

An articulated teleostome fish from the Late Silurian (Ludlow) of Victoria, Australia

Carole J. Burrow¹ and Gavin C. Young²

¹Department of Zoology, University of Queensland, St Lucia, Qld 4072;
email: CBurrow@zoology.uq.edu.au

²Department of Geology, The Australian National University, Canberra, ACT 0200

Abstract – The oldest articulated teleostome (?acanthodian) fish yet found in Australia, *Yealepis douglasi* gen. et sp. nov., is described from Yea in central Victoria. The specimen was associated with the Lower *Baragwanathia* Plant Assemblage in the Late Silurian (Ludlow) Yea Formation. The middle part of the body squamation is well preserved in part and counterpart, showing pectoral, pelvic and anal fins. The normal body scales are square-crowned, 0.8 to 1.5 mm wide, with a base wider than the crown. The crown bears short radial ridges along the anterior margin, and several vertical and/or radial ridges along the posterolateral sides. The only overlapping scales are the small, elongated scales near the distal margins of the fin webs. Dermal shoulder girdle plates, and fin and intermediate spines, are absent. The non-caudal fin webs do not bear the spines along the leading edges which are diagnostic for acanthodian fishes. This new genus is assigned to the Teleostomi, and provisionally to the Acanthodii, based on the type of scale and squamation pattern. Order and family are indeterminate, as it also lacks diagnostic characters for the recognized acanthodian orders. Alternatively, the new genus could represent a stem-group teleostome.

INTRODUCTION

Articulated acanthodian fish are generally rare in the fossil record, although acanthodian micro-remains are the most common vertebrate fossils in many Late Silurian-Early Devonian limestones in Australia (e.g. Turner 1991, 1993; Burrow 1995, 1997; Burrow and Simpson 1995). The oldest Australian articulated acanthodians described are from two sites of approximately similar age. The lacustrine middle-late Givetian Mt Howitt deposits in central Victoria have yielded two genera of acanthodians, the culmacanthid *Culmacanthus stewarti* (Long 1983) and the acanthodiform *Howittacanthus kentoni* (Long 1986). The lacustrine Bunga Beds (late Givetian/early Frasnian) on the southern coast of New South Wales (Young, in Fergusson *et al.* 1979) have also produced a few articulated acanthodians (Burrow 1996). All other Australian vertebrates previously recorded from Silurian deposits occur as micro-remains (Burrow and Simpson 1995; Burrow and Turner in press; Turner 1993).

The new specimen described below was collected from Limestone Road, south-east of Yea (Figure 1), by palaeobotanist Dr Jack Douglas during a field excursion to Heathcote, Yea and Kinglake West (Garratt *et al.* 1983). Thin laminated mudstones

exposed at this site contain the Lower Plant Assemblage of the *Baragwanathia* beds, and are assigned to the Yea Formation. The beds have been interpreted as a relatively deep water deposit, based on the occurrence of a *Nereites* ichnofauna. The pelagic shales and mudstones are interbedded with thick to medium-bedded sandstones (interpreted as turbidites) (Garratt *et al.* 1983). Flora and fauna recorded from the assemblage include the lycopod *Baragwanathia longifolia*, graptolites *Monograptus* sp. cf. *M. uncinatus uncinatus* and *Bohemograptus bohemicus*, brachiopods, bivalves, hyolithids and orthocerids (Garratt *et al.* 1983; Rickards and Garratt 1990). The *Baragwanathia* flora is the oldest known land plant assemblage. Until 1979, the Limestone Road site was a 50 m long, 4-5 m deep cutting. Unfortunately the exposure was razed to road level before it could be mapped and excavated. The fish specimen was found on a bedding plane at the edge of a small exposure which was subsequently excavated for the 1983 field party. One of us (G.C.Y.) was a participant of this excursion, and identified the specimen as part of an articulated acanthodian fish. However, a detailed search of surrounding rock rubble failed to locate missing parts of the specimen. The site has since been listed in the Register of the National Estate. The specimen is in the collections

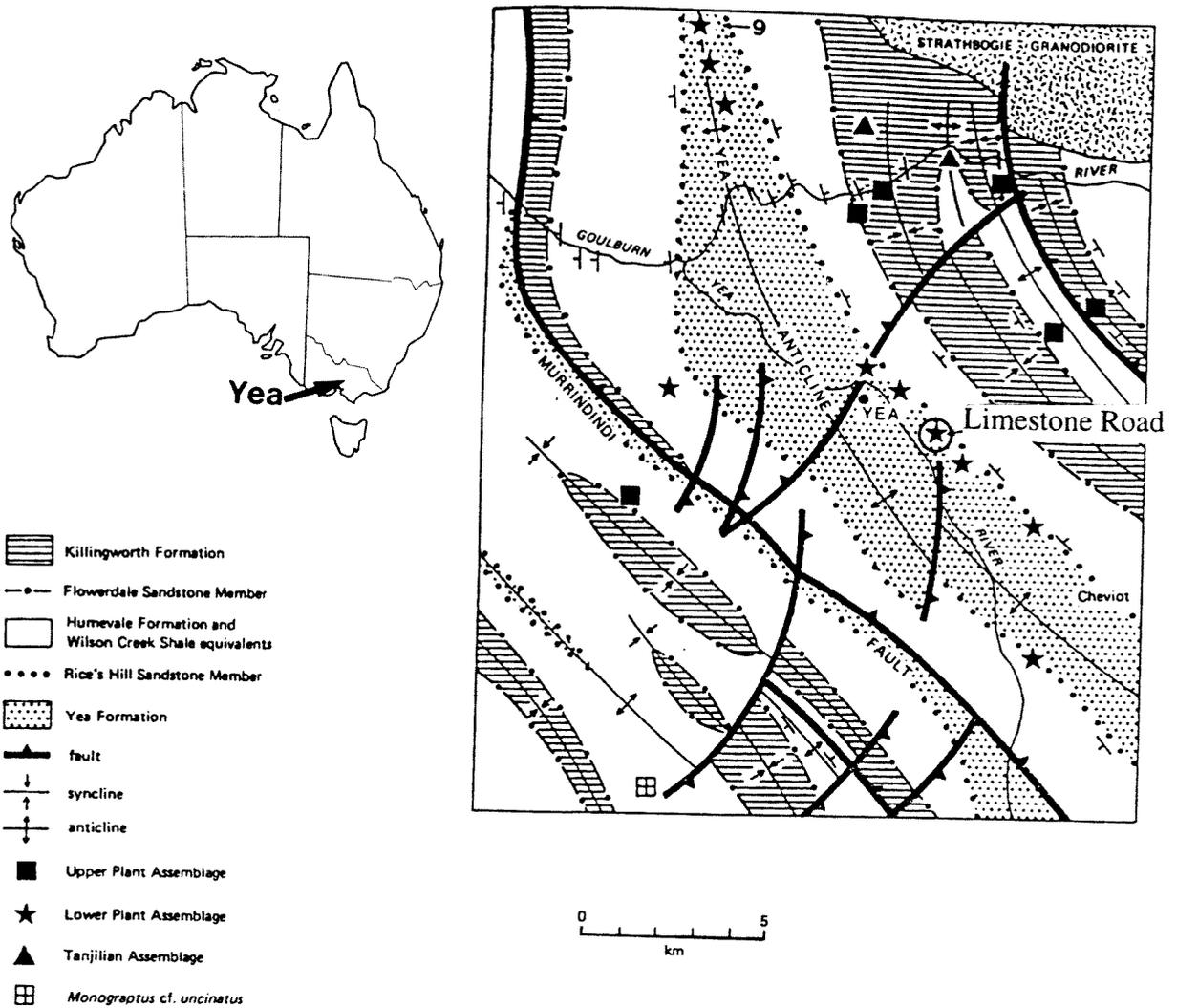


Figure 1 Locality map (after Garratt *et al.* 1983). Circled star represents the Limestone Road fish locality.

of the Geology Department, Australian National University, Canberra (prefix ANU V). Other abbreviations used: IVPP = Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; MMC = collection of the Geological Survey of New South Wales, Sydney.

SYSTEMATIC PALAEOLOGY

Superclass Teleostomi Huxley, 1861

Class Acanthodii Owen, 1846

Class Acanthodii?

Remarks

Details of the squamation and scale morphology, as far as preserved, are consistent with acanthodian affinity, so this specimen is

provisionally referred to the Acanthodii. However, fin spines, a diagnostic feature of this group, were apparently absent. Inclusion within the Teleostomi, either as currently defined to include acanthodians and osteichthyans (e.g. Janvier 1996), or enlarged to accommodate this new taxon as a stem-group teleostome, seems probable. The higher level relationships of the new taxon are considered more fully in the Discussion.

Order and Family indet.

Yealepis gen. nov.

Figures 2–7, 9

tail of an indeterminate acanthodian: Young 1993: 219

partial articulated acanthodian: Burrow and Young 1997: 16

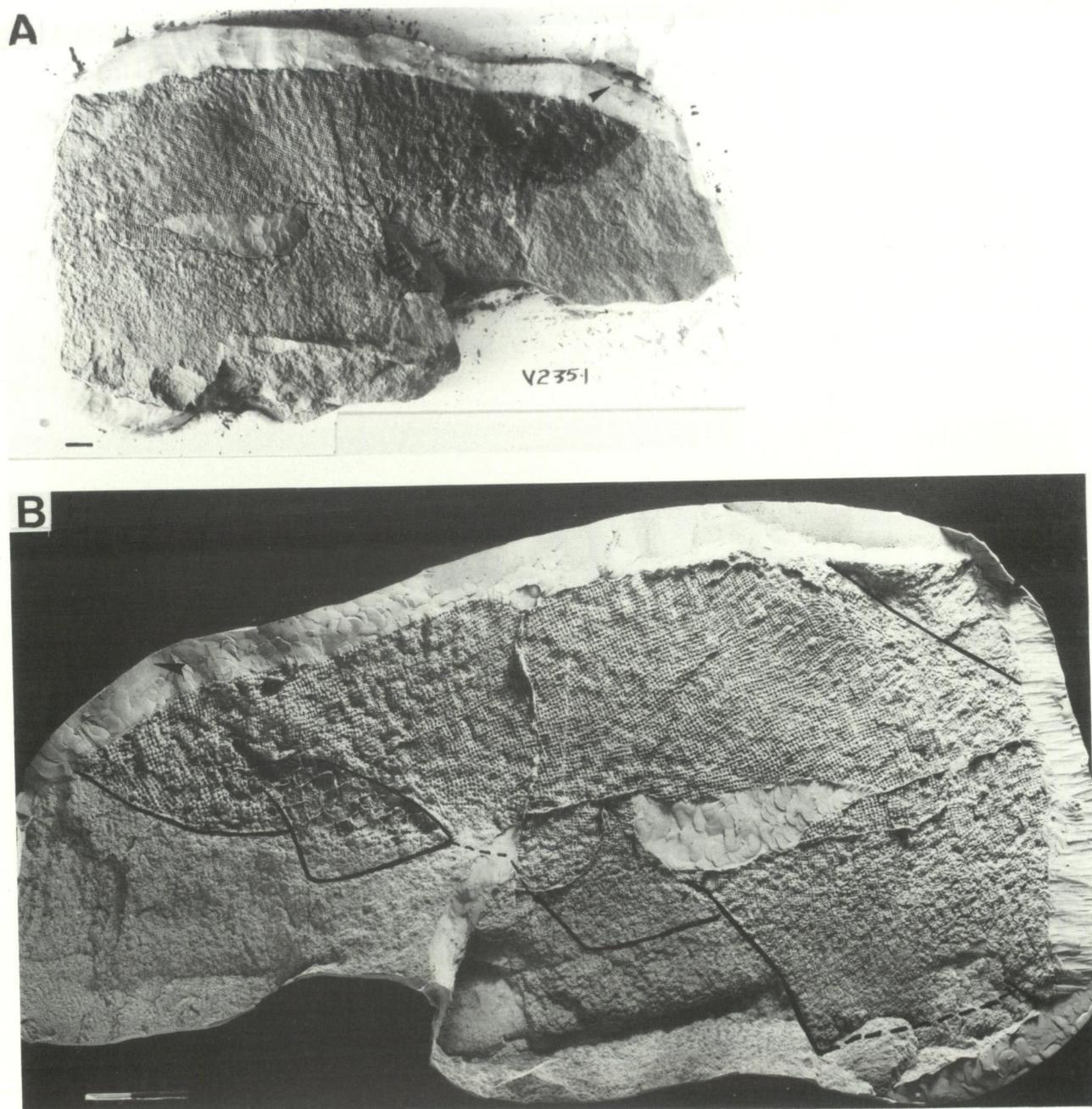


Figure 2 *Yealepis douglasi* gen. et sp. nov. from Yea, Victoria. Holotype and only known specimen, ANU V2351, preserved in part and counterpart. A, specimen (part). B, latex cast of part, whitened with ammonium chloride, with outline of fish added. Scale bars = 1 cm. Arrows point rostrally.

Type Species

Yealepis douglasi sp. nov.

Diagnosis

A moderately deep-bodied fish lacking pectoral and pre-pectoral dermal plates and fin spines; pectoral fin web with scale rows radiating from narrow base of fin; large fin webs on pelvic and anal fins, with scale rows perpendicular to the long body axis; flank scales non-overlapping, from 0.8 to 1.5 mm wide, with a low crown ornamented with four to seven short, radial ridges along the anterior

margin of the upper crown surface, and radial and/or vertical ridges rising from the posterolateral sides of the scale neck towards the posterior crown point; fin web scales with elongated crown drawn out to a posterior point extending beyond the base; scales with 'box-in-box' growth zones.

Etymology

From the Yea shire, where the specimen was collected; and for Dr Jack Douglas, palaeobotanist, who collected the specimen, in recognition of his work on fossils of the *Baragwanathia* beds.

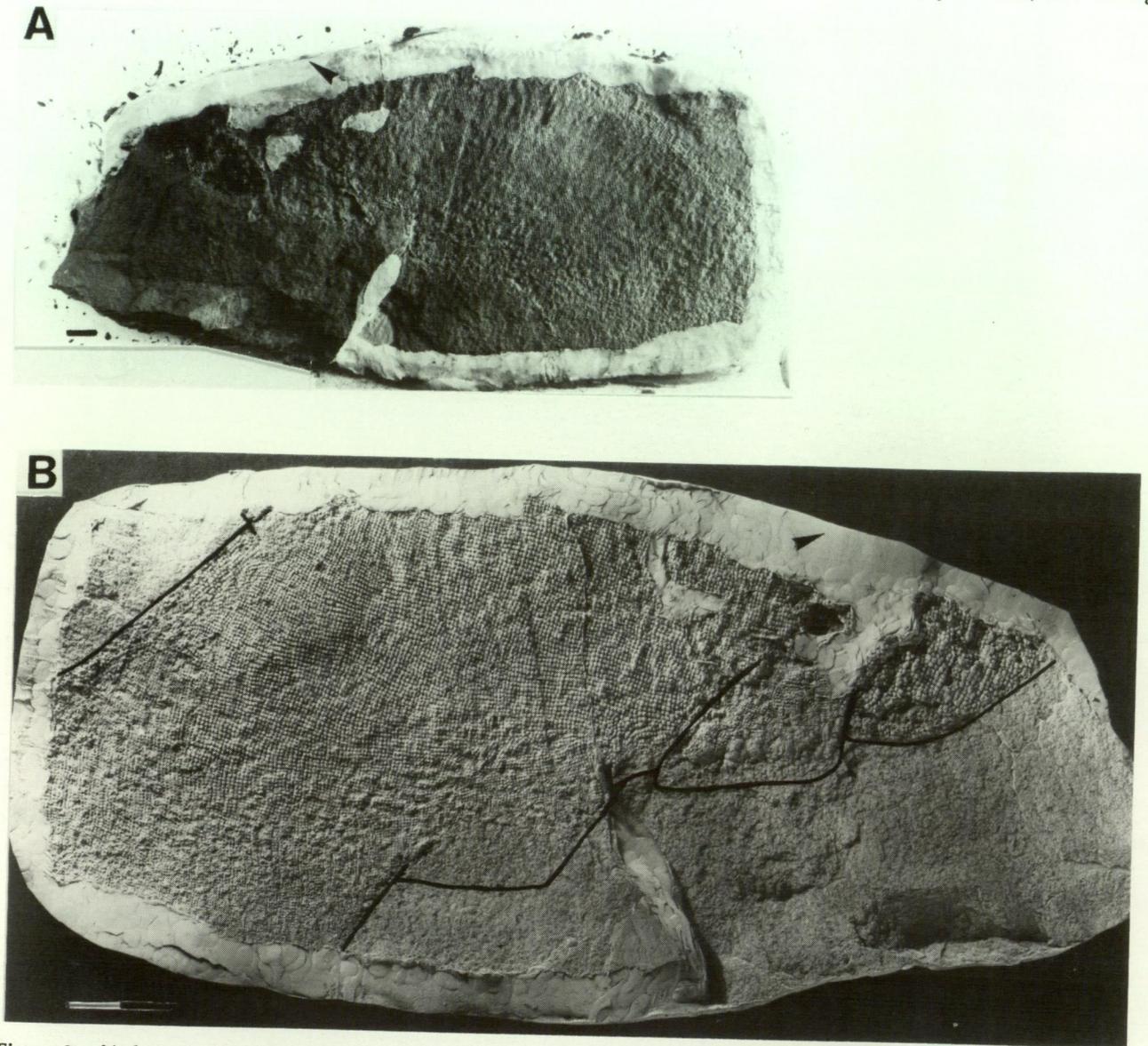


Figure 3 *Yealepis douglasi* gen. et sp. nov. from Yea, Victoria. Holotype and only known specimen, ANU V2351, preserved in part and counterpart. A, specimen (counterpart of Figure 2A). B, latex cast of counterpart, whitened with ammonium chloride, with outline of fish added. Scale bars = 1 cm. Arrows point rostrally.

Yealepis douglasi sp. nov.

Material Examined

Holotype ANU V2351, mid-body section preserved as part and counterpart, in lateral aspect (Figures 2, 3); only specimen.

Type Locality

Limestone Road road-cutting (Figure 1), which is locality 4 of Garratt (1978), near Yea, Victoria, Australia, in the Yea Formation, Late Silurian (Ludlow).

Diagnosis

As for genus, only species.

Description

The specimen is preserved in part (Figure 2A,B)

and counterpart (Figure 3A,B). The part has most of the squamation of both sides squashed together, with the right side of the fish exposed. Most of the scales, however, lack the upper crown layers, which are stuck on the counterpart. The latter then is mostly the impression of the squamation of the right side, though with the upper part of the scale crowns in the impressions, and only rare patches of the actual squamation. Only the middle section of the fish is preserved; the broken edges of the rock cut across the fish from anterior of the pectoral fin diagonally back to behind the posterior dorsal fin, and across the tail of the fish approximately at the level of the caudal peduncle. Thus the specimen shows the squamation from approximately 50 mm in front of the pectoral fin to the posterior end of the anal fin web ventrally; dorsally, only a short segment is preserved behind the posterior dorsal

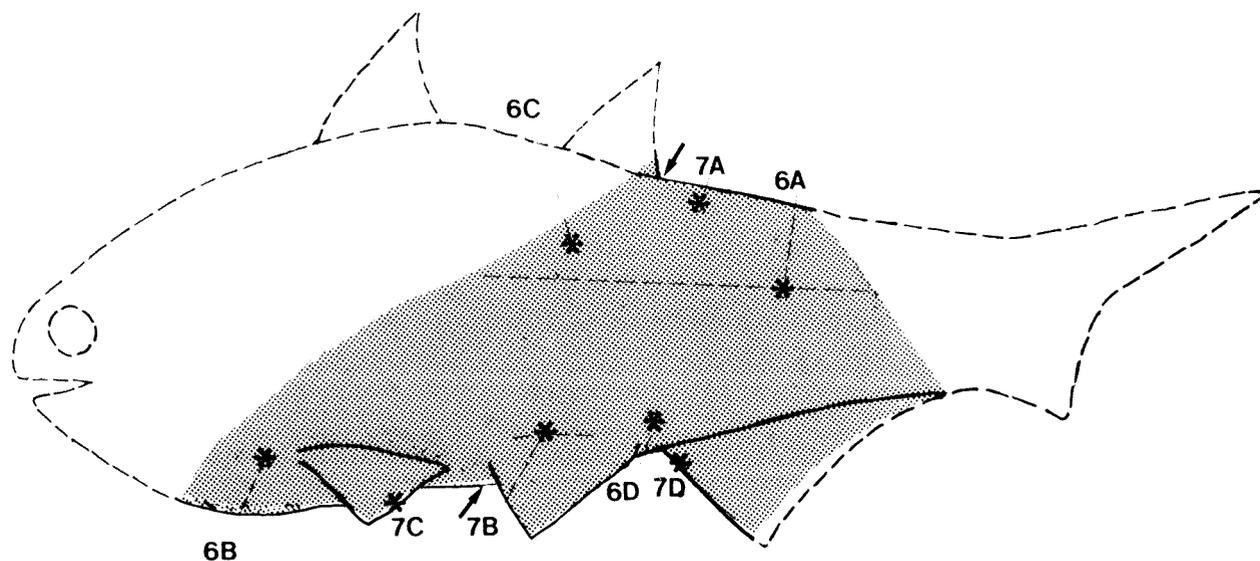


Figure 4 Hypothetical reconstruction of *Yealepis douglasi* gen. et sp. nov., with preserved portion stippled. Asterisks mark positions on the specimen for which close-ups of squamation are figured (figure numbers indicated). Scale count between arrows = 120.

fin web. Although less than half the fish is preserved, extrapolation of the known dimensions suggest that it was relatively deep-bodied. Reconstructed body length is estimated at about 400 mm, and greatest depth about 120 mm at the level of the pectoral fins (Figure 4). The distances from the leading edge of the pectoral fin to the leading edge of the pelvic fin is about 70 mm, with the same distance from the leading edge of the pelvic fin to the leading edge of the anal fin.

Fin spines are not preserved, despite the near-perfect articulation of the fin web scales and lack of disruption of the squamation at the base of the fin, and are assumed to have been absent. The pectoral fin inserts approximately 12 scales (or 15 mm) up from the ventral margin, and is preserved with the inner, or ventral, surface exposed. Scale rows on the fin web radiate out from the relatively narrow fin base (Figures 4, 5A,B). There is no indication of dermal shoulder girdle or pre-pectoral plates, as the normal squamation forms a complete cover in the area preserved in front of the pectoral fin. A bituminized lump in front of and above the pectoral fin, enclosed by the squamation of each side, could be the remains of the scapulocoracoid, but its exact shape is indeterminable. On the pelvic and anal fin webs, the scale rows run perpendicular to the long body axis (Figure 2A,B).

The scales are not well preserved, with little internal structure retained, and in the splitting of the slab the upper layer of the scale crowns had detached from the bases. The exposed natural sections through mid-crown of some of these broken scales show the 'box-in-box' internal structure typical of acanthodian scales (Figure 8F).

Scale morphology is only discernible by cleaning and studying the scale impressions. Scales decrease in size towards the tail, and dorsally and ventrally away from the mid-flank (Figure 2A). As only a short dorsal section of the fish is preserved, the anteriormost area enabling a scale count for an entire diagonal row is from the hind end of the posterior dorsal fin web down to the leading edge of the pelvic fin, which gives a scale count of approximately 120. Seven rows of scales run parallel to the mid-dorsal line behind the posterior dorsal fin (Figures 2A,B, 7A).

The lateral line is not clearly distinguishable, as it is not lined with specialized scales. It is possibly discernible as a faint ridge, and by a slight change in direction of the diagonal scale rows on either side (Figures 4, 6A). A possible ventrolateral line is vaguely distinguishable above the pelvic fin, with rows of scales meeting at a slightly oblique angle (Figures 2A, 7B).

Most of the body scales are square crowned, from 0.8 to 1.5 mm wide, with short, radially-directed ridges along the anterior crown margin (Figure 6B-E). The crown is smaller than the base, and thus most of the normal body scales have no overlap or imbrication with neighbouring scales. Vertical and/or diagonal ridges ornament the posterolateral sides of the crown below the upper crown surface (Figure 6D,E). The degree to which these lateral crown ridges are developed appears to depend on the location of the scale on the body. Scales on the mid-body, above mid-flank, have crowns with strongly developed side ridges, extending the length of the crown (Figure 6C). Scales in the rows parallel to the mid-dorsal line behind the dorsal fin (Figure 7A)

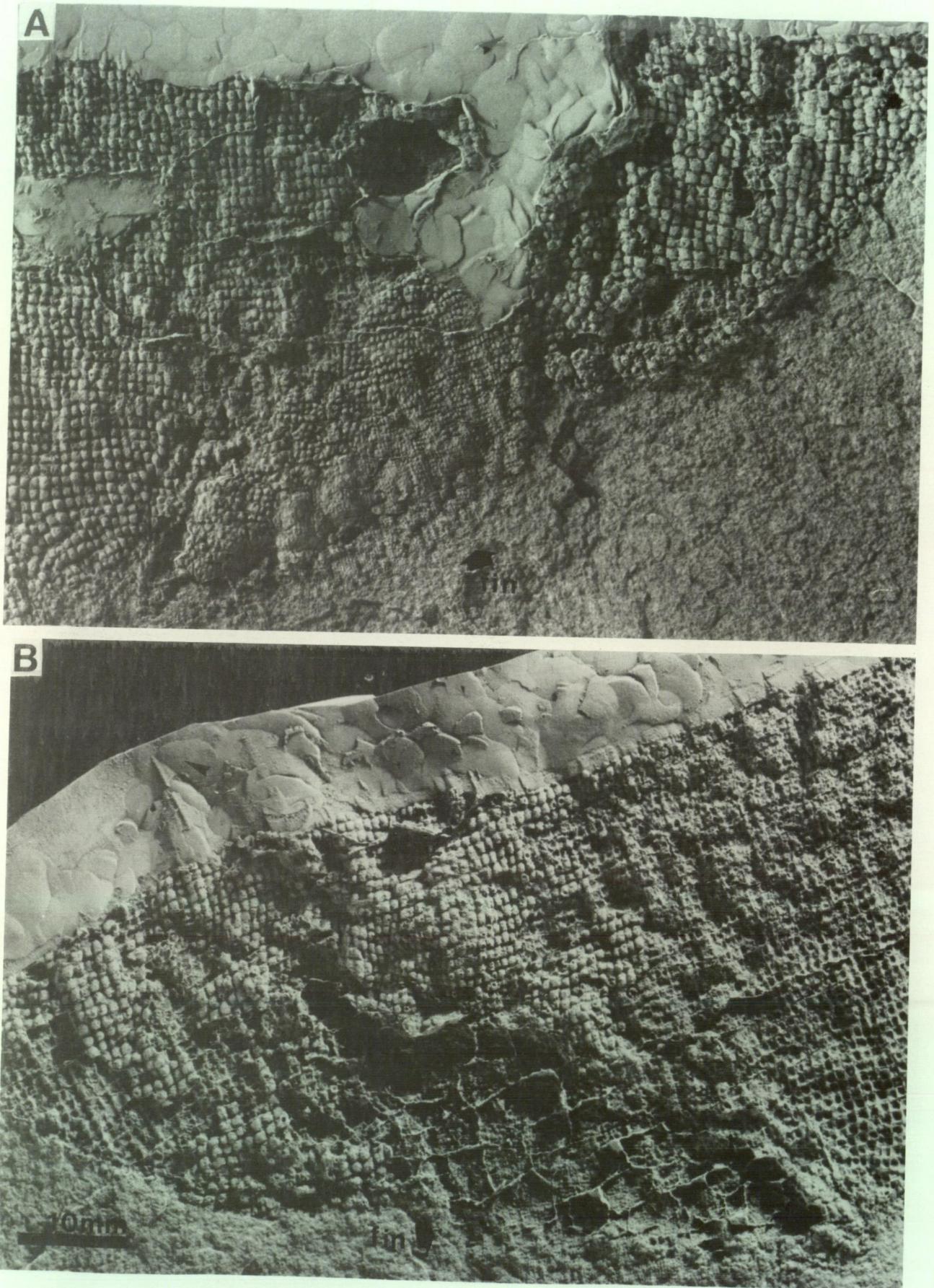


Figure 5 *Yealepis douglasi* gen. et sp. nov. Holotype, ANU V2351. A, pectoral fin on cast of counterpart. B, pectoral fin on cast of part. Both to the same scale – see 10 mm scale bar on B.

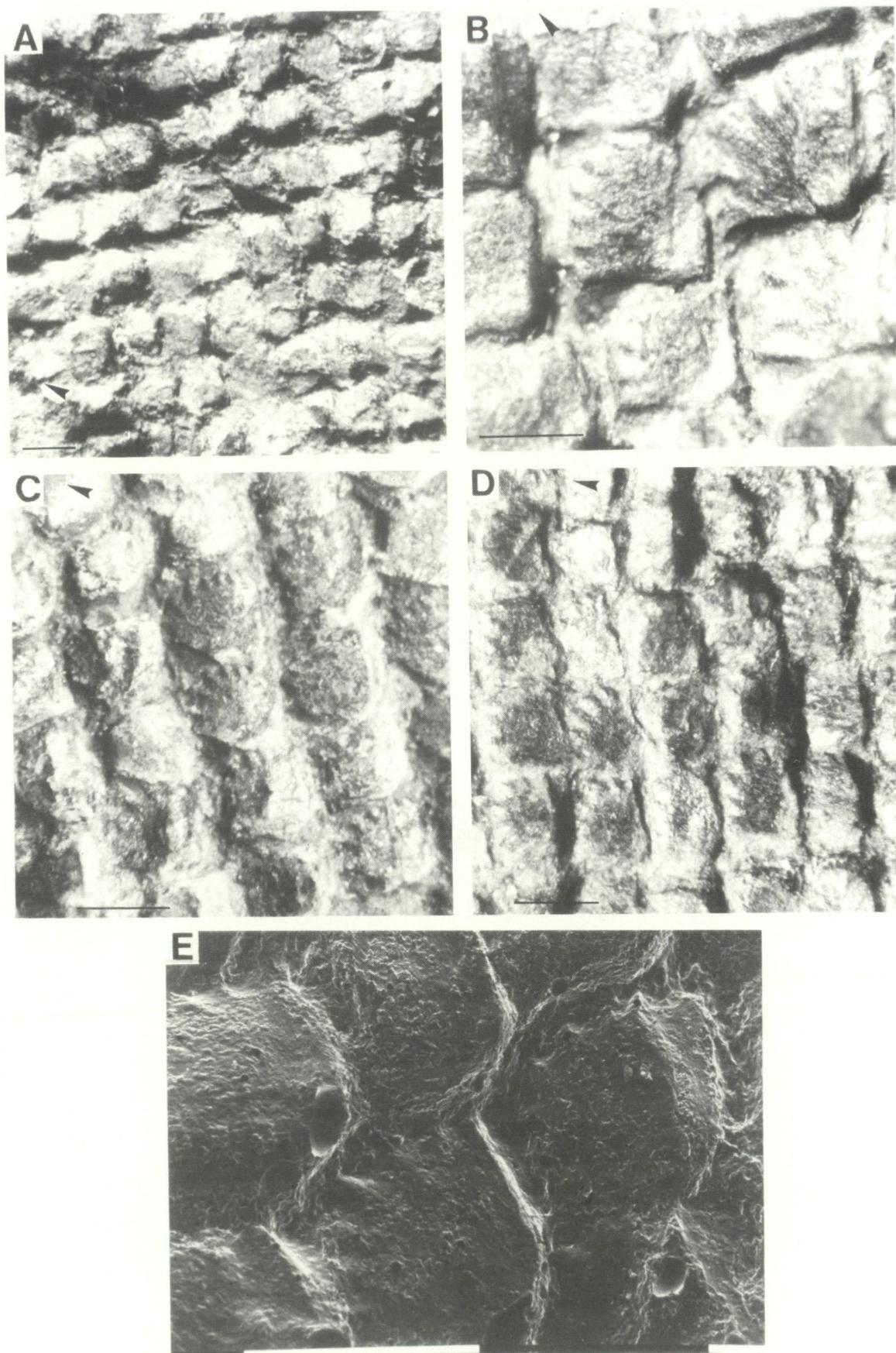


Figure 6 *Yealepis douglasi* gen. et sp. nov. Holotype, ANU V2351. Scale impressions on counterpart (see Figures 3, 4). A, mid-flank, with thin lateral line ridge. B, anterior to pectoral fin. C, high on the flank above pelvic fin. D, low on the flank, above the leading edge of anal fin. E, scanning electron microscope image of cast made of impressions anterior to pectoral fin. Scale bars = 1 mm (A, C-E), 0.5 mm (B). Arrows on A-D point rostrally.

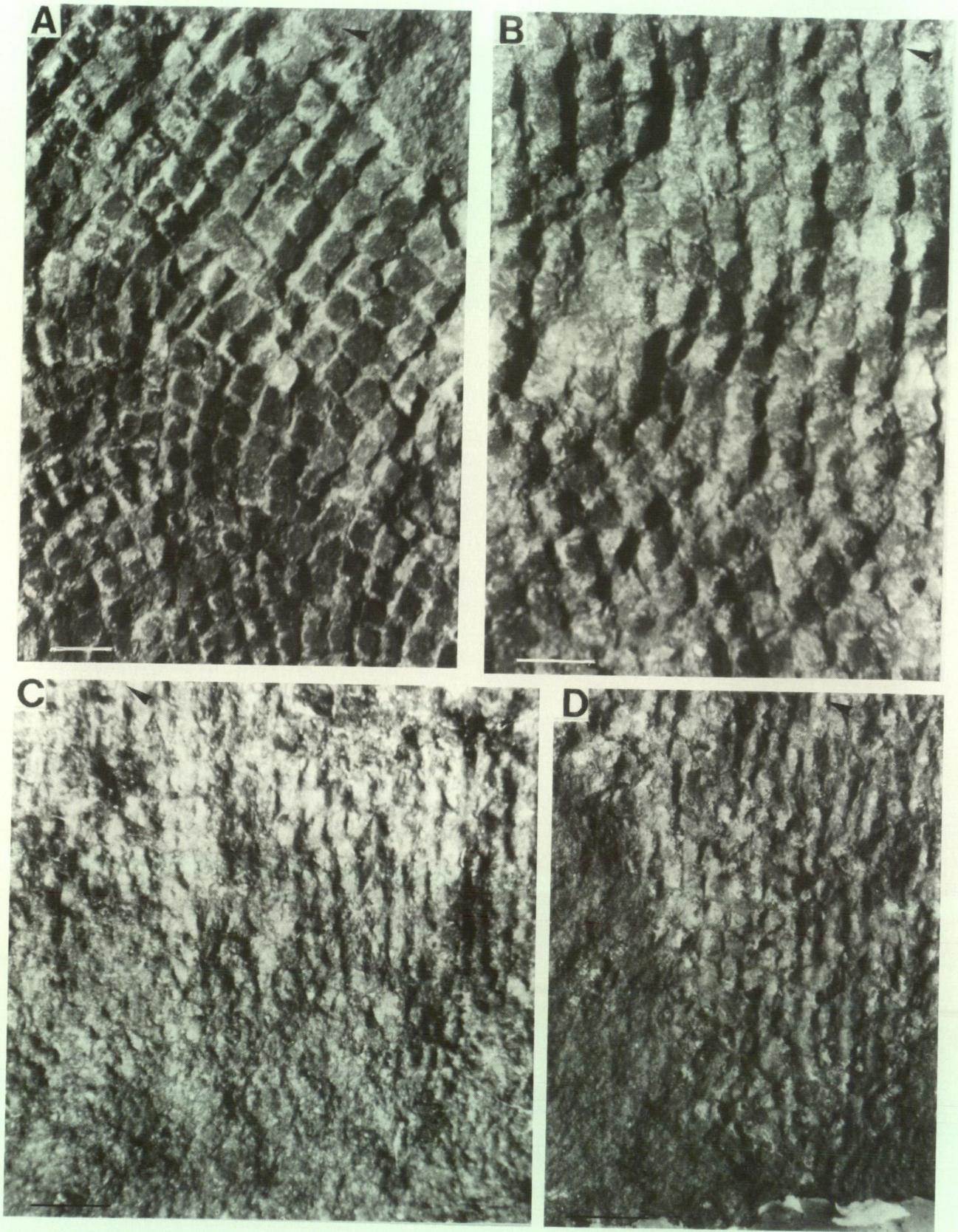


Figure 7 *Yealepis douglasi* gen. et sp. nov. Holotype, ANU V2351. Scale impressions on counterpart (see Figures 3, 4). A, paralleling the mid-dorsal line, with flank scale rows curving away. B, above the pelvic fin, ?ventrolateral line. C, distal part of pectoral fin web. D, anal fin leading edge. Scale bars = 2 mm (A, B, D), 1 mm (C). All arrows point rostrally.

have ridges which are short and only weakly developed, and the crown is slightly deeper than average. On scales close to the caudal peduncle, only a few short crown ridges diverge from the posterior point. Many of the scales are irregularly shaped in areas where diagonal rows converge or bifurcate, for example near the dorsal rostro-caudal rows and along the ventro-lateral line (Figure 7A,B). Often the last scale before a row bifurcates has a median groove, or perhaps two fused crowns. Many of the scales in these areas appear shaped to fit the space, being triangular, rounded or polygonal. Most scales have short, anterior, radial ridges, but random scales bear stronger, bifurcating ridges. On the fin webs, proximal scales are identical to normal body scales, with scales becoming smaller and more rectangular (long axis perpendicular to the long body axis) distally. Towards the distal fringe, the scales are very small, with an elongate crown drawn out to a sharp posterior point which extends beyond the scale base (Figure 7C). There are no specialized scales along the leading edges of the fins (Figure 7D).

DISCUSSION

Without a complete specimen, any suggestions about the palaeobiology of *Yealepis* are highly speculative, particularly as this specimen is the only vertebrate fossil known from the Yea Formation. However, we have reasonable information about scale morphology, so some comparisons can be made based on the strong morphological similarities to the scales of some extinct and extant fishes (Figure 9), including those of the modern Gulper shark, *Centrophorus granulosus* (Reif 1985, plate 5, text-figure 21G; Figure 8E). Non-overlapping scales indicate that streamlining was not important, which could suggest that *Yealepis* was a slow-swimming fish, and not subject to strong currents. On *C. granulosus*, "knob-shaped scales occur on all parts of the body were [sic] no high flexibility is required. In areas of high flexibility the scales are smaller, and elongate in an anterior-posterior direction. This is true for the ventral side of the head ... and for the fins" (Reif 1985, plate 5 caption). Whereas the scales on fins of *Centrophorus* are apparently oriented more or less antero-posteriorly (see also Reif 1985, text-figures 14, 15, for similar scale orientation over the body of other sharks), those on *Yealepis* are oriented perpendicular to the long body axis. The gulper shark is a demersal deep water species, with a maximum length of 1.5 m, which is always caught near the bottom. The Yea teleostome was preserved in a 13 mm thick, homogeneous layer of dark brown mudstone between finer, light brown layers, which could have been deposited as a turbidite, either smothering the fish if it occupied a similar niche to

that of the modern Gulper shark, or carrying the fresh carcass from shallower into deeper water.

Exact higher classification of this new genus is precluded by the lack of a head, by the absence of fin spines, and by poor histological preservation. If interpreted as an acanthodian, normal flank scales, and the rarer variations, superficially match most of the morphotypes (e.g. Figure 8A,B) from the Trundle Group of central New South Wales, which Burrow (1997, plate 1.5–8, plate 4.1–8) assigned to the acanthodian *Gomphonchus? guangxiensis* Wang,

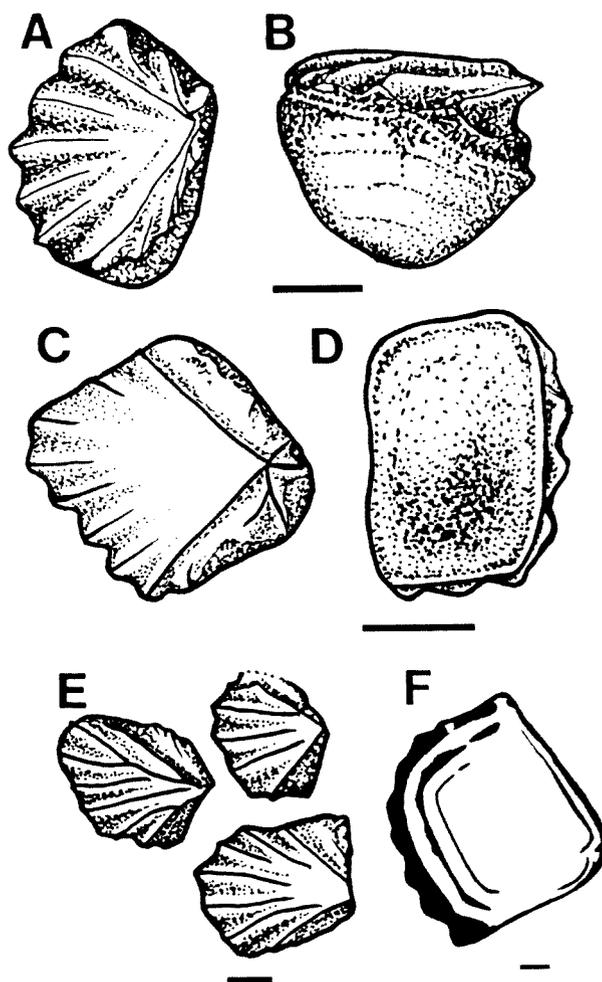


Figure 8 Comparison of scale morphology between *Yealepis douglasi* gen. et sp. nov., the acanthodian '*Nostolepis*', and the modern shark *Centrophorus*. A, B, '*Nostolepis*' *guangxiensis* scale, MMMC02220 from the Early Devonian Trundle Group, New South Wales (see Burrow 1997, plate 1, figure 4a,b). C, D, '*Nostolepis*' *guangxiensis* holotype scale (IVPP V9745,1), after Wang (1992, plate 1, figure 3a,b). E, scales from near a pit-organ of the modern gulper shark, *Centrophorus granulosus* (after Reif 1985, plate 5, figure B1). F, *Yealepis douglasi* gen. et sp. nov. Holotype (ANU V2351). Scale from mid-flank above the pelvic fin on part (see Figure 2), with upper crown layers missing to expose inner growth zones. Scale bars = 0.2 mm.

1992 (since revised to "*Nostolepis*" *guangxiensis*, Burrow *et al.* in press). The 'box-in-box' internal structure of the scales of *Yealepis* and most acanthodians differs from that of early actinopterygians. The latter have scales which grew by new layers added to base and crown, but these new ornament layers formed as individual 'ridges' (e.g. Gross 1966, and 1968, figure 7A-D), rather than over the entire crown surface as occurred in acanthodian scales and apparently in *Yealepis* (e.g. Figure 8F).

The head of the new specimen is missing so the dentition is unknown, and although the portion of squamation anterior to the pectoral fin comprises only normal body scales, the presence or absence of head tesseræ further rostrally is unknown. The pelvic fin is close behind the pectoral one. The ratio of the distances (pectoral fin insertion to leading edge of the pelvic fin) : (leading edge of pelvic fin to leading edge of anal fin) is 1:1. On nearly all climatiiforms (all of which, except gyracanthids and culmacanthids, have intermediate spines) the ratio is much higher, e.g. 2.4:1 on *Euthacanthus macnicoli*, 4:1 on *Ptomacanthus anglicus* (Denison 1979, figures 11A and 11G, respectively); even on *Uraniacanthus*

spinus, the only ischnacanthid known to have intermediate spines, the ratio is 2:1 (Denison 1979, figure 25B). The only climatiiform described which has a 1:1 ratio is *Kathemacanthus rosulentus* from the Lochkovian 'MOTH' locality, Northwest Territories, Canada (Gagnier and Wilson 1996a, text-figure 2). The latter species is unusual in that the pectoral fin is inserted high on the flank, "... at the middle of the height of the animal" (Gagnier and Wilson 1996a: 247). Elevated pectoral fins indicate extra lift, which in modern fish is compensated for by the forward position of the pelvic fins, so that they are in front of the centre of gravity. Although the pectoral fin is lower on the flank in *Yealepis* than in *Kathemacanthus*, it is also narrow-based, and flattened in a like manner to that of *Kathemacanthus*, with the inner, or ventral, side of the web exposed, and the leading edge of the fin along the upper fin margin as preserved. This mode of preservation indicates that in life the fin probably extended out from the body more or less horizontally.

Only a few known acanthodian species have scales with a crown smaller than the base, and all of these are sciotaxa (i.e. based on scales): the climatiids *Canadalepis linguiformis* Vieth, 1980

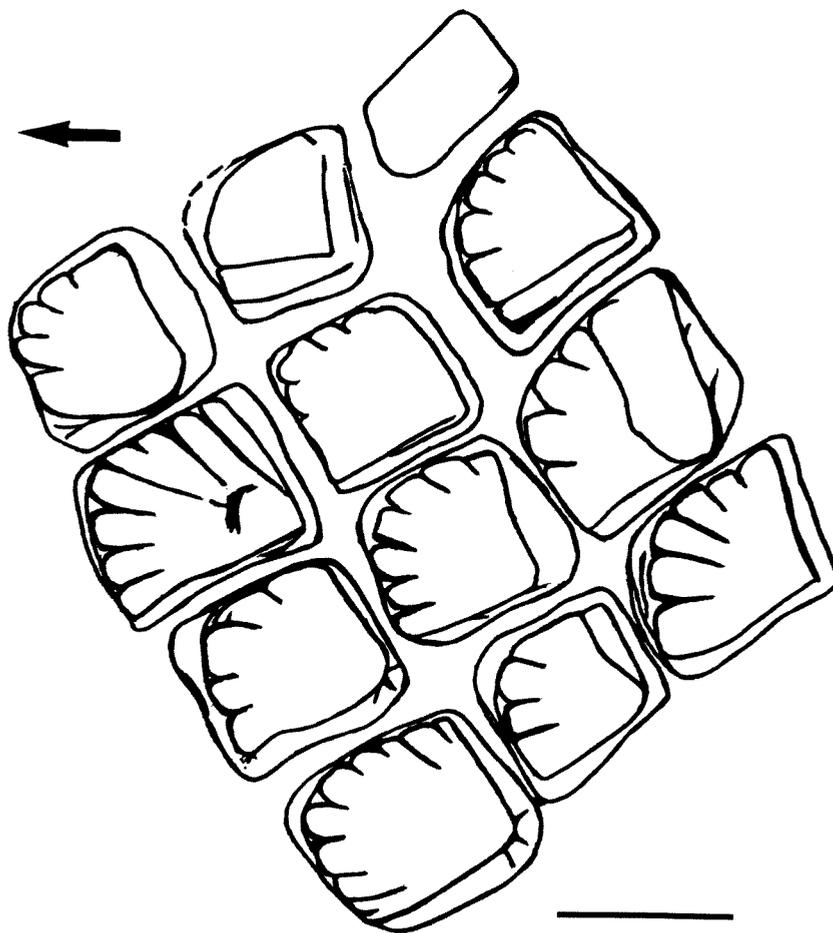


Figure 9 *Yealepis douglasi* gen. et sp. nov. Holotype (ANU V2351). Scale impressions on counterpart anterior to pectoral fin (see Figures 4, 6B). Scale bar = 1mm. Arrow points rostrally.

(Lochkovian, Arctic Canada), *Nostolepis laticristata* Valiukevicius, 1994 (Lochkovian; Arctic Canada and Tareya), "*Nostolepis*" *guangxiensis* (Wang, 1992) (Emsian; Guangxi and Beichuan Provinces, China), *Nostolepis curta* Valiukevicius, 1994 (Pragian and Emsian; Tareya), some scales assigned to *N. sinica* (Gagnier *et al.* 1989, plate 1.1–3) and *N. sp.* (Wang and Dong 1989), and perhaps *N. multangula* Valiukevicius, 1994 (Lochkovian; Timan-Pechora, and Emsian; Tareya). If the histology of scales of *Yealepis douglasi* corresponded to that of the morphologically similar, isolated scales from the Trundle Group assigned to "*Nostolepis*" *guangxiensis* (= *Gomphonchus?* *guangxiensis* in Burrow 1997), then (in the absence of information on head tesserae) scales of our new species would, until recently, have been referred to the climatiids. However, Valiukevicius (1997) mentioned a new specimen with characters of both ischnacanthiform and climatiid acanthodians, indicating that this is not a certainty. Some of the scales of *Nostolepis laticristata* superficially resemble those of the Yea teleostome, but *N. laticristata* has smaller scales with a moderately to highly swollen base. No scales with bifurcating ridges have been noted in *N. laticristata*.

Although the morphology, histology (as far as known) and arrangement of the squamation of *Yealepis* indicate acanthodian affinities, it lacks fin spines, a defining feature of this group. Denison (1979: 21) included the following features in his diagnosis of the Class Acanthodii: "all fins except the caudal have spines on their anterior edge ...". Janvier (1996) emphasized the uncertainties of acanthodian phylogeny, both within the group and with other gnathostomes. Within the Palaeozoic gnathostomes, paired fin spines are unique to the Acanthodii. However, the genus *Machaeracanthus* (based on disarticulated material) apparently had only asymmetrical paired fin spines and lacked unpaired fin spines (Janvier 1996: 181). Also, the variable development of fin spines along the ventro-lateral line, and a line perpendicular to this which incorporates the pectoral fin spine, in acanthodians described from the Lower Devonian of Canada (Gagnier and Wilson 1996a, 1996b), suggest great variability exists in the expression of fin spines. If we accept that the absence of spines on *Yealepis* is not an artifact of preservation, then one unlikely possibility is that it is unique amongst acanthodians in having lost its fin spines. However, as the gross morphological features displayed by the specimen (small scales, paired pectoral and pelvic, and unpaired caudal and anal fins) are widely considered to be primitive for gnathostomes generally (e.g. Janvier 1996), an alternative possibility is that *Yealepis* lies outside the Acanthodii, as a stem-group teleostome or gnathostome.

Although a dermal skeleton of small scales is considered by some scientists as primitive for

gnathostomes, small non-articulated scales superficially similar to those of acanthodians also occur in the Middle-Late Devonian actinopterygian *Cheirolepis*. The Actinopterygii has been proposed as the most primitive osteichthyan group, and there are several competing hypotheses about the higher group relationships amongst gnathostomes (e.g. Rosen *et al.* 1981; Gardiner 1984). Both of the extant gnathostome fish groups (osteichthyans and chondrichthyans) have been proposed as the closest relatives of the acanthodians. The primary evidence supporting a chondrichthyan relationship is the posterior orientation of the pharyngobranchials in *Acanthodes*, as in the cartilaginous fishes (Nelson 1968), but this condition is unknown in more primitive acanthodians. The alternative teleostome hypothesis of Miles (1973) placed the Acanthodii and the Osteichthyes as sister-groups within the higher taxon Teleostomi. Pearson (1982: 61) noted "... two major objections to the acanthodians as osteichthyan ancestors: their spinous precaudal fins and their lack of dentigerous dermal bones around the jaw and gill apparatus". However Reed (1992) described elements he interpreted as jointed fin spines of *Cheirolepis* cf. *canadensis* in the Red Hill fish fauna of Nevada, from close to the Middle/Upper Devonian boundary.

Given our limited knowledge of the morphology of *Yealepis*, this discussion is mainly concerned with comparative scale morphology and, to a lesser extent, histology in the relevant groups. Regarding the small, acanthodian-like scales of the actinopterygian *Cheirolepis*, Gross' (1947, 1973) histological studies indicated a purely superficial resemblance to acanthodian scales, a view supported by Schultze (1977, 1992), but disputed by Pearson and Westoll (1979: 371). Poplin *et al.* (1991) used histological characters to conclude that *Yaomoshania* from the Permian of China, another form known only from its squamation which comprises small, non-rhombic scales, was an actinopterygian. The tissue ganoine which typifies early actinopterygian scales, and has been proposed as a synapomorphy of the group (Patterson 1982; Gardiner 1984; Maisey 1986), was recently described in Siluro-Devonian acanthodian scales (e.g. Richter and Smith 1995). However, ganoine is a substance produced solely by ectodermal processes (Sire 1994). The enameloid-like tissue which is sometimes detectable in acanthodian scales, unlike ganoine, was probably produced by ectoderm-mesoderm interaction, as a clear boundary (as occurs in actinopterygian scales) does not always exist between the birefringent tissue and dentine in the crown growth zones. Acanthodian scales with nostolepid-type histology (including scales of all the species mentioned which have a morphological similarity to those of *Yealepis*) lack this enameloid-like tissue.

The superpositional growth of scales common to both actinopterygians and acanthodians could indicate a sister group relationship (Patterson 1982), whilst *Cheirolepis* has been (controversially) assessed as the primitive sister group of all other actinopterygians (Gardiner and Schaeffer 1989). The detailed discussion on *Cheirolepis* by Pearson and Westoll (1979) did not lead to a definitive opinion on this point, with Pearson (1982: 38, 46) suggesting that the resemblance to acanthodian scales was both "specialised" and "superficial", but also stating that "neither in scale structure nor arrangement does the micromery of *Cheirolepis* seem to be secondary". Schultze (1977, 1992) opposed this view, because of the advanced histological composition of its scales: multilayered ganoine in the scale crown is a derived state in actinopterygians, whereas separate dentine ridges with a single ganoine layer is thought to be the primitive state (Schultze 1992: 238). The palaeonisciform *Tegeolepis* from the Cleveland Shale Member (Famennian) of the Ohio Shale, Ohio, also has relatively small scales, similar to those of *Cheirolepis*, which Dunkle and Schaeffer (1973) recognized as a derived character. The palaeontological argument for small, acanthodian-like scales in actinopterygians being a derived condition is supported by the six stratigraphically oldest actinopterygian genera (*Andreolepis*, *Naxilepis*, *Ligulalepis*, *Terenolepis*, *Orvikuina*, and *Dialipina*) which all have rhombic scales. Although *Cheirolepis* is the oldest genus erected for articulated actinopterygians, several later genera including *Tegeolepis* in the Devonian, *Tarrasius* in the Carboniferous and *Yaomoshania* in the Permian also have secondarily-derived acanthodian-like scales.

Regarding distinguishing characteristics using external scale morphology, the diagonal long axis and anterodorsal process of typical *Cheirolepis* scales were considered by Patterson (1982) to represent an actinopterygian synapomorphy. The peg-and-socket articulation between scales, thought by Pearson (1982), for example, to be primitively absent in *Cheirolepis*, was subsequently identified in two scale rows of the tail lobe of the Middle Devonian *C. trailli* (Gardiner and Schaeffer 1989: 157), but both peg-and-socket articulation and anterodorsal processes are apparently absent in the Upper Devonian *C. canadensis* (Arratia and Cloutier 1996: 193). Again, a palaeontological argument of earlier fossil occurrence within the genus, and comparison with other palaeonisciforms (e.g. *Dialipina*, *Ligulalepis*) could be employed to conclude that the lack of articulation in the flank scales of *Cheirolepis* was secondary. The orientation of flank scales, and of their crown ornament, on *Yealepis* corresponds to that typical for acanthodians (e.g. Gross 1947, figure 25A), with ridges pointing rostrally. On *Cheirolepis*, the scale ornament is directed anterodorsally (Gross 1947, figures 25B, 26B).

In conclusion, there is insufficient evidence to confidently place the new form *Yealepis douglasi* within the Acanthodii. Its known characters, in particular the 'box-in-box' structure of the scales, exclude it from the Actinopterygii, in which the ornament layer in scales of early taxa grew by the addition of dentinous ridges. Nevertheless, it could be a basal teleostome.

ACKNOWLEDGEMENTS

We wish to thank Jack Douglas for making the specimen available for preparation and description. C.J.B. thanks the Australian Pacific Science Foundation for funding a field trip to visit the locality. R.W. Brown and H.M. Doyle (Australian Geological Survey Organisation) are thanked for carrying out initial preparation and photography of the specimen. G.C.Y. acknowledges provision of facilities at the Geology Department, Australian National University, which permitted research on this specimen to be finalized.

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Manuscript received 9 February 1998; accepted 21 September 1998.