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Biostratigraphy of Devonian microvertebrates from Broken River, North Queensland

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Abstract – Microvertebrate faunas from acid-leached residues from the Broken River region of north Queensland are dated by accompanying conodonts and span the interval *serotinus* (late Emsian) to *asymmetricus* (earliest Frasnian) zones.

Five major Devonian fish groups are represented: agnathan (thelodont), acanthodian (*Cheiracanthoides comptus, Nostolepis* cf. *costata, Nostolepis* spp., *Acanthoides* sp.), chondrichthyan (*Cladolepis* cf. *gunnelli, Ohiolepis* sp., phoebodont, indeterminate), placoderm (arthrodire, ptyctodontid), and osteichthyan (crossopterygian including *Onychodus* sp., palaeoniscoid, dipnoan).

Scales of *C. comptus* and *Cladolepis* cf. *gunnelli* both occur in horizons as young as *asymmetricus* Zone and are therefore longer ranging than previously reported. The stratigraphic range of the other Broken River forms falls within the range reported from elsewhere.

INTRODUCTION

The Broken River Group of North Queensland crops out as two shallow marine mixed carbonate platforms (northern Pandanus Platform and southern Dosey–Craigie Platform) covering approximately 320 square kilometres; it comprises five fossiliferous formations dated by conodonts as ranging from mid Emsian to earliest Frasnian (Mawson and Talent 1989). In the south (Figure 1), there are two limestone formations (Lomandra and Dosey limestones), and three mudstone/shale/siltstone units with nodular limestones (Bracteata Formation, Papilio Formation with associated Spanner Limestone Member, and Mytton Formation with associated Stanley Limestone Member); details of stratigraphy are given in the legend to Figure 1. Environments of deposition are interpreted as shallow marine (Lomandra Limestone, Mytton Formation), protected muddy shelf (Papilio Formation), deeper water muddy shelf (Bracteata Formation), shallow carbonate shelf (Dosey Limestone, Spanner Limestone), and carbonate shoal (Stanley Limestone) (Mawson and Talent 1989).

Previous work on the Broken River Group has resulted in reports of both microvertebrates and macrovertebrates. Reported from Early Devonian horizons are acanthodian scales and platelets, including *Nostolepis* sp., buchanosteid and radotinid tesserae, onychodontid teeth and an endemic turiniid from the Martins Well Limestone (Turner 1991, 1993), dated by conodonts as *pesavis–sulcatus* zones (Mawson *et al.* 1988; Withnall and Jell 1988). Middle Devonian forms reported are more diverse: antiarchs *Wurungulepis denisoni*, represented by scales, fin bones, and articulated trunk armour, and skull and dermal bones of *Nawagiaspis wadeae* from Eifelian and Givetian horizons (Young 1990); *Cheiracanthoides comptus* scales, onychodontid teeth and palaeoniscoid remains from the Eifelian–Givetian Fish Hill, and a phoebodont tooth from the Papilio Formation (*varcus* Zone) (Turner 1993); acanthodians *Acanthodes* sp., and an indeterminate ischnacanthid, chondrichthyan *Ohiolepis* sp., thelodont *Turinia* sp., placoderms cf. *Pterichthyodes* sp. and indeterminate asterolepidoid, brachythoracid and rhenanid? remains, dipnoan cf. *Chirodipterus* sp., onychodontid *Onychodus* cf. *sigmoides*, and palaeoniscoid *Ligulalepis toombsi* (Long and Turner 1984); and acanthodian *Machaeracanthus* sp., placoderms *Atlantidosteus* sp. and a new brachythoracid, and an indeterminate dipterid (Young 1993). A 50mm-long crossopterygian lower dentary, as yet undescribed but probably *Onychodus* sp., was recovered in 1993 from near Fish Hill, from a horizon dated by associated conodonts as close to the *costatus/australis* boundary (De Pomeroy *et al.* 1994).

For details of geology, interpreted depositional environment and conodont biostratigraphy, see Mawson and Talent (1989).

RESULTS OF STUDY

Twenty sections (comprising 586 samples, each weighing approximately 1 kg) were measured from the Dosey–Craigie Platform and the southernmost

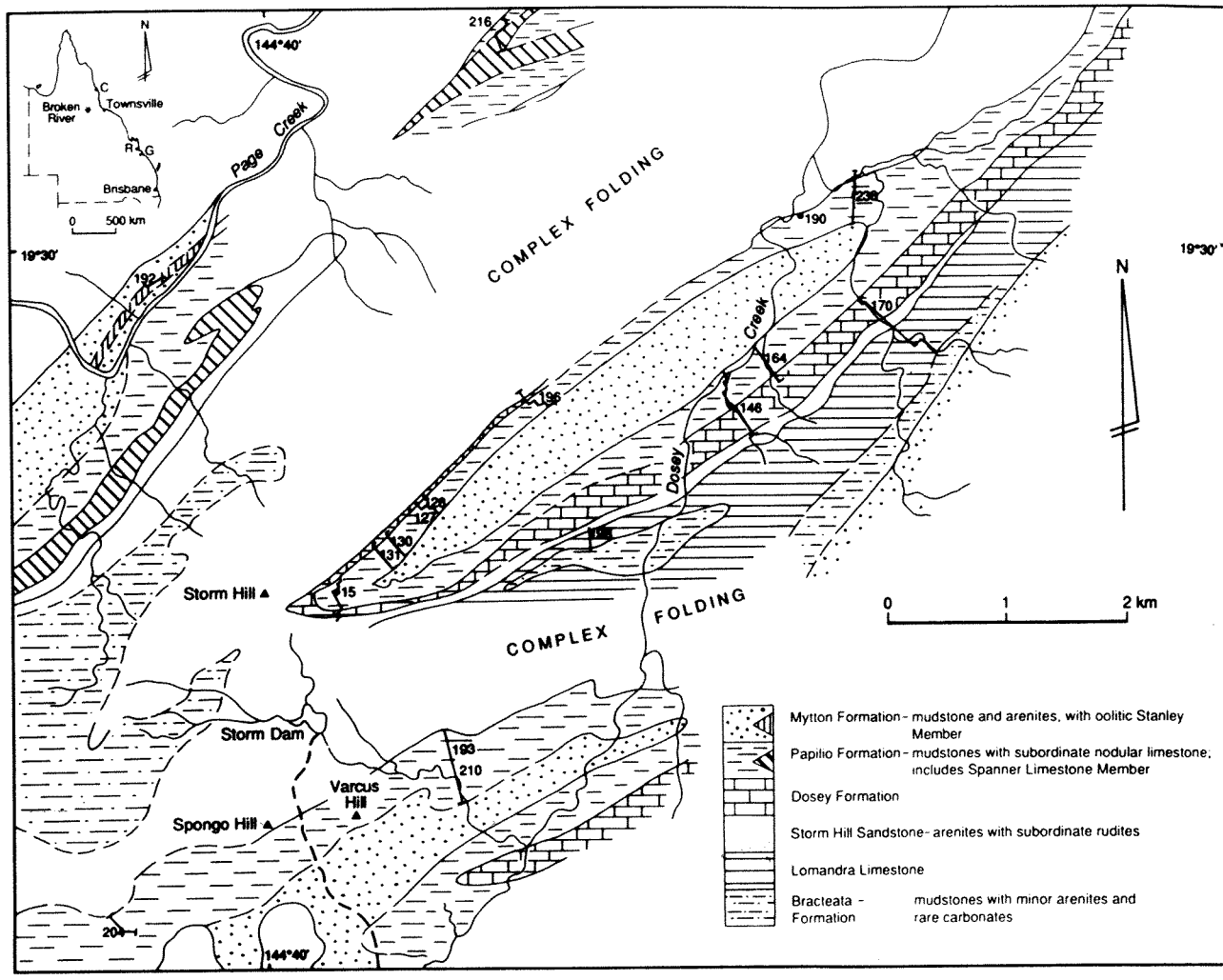

Figure 1 Broken River Group in the Dosey–Craigie Platform area showing location of stratigraphic sections. Sections bear prefix SD for Storm Dam (after Mawson and Talent 1989). Three sections are beyond the map boundaries: SD111 is approximately 3.6 km SW of Storm Dam; SAG is approximately 4.2 km east of Jessey Springs Hut; and SAGW is 94 m west of the original SAG section.

part of the Pandanus Platform. The microvertebrate faunas in the acid-leached residues from these samples have been precisely dated by the accompanying conodonts. Fish remains recovered include abundant acanthodian scales, chondrichthyan scales and teeth, onychodontid teeth; rare placoderm scales and bone fragments, onychodontid jaw fragments, and palaeoniscoid teeth; two onychodontid scale fragments, one palaeoniscoid scale, one thelodont scale, and one probable dipnoan toothplate.

The stratigraphic range of the forms reported here is compared with that from elsewhere. The presence of two forms in the Broken River Group extends the range later than that previously reported worldwide – the acanthodian *Cheiracanthoides comptus* and the chondrichthyan *Cladolepis* cf. *gunnelli*. Another acanthodian genus, *Nostolepis*, occurs later at Broken River than all other reported localities, with one exception. The ranges of the other forms recovered fall within the ranges reported from elsewhere (Figure 2).

SYSTEMATIC PALAEONTOLOGY

Figured material is lodged in the palaeontological collections of the Queensland Museum (prefix QMF). Locality information is given by section number, followed by metres above base of section of lowest and highest productive sample. Figure 1 gives location of sections.

Superclass Agnatha

Subclass Thelodonti

Order Thelodontida

Thelodont indet.
Figures 6M, N

Material

One head scale (QMF 31856).

Locality

Section SAG/26.8m – Chinaman Creek Limestone; see Mawson *et al.* 1988, figure 13.

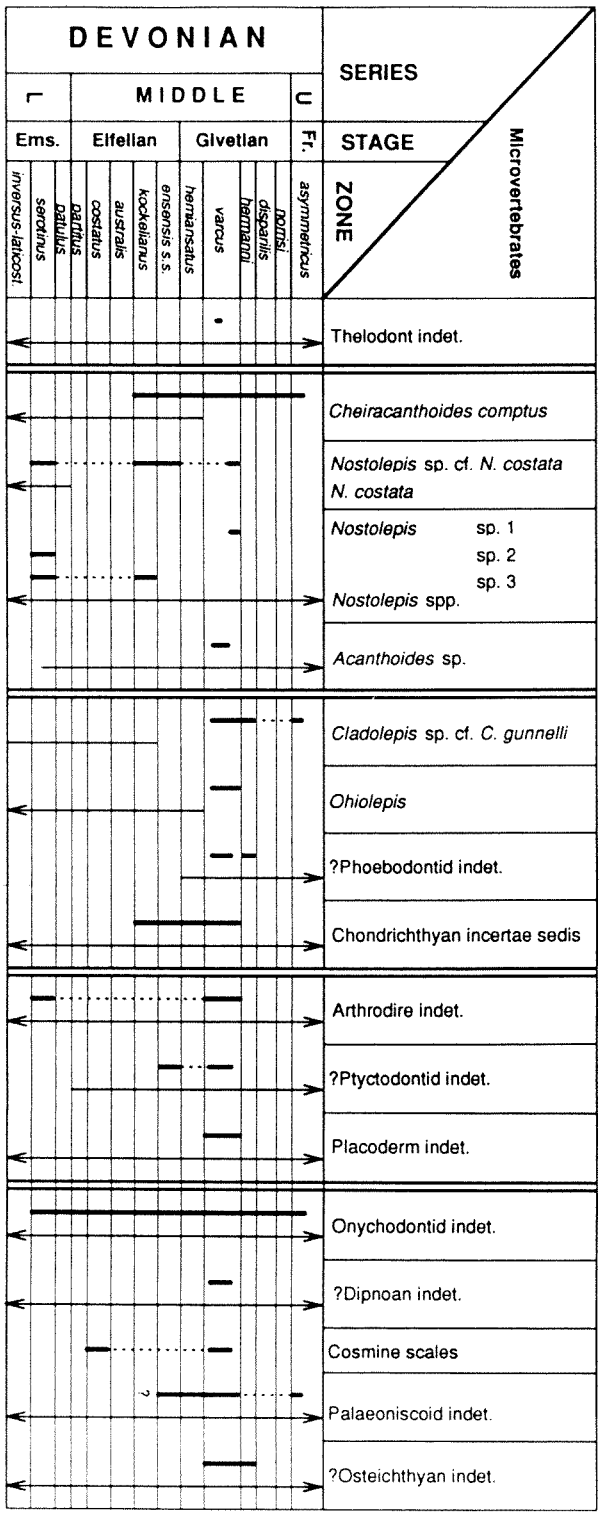

Figure 2 Stratigraphic ranges of microvertebrates discussed in text. Heavy line is range in Broken River Group; light line is range reported from other localities.

Stratigraphic level

Givetian (*varcus* Zone).

Remarks

All thelodonts have similar rounded head scales with undulating crown margins and radiating ribs, whereas trunk scales tend to be more distinctive (Turner 1986). The Broken River scale resembles head scales of *Australolepis seddoni* Turner and Dring, 1981 described from the Frasnian Gneudna Formation in the Carnarvon Basin of WA, in its rounded shape, bifurcated ridges radiating from a central plateau on the crown, and size (0.5 mm), but lacks the deep furrows on the crown and the stepped ridges on the vertical crown surface typical of this genus. However, the specimen cannot be unequivocally assigned to *Australolepis*. It also resembles head scales of the turiniid genus *Turinia* (e.g. Turner *et al.* 1981, figure 7G). For the present the Broken River scale is assigned in open nomenclature to Order Thelodontida. Turner and Dring (1981) suggest that *Australolepis* and *Turinia* are related, the former possibly being derived from the Early Devonian *T. australiensis* Gross, 1971. Turner (pers. comm.) considers *Australolepis* may be a neotenous form of *T. australiensis*.

Description

The scale has a gently rounded central crown extending outwards in five low, broad ridges. One anterior and one lateral ridge bifurcate slightly at the distal end (Figure 6M). The neck is smooth and low. The elliptical base is larger than the crown, with a wide rounded rim surrounding the central shallow pulp cavity (Figure 6N).

Discussion

Thelodonts, most commonly turiniids, have been reported from Australian localities ranging in age from close to the Siluro–Devonian boundary to the early Frasnian; these are listed by Long and Turner (1984) and Young (1993, 1995), and figured by Pickett *et al.* (1985), Turner *et al.* (1981), Young and Gorter (1981), Turner (1986, 1991, 1993), Young *et al.* (1987), and Long *et al.* (1988). No thelodont scales from the Broken River region are described or figured in the literature, but Young (1995) reports an endemic turiniid from the *pesavis–sulcatus* Martins Well Limestone, and Turner (1993) mentions, from the Broken River Group, a Lochkovian *Turinia australiensis* morphotype, and turiniid and nikoliviid-like scales of no specified age.

Subclass Acanthodii Owen, 1846

Order Climatiida Berg, 1940

Family Climatiidae Berg, 1940

Cheiracanthoides Wells, 1944

Type species

C. comptus Wells, 1944.

Diagnosis

Scales with flat or slightly convex crown,

extending beyond base posteriorly, ornamented with parallel or slightly radiating rounded ribs, usually only on anterior part of crown. Neck low, clearly separated from both base and crown, with small canal openings on front and back. Base convex, usually extends anterior to crown, concentrically striated. Mesodentine crown, with Stranggewebe in posterior half, has concentric, radial and ascending vascular canals. Tubules on top of the crown grouped into tufts in the furrows, with side branches extending into the ridges. Base of cellular bone.

Cheiracanthoides comptus Wells, 1944
Figure 3A–D

Material

280 scales (QMF 31819, 20 + 278 others).

Localities

SD15/59.1–113m, SD128/54.3–201.5m, SD130/32.5–73.1m, SD131/92.1m, SD146/418m, SD164/117.7–124.1m, SD170/710m, SD192/0–50m, SD193 (spot sample), SD204/115.9–120m, SD210/69.7–132.3m, SD216/26.7–95.3m, and SAG/26.8–121.9m; Lomandra, Stanley, Spanner and Chinaman Creek limestones, and Papilio Formation.

Stratigraphic range

Eifelian (*kockelianus* Zone) to earliest Frasnian (*asymmetricus* Zone).

Remarks

The scales have the flat or slightly convex crown with posteriorly converging ridges, the low indented neck, and convex base, described by both Wells (1944) in the original diagnosis, and by Denison (1979) as being typical of this genus. The Broken River scales are a similar size to those of Wells (1944).

Description

The scales have four to eleven radiating or subparallel rounded ridges on the anterior part of the crown. The anterior edge of the crown has a distinct rim (Figures 3A, C) that separates the flat crown from the indented neck, and connects the front edge of the coronal ridges; this is particularly visible in side view (Figure 3B). All specimens have a diamond-shaped, convex base. The crown extends posteriorly beyond the base, in some specimens further (Figure 3D) than in others (Eigure 3B). In most of the scales, the crown length and width is approximately equal, while the scale height is approximately one-third to one-half of the length/width measurement. The size range of the scales is 0.5–0.9 mm long, 0.4–1 mm wide, and 0.2–0.5 mm high. Thin sections reveal the typical *Nostolepis*-type histology, with a pyramid-shaped base of cellular bone showing concentric growth zones, and a crown with ascending and concentric vascular canals (Denison 1979, figures 9A–C and 10B), however preservation is insufficient in the prepared thin sections to reveal whether tubules are grouped into tufts in the furrows, a feature distinguishing this genus from *Nostolepis* (Denison 1979).

Discussion

Wells (1944) separated scales of this morphological type into six species in two genera. These were subsequently amalgamated into the single species *C. comptus* by Gross (1973), who considered the morphological differences intraspecific.

The anterior coronal rim found on all Broken River specimens is not specified by Wells (1944) as a character of the genus, but his illustrations (figures 4a–k, 5a–e, and especially the side view in figure 4c) show a clear delineation between the flat crown and deeply indented neck. Some later illustrations of *C. comptus* also show the rim (e.g. Gross 1973, plate 26 figures 24–26; Vieth-Schreiner 1983, plate 4 figures 32–33; Valiukevicius 1985, plate 8 figures 4–5). In contrast, other specimens have the coronal ridges running down the anterior edge of the scale to where the neck area joins the base (e.g. Giffin 1980, figure 5; Gross 1973, plate 27 figure 2c; and *Cheiracanthoides* cf. *comptus* illustrated by Boucot *et al.* 1989, text-figure 19). In these latter two examples the crown, in side view, appears thicker than the crown of specimens with the anterior rim. It is possible that this type of scale, without the anterior coronal rim, belongs to a different taxon, or at least occurs on a different region of the body.

An acanthodian scale with some morphological similarity to the Broken River specimens, including the anterior rim on the crown, has been figured and described as *?Gomphonchus* sp. by Long *et al.* (1988, figure 2F, G). Those authors discuss the differences between *Gomphonchus* and *Cheiracanthoides*, and these differences are sufficient to separate *Gomphonchus* and the Broken River material.

Scales assigned here to *C. comptus* Wells, 1944 are the most common acanthodian microvertebrates in the Broken River material occurring in horizons from Eifelian (*kockelianus* Zone) to earliest Frasnian (*asymmetricus* Zone). Specimens from Australian localities are figured by Giffin (1980 figure 5) and Turner (1991, plate 2A, F, plate 5C). The cosmopolitan genus has been reported elsewhere from the Early and Middle Devonian, particularly the Emsian and Eifelian (e.g. Wells 1944; Vieth 1980; Valiukevicius 1979, 1985), and also from the lowermost Givetian (*hemiansatus* Zone – Vieth-

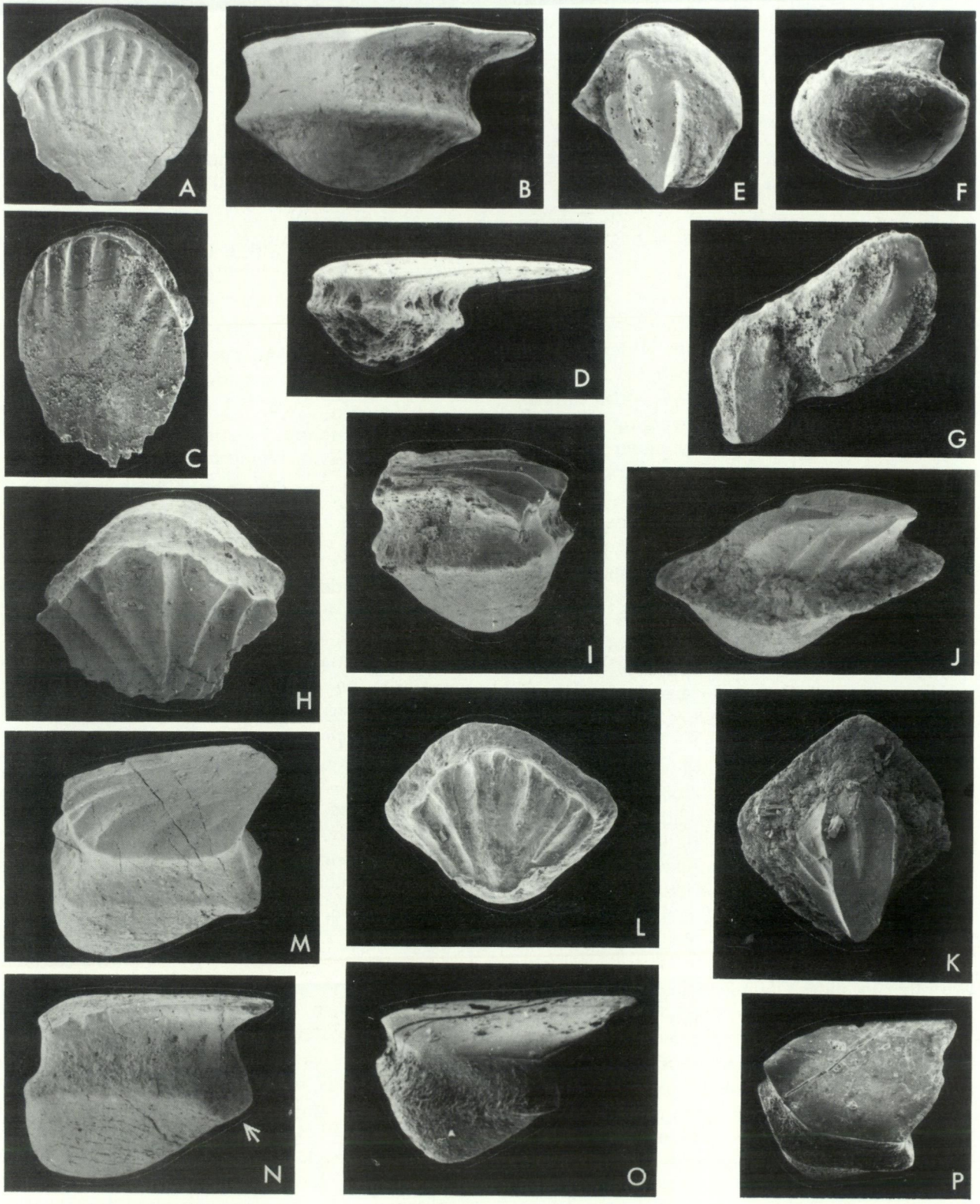

Figure 3 **A–D**, *Cheiracanthoides comptus* Wells, 1944. **A,B**, crown (x50) and lateral (x75) views of scale QMF 31819, SD204/120 m. **C,D**, crown (x50) and lateral (x75) views of scale QMF 31820, SD210/104 m.

E–G, *Nostolepis* sp. 2. E, crown view x90, **F**, latero–basal view x100 of scale QMF 31821, SD170/182–188.5 m. **G**, crown view of double scale QMF 31822, x75, SD170/182–188.5 m.

H,I,L, *Nostolepis* cf. *costata* Goujet, 1976. **H,I**, crown and lateral views of scale QMF 31823, x60, SD170/200 m. **L**, crown view of scale QMF 31824, x90, SD204/120 m.

J,K, *Nostolepis* sp. 1. **J**, lateral view x90, K, crown view x75, of scale QMF 31825, SD210/195.7 m.

M,N, *Nostolepis* sp. 3. Crown and latero–posterior views of scale QMF 31826, x60, SD170/700 m (appr).

O,P, *Acanthoides* sp. **O**, anterior view x100, **P**, crown view x90 of scale QMF 31827, SD204/120 m.

Schreiner 1983). There are no reports of these scales occurring elsewhere in horizons of *varcus* Zone or younger age. Correlation with associated conodonts at Broken River gives a definite age range for the species in eastern Australia, possibly the youngest occurrence globally.

Nostolepis Pander, 1856

Type species

N. striata Pander, 1856.

Remarks

In the almost 150 years since Pander erected the genus, scales and platelets with widely varying morphology have been ascribed to *Nostolepis*. Denison (1979) describes *Nostolepis* scales as being 'variously ornamented with converging or parallel ridges, or with strong ribs', and, along with more recent workers, emphasises the importance of histological examination to reveal the distinctive *Nostolepis*-type structure. Histological features typical of the genus include wide vascular canals, mesodentine in the crown, and Stranggewebe (C. Burrow, pers. comm.). It is likely that some specimens described as *Nostolepis* are a different taxon, and indeed, the whole concept of the genus is in need of review and clarification. However, the specimens from Broken River are ascribed to this genus for the present because of similarities with published forms (see below).

The genus is commonly found worldwide in Late Silurian and Early Devonian horizons (Obruchev and Karatajute-Talimaa 1967; Gross 1971; Goujet 1976; Denison 1979; Vieth 1980; Blieck *et al.* 1984; Wang 1984; Macadie 1985; Valiukevicius 1985,1988; Mader 1986; Pan Jiang and Dineley 1988; Turner and Murphy 1988; Boucot *et al.* 1989; Forey *et al.* 1992; Lelievre *et al.* 1993). *Nostolepis* has been reported from later than Early Devonian at only two other localities (Valiukevicius 1985,1988) – *N. kernavensis* Valiukevicius, 1985 from the Upper Narva Regional Substage (Narov "Gorizont") of Lithuania, broadly equivalent to *costatus* Zone (Reshenie 1990), and *Nostolepis* sp. no. 11 from the Frasnian Gauja Regional Stage of the Baltic Region of the former USSR. Scales assigned to *Nostolepis* have been reported from several Australian Early Devonian localities – Cravens Peak Beds of Queensland, Tumblong, Trundle Beds, Condobolin Formation and Yarra Yarra Creek Group of NSW, Silverband Formation, Coopers Creek Limestone, Tyers and Buchan in Victoria (Long and Turner 1984; Pickett *et al.* 1985; Turner 1991). No *Nostolepis* scales have been figured or described from the Broken River region, but *N. striata* is recorded as occurring in the Late Silurian Martins Well Limestone, and at Broken River Gorge, in strata of no given age (Long and Turner 1984). Two nostolepid scales in *varcus* Zone at Broken River (*Nostolepis* cf. *costata* and *Nostolepis* sp. 1 – see below) are thus, with the exception of the Frasnian species from the Baltic, the youngest recorded occurrence of the genus.

Nostolepis cf. *costata* Goujet, 1976

Figures 3H, I, L

Material

Nine scales (QMF 31823, 4 + seven others).

Localities

SD128/78m, SD170/200–710 m, SD204/120 m and SAGW/20 m; Lomandra and Chinaman Creek limestones, Papilio Formation.

Stratigraphic range

Emsian to Givetian (specimens occur in *serotinus, kockelianus, ensensis* and *varcus* zones).

Remarks

These scales are similar to those of *N. costata* Goujet, 1976, described from the Early Devonian of Saint-Céneré, France. However, the crown of the Broken River scales lacks lateral blades with a denticulate margin as in *N. costata*. This may simply be the result of abrasion, as all specimens show some signs of wear. Also, the Broken River scales are smaller than those from France; the latter reach up to about 2 mm in length and width (Goujet 1976).

These scales differ from those assigned to *C. comptus* (above) in the extension of the coronal ribs to the posterior point, the presence of bifuractions or short secondary ribs anteriorly, and the extension of the base beyond the crown on all sides.

Description

The flat crown, rounded anteriorly and tapering to a point posteriorly, has four or five strong, radiating ribs extending to the posterior point. These ribs may bifurcate at the anterior margin (Figure 3H), and there may be smaller, short secondary ribs between the main ones (Figure 3L). The shallow neck is indented and is deeper at the back (Figure 3I). The diamond-shaped base is strongly convex and extends beyond the crown on all sides (Figure 3L). Size of unbroken specimens is in the range 0.5–0.7 mm in length and width, with depth about 0.4–0.5 mm. Histological sections were not attempted because of the small number of specimens and the generally poor state of preservation.

Discussion

Forms assigned to *N. costata* are said to be

common in Lochkovian to Emsian limestones of NSW (Turner 1991); no examples are illustrated. The Broken River scales occur in horizons as young as Givetian; one specimen is from SD204/120m, in upper *varcus* Zone, dated by presence of conodonts *Polygnathus varcus, P. latifossatus* and *P. timorensis*.

Nostolepis sp. 1
Figures 3J, K

Material
1 scale (QMF 31825); other scales possibly belong to this taxon but are too abraded to assign with certainty.

Locality
SD210/196.4 m; Papilio Formation.

Stratigraphic level
Givetian (Upper *varcus* Zone).

Remarks
This scale differs from those assigned above to *Nostolepis* cf. *costata* in crown ornament: a central raised section, tapering posteriorly and with oblique ridges on the lateral edges, and with a flat, broad rim.

Description
The diamond-shaped scale is 0.5 mm long and wide, and 0.3 mm high. The central part of the crown is raised and smooth except for a median ridge (Figure 3K); the sloping lateral edges of this raised section have several oblique ridges (Figure 3J). The base is strongly convex. A distinct projecting rim encircles the scale at the crown/base junction.

Discussion
A similar nostolepid scale from the Pragian-early Emsian Jauf Formation of Saudi Arabia is figured by Boucot *et al.* (1989, figure 20a,b). Turner and Murphy (1988, figure 2.2) illustrate the crown view of a *Nostolepis*-type scale, which they consider resembles scales of *N.* striata, from the Windmill Limestone of the Simpson Park Range, Eureka County, Nevada; this scale is similar to the Broken River specimen. It is noted, however, that these figured scales are from the Early Devonian, whereas the Broken River specimen is dated Middle Devonian.

Nostolepis sp. 2
Figures 3E–G

Material
51 scales (QMF 31821,2 + 49 others).

Localities
SD170/185–200 m; Bracteata Formation.

Stratigraphic level
Emsian (*serotinus* Zone).

Description
These scales have the same diamond shape in crown view and deeply convex base as *Nostolepis sp.* 1, and a similar central, raised sloping section on the crown. They differ in having the raised crown section more triangular with the central ridge more pronounced and extending further anteriorly (Figure 3E), in the sloping lateral edges of the raised section being unornamented, and in lacking the protruding rim where the crown joins the base. The lateral and posterior corners of the crown are slightly extended into points (Figure 3E), while the anterior corner is rounded. Scales of this type are slightly smaller than *Nostolepis sp.* 1 – length and width are approximately 0.3 mm, and height about 0.2 mm. Fifty of the scales were recovered from the same sample (185m above base of section SD170). It is possible, therefore, that they are from a single fish, but preservation is not adequate to detect a noticeable variation among them, with the exception of the double scale illustrated in Figure 3G.

Discussion
The *Nostolepis*-type scale from the Lochkovian of Nevada figured by Turner and Murphy (1988, figure 2.3) bears a slight resemblance in crown view to the Broken River specimens, in the tripartite central raised section on the crown and in the overall diamond-shaped outline.

Nostolepis sp. 3
Figures 3M, N

Material
Three scales (QMF 31826 + two others).

Locality
SD170/185,710 m; Bracteata Formation, Dosey Limestone.

Stratigraphic range
Emsian (*serotinus* Zone) and Eifelian (*kockelianus* Zone).

Remarks
These scales differ from those of *Nostolepis* cf. *costata* discussed above by having a flat crown with low subparallel ridges only in the anterior half, in contrast to the strong, radiating ridges extending to the posterior of the crown in *Nostolepis* cf. *costata*, and in the lateral rounded projection. They

differ from *Nostolepis* sp. 1 and sp. 2 in the crown ornamentation.

Description

The crown is flat, rounded anteriorly and tapering posteriorly, with six subparallel ridges, the central two of which bifurcate at the anterior margin (Figure 3M). The neck is indented at anterior and posterior, with about six small holes at the posterior. The neck area is thickened laterally, extending into a rounded projection at each side of the scale where the neck joins the base. At the posterior corner, the lower edge of the neck dips to form a downward-curving arc (arrow in Figure 3N). The base is deeply convex, with the greatest depth towards the anterior end of the scale. Both length and width are approximately 0.6 mm, and depth of the scale is approximately 0.4 mm. Recovery of only three specimens precludes histological examination.

Order Acanthodida Berg, 1940

Family Acanthodidae Huxley, 1861

***Acanthoides* Brotzen, 1934**

Diagnosis

Acanthodian scales with smooth, glistening, usually more or less convex crown, translucent on edges, quadrangular to rhomboidal in outline, with short neck and thick, rounded inverted pyramidal base (Wells 1944:28).

***Acanthoides* sp.**
Figures 3O, P

Material

Eleven scales (QMF 31827 + ten others).

Locality

SD204/120 m; Papilio Formation.

Stratigraphic level

Givetian (Middle *varcus* Zone).

Description

The crown of the scales is flat and unornamented (Figure 3P), the pointed posterior edge extends beyond the base, and the anterior and lateral edges incline slightly ventrally. The neck is deep and indented, and the highly convex base is deepest towards the anterior of the scale (Figure 3O). These scales, together with *Nostolepis* sp. 2 described above, are the smallest of the acanthodian scales recovered, with length and width 0.3–0.4 mm, and height about 0.2 mm. The better-preserved scales have a transparent honey-coloured crown and an opaque black base; other scales are totally black.

Discussion

Confusion has arisen in the literature between scales assigned to the genera *Acanthodes* Agassiz, 1833 and *Acanthoides* Brotzen, 1934. Wells (1944) recognises *Acanthoides* as a form genus, distinct from the Carboniferous *Acanthodes*, whereas Denison (1979) acknowledges *Acanthodes* from the Carboniferous and Permian, but suggests that forms assigned to various species of *Acanthoides* are in fact synonymous with *Gomphonchus* Gross, 1971 and possibly *Nostolepis* Pander, 1856. Storrs (1987: 365) and Turner (Boucot *et al.* 1989:572) discuss this problem, Turner suggesting that the whole classification of smooth-crowned acanthodian scales from the Middle Devonian needs revision. The scales described here are assigned to *Acanthoides*, using Wells's concept of a form genus for smooth-crowned scales considered too old to belong to the Carboniferous and Permian genus *Acanthodes*.

The Broken River scales strongly resemble specimens named *Acanthodes? dublinensis* figured by Gross from the early Middle and late Late Devonian (1973, plate 27, figures 8–11 and 16–17), by Vieth from the Emsian and Eifelian (1980, plate 8, figures 21–22), and by Storrs from the Givetian and Frasnian (1987, figures 5–6), although these illustrations more closely fit the description given by Wells (1944:29) for *Acanthoides dublinensis* than that by Stauffer (1938:442) for *Acanthodes ? dublinensis*. In Australia, the genus *Acanthodes* has been reported, but not described or figured, from the Middle Devonian of Broken River, and Early Carboniferous of Victoria and Queensland (Long and Turner 1984). Also from Australia are scales of *Howittacanthus kentoni* from the Frasnian Mt Howitt locality in eastern Victoria (Long 1986). These small scales have a flat unornamented crown and are morphologically indistinguishable from those of *Acanthodes* (Long 1986).

Class Chondrichthyes Huxley, 1880

Infraclass Elasmobranchii Bonaparte, 1838

Order Cladoselachida Dean, 1894

Family Cladoselachidae Dean, 1909

***Cladolepis* Wells, 1944**

***Cladolepis* cf. *gunnelli* Wells, 1944**
Figures 4A–C

These specimens have been described and discussed elsewhere (De Pomeroy 1994). They are included here because the range of this form at Broken River is longer than previously reported.

Scales of *Cladolepis* cf. *gunnelli* Wells, 1944 (Figures 4A–C) occur in Givetian to earliest Frasnian (Middle and Upper *varcus, hermanni–*

cristatus and *asymmetricus* zones) horizons at Broken River. *Cladolepis* sp. scales have been reported from the early Eifelian Lauch Formation of Germany (Vieth-Schreiner 1983) in horizons of *patulus* Zone age (Weddige 1977); the late Emsian Santa Lucia Formation of Spain (Mader 1986); and the Middle Devonian of North America (Wells 1944; Gross 1973) in horizons dated *kockelianus* Zone or earlier (Klapper and Johnson 1980). None of these occurrences is as young as the Broken River specimens. Scales possibly belonging to the genus are reported from the middle Givetian-early Frasnian Holy Cross Mountains of Poland (Liszkowski and Racki 1992), and the *gigas* Zone (early Frasnian) Mostyn Vale Formation of NSW (Turner 1993).

Ohiolepis Wells, 1944

Ohiolepis sp. Wells, 1944

Figures 4D–G

These specimens have previously been described and discussed (De Pomeroy 1994). They are included here simply as part of the comparison of ranges of the Broken River fauna with occurrences reported elsewhere. Scales assigned to the genus are present in horizons of Middle and Upper *varcus* zones at Broken River (Figure 2), which is later than other reports. However, the concept of the genus appears to have become confused over the years (see De Pomeroy 1994) and is in need of revision, so the apparent late appearance of these scales at Broken River is at present considered of little significance.

Order Euselachii Hay, 1902

Superfamily Ctenacanthoidea Zangerl, 1981

Family Phoebodontidae Williams, 1985

?Phoebodontid indet.

Figures 4H, I

Material

Two broken cusps (QMF 31831 and one other).

Localities

SD128/134.1 m and SD164/124.1 m; Papilio Formation.

Stratigraphic range

Givetian (Middle *varcus* and *hermanni–cristatus* zones).

Remarks

The Broken River fragments are similar to cusps of *Phoebodus australiensis* and *P. politus* from the late Famennian of Thailand discussed and figured by Long (1990 figures 2–4). These two species have three- and four-cusped teeth with, respectively, three to four and seven to ten coarse vertical striae on the lingual surface (Long 1990), compared with six striae on the Broken River specimens. The Broken River specimens also resemble cusps of *P. bifurcatus*, where the labial face of some cusps bears strong, subparallel ridges, as found at late Frasnian localities in the South Urals (Ginter and Ivanov 1992: figures 4A–F, 5D–H). Turner (1982, figure 6A) illustrates a 3-cusped tooth assigned to *Phoebodus* cf. *politus*, from the Famenian Burdekin Star Shelf in Queensland. These cusps have longitudinal, raised striae, similar to the ornament on the Broken River specimens.

Description

The conical fragments are less than 1 mm long, with a small central pulp cavity, six straight longitudinal ridges on one side, and a circular cross-section. Under high magnification (Figure 4I), finer oblique striations are visible between the ridges; the other side of the cusp is smooth. Both fragments are apical ends of cusps, and are not curved.

Discussion

Phoebodont teeth are known from the Middle Devonian to Late Carboniferous (Zangerl 1981). Other reported Middle Devonian phoebodont teeth include the two species of *Phoebodus* erected by Wells (1944) from North American material, *P. floweri* with three to five slightly spiralling striations on one side of the cusp, and *P. ? bryanti* with smooth cusps and ovoid cross-section, figured by Gross (1973: plate 34, figure 23, plate 35, figures 7–8); those of the middle and late Givetian of the Holy Cross Mountains in Poland (Liszkowski and Racki 1992, figures 3, 4L–N); and a Givetian tooth from section SD146 at Broken River, reported by Turner (1993).

Chondrichthyan incertae sedis

Figures 4J–L

Material

Sixty-one teeth (QMF 31832,3 and 59 others).

Localities

SD15/115.6 m, SD127/43 m, SD128/68.6–132 m, SD130/25.5–109.3 m, SD164/40.2–80.8 m, SD210/75–104 m, SD216/25–106 m, and SAGW/20 m; Papilio Formation, Spanner and Chinaman Creek limestones.

Stratigraphic range

Givetian (*kockelianus* to *varcus* zones).

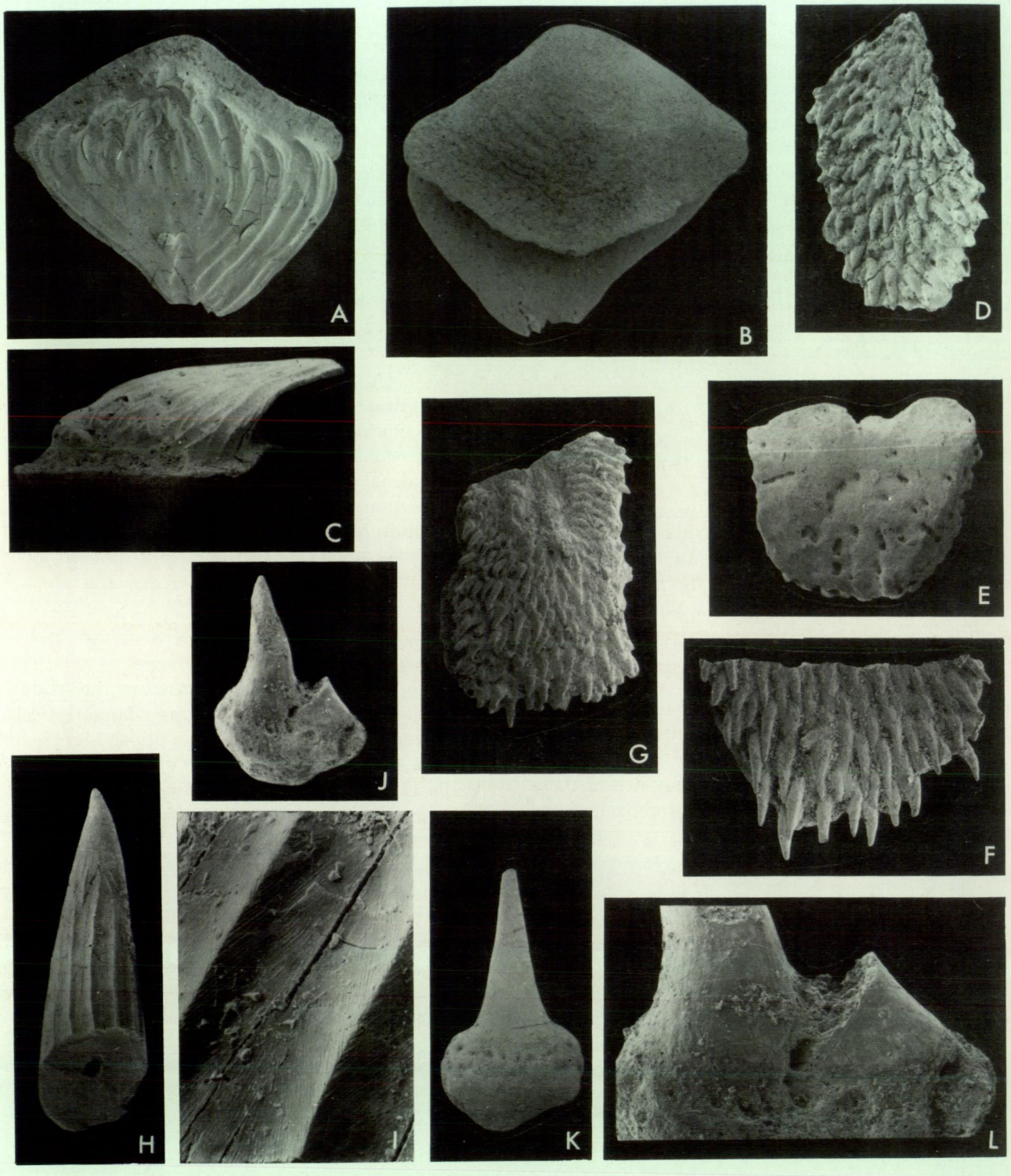

Figure 4 **A–C**, *Cladolepis* cf. *gunnelli* Wells, 1944. **A,B**, crown and base views x30, **C**, lateral view x40 of scale QMF26100, SD190/60.

D–G, *Ohiolepis* sp. Wells, 1944. **D**, crown view of scale QMF26103, x45, SD130/265.9 m. **E**, base view of scale QMF 31828, x45, SD204/120 m. **F**, crown view of broken scale QMF 31829, x60, SD204/120 m. **G**, crown view of scale QMF 31830, x45, SD204/120 m.

H,I, ?phoebodontid indet. **H**, x100, **I**, surface detail x220 of cusp QMF 31831, SD164/124.1 m.

J–L, chondrichthyan incertae sedis. **K**, lateral view of tooth QMF 31832, x55, SD15/187.6 m. **J**, lateral view x45, **L**, detail x110 of tooth QMF 31833, SD210/104 m.

Remarks

Few Palaeozoic chondrichthyan teeth figured in the literature are single-cusped, a condition considered by Zangerl (1981) to be the least specialised morphological type. One monocuspid form, however, is *Cobelodus aculeatus* (Cope) described by Zangerl and Case (1976) from the Late Carboniferous of North America; teeth from the upper dentition (Zangerl and Case 1976, figure 16; Zangerl 1981, figure 8E) are similar to the Broken River specimens in the single conical cusp being attached to a bulbous base, but differ in the cusp being longer and finely striated.

Figured teeth of *Antarctilamna prisca* and *"Xenacanthus"* sp. (the latter recently referred to a new genus *Portalodus* – Long and Young 1995) from the late Givetian or early Frasnian Aztec Siltstone in Antarctica (Young 1982, text-figure 3, plate 89, figures 1–4) bear a slight resemblance to the Broken River specimens. Histologically, the Broken River specimens have a similar structure to that described by Young (1982) for *Antarctilamna* teeth. However, the Antarctic teeth differ in being diplodont, in having the cusps curved, partly striated, perhaps with an accentuated striation or flattened side close to the base to form a cutting edge, and in the root being concave with a torus on the lingual side (Young 1982).

Description

The conical teeth are set centrally or towards one edge of a bulbous, subspherical base. One specimen (Figure 4J) from SD210/104 m in middle *varcus* Zone has a small second cusp; both cusps are broken distally. All other specimens are single-cusped. The cusps are about 0.4–0.5 mm long, smooth and uncurved, with a circular cross-section and blunt tip. Apart from the two-cusped specimen, the teeth are similar in size and shape; this lack of variation is common in Devonian elasmobranchs (Young 1982). The base has a ring of small holes close to the base of the tooth (Figure 4K). In some specimens, the central part of the base contains a spherical pulp cavity that extends a short distance into the cusp in a broad conical shape; in others, the base has no foramina or cavities.

Discussion

The samples containing these chondrichthyan teeth have also yielded numerous disarticulated scales, assigned to three new chondrichthyan form genera: *Gondwanalepis*, *Notiolepis* and *Aussilepis*, with respective ranges of *kockelianus* to younger than *varcus*, mid-*ensensis* to younger than *varcus*, and *ensensis* to younger than *varcus* (De Pomeroy 1994). As the stratigraphic ranges of these scales and that of the 61 teeth are similar, it is possible the teeth are from one of these genera.

Class Elasmobranchiomorphi

Subclass Placodermi

Order Arthrodira Gross, 1932

Arthrodire indet.

Figures 6G, H, J

Material

One possible arthrodire infragnathal (lower dermal jaw bone) (QMF 31852) and one scale (QMF 31853).

Localities

QMF 31852: SD198/67.6 m; Lomandra Limestone.
QMF 31853: SD170/200 m; Bracteata Formation.

Stratigraphic levels

QMF 31852: Givetian (*varcus* Zone).
QMF 31853: Emsian (*serotinus* Zone).

Remarks

This scale (QMF 31853) is dissimilar to the asterolepidoid antiarch *Wurungulepis* (see Young 1990, figure 13), the only other placoderm scale type described from this area. The ornament resembles that on scales of a buchanosteid arthrodire from Taemas (specimen CPC 16965, held at AGSO, Canberra). In the Broken River specimen the radiating ridges extend to the top of the tubercles, in contrast to the tubercles of CPC 16965, which are smooth in the centre and ridged only around the edges, but this scale type also occurs at Taemas (e.g. *'Ohioaspis tumulosa'* Giffin 1980, figure 3). Similar "buchanosteid"-type body scales are illustrated from the Lochkovian (*delta* Zone) of Nevada (Turner and Murphy 1988:962, figures 2.8–2.12).

Description

Fragment QMF 31852 (Figures 6G, H) measures almost 2mm long and just over 1mm high. Four spatulate denticles are ankylosed to the upper (dorsal) surface, with no obvious delineation between the material of the denticles and that of the bone. Two small foramina, probably for the passage of nerves or vessels (arrows in Figure 6H), are situated near the anterior margin of the bone. The ventral surface has a deep longitudinal groove, which would contain the meckelian cartilage if interpretation as an arthrodire infragnathal is correct. This groove starts a short way back from the blunt anterior tip of the bone, immediately posterior to a foramen (lower arrow in Figure 6H). The sides of this deep groove are composed of thin bone, in contrast to the more robust structure of the dorsal denticulate region and the solid anterior tip. One side extends further ventrally than the other (Figure 6G). Along one lateral surface a

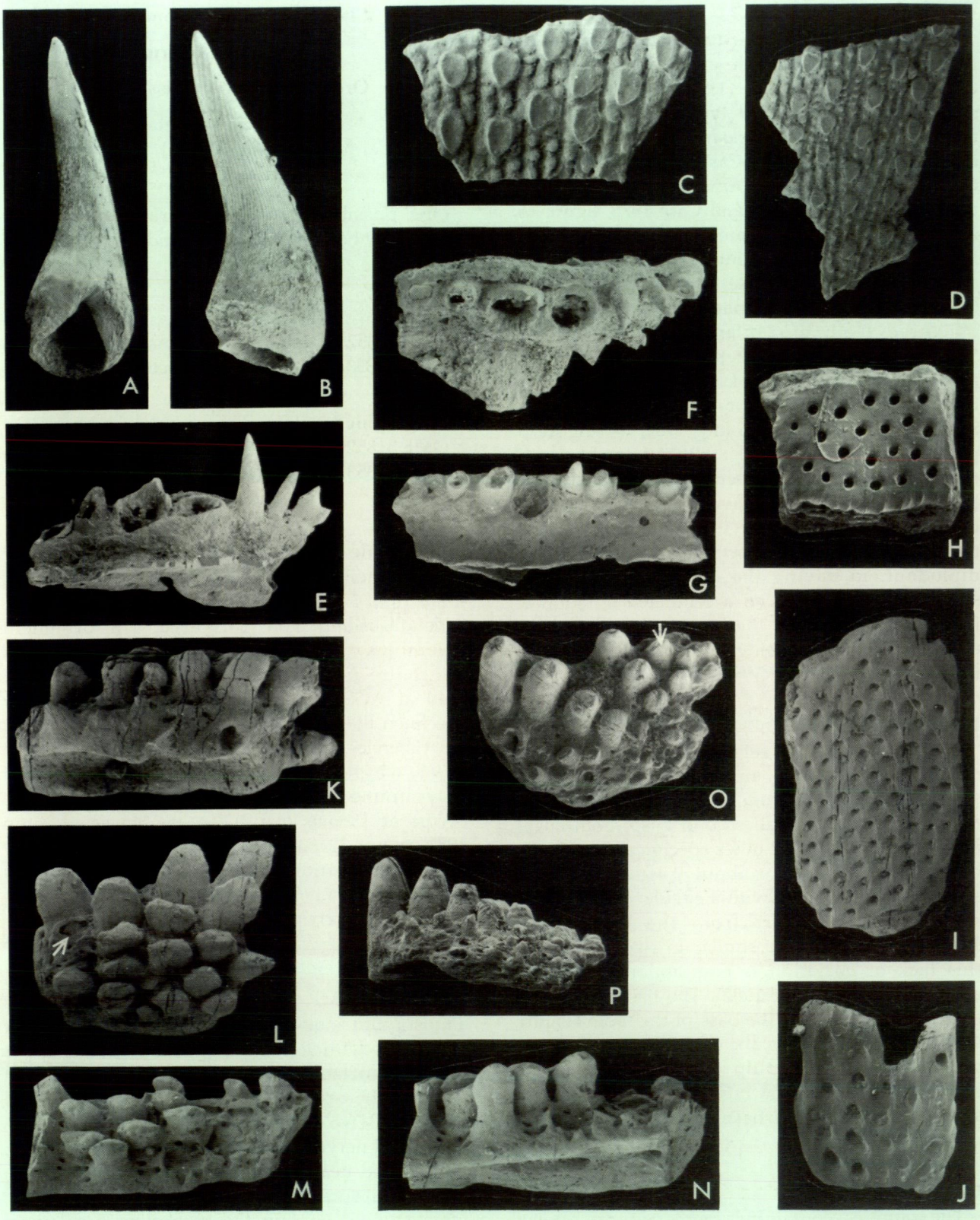

Figure 5 **A–G**, onychodontid indet. **A**, lateral view of tooth QMF 31834, x12, SD111/245 m. **B**, lateral view of tooth QMF 31835, x30, SD128/190 m. **C,D**, crown view of scale fragments. **C**, QMF 31836, x60, SD164/24.7 m. **D**, QMF 31837, x40, SD164/24.7 m. **E**, lateral and **F**, dorsal views of tooth-bearing bone fragment QMF 31839, x35, SD216/35 m. **G**, latero-dorsal view of tooth-bearing bone fragment QMF 31838, x30, SD210/87.7 m.

H–J, cosmine scales, all crown view. **H**, QMF 31840, x30, SD15/148.5 m. **I**, QMF 31841, x30, SD204/120 m. **J**, QMF 31842, x60, SD210/87.7 m.

K–N, ?osteichthyan indet. **K**, lateral view x50, **L**, dorsal view x45 of toothplate fragment QMF 31843, SD204/120 m. **M**, dorsal and **N**, lateral views of toothplate fragment QMF 31844, x45, SD204/115.9 m.

O,P, ?dipnoan indet. probable toothplate. Crown and lateral views of QMF 31845, x30, SD131/117.7 m.

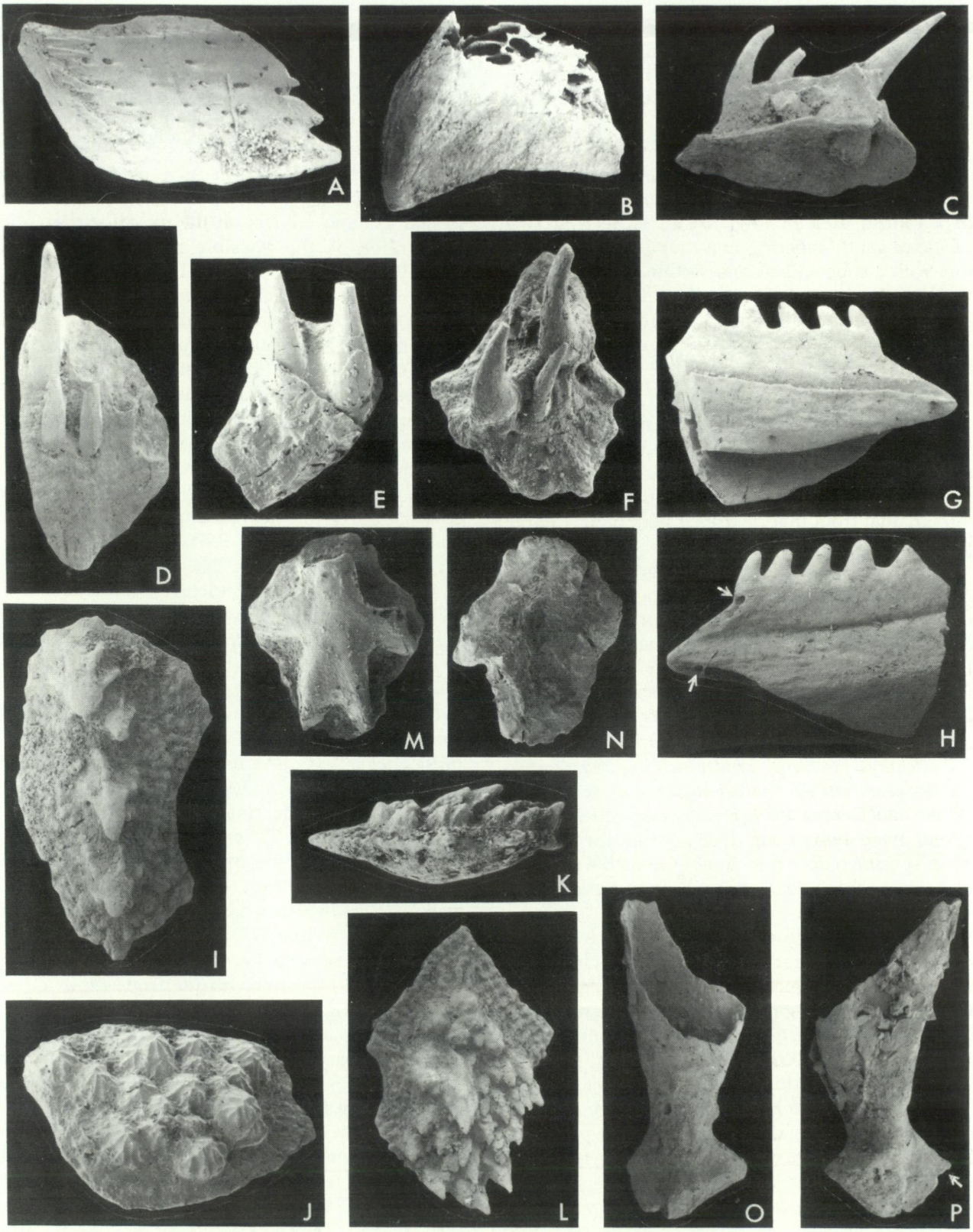

Figure 6 **A**, palaeoniscoid indet., crown view of scale QMF 31846, x30, SD192/60 m.
B, ?ptyctodontid indet., lateral view of probable supragnathal QMF 31847, x20, SD111/29 m.
C–F, palaeoniscoid indet. tooth-bearing plates. **C**, latero–basal view of QMF 31848, x75, SD204/95 m. **D**, top view of QMF 31849, x35, SD204/120 m. **E**, top view of QMF 31850, x65, SD15/148.5 m. **F**, top view of QMF 31851, x90, SD210/87.7 m.
G,H, arthrodire indet. infragnathal fragment, **G**, lingual, **H**, labial views of QMF 31852, x30, SD198/67.6 m.
I, placoderm indet., crown view of scale QMF 31855, x55, SD238/227 m.
J, arthrodire indet., crown view of scale QMF 31853, x60, SD170/200 m.
K, L, placoderm indet. **K**, lateral view x30, **L**, crown view x35 of scale QMF 31854, SD128/130.8 m.
M,N, thelodont indet. **M**, crown view, **N**, basal view of scale QMF 31856, x60, SAG/26.8 m.
O,P, ?ptyctodontid indet. quadrate, QMF 31857, x20, SD15/145.6 m.

shallow groove runs parallel to the dorsal margin (Figure 6H); on the other lateral surface a narrow lengthwise ledge is found in the same position (Figure 6G). The posterior part of the bone is broken (Figure 6G).

The scale QMF 31853 (Figure 6J) measures 1mm across the greatest diameter, with a gently convex base and no discrete neck. The ornament consists of a central area of low, broad, closely-packed tubercles gently tapering to a rounded point at the top, with a subcircular cross-section, and up to ten irregularly radiating, sometimes bifurcating, ridges, and small, indistinct nodes on the margins of the scale.

Discussion

Young (1993) mentions the presence in the Broken River Formation of large eubrachythoracid arthrodires, such as the homostiid *Atlantidosteus*. However, homostiids have a different type of infragnathal from that described here (G C Young, pers. comm.).

Infragnathals have been described from other Australian arthrodires, all eubrachythoracids: *Goodrdigbeeon australianum* from the Early Devonian Taemas Formation at Taemas and Wee Jasper, NSW (White 1978), and from the Frasnian Gogo Formation in WA *Harrytoombsia elegans, Camuropiscis concinnus, Rolfosteus canningensis, Tubonasus lennardensis, Bruntonichthys multidens, Bullerichthys fascidens, kendrickichthys cavernosus, Incisoscutum ritchiei* and *Latocamurus coulthardi* (Miles and Dennis 1979; Dennis and Miles 1979a, 1979b, 1980, 1981; Long 1988). While the Broken River specimen does not strongly resemble any one of these published forms, it does have some common characters.

Arthrodire infragnathals consist of two main regions – the anterior biting region, usually accupying approximately half the total length of the bone, and commonly bearing one or more rows of teeth, and a posterior expanded blade (Miles and Westoll 1968; White 1978; Miles and Dennis 1979; Dennis and Miles 1979a, 1979b, 1980, 1981). This specimen is interpreted as part of the anterior biting region of the infragnathal, with the posterior blade missing. It possesses, in common with other described specimens, the deep ventral longitudinal groove for meckels cartilage, a shallow groove on the lateral surface, and denticles or teeth in the biting region. The Broken River specimen differs from previously described specimens in the anterior region, the position of the shallow lateral groove, and the shape and position of the denticles.

The deep ventral groove, found in the Broken River specimen, is commonly, but not always, present in arthrodire infragnathals. A ventral groove for the mentomeckelian bone has been described in *Goodradigbeeon* (White 1978), *Bruntonichthys, Bullerichthys* and *Kendrickichthys* (Dennis and Miles 1980), and in Northern Hemisphere arthrodires *Coccosteus cuspidatus, Dunkleosteus, Titanichthys, Malerosteus* and some arctolepids, from the Middle Old Red Sandstone of Scotland (Miles and Westoll 1968).

The shallow lateral groove extends to the anterodorsal edge of the specimen (Figure 6H). A similar shallow groove, on the mesial surface and interpreted as the possible path of the ramus mandibularis internus VII, is reported in infragnathals of *Coccosteus, Harrytoombsia, Camuropiscis, Rolfosteus* and *Incisoscutum* (Miles and Westoll 1968; Miles and Dennis 1979; Dennis and Miles 1979a, 1979b, 1981), but occurring only on the posterior blade region parallel to the ventral margin, not on the anterior biting region as in the Broken River specimen. A shallow mesial groove has not been reported in *Goodradigbeeon, Bruntonichthys, Bullerichthys, Kendrickichthys* or *Latocamurus* (White 1978; Dennis and Miles 1980; Long 1988).

The nature of teeth on the biting region varies, and in some genera is difficult to determine as a result of the amount of wear caused by either the anterior or posterior supragnathal, or both (e.g. Dennis and Miles 1980). *Camuropiscis, Bruntonichthys* and *Incisoscutum*, for example, have two dorsal or mesial rows of teeth and a short anterior row of symphysial teeth (Dennis and Miles 1979a, 1980, 1981). The unworn part of the dorsal tooth row in *Bullerichthys* comprises ten pointed, forward-facing teeth, smallest posteriorly (Dennis and Miles 1980). *Tubonasus*, in contrast, has shearing edges on the infragnathal rather than a biting surface with teeth (Dennis and Miles 1979b), while *Goodradigbeeon* has no apparent teeth or cutting edges (White 1978).

The spatulate denticles on the dorsal edge of the Broken River specimen differ from these other arthrodires. The biting region is not flattened, but the denticles are aligned longitudinally aong a narrow dorsal ridge. There are no anterior symphysial teeth; the anterior extremity of the Broken River infragnathal narrows and extends slightly ventrally, in contrast to the dorsally-curving anterior end of other described infragnathals (e.g. *Camuropiscis* Dennis and Miles 1979a, figure 14a, b; *Bullerichthys* Dennis and Miles 1980, figure 12A, C; *Kendrickichthys* Dennis and Miles 1980, figure 20A, B).

Abundant buchanosteid-type scales occur in the Emsian Taemas-Buchan fauna (Schultze 1968; Giffin 1980; G.C. Young, pers. comm.), in horizons of a comparable age to those at Broken River where only a single similar specimen was recovered, despite extensive sampling (particularly in section SD170). These two regions, although separated by approximately 2000 km, were both shallow marine

environments situated on the northeastern margin of Gondwana during the Devonian (Scotese and McKerrow 1990), and so could be expected to have similar faunas. Indeed, preliminary studies of microvertebrate faunas from Buchan and Taemas reveal cheiracanthoid and nostolepid scales and onychodontid teeth, not unlike those found at Broken River.

Order Ptyctodontida Gross, 1932

Family Ptyctodontidae Woodward, 1891

?Ptyctodontid indet.

Figures 6B, O, P

Material

One probable supragnathal (upper toothplate) fragment (QMF 31847; Figure 6B) and one quadrate (QMF 31857; Figures 6O, P).

Localities

QMF 31847: SD111/29 m; Dosey Limestone.
QMF 31857: SD15/145.6 m; Papilio Formation.

Stratigraphic levels

QMF 31847: Eifelian (*ensensis* Zone).
QMF 31857: Givetian (Middle *varcus* Zone).

Remarks

Specimen QMF 31847 (supragnathal) is placed tentatively in the family Ptyctodontidae as is has a wedge-shaped cross-section similar to *Ctenurella gardineri* (and as reported by Watson 1938 in *Rhamphodopsis*) and the anteroventral corner of the biting edge extended into a slight, rounded beak as in *C. gardineri* and *Campbellodus decipiens* (Miles and Young 1977). The Broken River specimen also resembles figured *Rhynchodus*-type supragnathals from the Frasnian and Famennian of Iran (Lelièvre *et al.* 1981: figure 23A,B). The broken dorsal edge of the specimen prevents observing the presence of an anterior dorsal process, found in *Ctenurella, Campbellodus* and *Rhamphodopsis trispinauts* (Miles 1967; Miles and Young 1977). The mesial surface just behind the anterior margin lacks the grooves common in ptyctodontids (Miles and Young 1977).

Specimen QMF 31857 (quadrate) is also placed tentatively in this family as it is similar to a quadrate of *C. gardineri* (Miles and Young 1977) recovered from the Frasnian Gogo Formation. This specimen differs from *C. gardineri*, however, in lacking the lateral and mesial ridges adjacent to the main shaft of the bone that articulated with the upper toothplate, and in possessing an articular process (arrow in Figure 6P) at the posteroventral end. Indeed, any placoderm group without dermal bones in the cheek (e.g. phyllolepids) could have a quadrate similar to this specimen (G.C. Young, pers. comm.).

Description

QMF 31847: The 2 mm long fragment is incomplete dorsally and posteriorly, with open spongy bone visible along the dorsal margin. the anterior margin is extended ventrally into a slight, rounded beak. The surface is unornamented and shows no evidence of lamellae or grooves.

QMF 31857: This fragment is about 2.5 mm long. The open, flared anterior end (Figure 6O) is hollow for about half the total length of the fragment. The opposite, posteroventral end has a solid, rounded condyle, interpreted as the articulating surface with the articular bone of the mandibular joint, and a separate shallow, hollow cylindrical process (arrow in Figure 6P).

Discussion

Quadrates from several arthrodires from the Frasnian Gogo Formation have been figured and described; none resemble the Broken River specimen. The quadrate of *Camuropiscis* is co-ossified with the palatoquadrate (Dennis and Miles 1979a), and that of *Rolfosteus* and *Kendrickichthys* with the postsuborbital plate (Dennis and Miles 1979b, 1980). In *Incisoscutum* and *Latocamurus* the quadrate is a separate, elongate bone (Dennis and Miles 1981; Long 1988).

Ptyctodontids had a pair of upper and lower toothplates that operated by crushing, grinding or shearing (Denison 1978). *Ctenurella, Campbellodus* and *Rhamphodopsis* have a shearing edge on the lingual surface (Miles 1967; Miles and Young 1977), whereas the biting areas of *Ptyctodus* and *Palaeomylus* bear tritors and rounded tritoral cusps, respectively (Ørvig 1960). The family has been reported from the Early Devonian of Iran and the Soviet Arctic, the Emsian Taemas–Buchan fauna of southeastern Australia, and the Eifelian to Famennian of North America, Europe, Scotland, former USSR, Iran, Libya and Australia (Hussakof and Bryant 1918; Ørvig 1960; Miles 1967; Miles and Young 1977; Denison 1978; Lelièvre *et al.* 1981, 1988).

Placoderm indet.

Figures 6I, K, L

Material

Three scales (QMF 31854,5 and one other).

Localities

SD128/137 m and SD238/227 m; Papilio Formation.

Stratigraphic level

Givetian (*varcus* Zone).

Description

The figured scales measure 1.1–1.2 mm along the

greatest diameter, and have a gently convex or flat base. The crown ornament consists of a central area of posteriorly-inclined, pointed, stellate tubercles. In one specimen (Figure 6K, L), the tubercles are closely-packed, with larger ones in the centre; in the other figured specimen (Figure 6I) the tubercles are more widely spaced. In both specimens the central tuberculated region of the crown is surrounded by a marginal area of small rounded nodes in concentric rows.

Discussion

Similar scales are figured by Obruchev and Karatajüte-Talimaa (1967, plate 1, figure 9), assigned to a rhenanid related to *Radotina* from the Early Devonian of eastern Europe; by Goujet (1976, plate 62, figures 12 and 14), assigned to an indeterminate radotinid from the Lochkovian–Pragian of France; and mentioned by Turner and Murphy (1988) from the Pragian Martin's Well Limestone at Broken River and from the Early Devonian of NSW.

Class Teleostomi

Subclass Osteichthyes Huxley, 1880

Infraclass Crossopterygii Huxley, 1861

Order Struniiformes Jessen, 1966

Family Onychodontidae Woodward, 1891

Onychodontid indet.

Figures 5A–G

Material

430 whole or parts of teeth (QMF 31834–5 and 428 others; Figures 5A, B); Two scale fragments (QMF 31836–7; Figures 5C, D); Eight tooth-bearing bone fragments (QMF 31838–9 and six others; Figures 5E–G).

Localities

QMF 31834–5: SD15/14.2–213.8 m, SD111/31–240 m, SD128/54.3–201.5 m, SD130/3.6–63.5 m, SD131/92.1–207.4 m, SD146/429.5 m, SD164/80.8–124.1 m, SD170/200–850 m, SD192/0–60 m, SD198/111.9 m, SD204/95–120 m, SD210/69.7–104 m, SD216/0–107 m, SAG/16.1–112 m and SAGW/17.1–20 m; Papilio and Bracteata formations, Lomandra, Dosey, Spanner, Stanley and Chinaman Creek limestones.

QMF 31836–7: SD164/24.7 m; Papilio Formation.

QMF 31838–9: SD15/107.9 m, SD128/104.2–118.8 m, SD204/114.2–115.9 m, SD210/87.7 m and SD216/29.2 m; Papilio Formation and Spanner Limestone.

Stratigraphic ranges

QMF 31834–5: Emsian (*serotinus* Zone) to earliest Frasnian (*asymmetricus* Zone).

QMF 31836–7: Givetian (Upper *varcus* Zone).

QMF 31838–9: Givetian (Lower and Middle *varcus* zones).

Remarks

The teeth are compatible with the description by Wells (1944:44) of the prearticular and coronoid series set in the jawbone between the longer, more slender dentary teeth.

The scale fragments resemble the *Onychodus* scales discussed and figured by Wells (1944:44, figure 9c). Scales with ornament of horseshoe-shaped denticles with a flattened or slightly concave top face have also been described or figured in the literature from porolepiforms and dipnoans: on scales of the porolepiforms *Heimenia ensis* Ørvig 1969 (figure 6D) and *Porolepis* (Ørvig 1957, figure 8C) along the anterior border, and *Laccognathus* and *Glyptolepis* (Ørvig 1957, figures 2B, 4C, 10B) on the overlapped portion; scales of the onychodontid *Onychodus* (Ørvig 1957, figures 7C, E); and the dipnoan *Iowadipterus halli* Schultze, 1992 (figure 9A). However, in none of these scales are the horseshoe-shaped tubercles interspersed with smaller, rounded tubercles arranged linearly, as in the Broken River specimens.

The tooth-bearing bone fragments resemble those of *Onychodus* sp. (e.g. Wells 1944, plate 3, figure 37; Vieth-Schreiner 1983, plate 4, figures 44–45), and are socketed in the jawbone. However, these teeth are smooth, in contrast to the striated teeth of *Onychodus*.

Description

QMF 31834–5: The teeth are slender, conical and curved with fine longitudinal striations; the striations cover the whole surface of the cusp, unlike the chondrichthyan phoebodont cusp discussed above, with striations only on the labial surface. Length ranges from 0.5 mm to approximately 2.5 mm. The base of most specimens is tapering and nonfluted.

QMF 31836–7: Surface ornament is of coarser horseshoe-shaped, flattened denticles about 100 µm long and 50 µm high, interspersed with rows of finer tubercles (Figure 5C). The base of the scale fragments is flat and unornamented.

QMF 31838–9: The fragments are up to about 2 mm long, with smooth, conical, socketed teeth up to about 0.5 mm long. Broken cusps show a central pulp cavity (Figures 5F, G).

Discussion

A specimen from the Emsian *Spirifer yassensis* Limestone of the Murrumbidgee area, NSW, described by Ørvig (1969, figure 11c) as a pre-maxillary of a struniiform crossopterygian, has conical, socketed teeth with a central pulp cavity,

as found in the Broken River specimens (Figures 5F, G). Similar specimens are currently emerging from acid-leaching of material from Fish Hill, a limestone outcrop approximately 10 km northeast of SD216 (S. Turner, pers. comm.).

Onychodus sp. has been reported from the Early to Late Devonian of Australia, North America, Europe and the Middle East (Wells 1944; Blieck *et al.* 1980; Giffin 1980; Vieth-Schreiner 1983; Lelièvre *et al.* 1988; Turner and Murphy 1988). The distinctive conical, finely striated teeth of onychodontids are common in Australian microvertebrate residues throughout the Devonian (S. Turner, pers. comm.).

Infraclass Dipnoi Muller 1844

?Dipnoan indet.

Figures 5O, P

Material

One probable dipnoan toothplate (QMF 31845).

Locality

SD131/117.7 m; Papilio Formation.

Stratigraphic level

Givetian (Middle *varcus* Zone).

Description

The specimen is about 1.5 mm long, and has radiating rows of rounded conical denticles that increase in size towards the outer edge of the plate. The anterior edge of the fragment (to the bottom in Figure 5O) has closely-packed, smaller denticles. The underside is slightly concave, unornamented, and appears to be slightly rougher in texture than the smooth denticles. Possibly the specimen has split from the underlying bone along a basal pulp cavity, so that the base of the toothplate is missing.

Discussion

Three types of lungfish are known from Fish Hill at Broken River, approximately 10 km northeast of the present study area (S. Turner, pers. comm.).

Cosmine scales

Figures 5H–J

Material

Six scales or fragments (QMF 31840–2 and three others).

Localities

SD15/145.6–148.5 m, SD170/483 m, SD204/120 m, SD210/87.7 m, SD216/48.5 m; Papilio Formation, Lomandra and Spanner limestones.

Stratigraphic range

Eifelian (*costatus* Zone) and Givetian (Middle *varcus* Zone).

Remarks

Cosmine, a hard tissue composed of enamel plus dentine and perforated by pores, formed the surface layer of scales of Devonian crossopterygians and dipnoans.

Description

The scales have a shiny, coarsely porous surface layer. The pores are of similar size, fairly closely-packed, and regularly arranged (Figures 5H, I). The pores may open obliquely within semi-elliptical depressions (e.g. Figures 5I, J), or directly to the surface (Figure 5H).

Discussion

One scale (Figure 5H) has a square bse with a deep, wide groove running across the scale, and is much deeper than the others. It resembles lepidotrichia of the dipnoan *Dipterus* described and illustrated by Campbell and Barwick (1988, figures 29C, 30, 31A, B, C).

The semi-elliptical depressions in the cosmine have been illustrated in porolepiform rhipidistians (e.g. Schultze 1977, plate 13, figure 1a) but are absent in dipnoans, although this distinction may not be apparent in Early Devonian forms (V. Karatajute-Talimaa, pers. comm., 1994; E. Mark-Kurik, pers. comm., 1994). This generalisation may not apply in all cases, however, since porolepiforms and dipnoans are closely related (Chang and Smith 1992).

Infraclass Actinopterygii

Order Palaeonisciformes Hay, 1929

Palaeoniscoid indet.

Figures 6A, C–F

Material

One scale (QMF 31846) and 34 tooth-bearing plates (QMF 31848–51 and 30 others).

Localities

QMF 31836: SD192/60 m; Stanley Limestone.

QMF 31848–51: SD15/148.5 m, SD128/78.2–196.6 m, SD130/73.6–143 m, SD131/92.1 m, SD204/95–120 m, SD210/87.7 m, SD216/30.3 m and SAG/117.7 m; Papilio Formation, Spanner and Chinaman Creek limestones.

Stratigraphic range

QMF 31836: Earliest Frasnian (*asymmetricus* Zone).

QMF 31848–51: Eifelian (*ensensis* Zone) to Givetian (Upper *varcus* Zone), with one specimen from a horizon older than *ensensis* Zone.

Remarks

The Broken River scale is a similar shape to those of *?Moythomasia* sp. figured by Storrs (1987, figures 5.1 and 5.2) from the Givetian to Frasnian of Iowa, although these scales lack the surface holes of the Broken River specimen. Two scales figured by Liszkowski and Racki (1992, figures 9F and 9I), described respectively as *Moythomasia* (?) sp. and undet-ermined palaeoniscoid, resemble the Broken River scale in general morphology.

Description

The slightly broken, abraded scale measures almost 2 mm in length. It is thin and flat, and ornamented with rows of irregularly spaced canal pores. These rows of pores lie between the ganoine ridges (Janvier 1974). The area of overlap by adjacent scale(s) is smooth (Stamberg 1988). There is evidence of a series of parallel ridges, now worn, alongside the anterior margin. The posterior edge extends into short, broad denticles (Figure 6A).

The thin, conical teeth are attached to plates or bases (Figures 6C–F). The cusps range in length up to about 0.6 mm. The bases are generally thin and flat, and appear to consist of a less dense, bone-like tissue in contrast with the smooth, dense cusp material. Very few specimens have the acrodin tip still intact; in these, the delineation between the opaque enamel-coated main part of the tooth and the transparent tip is clearly marked.

Discussion

Moythomasia sp. is described as a whole specimen from the late Middle and early Late Devonian of Germany (Gross 1953) and the Frasnian Gogo Formation of WA (Gardiner 1984), and reported from Late Devonian unspecified horizons at Pandanus Creek, Broken River, Queensland (Long and Turner 1984), the Givetian of France (Lelièvre *et al.* 1986), and the Late Devonian of Iran (Bartram 1981). The Broken River scale differs in shape and ornament from other Early and Middle Devonian palaeoniscoid scales from eastern Australia, such as *Ligulalepis toombsi* (Schultze 1968; Giffin 1980) and indeterminate palaeoniscoid scales (Giffin 1980, figure 11) from the Early Devonian Taemas Formation.

The Broken River scale lacks the peg and socket articulation so it may have come from the area near the tail of the fish (Area D in Esin 1990, figure 2). In such scales the length exceeds the height, the peg and socket articulation is absent, and sculpture on the free field area of the scale is minimal (Esin 1990). Also, the Broken River scale has a similar rhombic shape to the *Amblypterina costata* (Eichwald) scale from Area D near the tail, figured by Esin (1990, plate VIII, figure 1).

?Osteichthyan indet.

Figures 5K–N

Material

Fifteen toothplate fragments (QMF 31843,4 and thirteen others).

Localities

SD15/66 m, SD128/78.2–188.4 m, SD131/117.7–208.3 m, SD164/24.7–117.7 m, SD204/115.9–120 m and SD216/96.2 m; Papilio Formation and Spanner Limestone.

Stratigraphic range

Givetian (Lower *varcus* to *hermanni–cristatus* Zones).

Description

The fragments range up to about 2 mm long. The top is covered by closely-packed, blunt spatulate denticles (Figures 5L,M); the longer side of these denticles is parallel to the longer edge of the fragments. The denticles are up to 0.3 mm high, and have a central pulp cavity (arrow in Figure 5L). The bony base has a wide shallow longitudinal groove on the underside, and its surface appears slightly porous and less dense than the surface of the unornamented denticles.

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