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Ancient Fishes and their Living Relatives: a Tribute to John G. Maisey. Alan Pradel, John S. S. Denton & Philippe Janvier (eds.): pp. 239–245, 7 figs. © 2021 by Verlag Dr. Friedrich Pfeil, München, Germany – ISBN 978-3-89937-269-4

# Fossil chondrichthyan remains from the Middle Devonian Kevington Creek Formation, South Blue Range, Victoria

John A. Long\*,\*\*, Victoria Thomson\*,\*\*\*, Carole J. Burrow\*\*\* and Susan Turner\*\*\*

#### **Abstract**

Chondrichthyan teeth are described from a new site located in the upper section of the Middle Devonian Kevington Creek Formation, NW Victoria. Our review of the genus Mcmurdodus White, 1968 indicates that the Australian teeth previously assigned to this genus, which have up to eight large asymmetric cusps, belong in a separate genus from the type species, which has a central row of median cusps separating three larger lateral cusps. We refer the Australian species M. whitei Turner & Young, 1987 to Maiseyodus new genus, and describe a new occurrence of this species from the South Blue Range assemblage. The co-occurrence supports an Eifelian age for the South Blue Range unit, as M. whitei is otherwise known only from the late Early/early Middle Devonian Cravens Peak Beds of western Queensland (Emsian–Eifelian boundary). The younger oc-

currence of the type of the genus *Mcmurdodus* in the Aztec Siltstone of Antarctica (Eifelian–Givetian) and the presence of *Aztecodus* sp. cf. *A. harmsenae* and *Antarctilamna prisca* in the Kevington Creek Formation fauna would also support an older age than previously estimated for the South Blue Range Devonian succession. Revised U-Pb dates on the nearby Toombullup Ignimbrites supports an older age for the fish-bearing sequence at the base of the Mansfield Basin sequence. Biostratigraphic correlation of key chondrichthyan species found in the Aztec Siltstone of Antarctica and the Cravens Peak Beds limestone member suggests that the South Blue Range succession is much older than previously placed. It is likely a correlate of the lower part of the Aztec Siltstone succession.

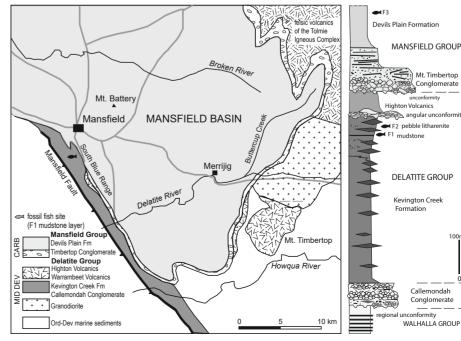
#### Introduction

Fossil fishes were first discovered from the South Blue Range (SBR), near Mansfield (Fig. 1), in the early 1930s and described by Hills (1936). Hills identified Bothriolepis and Phyllolepis, placoderm fish taxa both known from northern hemisphere sites in the USA, Europe and Russia, where they characterise Late Devonian deposits. In earlier work at Taggerty, Hills (1929, 1932) identified these taxa in Australia for the first time and suggested that a Late Devonian age could be placed on the Cerberean Cauldron volcanic sequence. Long & Werdelin (1986) proposed lithostratigraphic and biostratigraphic correlations using Devonian fish faunas throughout the central Victorian sites, and suggested an older, Givetian (upper Middle Devonian) age for the SBR fauna based on its relationship with key volcanic events and the composition of the fish fauna.

A large number of sites in both Australia and Antarctica contain the presumed freshwater fish fauna typical of the northern hemisphere Late Devonian (with key placoderm genera *Bothriolepis*, *Groenlandaspis*, and phyllolepids) in much older, well-dated sites (Young 1974, 1989a, 2010a, 2010b). We now know that *Bothriolepis* ranges from the Early Devonian in China (Zhao & Zhu 2010) and earliest Middle Devonian in Australia and Antarctica (Young 1974, 2010a), but is restricted to the Late Devonian in Europe, Russia, Greenland and North America (Young 1974, Stensiö 1948). The genus *Groenlandaspis* is restricted to the latest Devonian (Famennian stage) in Europe, South Africa and North America, but is established

The genus *Phyllolepis* is also tied to latest Devonian strata in the northern hemisphere (Famennian, USA, UK, France, USSR, Long & Daeschler 2013) with several endemic genera of phyllolepids having been described from Australia and Antarctica (Long 1984, Ritchie 1984, 2005, Young & Long 2005, Young 2007) in Middle–Late Devonian strata, and an unnamed phyllolepid from the Frasnian of Turkey (Janvier 1983). Tying down the age of terrestrial sedimentary sequences using placoderm faunas relies on having a well-preserved, diverse fauna where taxa can be accurately identified down to species level. The

Fig. 1. Map showing geology and stratigraphic column for Mansfield region (modified after Cas et al., 2003).



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as occurring in the Eifelian and Givetian of the Australian and Antarctic sequences.

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relatively few specimens of placoderms so far described from the SBR mudstone lens are mostly placed in indeterminate species in cosmopolitan genera (*Bothriolepis* sp., *Groenlandaspis* sp.) apart from the phyllolepid *Austrophyllolepis* edwini (Long 1989).

More recently, use of shark teeth as key biostratigraphic indicators of precise ages within the Devonian strata has greatly increased (e.g. Turner 1993, Ginter & Ivanov 1992, Ginter 2002, Ginter et al. 2008, 2010, Burrow et al. 2010). The new discovery of fossilised shark teeth within the SBR succession in a thin mudstone lens in the middle section of the Kevington Creek Formation enables more precise dating of the succession, as inferred from the presence of key species known from sections in other regions that represent reasonably well-constrained biostratigraphic frameworks, in particular the Aztec Siltstone of Antarctica and Cravens Peak Beds limestone of the Georgina Basin in Queensland.

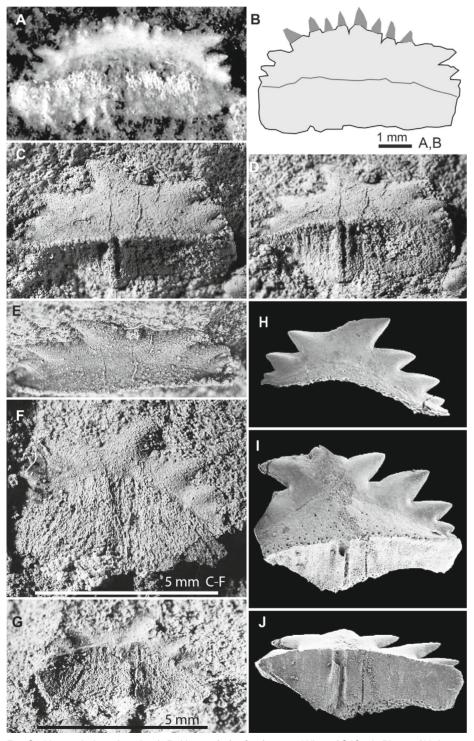


Fig. 2. Mcmurdodontid teeth. A, B. Mcmurdodus featherensis White, 1968. A. Photo of Holotype NMHUK PV P.49157 (from Ginter et al., 2010, fig. 97E); B. interpretation of restored tooth based on a camera lucida sketech of the Holotype by JAL. C-G. Maiseyodus gen. nov. sp. cf. M. whitei. South Blue Range specimens, MV P228244: C. in labial view; D. in ventrolabial view; E. in lingual view; F. crown view; G. in ventral view. H-J. Maiseyodus whitei new genus (Turner & Young 1987), Craven Peak beds limestone (Burrow et al. 2008, fig. 1D, B, A respectively).

This discovery is the first time that any chondrichthyan teeth have been identified from the continental Middle–Late Devonian sedimentary successions anywhere within Victoria. Older stem chondrichthyan remains were reported from the Silverband Formation in the Grampians of western Victoria by Chapman (1917) and Talent & Spencer-Jones (1963), and the fauna extensively revised by Turner (1986) and Burrow (2003) with thelodont scales and stem chondrichthyan (acanthodian) scales and fin spines identified. The age of this fauna remains unclear, due to dating constraints with nearby volcanics. Burrow (2003) suggested a Late Silurian (Ludlow) age based on the presence of Sinacanthus and Radioporacanthodes.

Garvey & Turner (2006) described shark teeth and scales from the Mansfield district, from the slightly younger Devils Plain Formation, comprising teeth of Ageleodus altus and scales of Tristychius sp. and Ctenacanthus sp., representing genera known from the very latest Devonian (upper Famennian) and Early Carboniferous beds of the northern hemisphere (fish fauna F3, Fig. 1).

#### Material and methods

The new material described herein is housed at the Melbourne Museum (Museum Victoria) in the Geosciences collections. Specimens were collected in situ and as the bone was not well preserved, the rocks were soaked in solutions of dilute HCL (10%) to clean the surfaces of weathered bone fragments. The cleaned rock surfaces were cast with blackened latex rubber; casts were then photographed with an Olympus Microscope U-TVO.5XC-3 attachment after being whitened with ammonium chloride sublimate.

Specimens were collected by the lead author and colleagues from a new fossil locality occurring within the top 50 m of the Kevington Creek Formation in the northern end of the South Blue Range, near Mansfield, Victoria (Fig. 1). The new site was uncovered during a CAVEPS (Conference on Australian Vertebrate Evolution, Palaeontology and Systematics) field trip in April 2007. It comprises a thin layer (c. 10 cm thick, Fig. 1, F1) of dark grey silty mudstone that outcrops about 40-50 m below the highest point of the range in its northern end, almost directly opposite the intersection of the two major roads along the western side of the South Blue Range (Fig. 1). The mudstone layer is bracketed by medium-grained buff sandstones above and below it, grading upwards into intraclast conglomerate lenses and pebble litharenite layers towards the top of the range where impressions of placoderm fish plates are also found (Fig. 1, F2). Long (1989) collected and described the remains of the phyllolepid Austrophyllolepis edwini from this locality above the mudstone layer.

Institutional Abbreviations. CPC, Commonwealth Palaeontological Collections, Geoscience Australia, Fyshwick, ACT. MV P, Melbourne Museum (Museum Victoria); NHMUK PV, Natural History Museum, London, UK; QM, Queensland Museum, Brisbane.

### Systematic palaeontology

Class Chondrichthyes Huxley, 1880 Order indet.

Family Mcmurdodontidae White, 1968

Revised diagnosis. Chondrichthyan teeth with up to seven large asymmetric flat weakly serrated cusps forming each side of the crown, with or without series of central medial cusps. Root is broad and subrectangular with distinct medial basal canal through raised tube in midline of ventral surface of the root. The base is angled lingually away from the crown, being subequal in size to the crown, and sloping down towards the lingual edge.

#### Mcmurdodus White, 1968

Revised diagnosis. Selachian teeth up to 8 mm long and 5 mm high, multicuspid asymmetrical crown strongly compressed labiolingually. Lateral cusps are triangular in shape, sometimes elliptical in section, with upper cutting edges weakly to strongly serrated, maximum number of cusps is seven for each side, with third cusp in from each side being the largest on the crown; central row of at least four smaller narrow cusps. The cusp axes are progressively more inclined from the vertical so that the distal cusp axis is almost parallel to the crown root junction. There is a prominent medial groove on the basal surface with a large foramen opening at the labial end.

**Type species.** Mcmurdodus featherensis, NHMUK PV P49157, Mt. Feather, southern outcrop of Aztec Siltstone, South Victoria land, Antarctica (cf. Eifelian–Givetian age range).

#### Maiseyodus, new genus

Diagnosis. A mcmurdodontid with teeth having 8–10 major cusps, ranging between 4–6 major cusps on each side, increasing rapidly in size in the first three cusps from the edge of the crown with the fourth or fifth cusp being sometimes slightly smaller than the third cusp from the edge. Serrations either absent or developed on the occlusal cutting edge between the principal (medial) and second largest cusps on each side. A series of ca. 8–10 foramina on the lingual surface within a pitted triangular area above the crown-base interface. Holaulacorhize base, with D shaped profile in ventral view.

Type species. Mcmurdodus whitei Turner & Young, 1987, p. 235

**Holotype.** CPC 25765, Cravens Peak Beds (limestone unit), Georgina Basin, Queensland (upper Emsian), Turner & Young (1987, fig. 2), a relatively complete tooth although many of the cusps have their tips broken off.

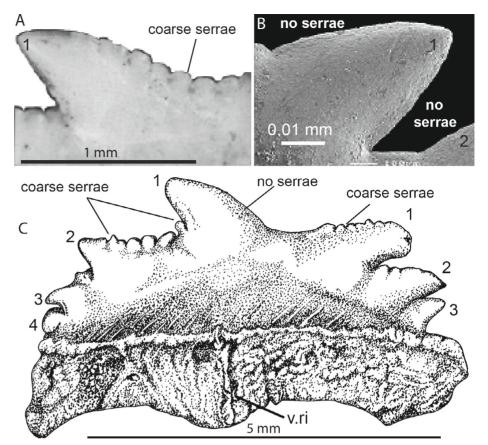
**Etymology**. In honour of Dr. John Maisey for his outstanding contributions to our understanding of the evolution and anatomy of sharks.

Remarks. The diagnosis is modified from Turner & Young (1987, p. 235) to distinguish cusp morphology from M. featherensis, which appears to have 12-14 cusps as evidenced by broken cusps clearly visible on the holotype (Fig. 2A, B), and with smaller cusps medially located. M. whitei has the largest cusps developed towards the central region of the crown (Turner & Young 1987, figs. 2, 3A). The known specimens of M. whitei suggest that Maiseyodus had a dentition somewhat similar to that of the hexanchoids (Turner & Young 1987), though the teeth bear a stronger resemblance to those of the sister group of the hexanchoids, the echinorhinoids (Burrow et al. 2008). Whereas hexanchoids have different dentitions on the upper and lower jaws (Herman et al. 1987), Echinorhinus has similar teeth on both jaws (Herman et al. 2003). The lack of marked variation in the known examples of M. whitei indicates that its dentition closely resembles that of Echinorhinus, particularly E. cookei. By comparison, the difference in cusp length is not due to differentiation within the dentition. Extant hexanchoid sharks have little variation between adult and juvenile dentitions, with possible lack of serration found in juveniles (Springer & Waller 1969; Herman et al. 1987, 1994, 2003). However, extant Echinorhinus spp. show variation in the number of cusps between adults and juveniles, with adults having a larger number of cusps (Garrick 1960).

Maiseyodus whitei specimens from the Cravens Peak Beds (Turner & Young 1987) have been completely removed from limestone by acetic acid digestion, whereas the two specimens described here from the SBR were studied from latex peels of the natural moulds.

## Maiseyodus sp. cf. M. whitei (Figs. 2C-G, 3A,C)

**Description**. MV P228244, preserved in part and counterpart moulds (Fig. 2C, D, F, 3A, C) from the SBR, has a width of 6 mm, with crown height of 2.5 mm. It has 3–5 coarse, rounded serrations well developed between the central, and largest, three



cusps, but lacking on the median cusp oral edge, a feature distinguishing it from all known examples of *Maiseyodus whitei* (Fig. 3B). MV P254493 (Fig. 2E,G) is a second complete tooth from the same locality showing similar morphology although the crown-root line is more strongly convex than in the P228244. It also shows a similar distribution of the serrations with a nonserrate median oral edge between the main cusps.

Comparison. Maiseyodus sp. cf. M. whitei from the SBR resembles M. whitei from the Cravens Peak Beds (limestone) in overall crown shape, having multiple broad-based cusps, and a flat base with a central labio-lingual canal. However, unlike Maiseyodus whitei with cusp 1 and 3 on both sides of the crown being larger than cusp 2 (Turner & Young 1987), M. sp. cf. M. whitei from the SBR shows a decrease in size outwards from cusp 1 on both sides of the crown, like in hexanchids Eonotidanus, Notorynchus, and Weltonia (Ginter et al. 2010; Herman et al., 1987, 1994), and Mcmurdodus featherensis (White 1968, fig. 1). As the teeth from the Cravens Peak Beds (and in Echinorhinus) show little morphological variation, it is possible that the new South Blue Range Maiseyodus is not conspecific with M. whitei, but the limited material precludes us from erecting a new species.

Family Aztecodontidae Hairapetian, Ginter & Yazdi, 2008 Aztecodus Long & Young, 1995 Aztecodus harmsenae Long & Young, 1995

## **Aztecodus sp. cf. A. harmsenae** (Fig. 4A-C)

**Description.** Aztecodus sp. tooth NMV P254494 is 5 mm in width with a crown height of 3 mm, with a partially missing base. Both labial and lingual crown surfaces appear smooth with no external striae. The two cusps are widely separated and twisted in different planes. The ridge between the two cusps appears smooth, although some of it is obscured by matrix (Fig. 4A,B). The anterior and posterior edges of the tooth are perpendicular to its long axis. The base is relatively shallow, and only slightly wider than the crown labio-lingually (Fig. 4A,C). The basal surface has labio-lingually oriented ridges and furrows.

**Comparison.** The single tooth from the SBR succession is only half the size of the type specimens of *A. harmsenae* from the Aztec Siltstone, which are up to 2 cm wide (Long & Young, 1995, figs. 8, 9). The lack of crenulations on the connecting

Fig. 3. Comparison of Maiseyodus new genus specimens from South Blue Range. A, C. MV P 228244), B. Cravens Peak Beds limestone, specimen QMF 52817 (Burrow et al., 2008, fig. 1C).

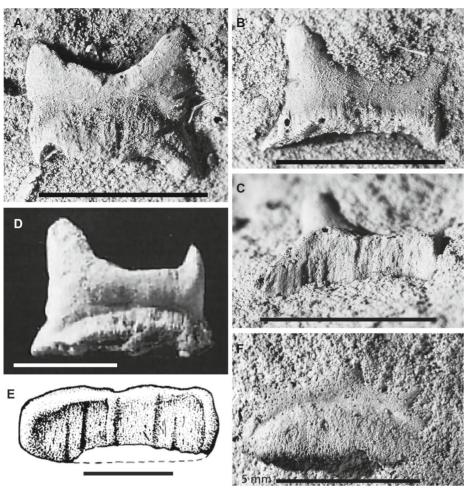


Fig. 4. A–C. Aztecodus sp. cf. A. harmensae tooth MV P 254494 from South Blue Range; D, E. Aztecodus harmensae teeth from the Aztec Siltstone, Antarctica (Long & Young, 1995, figs. 8F, 9B respectively). F. Maiseyodus new genus sp. cf. M. whitei. MV P254493 in lingual view.

ridge between the two cusps on the SBR tooth might be related to the small size of the tooth; the smallest of the type specimens (Long & Young, 1995, fig. 8F,G) appear to have only weakly developed crenulations, compared with the larger type teeth. The orientation and wide separation of the cusps on the SBR tooth make it most similar to type tooth WAM 92.3.71 (Long

conclusion as no new specimens of *Anareodus* were collected.

Order Antarctilamniformes Ginter, Liao & Valenzuela-Ríos, 2008
Family Antarctilamnidae Ginter, Liao & Valenzuela-Ríos, 2008 *Antarctilamna* Young, 1982

& Young, 1995, fig. 8F; Fig. 4D,E). Ginter et al. (2010) suggested that *Anareodus* Long & Young, 1995 is a variation of the *Aztecodus* style tooth, as both are found together in the same layers of the Aztec Siltstone. Increased numbers of specimens of shark's teeth from JAL's recent Antarctic field trips over 2016 and 2018 summer field seasons would appear to validate this

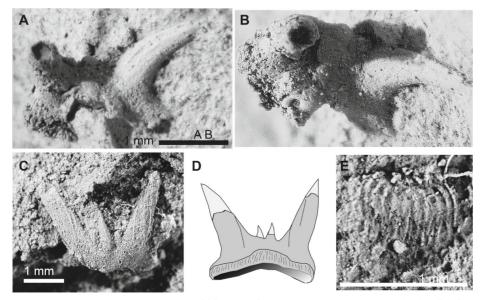
## Antarctilamna prisca Young, 1982 (Fig. 5)

Description. Two nearly complete teeth have been identified, plus some isolated cusps which will not be dealt with herein. The teeth are small (2-3 mm high) with large divergent striated cusps and a small central nub at the confluence of the cusps and in general closely resemble the type species A. prisca (Young 1982, Fig. 5D). The first specimen (NMV P254494, Fig. 5A, B) shows two nearly complete curving lateral cusps, each with 4-5 striae along the lingual face and broken cross-sections suggesting the presence of a median cusplet. The tooth base is broad, semicircular with a small torus well defined on the lingual surface (Fig. 5B). The base is strongly convex along the lingual margin, but incomplete on its labial margin. NMVP254495 is the most complete, showing both lateral cusps, small median cusplets and most of the extent of the tooth base (Fig. 5C). As well as teeth, two scales (one shown in Fig. 5H) have been identified, which show 'ctenacanthid' morphology comprising multiple thin odontodes oriented anteroposteriorly, forming the crown.

Comparison. The teeth conform to the species definition of Antarctilamna prisca, known from the Aztec Siltstone of Antarctica and Bunga Beds of New South Wales (Fig. 5D). The isolated scale(s) show the same crown morphology as those on the articulated A. prisca specimens from the Bunga Beds (Young 1982, fig. 4D). The same type of scale is also found on other early sharks including the Early Devonian Doliodus (Miller et al. 2003) as well as Late Devonian and Carboniferous ctenacanthiforms (e. g. Williams 1998).

#### Discussion

Range and distribution of *Antarctilamna*. According to Ginter et al. (2010), teeth belonging in the Order Antarctilamniformes range through the Middle-Upper Devonian, with the genus



**Fig. 5.** Antarctilamna prisca Young, 1982. **A, B.** South Blue Range specimen NMV P24495: **A.** linguocrown view; **B.** crown views; **C.** NMV P224496, in labial view showing striae on lateral cusps and median cusplets. **D.** tooth sketch based on the holotype specimen CPC 21198 (after Young 1982, plate 89, 8), Aztec Siltstone, Antarctica. **E.** scale from the South Blue Range mudstone layer, NMV P256966.

Antarctilamna also having a range span from the Middle-Upper Devonian, although this estimate was based on earlier work presenting a younger age estimate for the Aztec Siltstone (Young 1982, 1988). More recent appraisal of the strata (Young 2007), with comparisons made based on Maiseyodus teeth occurring in both the Cravens Peak Beds limestone (Emsian-Eifelian boundary?) and the lowest section of the Aztec Siltstone at Mt. Feather, suggest an older date for the base of the Aztec Siltstone. Antarctilamna is known only from its lowest levels, from sites at Portal Mt., Mt. Crean, Lashley Mt., and was recently found at Mt. Fleming (lowest horizons of the unit). The thelodont Neoturinia antarctica (Turner & Young, 1992) occurs at all these sites, but has not been found outside Antarctica (Turner 1997a) although similar scales are known from Australia (Long & Trinajstic 2000, Hairapetian et al. 2016).

Whilst spines assigned to Antarctilamna vary, with some likely to be from other taxa, teeth having Antarctilamna characteristics are known from fewer sites, namely the Aztec Silstone of Antarctica (Eifelian?-lower Givetian) and the Bunga Beds of NSW (?Emsian-Eifelian) in Eastern Gondwana. Gess & Coates (2014) assigned an articulated shark with similar teeth from the Famennian of South Africa to a new species Antarctilamna ultima. This latter occurrence marks the youngest and higest latitude record for the genus, so might be a relict survivor. Alternatively, it could be referrable to another genus based on the robust shape of the teeth (e.g. Gess & Coates 2014, fig. 7), quite unlike the very slender teeth found in the only other member of the genus, the type species A. prisca. These are all the known instances of teeth confidently attributed to Antarctilamna, although one tooth fragment from the Givetian

of Spain has also been tentatively assigned to *Antarctilamna*? sp. (Ginter et al. 2008, fig. 2P). The only other possible occurrence of teeth from this genus is in the Givetian–Frasnian boundary beds of the North Evans Limestone, New York. Teeth of *Wellerodus priscus* (Eastman, 1899) closely resemble those of *A. prisca* (Turner, 1997b), and Ginter et al. (2008, 2010) supported Turner's hypothesis that they could be congeneric (Burrow et al. 2010). *Wellerodus* is now known from several localities in the Middle to Late Devonian of North America in marine settings (Turner 1997b, Potvin-Leduc et al. 2015).

Associated fauna at the new SBR locality. Placoderm plates and acanthodian fin spines and a cheek plate have also been collected from the mudstone lens (Fig. 6). The placoderms include Venezuelaspis sp. represented by an anterior median dorsal plate (Fig. 6A, B), similar to specimens formerly identified as Pambulaspis by Young (1988). The distinct narrow anterior margin and split median ventral ridge make this plate distinctive for the genus (Young & Moody, 2002). A large anterior median ventral plate of the arthrodire Groenlandaspis is also identified from the assemblage (Fig. 6C) but beyond generic identification nothing more can be noted about this large specimen. The acanthodian specimens are fin spines of Striacanthus sp. (Hills, 1931, Fig. 6D) and a cheek plate of the diplacanthiform  $\mbox{\it Culmacanthus}$  sp. (Fig. 6E).  $\mbox{\it Culmacanthus}$ is well-known from the Mt. Howitt fauna (Long, 1983a) and has also been described from a cheek plate from the Aztec Siltstone at Mt. Crean, Antarctica, from the Pambula River assemblage (Young 1989b), and partial articulated fish from the Bunga Beds (Burrow & Young, 2012). In addition, a number of isolated antiarch plates attributed to Bothriolepis sp. have been found in the assemblage, but these are beyond the scope of this paper to describe in detail.

**Geological and Biostratigraphic Implications**. New radiometric dating for the Cerberean Volcanics by Clemens et al. (2014) indicated older dates were unreliable. The new, reliable date

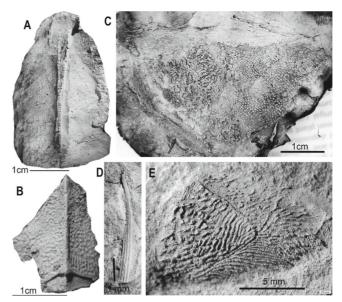


Fig. 6. Placoderm and acanthodian remains form the mudstone lens, South Blue Range, Mansfield. A, B. Venezuelepis sp. MV P254499, Anterior Median Dorsal plate in ventral (a) and dorsal view (b). C. Groenlandaspis sp. MV P228259. Anterior Median Ventral plate in ventral view; D. Striacanthus sp. MV P254497, fin spine, lateral view. E. Culmacanthus sp., left cheek plate MV P254498 in lateral view. Scale bar = 1mm

placed on the upper part of the Toombullup Formation at the top of the CVC is  $377\pm2\,\text{Ma}$ , placing the upper section of the volcanic event as middle Frasnian (IUGS 2018 chart). The sediments of the Blue Range Formation containing a diverse fish fauna lie well below the newly dated volcanics, separated by several major volcanic eruption events (Fig. 7).

The Snobs Creek Volcanics, situated below the Blue Range Formation, are one of the re-dated units with Pb/Ur radiometric dates at  $373.2\pm1.8$  and  $375\pm2$  Ma (Compston 2004), which would place the fish fauna at Taggerty in the Taggerty Formation well within the Frasnian, if the dates are reliable. This date would thus split the vertebrate zonation MAV 8 (Taggerty-Mt. Howitt fauna) of Young (1993) and place the Taggerty fauna within MAV 10 (Pambula River fauna) or MAV 11 (Nettletons Creek fauna) in the mid Frasnian. Whilst this might be consid-

Fig. 7. Revised scheme of biostratigraphic correlations based on fish faunas for central Victoria (modified stratigraphic columns from Cas et al. (2003), with added radiometric dates for the Toombullup Formation from Compston (2004) and Clemens et al. (2014). Age ranges of key species taken from Young (1993, 2007) and Long (1983b).

|               |                    |            | Central<br>Victorian<br>Caldera<br>Complexes | Tolmie<br>Igneous<br>Complex        | Mansfield<br>Basin | North<br>Macalister<br>Synclinorium | Freestone<br>Anticlinorium<br>Mitchell<br>Synclinorium | Victorian<br>Vertebrate Faunas<br>(Young 1993)   | Key taxonomic ranges                       |                   |  |
|---------------|--------------------|------------|--|-------------------------------------|--------------------|-------------------------------------|--|--|--|-------------------|--|
| CARB.         | Tournasian         | 359        | ??   | ??                                  | ??                 |                                     | ?? West  | Mansfield Fauna (8)  | Chondrichthyes                             | Phyllolepids      | Bothriolepids                                  |
| LATE DEVONIAN | Frasnian Famennian | 372        | ??  Cerberear Caldera Volcanics  Volcanics   | Toombull Formatio Ryan's C Rhyolite | up<br>n            | lo°o⊓<br>ding <i>‱</i>              |  | MAV 15 Grenfell fauna  MAV 14 Worange Point fauna  MAV 13 JemalCanow. fauna  MAV 12 Twofold Bay fauna  ?Taggerty (3)  MAV 11 Nettletons Ck Fauna  MAV 10 Pambula River | isca                                       |                   |  |
| OLE DEVONIAN  | Eifelian Givetian  | 383        | Wightman's                                   | Holland's Creek Rhyodaci            | Highto             | on nics Fm Rose River Volcanics     | Wellington Volcanic Gp Moroka Glen Fm                  | MAV 9 Bindaree Rd (5) – Freestone Ck (6, 7)  MAV 8 Mt. Howitt (4)  MAV 6 Aztec Siltstone fauna Antarctica  [ MAV 7 Tatong (1) – SBR (2)]                               | Maiseyodus Mcmurdodus Antarctilamna prisca | Austrophyllolepis | ensis<br>B.cullodenensis<br>B. gippslandiensis |
| MIDDLE        | Emsian             | 393<br>407 | TABBERABBERAN DEFORMATION                    |                                     |                    |                                     |  | MAV 4-5 Naw-War-Atland. fauna MAV 3 Hatchery Crk-Bunga fauna MAV 2 Cravens Peak fauna MAV 1 Taemas-Buchan fauna  |  | Ą                 | B. tatongensis<br>B.c<br>B. gip                |

ered problematic, the long age ranges of taxa here discussed (Fig. 7) would support the possibility that the Taggerty fauna is a much younger assemblage than Mt. Howitt.

Thus, the presence of faunal elements common to the SBR succession and the Aztec Siltstone of Antarctica (co-occurrence of chondrichthyan species in units bearing thelodonts) further suggests the succession at South Blue Range should be older than Late Devonian. Recent reassessment of the thelodont bearing units in southern NSW included the suggestion that the Hatchery Creek Formation fauna, containing thelodonts, placoderms and basal osteolepidids, should now be considered Emsian in age (Hunt & Young 2011). The realignment of the Hatchery Creek assemblage as upper Emsian, combined with the suggested placement of the Bunga Beds assemblage at early Eifelian (Young 2007; MAV 3 equivalent, Young 1993) has implications for assemblages containing the species Antarctilamna prisca, such as the Aztec Siltstone and South Blue

Range faunas, indicating these are likely to be older than previously suggested. Figure 7 presents these vertebrate faunal assemblages in a re-aligned order, tied in to existing reliable radiometric dates (Compston 2004, Clemens et al. 2014). Young's (1993) vertebrate assemblage previously referred to as MAV 7 (South-Blue Range-Tatong faunas) is here correlated with the lower section of the Aztec Siltstone, because of the shared species of Antarctilamna prisca, Maisevodus sp. cf. M. whitei, and Aztecodus. The presence of Maiseyodus in the much older Cravens Peak Beds limestone member (MAV2, Young 1993) suggests the SBR and Tatong assemblages are likely to be equivalent to the lowermost section of the Aztec Siltstone fauna (MAV 6, Young 1993). The notable absence of thelodonts from the SBR and Tatong assemblages might be due to differing environmental conditions, the latter assemblages being from smaller fluviatile systems than those envisaged for the Aztec Siltstone.

#### Acknowledgments

CJB and ST thank the Board of the Queensland Museum for basic facilities. JAL acknowledges the support of Museum Victoria, the Australian Research Council (DP0558499) and the Flinders University Strategic Professor fund. Dr Gavin Young, ANU, provided helpful

discussion of the topic. We also thank Tim Zeigler, Museum Victoria, for access to collections and support whilst working at Museum Victoria, and the reviewers for their helpful comments.

#### Literature cited

- Burrow, C. J. 2003. Redescription of the gnathostome fish fauna from the Mid-Palaeozoic Silverband Formation, the Grampians, Victoria. Alcheringa, 27: 37–49.
- Burrow, C. J., D. C. Hovestadt, M. Hovestadt-Euler, S. Turner & G. C. Young. 2008. New information on the Devonian shark Mcmurdodus, based on material from western Queensland, Australia. Acta Geologica Polonica, 58: 151–159.
- Burrow, C. J., S. Turner & G. C. Young. 2010. Middle Palaeozoic microvertebrate assemblages and biogeography of East Gondwana (Australasia, Antarctica). Palaeoworld, 19: 37–54.
- Burrow, C. J. & Young, G. C. 2012. New Information on *Culmacanthus* (Acanthodii: Diplacanthiformes) from the ?Early–Middle Devonian of Southeastern Australia. Proceedings of the Linnean Society of New South Wales 134: 21–29.
- Cas, R., G. O'Halloran, J. A. Long & A. Vandenberg. 2003. Middle Devonian to Carboniferous: late to post tectonic sedimentation and magmatism in an arid continental setting. In W. D. Birch (ed.) Geology of Victoria. Geological Society of Victoria, Special Publication, 23: 157–194.
- Chapman, F. 1917. On the occurrence of fish remains and a Lingula in the Grampians, western Victoria. Records of the Geological Society of Victoria, 4: 83–104.
- Clemens, J. D., D. Frei & F. Finger. 2014. A new precise date for the Tolmie Igneous Complex in northeastern Victoria. Australian Journal of Earth Sciences, 61: 951–958. DOI: 10.1080/08120099.2014.955058
- Compston, W. 2004. SIMS U-Pb zircon ages for the Upper Devonian Snobs Creek and Cerberan Volcanics from Victoria, with age uncertainty based on UO2/UO v. UO/U precision. Journal of the Geological Society of London, 161: 223–228.
- Eastman, C. R. 1899. Some new American fossil fishes. Science, 2: 642-643.
- Garrick, J. 1960. Studies on New Zealand Elasmobranchii. Part X. The genus *Echinorhinus*, with an account of a second species, *E. cookei* Pietschmann, 1928, from New Zealand waters. Transactions of the Royal Society of New Zealand, 88: 105–117.
- Garvey, J. M. & S. Turner. 2006. Vertebrate microremains from the presumed earliest Carboniferous of the Mansfield Basin, Victoria. Alcheringa, 30: 43–62. DOI: 10.1080/03115510608619344
- Gess, R. & M. Coates. 2014. High-latitude chondrichthyans from the Late Devonian (Famennian) Witpoort formation of South Africa. Paläontologische Zeitschrift, 89: 147–169. DOI: 10.1007/ s12542-014-0221-9
- Ginter, M. 2002. Chondrichthyan fauna of the Frasnian-Famennian boundary beds in Poland. Acta Palaeontologica Polonica, 47: 329–338.
- Ginter, M. & A. Ivanov. 1992. Devonian phoebodont shark teeth. Acta Palaeontologica Polonica, 37: 55–75.
- Ginter, M. & A. Ivanov. 1995. Middle/Late Devonian phoebodontbased ichthyolith zonation. Géobios, Memoire Special 19: 351–355.

- Ginter, M., J.-C. Liao & J. I. Valezuela-Ríos. 2008. New data on chondrichthyan microremains from the Givetian of the Renanué section in the Aragonian Pyrenees (Spain). Acta Geologica Polonica, 58: 165–172.
- Ginter, M., O. Hampe & C. Duffin. 2010. Chondrichthyes VI. Paleozoic Elasmobranchii. Teeth. – In H.-P. Schultze (ed.) Handbook of Paleoichthyology. 168 pp, Friedrich Pfeil, Munich.
- Hairapetian, V., M. Ginter & M. Yazdi. 2008. Early Frasnian sharks from central Iran. Acta Geologica Polonica, 58: 173–179.
- Hairapetian, V., H. Blom & S. Turner. 2016. Early Frasnian thelodont scales from central Iran and their implications for turiniid taxonomy, systematics and distribution. Journal of Vertebrate Paleontology, 36: e1100632. DOI: 10.1080/02724634.2016. 1100632
- Herman, J., M. Hovestadt-Euler & D. C. Hovestadt. 1987. Herman, J., M. Hovestadt-Euler & D. C. Hovestadt. 1987. Contributions to the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of chondrichthyan fishes. Part A: Selachii. No. 1: Order: Hexanchiformes Family: Hexanchidae. Commissural teeth. M. Stehmann (ed.), Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie, 57: 43–56.
- Herman, J., M. Hovestadt-Euler & D. C. and Hovestadt. 1994. Contributions to the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of chondrichthyan fishes. Part A: Selachii. No. 1: Order: Hexanchiformes Family: Hexanchidae. Odontological results supporting the validity of *Hexanchus vitulus* Springer & Waller, 1969 as a third species of the genus *Hexanchus* Rafinesque, 1810, and suggesting intrafamilial reordering of the Hexanchidae. M. Stehmann (ed.), Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie, 64: 147–163.
- Herman, J., M. Hovestadt-Euler & D. C. Hovestadt. 2003. Contributions to the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of chondrichthyan fishes. Part A: Selachii. Addendum to 1: Order Hexanchiformes-Family Hexachidae, 2: Order Carcharhiniformes, 2a: Family Triakidae, 2b: Family Scyliorhinidae, 2c: Family Carcharhinidae, Hemigaleidae, Leptochariidae, Sphyrnidae, Proscylliidae and Pseudotriakidae, 3: Order Squaliformes: Family Echinorhinidae, Oxynotidae and Squalidae. Tooth vascularization and phylogenetic interpretation. S. Springer & R. Waller (eds.), Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie, 73: 5–26.
- Hills, E. S. 1929. The geology and palaeontology of the Cathedral Range and the Blue Hills, in northwestern Gippsland. Proceedings of the Royal Society of Victoria, 41: 176–201.
- Hills, E. S. 1931. The Upper Devonian fishes of Victoria, Australia, and their bearing on the stratigraphy of the state. Geological Magazine, 68: 206–231.

- Hills, E. S. 1932. The geology of Marysville, Victoria. Geological Magazine. 69: 145–166.
- Hills, E. S. 1936. Records and descriptions of some Australian Devonian fishes. Proceedings of the Royal Society of Victoria, 48: 161–171.
- Hunt, J. R. & G. C. Young. 2011. A new placoderm fish of uncertain affinity from the Early-Middle Devonian Hatchery Creek succession at Wee Jasper, New South Wales. Alcheringa, 35: 53–75. DOI: 10.1080/03115511003793645
- Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly the Mammalia. Proceedings of the Zoological Society of London, 1880: 649–662.
- Janvier, P. 1983. Les vertébrés dévonien de la Nappe Supérieure d'Antalya (Taurus Lycien occidentale, Turquie). Géologie Méditerranéenne, 10: 1–13.
- Long, J. A. 1983a. A new diplacanthoid acanthodian from the Late Devonian of Victoria. Memoirs of the Australasian Association of Palaeontologists, 1: 49–58.
- Long, J. A. 1983b. New bothriolepid fish from the Late Devonian of Victoria, Australia. Palaeontology, 26: 295–320.
- Long, J. A. 1984. New phyllolepids from Victoria and the relationships of the group. Proceedings of the Linnean Society of New South Wales, 107: 263–308.
- Long, J. A. 1989. Phyllolepid placoderm fishes from the Late Devonian of eastern Victoria. Pp. 52–58 in R. Le Maitre (ed.) Pathways in Geology. E. S. Hills Memorial Volume, Blackwell Press, Melbourne.
- Long, J. A. & L. Werdelin. 1986. A new Late Devonian bothriolepid (Placodermi, Antiarchia) from Victoria, with description of other species from the state. Alcheringa, 10: 355–399.
- Long, J. A. & G. C. Young. 1995. New sharks from the Middle-Late Devonian Aztec Siltstone, southern Victoria Land, Antarctica. Records of the Western Australian Museum, 17: 287–308.
- Long, J. A. & K. Trinajstic. 2000. Devonian microvertebrate faunas of Western Australia. Courier Forschungsinstitut Senckenberg, 223: 471–485.
- Long, J. A. & E. B. Daeschler. 2013. First articulated phyllolepid placoderm from North America, with comments on phyllolepid systematics. Proceedings of the Academy of Natural Sciences of Philadelphia, 162: 33–46.
- Miller, R. F., R. Cloutier & S. Turner. 2003. The oldest articulated chondrichthyan from the Early Devonian period. Nature, 425: 501–504.
- Potvin-Leduc, D., R. Cloutier, E. Landing, L. V. Hernick & F. Mannolini. 2015. Givetian (Middle Devonian) sharks from Cairo, New York (USA): evidence of early cosmopolitanism. Acta Palaeontologica Polonica, 60: 183–200.
- Ritchie, A. 1984. A new placoderm, *Placolepis* gen. nov. (Phyllolepidae) from the Late Devonian of New South Wales, Australia. Proceedings of the Linnean Society of New South Wales, 107: 321–353.
- Ritchie, A. 2005. Cowralepis, a new genus of phyllolepid fish (Pisces, Placodermi) from the late Middle Devonian of New South Wales, Australia. Proceedings of the Linnean Society of New South Wales. 125: 215–259.
- Springer, S. & R. A. Waller. 1969. *Hexanchus vitulus*, a new Sixgill Shark from the Bahamas. Bulletin of Marine Science, 19: 159–174
- Stensiö, E. 1948. On the Placodermi of the Upper Devonian of East Greenland. II. Antiarchi: subfamily Bothriolepinae. With an attempt at a revision of the previously described species of that subfamily. Meddelelser on Grønland 139: 1–622.
- Talent, J. A. & D. Spencer-Jones. 1963. The Devono-Carboniferous fauna of the Silverband Formation, Victoria. Proceedings of the Royal Society of Victoria. 76: 1–11.

- Turner, S. 1986. Vertebrate fauana of the Silverband Formation, Grampians, Victoria. Proceedings of the Royal Society of Victoria, 76: 1–11.
- Turner, S. 1993. Palaeozoic microvertebrate biostratigraphy of Eastern Gondwana. In J. A. Long (ed.) Paleozoic Vertebrate Biostratigraphy and Biogeography. Pp. 174–207, Belhaven Press, London.
- Turner, S. 1997a. Sequence of Devonian thelodont scale assemblages in East Gondwana. Geological Society of America Special Publication, 321: 295–315.
- Turner, S. 1997b. Restudy of Late Givetian/early Frasnian "Dittodus" specimens of Hussakof and Bryant 1918 and other American xenacanthid-phoebodont type teeth. Modern Geology, 21: 87–119
- Turner, S. & G. C. Young. 1987. Shark teeth from the Early–Middle Devonian Cravens Peak Beds Georgina Basin. Alcheringa, 11: 233–244.
- Turner, S. & G. C. Young. 1992. Thelodont scales from the Middle– Late Devonian Aztec Siltstone, southern Victoria Land, Antarctica. Antarctic Science, 4: 89–105.
- White, E. I. 1968. Devonian fishes of the Mawson-Mulock area, Victoria Land, Antarctica. Trans-Antarctic Expedition 1955–1958. Scientific Reports, Geology, 16: 1–26.
- Williams, M. E. 1998. A new specimen of *Tamiobatus vetustus* (Chondrichthyes, Ctenacanthoidea) from the Late Devonian Cleveland Shale of Ohio. Journal of Vertebrate Paleontology, 18: 251–260.
- Young, G. C. 1974. Stratigraphic occurrences of some placoderm fishes in the Middle and late Devonian. Newsletters in Stratigraphy, 3: 243–261.
- Young, G. C. 1982. Devonian sharks from southeastern Australia and Antarctica. Palaeontology, 25: 817–843.
- Young G. C. 1988. Antiarchs (placoderm fishes) from the Devonian Aztec Siltstone, southern Victoria Land. Antarctica. Palaeontographica A, 202: 1–125.
- Young, G. C. 1989a. The Aztec fish fauna (Devonian) of Southern Victoria Land: Evolutionary and biogeographic significance. In J. A. Crame (ed.) Origins and Evolution of the Antarctic Biota. Geological Society Special Publication, 47: 43–62.
- Young, G. C. 1989b. New occurrences of culmacanthid acanthodians (Pisces, Devonian) from Antarctica and southeastern Australia. Proceedings of the Linnean Society of New South Wales, 111: 12–25.
- Young, G. C. 1993. Middle Palaeozoic macrovertebrate biostratigraphy of Eastern Gondwana. – Pp. 208–251 in J. A. Long (ed.) Palaeozoic Vertebrate Biostratigraphy and Biogeography. Belhaven Press, London.
- Young, G. C. 2007. Devonian formations, vertebrate faunas and age control on the far south coast of New South Wales and adjacent Victoria. Australian Journal of Earth Sciences, 54: 991–1008.
- Young, G. C. 2010a. Placoderms (Armored Fish): Dominant vertebrates of the Devonian Period. Annual Review of Earth and Planetary Sciences, 38: 523–550. DOI: 10.1146/annurevearth-040809-152507
- Young, G. C. 2010b. Analytical methods in palaeobiogeography, and the role of early vertebrate studies. Palaeoworld, 19: 160–173. DOI: 10.1016/j.palwor.2009.10.001
- Young, G. C. & J. A. Long. 2005. Phyllolepid placoderm fish remains from the Devonian Aztec Siltstone, southern Victoria Land, Antarctica. Antarctic Science, 17: 387–408.
- Young, G. C. & J. M. Moody. 2002. A Middle–Late Devonian fish fauna from the Sierra de Perija, western Venezuela. South America. Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe 5: 155–206.
- Zhao, W.-J. & M. Zhu. 2010. Siluro-Devonian vertebrate biostratigraphy and biogeography of China. Palaeoworld, 19: 4–26. DOI: 10.1016/j.palwor.2009.11.007



John G. Maisey (right) and the publisher visiting Neuschwanstein castle in Bavaria on Nov. 11, 2014

Knowledge of fossil sharks (chondrichthyans) has advanced tremendously over the past decade, giving scientists a window into a historically understudied branch of the evolutionary tree of fishes, and revealing anatomies and ecologies just as diverse and fascinating as those of bony fishes (osteichthyans). This volume assembles cutting-edge research on the biology, anatomy, and evolution of sharks and bony fishes, featuring works by paleobiologists and associated researchers from 11 countries, spanning topics from taxonomy to statistical methodology, in honor of Professor John G. Maisey, for his pioneering work on Paleozoic chondrichthyan anatomy, taxonomy, and paleobiogeography over his half-century career at the American Museum of Natural History. With an introduction and 16 chapters, this volume erects two new families and two new genera, and provides 160 figures and illustrations, and 29 plates, including the most comprehensive collection of high-resolution images of a rare fossil shark held predominantly in private collections.

