

New Information on *Culmacanthus* (Acanthodii: Diplacanthiformes) from the ?Early–Middle Devonian of Southeastern Australia

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A new articulated acanthodian from the Devonian Bunga Beds on the south coast of New South Wales is assigned to *Culmacanthus* sp., and reveals that this diplacanthiform has smooth dental plates on the occlusal surfaces of the lower jaws. Within the Acanthodii, this type of element was first identified in “*Gladiobrachus*” *probaton* from the earliest Devonian MOTH locality, Northwest Territories, Canada, and has now also been identified in “*Euthacanthus*” *curtus* (Lochkovian, Lower Old Red Sandstone, Scotland) and *Diplacanthus* spp. (Givetian, Scotland and Frasnian, Canada). The dental plates in *Culmacanthus* have the same morphology as those of “*Gladiobrachus*” *probaton* and “*Euthacanthus*” *curtus*. Reexamination of type specimens of *Culmacanthus* shows that its pectoral fin spines do not have long insertions, and the purported lack of prepectoral, admedian and prepelvic fin spines could be due to loss of the elements before burial rather than morphological absence.

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INTRODUCTION

Exposures of Devonian sedimentary and igneous rocks along the southern coastline of New South Wales have been recognized since the mid-19th century (Young 2007). Detailed geological mapping by students of the Australian National University Geology Department during the 1970s led to discovery of fossil fish remains at several levels within the sedimentary sequence, including dark shales referred to the ‘Bunga Beds’, which preserve abundant plant remains and rare vertebrates, and have been interpreted as a deep freshwater lake deposit. Fergusson et al. (1979) assigned the Bunga Beds to a ‘Flyschoid facies’ within the Boyd Volcanic Complex, and suggested an age ‘not older than Givetian’ (late Middle Devonian). However, Hall (1959, 1960) had suggested an Early–Middle Devonian age, and recent comparisons of the plants and vertebrates with similar taxa occurring elsewhere also suggest an

older (Eifelian, possibly Emsian) age (Young 2007, Young et al. 2010). Apart from acanthodians, other vertebrates in the Bunga Beds assemblage include the chondrichthyan *Antarctilamna prisca* Young, 1982, remains of a tristichopterid sarcopterygian (including partial skull and jaw remains, many scales, and a cleithrum from the shoulder girdle; see Young 2007:fig. 3a), and a single partly articulated actinopterygian named ?*Howqualepis youngorum* (sic) by Choo (2009). Acanthodians include the probable ischnacanthid described by Burrow (1996), the tail of a large acanthodiform acanthodian, and the diplacanthiform acanthodian described here. The Bunga Beds assemblage is unusual in that placoderm remains have not been found (Young 2007), even though phyllolepid placoderm plates with highly distinctive ridged ornament are well represented at other fossil fish localities (Pambula River) in sedimentary interbeds presumed to be higher (younger) within the Boyd Volcanic Complex (e.g. Young 2005).

A NEW ARTICULATED ACANTHODIAN

Culmacanthus stewarti Long, 1983, the type species of *Culmacanthus*, comes from Late Devonian lacustrine shales at Mt Howitt, Victoria. Two additional species, *C. antarctica* Young, 1989 and *C. pambulensis* Young, 1989 are based on distinctive cheek plates from the Aztec Siltstone, Antarctica, and the Boyd Volcanic Complex (Pambula River), respectively. The Pambula River locality represents another sedimentary facies of the Boyd Volcanic Complex, and is some 60 km to the south of the Bunga Beds locality (Fig. 1). In this paper we describe a newly discovered acanthodian specimen showing distinctive dental elements. The same elements are identified in a previously undescribed specimen of the type species of *Culmacanthus*. We also reinterpret some other features of the type species.

GEOLOGICAL SETTING

The Boyd Volcanic Complex was defined by Fergusson et al. (1979) to include the 'Eden Rhyolite' and 'Lochiel Formation' of earlier authors. Previously the 'Eden Rhyolite' was interpreted as the basal unit of the Devonian sequence, which was unconformably overlain by two Upper Devonian formations, the 'Lochiel Formation' and the 'Merrimbula Formation' (e.g. Brown 1930; Hall 1959, 1960). More detailed mapping indicated a complex interfingering between the intrusive and extrusive silicic rocks and the basalts and associated sediments, and on this evidence the Boyd Volcanic Complex was named, and described in terms of eight facies associations (Fergusson et al. 1979). One of these ('Flyschoid facies') represented the 'dark coloured shales containing abundant *Lepidodendron clarkei*' recorded by Hall (1959:7) in the vicinity of Bunga Head. This sedimentary unit mapped as lying beneath the 'Eden Rhyolite', and the plant fossils establishing a Devonian age for strata that at some localities rest unconformably on folded Ordovician of similar lithology (Powell 1983; Young 2007). The outcrop of sediments and associated volcanics in the Bunga Head area is separated by some 20 km from the main outcrop of the Boyd Volcanic Complex, which extends from Tathra to the south through Pambula and Eden (Fig. 1).

Within this northern outlier, the Bunga Beds (finely bedded carbonaceous dark shales and sandstones) were first described from three separate exposures, with an apparent erosion surface separating them from the overlying volcanics (Hall 1969). The Bunga Beds are best exposed for about 9 km along the coast between Picnic Point and Goalen Head, where they are intruded by the Goalen Head Gabbro.

The northern sedimentary outcrop is the largest, and extends some 3 km inland (Rickard & Love 2000: fig. 1). Student mapping (Bucknell 1969; Scott 1972) established a range of sedimentary lithologies including black shale, siltstone, sandstone and conglomerate. Fergusson et al. (1979:fig. 15) indicated the sequence at Bunga Head to be some 200 m thick, based on the work of Scott (1972), and this thickness was attributed by Lewis et al. (1994) to the basin margin. Cas et al. (1990) illustrated measured sections of stratified volcanoclastic successions less than 40 m in coastal exposures. The published geological map (Lewis et al. 1994) closely follows the student maps of Bucknell (1969) and Scott (1972); the only other published map (Rickard & Love 2000:fig. 1) shows less detail of the sedimentary outcrop. Bucknell (1969) and Scott (1972) both recorded several plant fossil localities, but no fish. Plant fossils may be locally abundant, for example in the gravel quarry (Bunga Pinch Quarry) on the main Tathra–Bermagui Road about 2.5 km north of Lake Wapengo (examples figured by Young 2007:fig. 3d-f). This is about 2.5 km inland from the coastal outcrop on Bunga Beach that has produced, in addition to similar plant remains, the shark, sarcopterygian and actinopterygian fossils documented by Young (1982, 2007), Long and Young (1995) and Choo (2009). About 2.5 km to the north of Bunga Pinch Quarry along the Tathra–Bermagui Road black shales can be exposed in small gravel pits and road cuttings in the vicinity of the intersection with Hergenahs Road (Murrah 1:25 000 Topographic Map 8924-4N, second edition). This is the area that produced the acanthodians described by Burrow (1996), and also the new specimens described here (collected in February, 2008).

The detailed map of Bucknell (1969) suggests that the vicinity of the Hergenahs Road intersection (locality 1, Fig. 1) is at a similar stratigraphic level to the main *Antarctilamna* locality at Bunga Beach (locality 2, Fig. 1), whereas the Bunga Pinch Quarry (locality 3, Fig. 1) may be considerably higher stratigraphically. Bucknell (1969) and Scott (1972) mapped two east-west trending conglomerate bands separated by volcanics which evidently lie stratigraphically beneath the acanthodian fish localities, and showed a general dip of strata to the south-west with dips of up to 35°. Although the sequence is made complex by interbedding of volcanics (Cas et al. 1990), and faulting and folding (but the folds are moderate to gentle; Rickard and Love 2000), the general dip and south-easterly strike indicates that the Bunga Pinch Quarry locality is considerably higher in the sequence than the other fish horizons. Scott's (1972) detailed stratigraphic analysis was confined to the limited

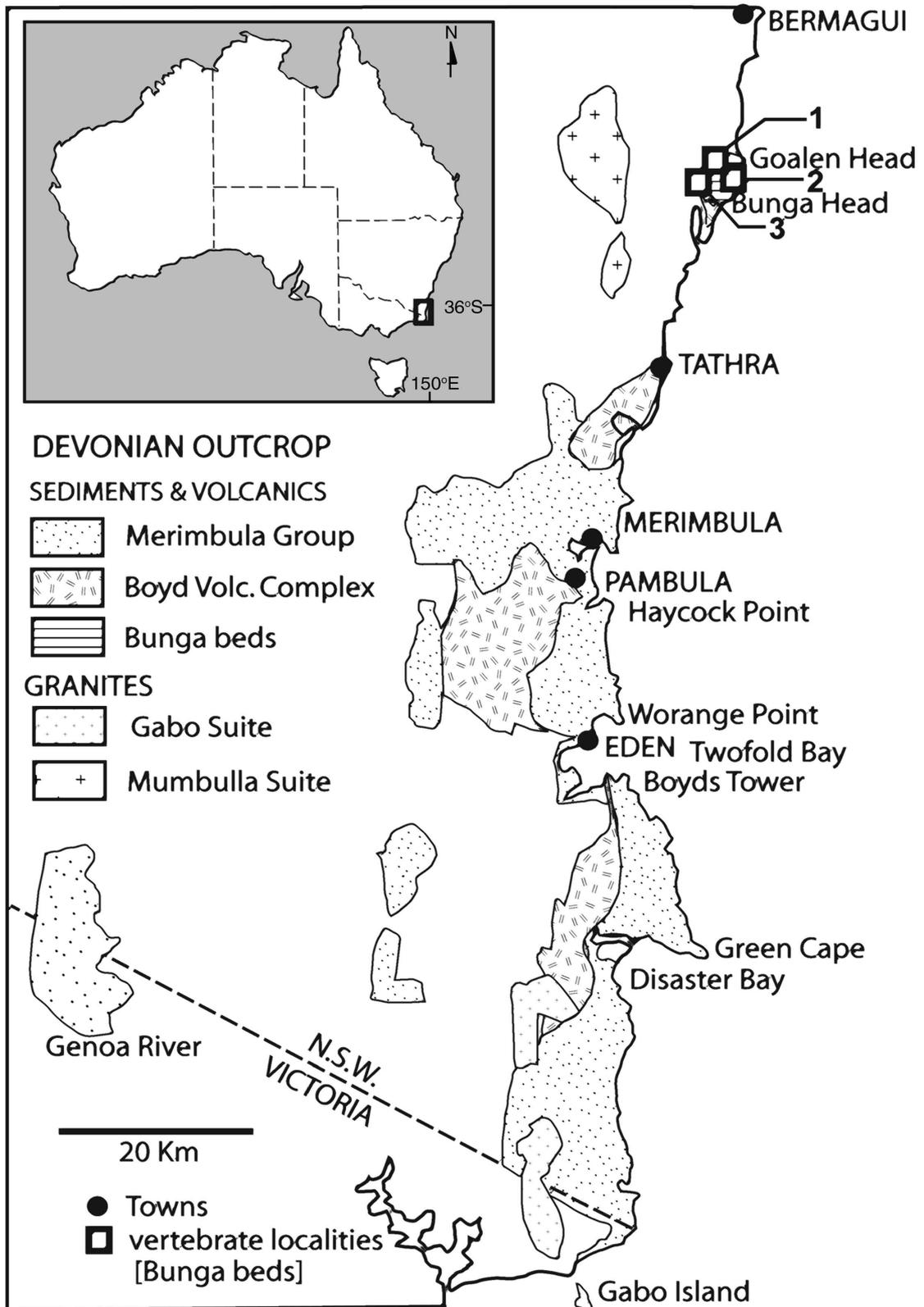


Figure 1. Generalised Devonian geology of the far south coast of New South Wales (after Young 2007), showing the three main fossil fish localities within the Bunga Beds discussed in the text: 1, Hergenhans Road intersection; 2, Bunga Beach; 3, Bunga Pinch Quarry.

A NEW ARTICULATED ACANTHODIAN

sedimentary sequence well exposed on the coast, but Scott (1972:45) also mentioned overlying 'arenites and coarse lutites' more than 450 m thick extending inland, and assuming a general dip of 35° to the SW, without folding or faulting, the Bunga Pinch Quarry locality could be perhaps more than 1 km higher than the other localities. This locality produced the undescribed tail of a large acanthodiform mentioned above. Note that the suggestion (Cas et al. 1990:160) that the fossil fish from the Bunga Beds are most likely marine is unsupported by any evidence.

MATERIALS AND METHODS

Bunga Beds specimens ANU V3374, V3375, 3376, and 3377 were collected in 2008 in a laminated black shale exposed in a road cutting on a road providing access to the beach on the northern side of Goalen Head, south of Bermagui, NSW. *Culmacanthus stewarti* specimen NMV P230281 was collected from Mt Howitt, Victoria by Ian Stewart in the 1990s.

Institutional abbreviations: ANU V, College of Science palaeontological collection, Australian National University; CMN, Canadian Museum of Nature collection; NMS G., National Museums Scotland, geology collection; NMV P, Museum Victoria palaeontological collection; UALVP, University of Alberta vertebrate paleontology collection.

SYSTEMATIC PALAEOLOGY

CLASS ACANTHODII Owen, 1846

ORDER DIPLACANTHIFORMES Berg, 1940

Diagnosis.

See Newman et al. (in press) for a revised diagnosis.

Family Culmacanthidae Long, 1983

Diagnosis

(revised). Diplacanthiform acanthodian lacking prepelvic and admedian spines; paired pinnal plates and anterior loral plate ornamented with flat sinuous narrow ridges; large cheek plate with the same ornament, plus sensory lines, extending from just behind eye almost to scapulocoracoid; two or three anterior circumorbital plates ornamented with spiky tubercles; lower jaws each have a short ossified plate with a high dorsally-directed process near the posterior end; scapulocoracoid tall and slender with a narrow posterior flange; pectoral fin spine not attached to dermal plates; anterior and posterior dorsal fin

spines of equal length, twice the length of the pelvic fin spines and slightly longer than the anal fin spine; scales with strongly convex bases and flat crowns bearing six or seven weak longitudinal ridges.

Remarks.

Absence of admedian spines is assumed based on their absence in all known specimens, but this could result from disarticulation and/or loss of the pectoral spines, as discussed below.

Genus *Culmacanthus* Long, 1983

Diagnosis.

As for the family.

Type species.

Culmacanthus stewarti Long, 1983.

Culmacanthus sp.

Description.

ANU V3376a, b (Fig. 2a, 2b) comprises an articulated fish, poorly preserved in part and counterpart. Most fine detail and nearly all of the hard parts are weathered away, and the fish is mainly preserved as impressions of each side, but with the head dorsoventrally compressed. No details of the squamation are preserved, except its extent. The 25 mm-long anterior and posterior dorsal fin spines and the 17 mm-long anal fin spine are in situ; two shorter, displaced fin spines preserved between the anal and anterior dorsal spines are interpreted as the pelvic fin spines. The insertion on the anterior dorsal fin spine (Fig. 2e) is one-third of total spine length, and is ornamented with fine parallel ridges. The exerted two-thirds has about seven parallel longitudinal dentine ridges per side. These ridges are very narrow near the trailing edge and wider towards the leading edge. No other spines are distinguishable. One scapulocoracoid lies horizontally behind the head region and the other is preserved as a worn impression, vertically oriented above the head. These elements are c. 10 mm high, with tall straight slender shafts, and a short flared base. On the counterpart, two plates overlies the base of the scapulocoracoid preserved above the head (Fig. 2c, 2d). As this scapulocoracoid has been displaced, it is not clear if it is preserved under or on top of the head. No ornament is visible on the two plates, but their shape is comparable with that of the median loral plus a pinnal plate of *Culmacanthus stewarti* (Long 1983:fig. 2A). The lack of ornament suggests that the internal surfaces are exposed, indicating that the dorsal side of the head is uppermost. At

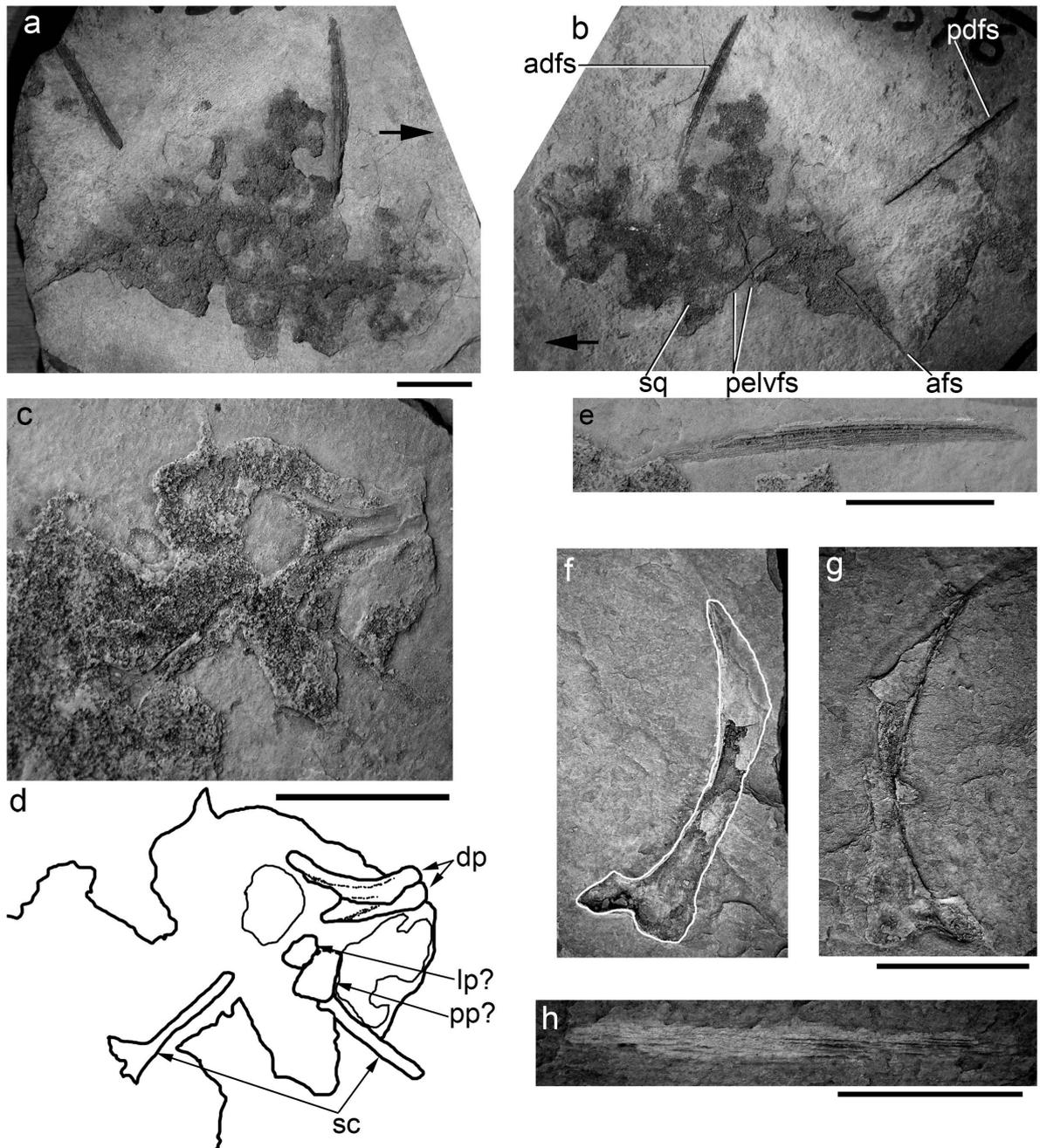


Figure 2. *Culmacanthus* sp. from the Bunga Beds, southern coast New South Wales. a-c. articulated fish ANU V3376. a, part. b, counterpart. c, closeup of head region of counterpart (specimen rotated 180° to right). d, diagrammatic sketch of c. e, anterior dorsal fin spine on counterpart. f, g, isolated scapulocoracoid ANU V3374, two sides b and a. h, isolated fin spine, ANU V3377. adfs, anterior dorsal fin spine; afs, anal fin spine; dp, dental plates; lp, lorical plate; pdfs, posterior dorsal fin spine; pelvfs, pelvic fin spine; pp, pinnal plate; sc, scapulocoracoid. Scale bar is 1 cm.

the anteriormost end of the counterpart (Fig. 2c, 2d) are impressions of two curved spathiform jaw ossifications, each about 7 mm long. A smooth oval area forming a gap in the squamation behind the jaws on the counterpart possibly represents the area where

one of the dermal cheek plates has detached. No pectoral or associated fin spines are present, nor are any details of the squamation discernible.

The isolated scapulocoracoid ANU V3374 (Fig. 2f, 2g) is 26 mm high, with a short base and high

A NEW ARTICULATED ACANTHODIAN

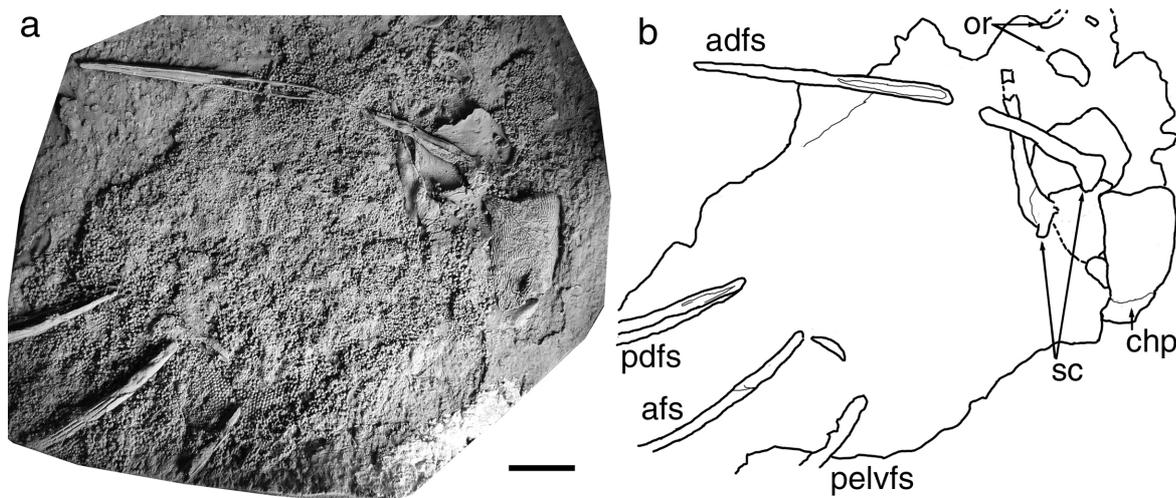


Figure 3. a, b. Cast of *Culmacanthus stewarti* NMV P230281 (part) from the Givetian of Mt Howitt, central Victoria. a, latex of specimen whitened with ammonium chloride sublimate; b, diagrammatic sketch of specimen. adfs, anterior dorsal fin spine; afs, anal fin spine; chp, ornamented cheek plate; or, sclerotic or circumorbital plates; fw, fin web; pdfs, posterior dorsal fin spine; pelvfs, pelvic fin spine; sc, scapulocoracoid; sq, squamation. Scale bar is 1 cm.

curved shaft. The element is exposed in transverse section, showing an anteroposterior oriented ventral groove for articulation with the pectoral fin spine. The element is much larger than the scapulocoracoid on the articulated *Culmacanthus* sp. from Bunga Beds, but is a similar size to those on the type specimens of *C. stewarti* from Mt Howitt, which also have a ventral groove for the pectoral spine articulation (Long 1983: fig. 6).

Isolated fin spine ANU V3377 (Fig. 2h) is a poorly preserved straight spine, 26 mm long, with longitudinal ridges comparable to those on the articulated *Culmacanthus* sp. It is tentatively assigned to this taxon. Remnants of a similar spine are preserved near the scapulocoracoid on ANU V3374.

DISCUSSION

The general dimensions, and number, size and orientation of the fin spines on ANU V3376 compare closely with *Culmacanthus stewarti* specimen NMV P230281 (Fig. 3) from Mt Howitt. In the original description of *Culmacanthus*, Long (1983:figs. 3A, 4D) labelled several fin spines as pectorals, but on reexamination we interpret these as anterior dorsal fin spines. We suggest that the specimen in his figure 3A preserves the right side with the anterior dorsal fin spine, rather than the left side with the pectoral fin spine (to view the specimen with dorsal side uppermost, the image should be rotated 180°). In

his figure 4D, the fin spine on the left is the pectoral, and the one on the right is the anterior dorsal, with the main lateral line visible running through the squamation between the two spines. In this interpretation, none of the original specimens show the pectoral region preserved intact; the pectoral fin spines have been disarticulated and lost in all of the most complete specimens. Based on reinterpretation of the spine with a long insertion as a dorsal fin spine, pectoral fin spines in *Culmacanthus*, like those in all other acanthodians, lack a deep insertion (contra Long 1983). Even on NMV P160709 (Fig. 4a), which shows the dermal pectoral plates articulated together and the disarticulated scapulocoracoids, the pectoral fin spines are missing. The possibility that *Culmacanthus* had prepectoral and/or admedian spines cannot thus be discounted, as they would likely have been dislocated when the pectoral fin spines were lost. The lack of pectoral fin spines on ANU V3376 is consistent with its assignment to *Culmacanthus*, by comparison with the loss of these spines in known specimens of *C. stewarti* (assuming the fish actually had pectoral fin spines!). Although ANU V3376 is poorly preserved, the impression on the counterpart of the insertion area on the anterior dorsal fin spine (Fig. 2e) shows the fine parallel ridges characteristic of diplacanthiform acanthodians (Burrow 2007:835). This spine also shows that the exerted ridges near the trailing edge are markedly narrower than the ridges towards the leading edge, unlike the equal-width ridges on *C. stewarti* fin spines. The isolated

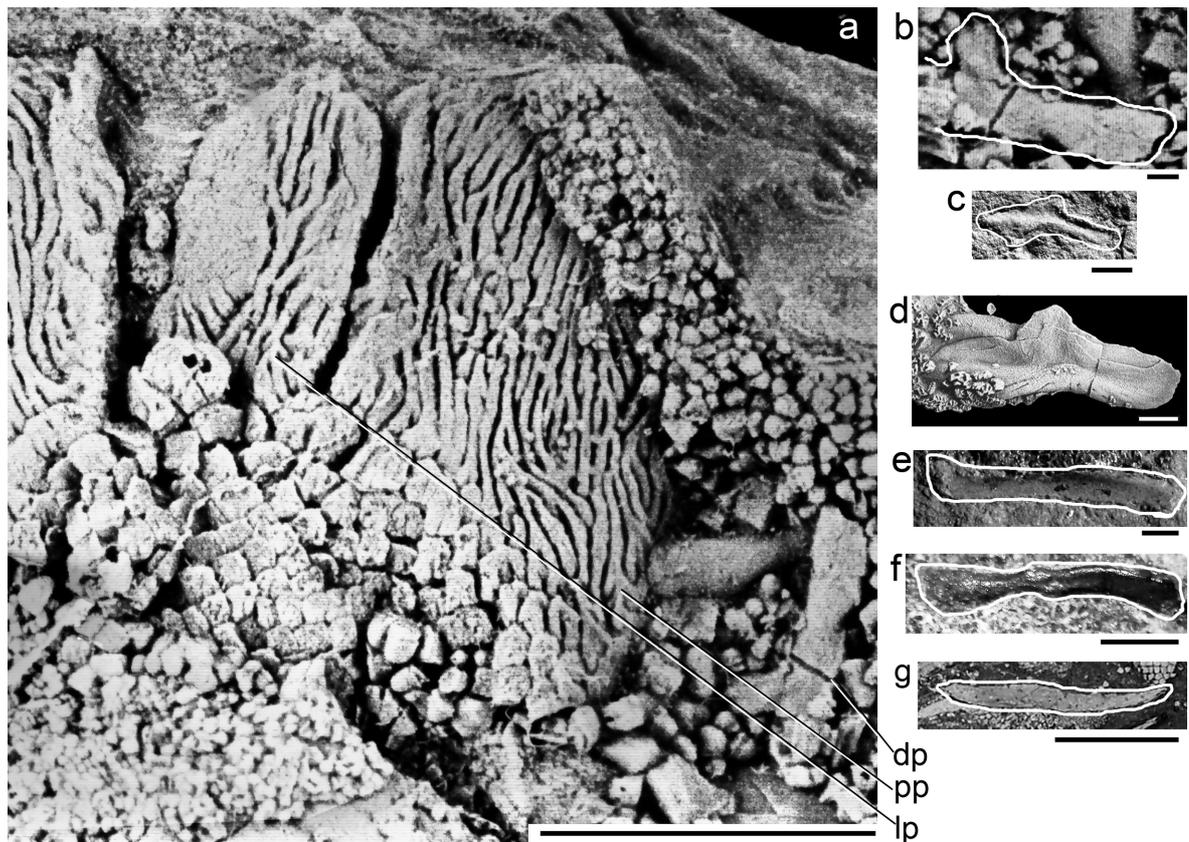


Figure 4. Lower jaw dental plates in diplacanthiform acanthodians. a, b. *Culmacanthus stewarti* NMV P160709 from the Givetian of Mt Howitt, central Victoria: a, ventral surface; b, cast of ?external surface of right dental plate. c, *Uraniacanthus curtus* NMS G.1891.92.250 from the Lochkovian of Tillywhandland Quarry, Scotland; right plate. d, *Uraniacanthus probaton* UALVP42095 from the Lochkovian MOTH locality, Northwest Territories, Canada; image flipped from Hanke & Davis 2008, figure 9D. e, *Diplacanthus longispinus* NMS G.1891.92.338 from the ?Eifelian of Gamrie, Scotland; external impression of right plate, image flipped horizontally. f, *Diplacanthus horridus* CMN 8570 from the Frasnian Escuminac Formation, Miguasha, Canada; occlusal/external surface of right plate, image flipped horizontally. g, *Milesacanthus antarctica* ANU V773, fish 1; lateral view of left plate, image flipped horizontally. cp, coronoid process; lp, lorical plate; pp, pinnal plate. Scale bar is 1 cm in a, g, 1 mm in b-f.

spine ANU V3377 (Fig. 2g) shows parallel ridges on the exerted part, but it is not possible to determine the variation in ridge width. This spine has only a short insertion, so could possibly be a pectoral fin spine; its size and type of ornament support its assignment to *Culmacanthus* rather than the unnamed ischnacanthid described by Burrow (1996), the only other acanthodian known from the Bunga Beds with spines preserved. The scapulocoracoids on ANU V3376 are of comparable dimensions to those of *C. stewarti*, with a narrow posterior flange on the scapula shaft and only a short low ventral expansion. The isolated scapulocoracoid ANU V3374 (Fig. 2h) differs from known *Culmacanthus* scapulocoracoids in having a curved rather than a straight shaft, but this could result from the structure on other specimens

being preserved in lateral or medial view, rather than anterior/posterior, with the curve of the element in the latter type of preservation matching the curve of the body.

The mouth region was not described in any of the type specimens of *C. stewarti*, however we have observed a short spathiform bone with a marked process perpendicular to the long axis, on examination of the cast of the ventral surface on NMV P160709 (Long 1983:fig. 2A; Fig. 4a, 4b). Recent work on Early Devonian diplacanthiforms from Canada and Britain has shown that *Uraniacanthus probaton* (Bernacsek & Dineley, 1977), previously *Gladiobranchus probaton*, and *Uraniacanthus curtus* (Powrie, 1870), previously *Euthacanthus curtus*, have ossified spathiform lower jaws of a comparable shape to this bone, also with

A NEW ARTICULATED ACANTHODIAN

a dorsally-directed process (Hanke and Davis 2008; Newman et al. in press; Fig. 4c, 4d). Hanke and Davis (2008) described the latter as a “coronoid” process; there is no evidence that this process is homologous to the structure of the same name in other gnathostome groups. Elements previously identified as mandibular bones in *Diplacanthus* spp. and *Milesacanthus antarctica* Young and Burrow, 2004 have been recharacterized as occlusal ossifications of the lower jaws, rather than bones supporting the ventral edge of the jaw cartilages (Newman et al. in press; Figure 3e-3g). Thus, all the elements previously described as mandibular bones or splints in diplacanthiforms have been reinterpreted as ossifications of the whole lower jaw, or of their occlusal surface. *Tetanopsyrus* spp. from the Lochkovian MOTH locality in Canada differ from other diplacanthiform taxa in having upper jaw ossifications as well (Hanke et al. 2001).

All determinable characters on ANU V3376 – inferred body shape and size; position, structure and relative dimensions of fin spines; scapulocoracoid shape; spathiform Meckel’s cartilage ossifications; probable pectoral plate shapes – support assigning the specimen to *Culmacanthus* rather than any other acanthodian genus. Although the highly distinctive cheek plates that characterize *Culmacanthus* have not been preserved on the specimen, there is a gap in squamation on the cheek region where such a plate would be positioned, suggesting that they were lost before burial of the fish. Such a loss is consistent with *C. pambulensis* and *C. antarctica* being known only from isolated plates. Unlike acanthodian scales, which have Sharpey’s fibres fixing the scale bases in the skin, the smooth inner surface of dermal plates of *Culmacanthus* lack evidence of fibrous attachment to the dermis and could thus be more easily detached from the carcass.

Because *C. pambulensis* is only known from isolated cheek plates, and the cheek plates have not been preserved on ANU V3376, it is not possible to assign this specimen to species level. The lower jaw ossifications of *Culmacanthus*, with their “coronoid” process, resemble those of the earliest Devonian (Lochkovian) genus *Uraniacanthus* from Britain and Canada rather than the simpler occlusal ossifications of the younger diplacanthiforms *Milesacanthus antarctica* from Antarctica and *Diplacanthus* spp. from Britain and Canada.

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