984) assigned *Echinorhinus* to the Squaliformes. Most workers acknowledge a long branch for echinorhinids from a node preceding their oldest Mesozoic record in the Early Cretaceous, referring the group to ordinal or even superordinal rank (de Carvalho 1996).

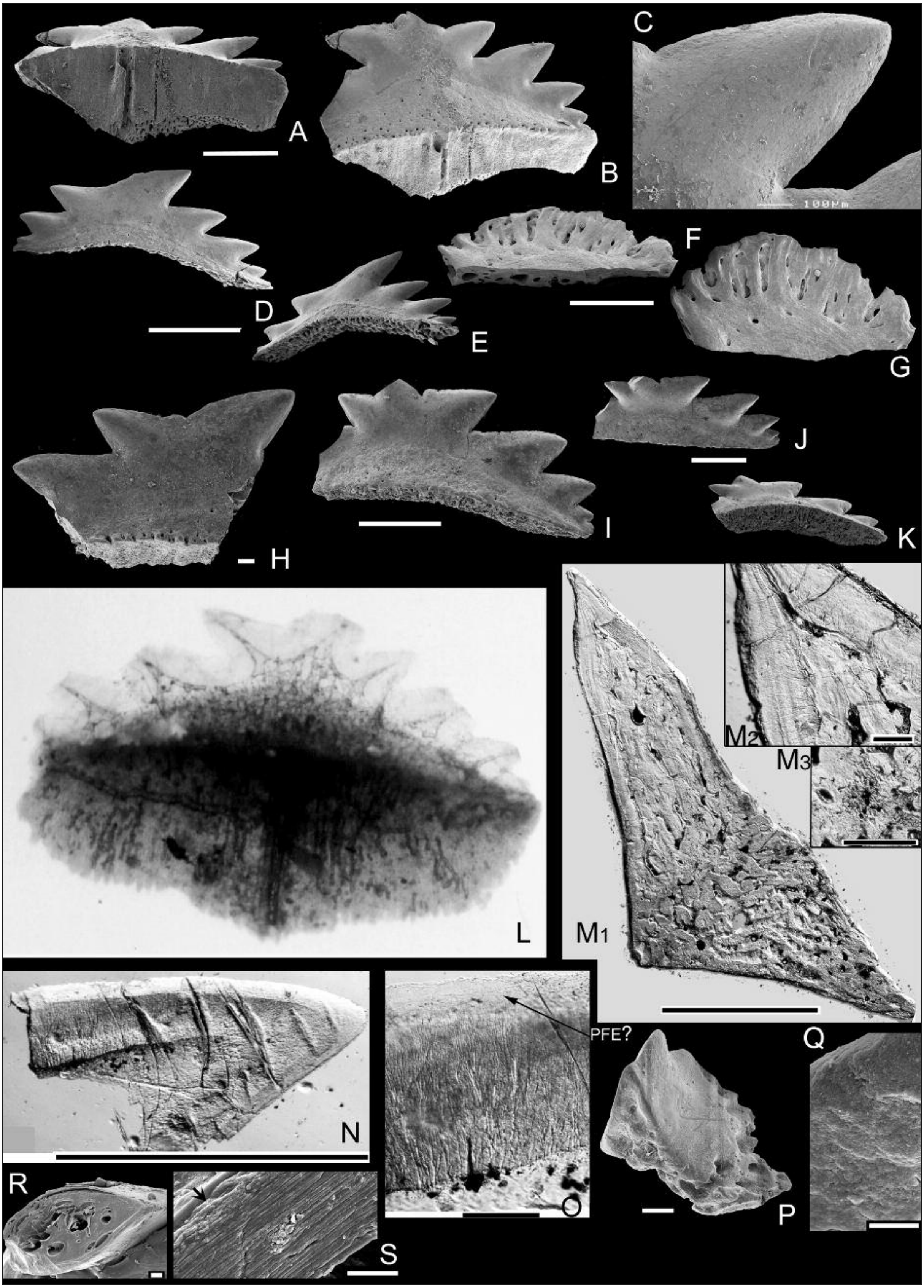
Phylogenetic analyses of the Neoselachii based on morphological data indicate a close relationship between *Echinorhinus* and the Hexanchiformes (e.g. de Carvalho 1996, Shirai 1996). In the only analysis based on molecular data that included *Echinorhinus* (Maisey & *al.* 2004), the taxa were more widely separated. None of these analyses regarded any pre-Triassic taxa as neoselachians. Assignment of teeth of the genus *Cooleyella* from the Early Carboniferous of Britain (Duffin & Ward 1983) and the Late Carboniferous of North America and Brazil (Duffin & *al.* 1996) to the Neoselachii has generally been dismissed (Cuny 1998), as these teeth lack the triple-layered enameloid (TLE) which Reif (1973) recognized as a synapomorphy of the group. Gillis & Donoghue (2007) undertook a survey of tooth enameloid microstructure in selected fossil sharks including the holocephalan *Helodus*, of Late Devonian to Early Permian age, as well as three living neoselachian taxa, *Carcharinus*, *Carcharias*, and *Chlamydoselachus*. Their investigations generally supported the presence of TLE as a neoselachian character, as it was fully developed in the basal squalean/neoselachian *Chlamydoselachus* and absent in all the fossil taxa examined. However, neither *Echinorhinus* nor *Mcmurdodus* were studied by these authors.

In order to test the possible relationships of *Mcmurdodus whitei* to other chondrichthyans, we investigated the morphological and histological structure of teeth, and associated prismatic calcified cartilage, scales and spines, which probably all belong to the taxon. Because of the morphological resemblance of *Mcmurdodus* teeth to those of *Echinorhinus*, we are also studying the structure of *Echinorhinus* teeth and dermal elements.

MATERIALS AND METHODS

DCH and MH-E photographed the holotype tooth of *Mcmurdodus whitei* (Turner & Young 1987, fig. 2) submerged in anise oil, during a visit to Australia in 1998. New material was collected from the type locality in 2006 on a field trip to the Cravens Peak Beds; material is housed at the Queensland Museum, Hendra Geosciences annex (QMF). Several more teeth and tooth fragments (QMF52817-19, 52833-35, 52838, 52839) plus many pieces of prismatic calcified cartilage (QMF52820-22, 52840) also presumed to be from *M. whitei*, as well as possible scale and fin spine fragments (QMF52823-25, 52836, 52841, 52842), came from samples collected at sites GY77/7, /7.5, /8, /8.5, /10 and /11 in the small limestone outcrop in the Toomba Range (see Turner & Young 1987 for locality details). Thin sections were ground from tooth fragments, cartilage, a spine and scales, and imaged using an Olympus BX-50 transmission microscope and DP-12 imaging system. Two cusp fragments were placed in 10% HCl for a short period to etch the fracture surfaces; one fragment dissolved rapidly, and the other was removed after 20 seconds. The etched specimen plus other teeth, patches of prismatic calcified cartilage, spine fragments, scales and a ring element (QMF52837) from the Cravens Peak Beds samples, as well as a sectioned and etched tooth and a skin patch with scales and lateral line rings from *Echinorhinus cookei* Pietschmann, 1928 specimen NMV A 21728 from Museum Victoria, were coated with platinum and imaged in a JEOL JSM-6300F scanning electron microscope. Figures were compiled using Adobe Photoshop®. For terminology concerning tooth vascularization we refer to Radinsky (1961).

Fig. 1. **A-Q**, *Mcmurdodus whitei* teeth from limestone outcrop localities GY77/7-11; A-C – slightly broken tooth QMF52817 in (A) basal, (B) labiobasal views, and (C) closeup view of cusp; D-E – tooth crown QMF52818 in (D) labial, (E) labiobasal views; F-G – detached base QMF52819, upper surface; H, tooth fragment QMF52834; I-K – tooth lacking lingual extension of base QMF52835 in (I) lingual, (J) occlusolingual and (K) basal views; L – holotype tooth CPC25765 in anise oil, showing vascularization; M_1, labiolingual cross-section of tooth QMF52838, with (M_2) closeup view of cusp structure towards apex, and (M_3), closeup of possible bone cell lacunae in base; N-O – thick mesiodistal section of distal tooth cusp QMF52839; P-Q – HCl-etched tooth fragment QMF52833. R-S – cross-section of tooth cusp from *Echinorhinus cookei* specimen NMV A 21728, HCl-etched, with the single layer of parallel-fibred enameloid (dentine/enameloid junction marked by arrow) magnified in (S).
Bar: 1.0 mm in A, B, D-G, I-L, M_1, N; 0.1 mm in C, H, M_2, M_3, O, P, R; 0.01 mm in Q, S


A
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MORPHOLOGY OF *MCMURDODUS WHITEI* TEETH

The new specimens (Text-fig. 1A-K) show little variation from the types, with size being the main variable; the smallest tooth is 3 mm long, and the largest (fragments only preserved; one sacrificed for sectioning: Text-fig. 1M) estimated at 7-8 mm long, similar to the paratype tooth (Turner & Young 1987, fig. 3). By comparison, in the extant shark *Echinorhinus cookei*, the smallest adult teeth are half the width of the largest (Garrick 1960, text-fig. 2I, J: ca. 2 metre-long male has teeth 6.5-13 mm long). Unlike the type specimens of *M. whitei*, serrations along the occlusal edge of the cusps in the new specimens are rare (Text-fig. 1I).

HISTOLOGICAL STRUCTURE OF *MCMURDODUS WHITEI* TEETH

Immersion in anise oil made the holotype tooth translucent, revealing the distribution of osteodenteons and vascular canals (Text-fig. 1L). In general, the tooth vascularization can be subdivided vertically into three sections (Text-fig 2A): a, upper, including the cusps; b, middle; and c, lower. By comparison with the *Echinorhinus* dentition (Garrick 1960), the left end as figured is considered to be mesial, based on the smaller number of cusplets compared to the right end, and on the shape of the central cusps.

The middle section (b) is thickest and possesses large, cavity-like osteodenteons, which are more or less vertically directed in the centre and horizontally directed in the mesial and distal parts. The mesial part exhibits a horizontal canal that connects the large central osteodenteons with those mesiad. Smaller, vertically directed canals are present in the lower section (c); these mainly branch off from the larger canals of (b). Most of the cusplets in (a) possess a cavity connected to the osteodenteons and canals of (b) via a reticulated system of relatively smaller canals, present in the lower part of (a). Circumpulpar dentine is not visible when the tooth is immersed in anise oil, but can be seen clearly in the labiolingual ground thin section through a central cusp and base (Text-fig. 1M). This thin section shows the dense osteodentine network forming (b); possible bone cell lacunae (Text-fig. $\mathrm{1M}_3$) are visible between the vascular canals forming (c). The outer orthodentine layer, of relatively constant width, extends from just above the labial base of the cusp up to the apex and down to the lingual base of the cusp in (a). A relatively thick mesiodistal section of a distal-side cusp (Text-fig. 1N,

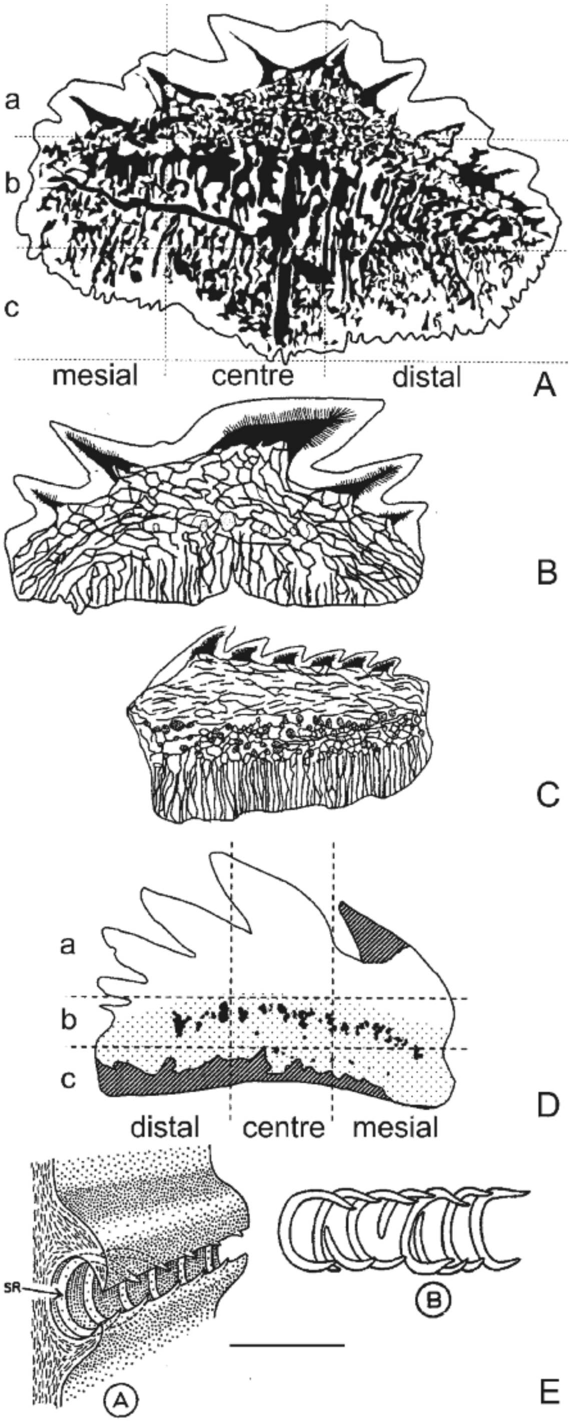

Fig. 2. **A-C**, comparative drawings of tooth vascularization; A – *Mcmurdodus whitei* holotype CPC25765; B – *Echinorhinus* (Herman & *al.* 2003, text-fig. 49); C – *Hexanchus griseus* (Herman & *al.* 2003, text-fig. 2). **D**, Upper Permian tooth from Japan assigned to Hexanchidae gen.indet.sp.indet. (after Goto 1994, fig. 5); hatching represents reconstructed areas). **E**, *Echinorhinus cookei* lateral line rings (Garrick 1960, text-fig. 1A, B)

O) shows a wide central pulp cavity with fine branching orthodentine tubules coalescing in from the tooth surface, without a distinctly differentiated enameloid layer (the shiny outer area in Text-fig. 1N is the surface of the cusp). However, thin wavy structures (PFE?) visible parallel to and just below the tooth surface, might be parallel-fibred enameloid. The rapid dissolution in ca. 30 seconds of an isolated cusp placed in 10% HCl, and the lack of differentiation in the outer layer of a second tooth fragment placed in 10% HCl for 20 seconds (Text-fig. 1P, Q) led to no other clear evidence for a structured enameloid layer or layers. This specimen was ground down, etched, recoated and scanned, but still no differentiation was noted.

OTHER PROBABLE ELEMENTS OF *MCMURDODUS WHITEI*

Prismatic calcified cartilage: Isolated patches of prismatic calcified cartilage are relatively common elements in the residues from all the Cravens Peak Beds limestone samples (Text-fig. 3; Turner & Young 1987, fig. 3D). The tesserae are preserved in single or double layers (Text-fig. 3A-C), and occasionally as cylinders (Text-fig. 3D). Horizontal thin sections through the tesserae show waves of Liesegang (Text-fig. 3E-F), and vertical sections in polarized light show the characteristic prisms (Text-fig. 3G).

Spine fragments: Whereas spines of the acanthodiform *Teneracanthus toombaensis* Burrow & Young, 2005 and osseous fin rays/spines are common, fragments of dentinous spines with ctenacanthiform-like ornament ridges are rare (Text-fig. 4A-F). These slender spines have overlapping nodes on the longitudinal lateral and leading edge ridges, and a double row of proximally-inclined denticles along the trailing edge. The surface between the denticle rows appears relatively flat; the internal cavity of the spine is bipartite, with upper and lower cavities separated by a ?bony shelf. A ground thin section of a short length of spine, which collapsed during SEM work (Text-fig. 4G,H), shows only a few fine dentine tubules visible in the outer layer of the leading edge ridge (Text-fig. 4G).

Scales: Other scales (acanthodiform *Teneracanthus toombaensis* and machaeracanthid *Machaeracanthus pectinatus* Burrow & Young, 2005) are abundant in the residues, but rare shark-like scales are also seen, confirming the identification of Turner & Young (1987). The crowns resemble those of *M. pectinatus* but overall the scales have a thin, concave base and a much thinner crown (Text-fig. 4K,L).

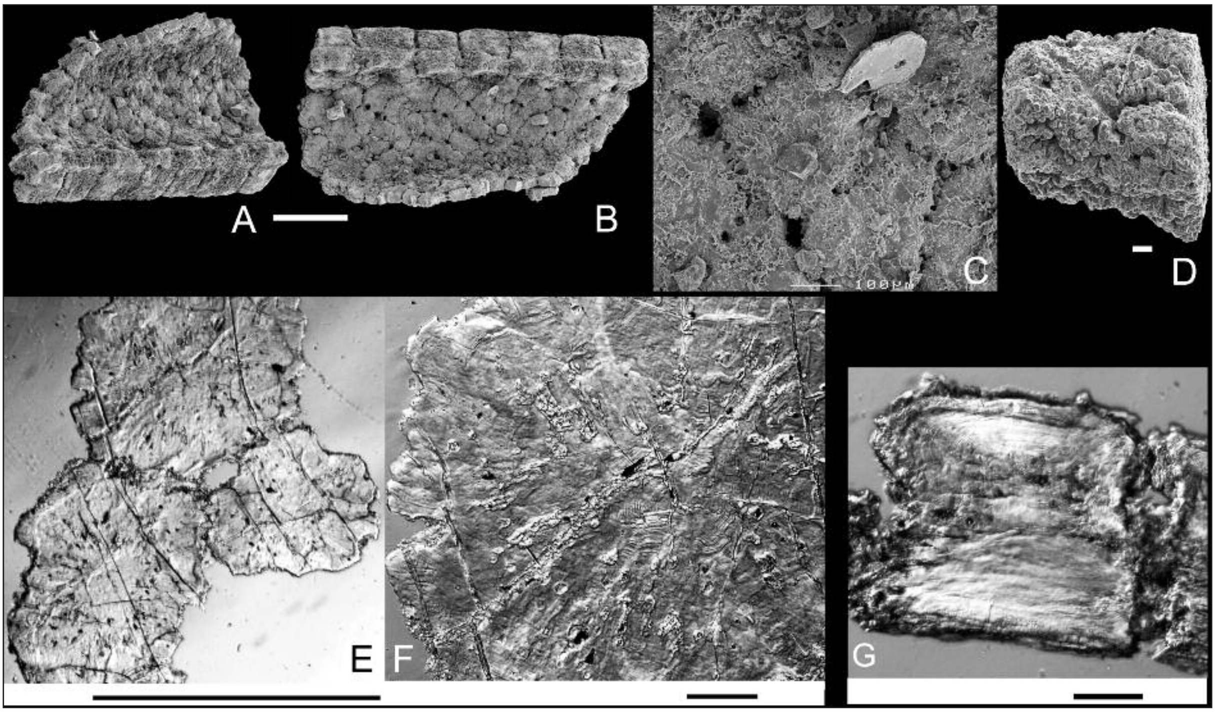

Fig. 3. Prismatic calcified cartilage tesserae from limestone outcrop localities GY77/7-11, south Toomba Range, western Queensland; A-C – double and single layered fragment QMF52820; D – cylindrical fragment QMF52821; E-F – horizontal thin section QMF52840; G – vertical section QMF52822. Bar: 1.0 mm in A, B, E; 0.1 mm in C, D, F, G.

Ring-like elements: Several distinctive rings of bone (Text-fig. 4M-N) were also found. The ends of the better preserved element do not appear to be broken, indicating that the original structure was an incomplete ring with a diameter ca. 2.5 mm and width ca. 0.5 mm. The rings are flat from side to side, not curved as would be expected if they were sclerotic rings.

COMPARISON

Morphologically, as noted by TURNER & YOUNG (1987), *Mcmurdodus* teeth most closely resemble those of the Echinorhinidae. COMPAGNO (1984) listed the diagnostic features of hexanchid teeth as: well differentiated in upper and lower jaws, upper anteriors small, narrow, with a main cusp and often smaller cusplets, lowers very broad, compressed and saw-like, with series of large cusplets and a short elongated cusp; posterior teeth small and granular at corners of dental bands. The teeth of the Echinorhinidae are diagnosed as having 3-7 cusps with the middle cusp largest and strongly oblique so that the inner margin of adjacent middle cusps form an almost continuous cutting edge along the jaw (after GARRICK 1960). A distinctive central groove running labiolingually across the base of the tooth is present in both *Mcmurdodus* (TURNER & YOUNG 1987, fig. 4B; Text-fig. 1A, B) and *Echinorhinus* (e.g. KEMP 1991, pl. 4P). The relative abundance of prismatic calcified cartilage, the scarcity of *Mcmurdodus* teeth in the Cravens Peak Beds samples, and the lack of variation in morphology, suggest that, like *Echinorhinus* (GARRICK 1960, text-fig. 2C, I, J), *Mcmurdodus* probably had a limited number of functional teeth and tooth families.

As described and illustrated by HOVESTADT & HOVESTADT-EULER (1993) and HERMAN & *al.* (2003), hexanchid and echinorhinid taxa possess a similar kind of

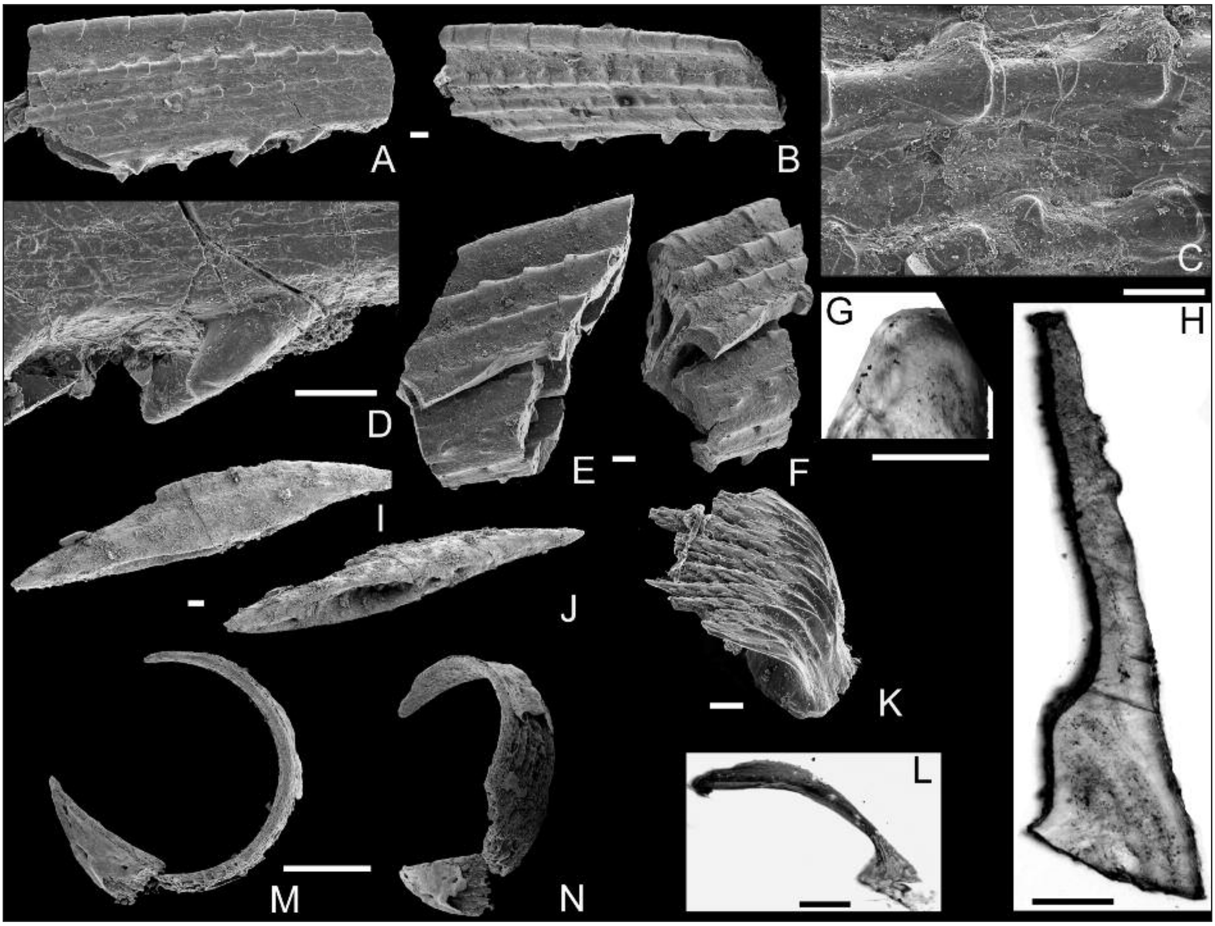

Fig. 4. Spines, scale, and bony ring possibly from *Mcmurdodus whitei*, from limestone outcrop localities GY77/7-11, south Toomba Range, western Queensland; A-D – spine fragment QMF52841; E-F – spine fragment QMF52836; G-H – vertical thin section of spine fragments QMF52823; I-J – small spinelet QMF52842; K – scale QMF52824 in laterocrown view, anterior to right; L – vertical longitudinal section QMF52825 of half of scale in (K); M-N, incomplete bony ring QMF52837. Bar: 0.1 mm in A-L; 1.0 mm in M, N

tooth vascularization. The entire mid-section of the tooth shows a series of relatively large osteodenteons, from which vertical, more or less parallel canals pierce the lower root part and end at the lingual face of the root as an opening to the vascular system outside. Above the mid-section, the osteodenteons become narrow to form a reticulated system of more or less horizontal canals. This system is connected to separate triangular-shaped pulp cavities in each mesial cusplet of the crown. From these cavities, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusplets (Text-fig. 2B,C). Although the tooth vascularization of *Mcmurdodus* is not identical, it shares the following characters considered to be significant:

1. A series of relatively large osteodenteons in the midsection, from which more or less vertically directed canals pierce the lower root and end at the lingual face of the root as an external vascular opening.
2. Osteodenteons above the midsection become narrower forming a reticulated system of canals connected to separate triangular-shaped pulp cavities in the crown cusplets.

Thin sectioning and acid etching of the teeth has shown that the cusps have branching orthodentine tubules that extend from just below the outer surface to the pulp cavities, without, or with a very thin, enameloid layer. The teeth lack the triple-layered enameloid of shiny-layered enameloid (SLE), middle parallel-fibred enameloid (PFE) and inner tangle-fibred enameloid (TFE), which REIF (1973) regarded as characteristic of neoselachian teeth, despite its absence in some extant genera including *Hexanchus*, which has only the PFE layer (REIF 1973, fig. 15). TLE is also absent in the oldest recognized neoselachian *Palaeospinax* (DE CARVALHO 1996). Only the PFE layer is now considered apomorphic for neoselachians, but even that is not found in all groups (DUFFIN & WARD 1983, pl. 1; MAISEY & *al.* 2004). Apart from the vascularization studies of HERMAN & *al.* (2003), the histology of echinorhinid teeth had not previously been examined. Our preliminary work reveals that, like *Hexanchus*, *Echinorhinus cookei* has only the PFE layer (Text-fig. 1R, S).

The possible *Mcmurdodus* spines and scales found show no neoselachian characters, but rather compare with those of other Devonian sharks (e.g., *Antarctilamna* YOUNG, 1982). If they belong to *Mcmurdodus*, this could support the interpretation that the close morphological similarity between *Mcmurdodus* and *Echinorhinus* teeth is by convergence rather than a close phylogenetic relationship. *Echinorhinus* is anacanthous, and has small and large, unusual stellate scales scattered over the body (GARRICK 1960, pl. 7, figs. B-D, text-figs. 2E, 3C). *Echinorhinus* also lacks an anal fin, which is regarded as a derived character in cladistic analyses, because (possibly using circular reasoning) possessing an anal fin is considered to be plesiomorphic for neoselachians. Other 'primitive' characters for *Echinorhinus* include an unsegmented notochord and a poorly calcified vertebral column (KEMP 1991).

The bony rings (Text-fig. 4M, N) are highly distinctive elements. We considered the possibility that they could be sclerotic rings. Dipnoans, several sarcopterygians (YOUNG & SCHULTZE 2005) and an antiarch placoderm (YOUNG 1984) occur at this locality, but sclerotic rings are formed of multiple, articulating or fused, ornamented plates (e.g. MILES 1971, 1977). Rather, the rings closely resemble the diagnostic elements that support the lateral line canal in *Echinorhinus* spp. (GARRICK 1960, text-fig. 1; Text-fig. 2E), and which are not found in any other modern shark, but are present in chimaeroids, which suggests that they are a plesiomorphic character retained in echinorhinids.

The only other Palaeozoic record of a possible hexanchiform or echinorhiniform is a single tooth from the Upper Permian of Japan, listed as Hexanchidae gen. sp. indet. (GOTO 1994) and later figured by GOTO (2002, fig. 5). The tooth is imbedded in its original matrix revealing the labial view only, but several hexanchid tooth characters are notable, as seen in the reconstruction (Text-fig. 2D) based on the shape of the non-fractured parts of the tooth and the shape of early Mesozoic hexanchids. The tooth is more similar to Early Jurassic teeth, e.g., *Notidanoides muensteri* (AGASSIZ, 1843), than to *Mcmurdodus*, but the record is valuable in pointing to an extremely long ghost lineage for the two neoselachian groups.

Recent phylogenetic analyses of modern elasmobranchs based on morphological and molecular data have yielded strongly conflicting results (MAISEY & *al.* 2004), but despite some dissention (e.g. DUFFIN & WARD 1983) a broad consensus maintains a Mesozoic, rather than Palaeozoic, origin for the neoselachians. The few studies that mentioned *Mcmurdodus* (e.g. CAPPETTA & *al.* 1993, CUNY 1998, MAISEY & *al.* 2004) preferred the interpretation that similarity in tooth morphology and vascularization result from convergence rather than close phylogenetic relationship. However, it is perhaps surprising that no other teeth from the Devonian or Carboniferous bear any resemblance to those of *Mcmurdodus*, a genus now known from three separate localities – Antarctica, western Queensland, and Victoria (J. LONG pers. comm. 2007), albeit all in Eastern Gondwana. While these occurrences were from relatively shallow water deposits, extant *Echinorhinus* is now a rarely seen, deepwater shark, although in the Cretaceous echinorhinids were common scavengers on dinosaur carcasses [D. Ward, pers. comm., ST pers. obs]. The evidence which we have presented here on the morphology, enameloid structure and vascularization of teeth, plus possible lateral line rings in *Mcmurdodus*, support a phylogenetic relationship rather than convergence with *Echinorhinus*. If *Mcmurdodus* was a stem echinorhinid or hexanchid, the long gaps between appearances in the fossil record (Devonian to Permian to Early Jurassic, or Devonian to Early Cretaceous) could result from a post-Middle Devonian change in lifestyle for the clade(s).

Acknowledgements

DCH and MH-E thank J. & C. Hartman, Fitzroy Falls, for their hospitality and help in Australia. We thank Prof. Dr M. Goto (Tokyo) and Dr J. Long (Melbourne) for sending photographs for examination, D. Ward (London) for sharing information, and D. Bray (MV) for extracting *Echinorhinus cookei* teeth and skin for our study. GCY and CJB acknowledge the support of Australian Research Council Discovery grant DP0558499 for the field trip to western Queensland, and thank the Rule family (Cravens Peak Station) for their extensive help. ST & CJB thank the Queensland Museum Board for on-going basic support, CJB acknowledges use of facilities at the Centre for Microscopy and Microanalysis, University of Queensland, and GCY acknowledges use of facilities at the Research School of Earth Science, Australian National University. We thank Dr O. Hampe and an anonymous reviewer for their helpful suggestions.

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Manuscript submitted: 31th October 2007
Revised version accepted: 15th April 2008