Earliest Devonian gnathostome microremains from central New South Wales (Australia)

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ABSTRACT

The vertebrate faunas in limestone samples of earliest Devonian age, which were collected from 10 localities near Trundle, central New South Wales, Australia, include scales of acanthodians *Nostolepis lacrima* Valiukevicius, 1994, *Radioporacanthodes porosus* (Brotzen, 1934), *Gomphonchus sandelensis* (Pander, 1856), *Trundlelepis* sp. and *Gomphonchoporus hoppei* (Gross, 1947), as well as scales and dermal bone fragments from romundinid, palaeacanthaspid and ?brindabellaspid placoderms, and scales of the palaeoniscoid *Terenolepis turnerae* Burrow, 1995. Although the vertebrate remains are not plentiful, the assemblages are significant in being dominated by taxa which are found in coeval deposits of the circum-Arctic region.

KEY WORDS
Acanthodii,
Placodermi,
palaeoniscoid,
Devonian,
Lochkovian,
Cookeys Plains Formation,
Australia.

RÉSUMÉ

Les plus anciens microrestes de gnathostome dévonien de Nouvelle-Galles du Sud centrale (Australie).

Dans des calcaires d'âge dévonien inférieur, des faunes de vertébrés ont été récoltées dans 10 localités près de Trundle, en Nouvelle-Galles du Sud centrale (Australie). Ces faunes incluent des écailles d'acanthodiens : *Nostolepis lacrima* Valiukevicius, 1994, *Radioporacanthodes porosus* (Brotzen, 1934), *Gomphonchus sandelensis* (Pander, 1856), *Trundlelepis* sp. et *Gomphonchoporus hoppei* (Gross, 1947), ainsi que des écailles et des fragments dermiques de placodermes romundinide, paleacanthaspide et ? brindabellaspide ; y sont associées des écailles de paleoniscoide *Terenolepis turnerae* Burrow, 1995. Bien que les restes vertébrés ne soient pas abondants, leurs assemblages sont significatifs. On y retrouve des taxons connus dans les dépôts de même âge de la région circum-arctique.

MOTS CLÉS
Acanthodii,
Placodermi,
paleoniscoide,
Dévonien,
Lochkovien,
Formation de Cookeys Plains,
Australie.

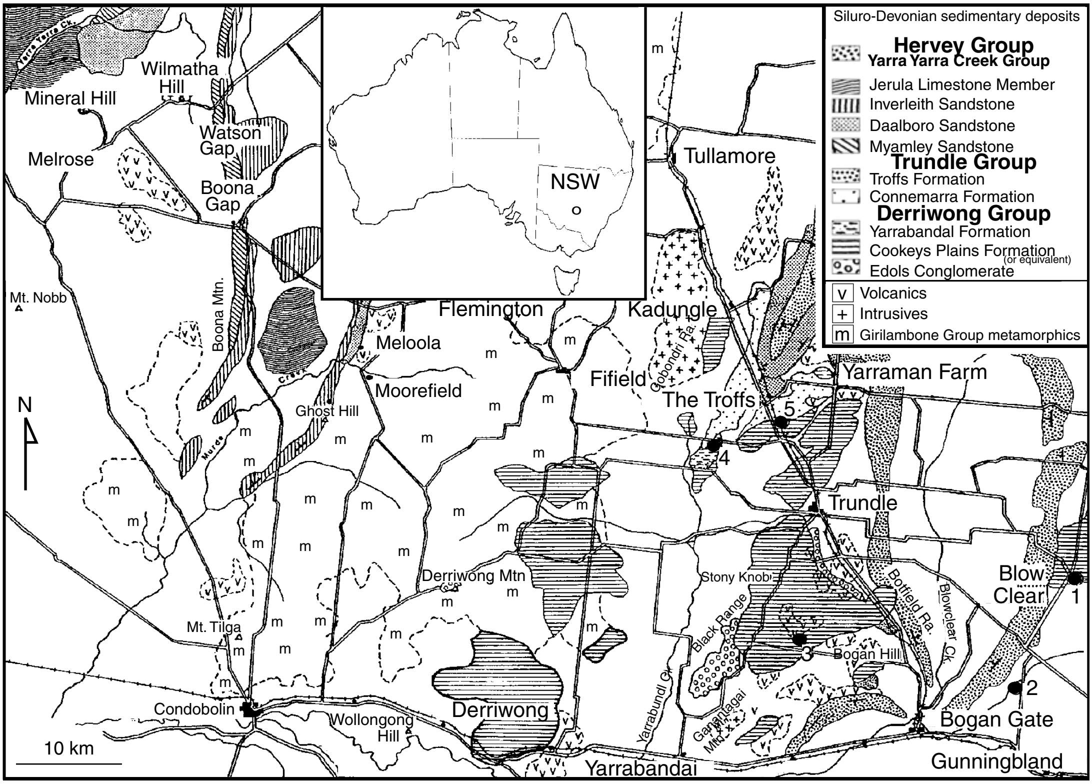

FIG. 1. — Locality and schematic geological map of the Trundle-Condobolin-Mineral Hill area of central New South Wales, Australia, showing approximate localities (•) which yielded the microvertebrate samples (after Földvary 2000: fig. 1): **1**, C920; **2**, C923-5, C937; **3**, Y4; **4**, C864-5; **5**, C866-7.

INTRODUCTION

Vertebrates from the earliest Devonian (early Lochkovian; *woschmidti-eurekaensis* Conodont zones) of Australia are relatively scarce, with faunas recorded from the Tumblong Oolite (Pickett *et al.* 1985; Burrow 2001), Clandulla Limestone and Yellowmans Creek Formation (Colquhoun 1995), and Windellama and Camelford limestones (Parkes 1995; Parkes *in* Basden *et al.* 2000) of New South Wales. The assemblages described in this study were in limestone samples from central New South Wales (Fig. 1; Table 1) which were collected by G. Dargan (GSNSW) for his investigations of the coral and conodont faunas (Dargan 1993) of this region. Most of the samples were collected from earliest Devonian limestones of the late Pridoli-early Lochkovian Cookeys Plains Formation, Derriwong Group (Sherwin 1996; Sherwin *et al.* 2000). The Derriwong Group rests unconformably on older units, and is overlain by the Early Devonian Trundle Group (Sherwin *et al.* 2000). The Cookeys Plains Formation includes a variety of poorly outcropping sedimentary rock types, mainly mudstones and well laminated siltstones, fine-medium sandstones, and small limestone lenses; the latter presumably represent areas of shallower deposition (Sherwin 1996). The type area is about 16 km WNW of Bogan Gate (see Fig. 1). Pickett & Ingpen (1990) and Pickett & McClatchie (1991) described the conodont faunas from several localities in the Formation, and Földvary (2000) described and analysed the Siluro-Devonian invertebrate fauna from 17 localities in the Cookeys Plains and Yarrabandai formations in

TABLE 1. — Vertebrate taxa in samples from Early Devonian limestones of the Cookeys Plains Formation and ?Connemarra Formation, central New South Wales, Australia. Symbols: **x**, < 10 scales/scale fragments/dermal bone fragments; **xx**, > 10 scales.

Taxon / Sample No.	**C864**	**C865**	**C866**	**C867**	**C920**	**C923**	**C924**	**C925**	**C937**	**Y4**
ACANTHODII		-		-			-			
Nostolepis lacrima					?1	8		24		1
"*N. applicata*"-type scale						1		1		
Nostolepis sp.						1		2		
Nostolepis sp. ?branchial scale								1		
Nostolepis sp. toothwhorl								1		
"*Nostolepis*" *guangxiensis*									4	
Gomphonchus sandelensis						4		13	2	
Radioporacanthodes porosus	1					5		3		
Gomphonchoporus hoppei	2							3		2
Trundlelepis sp.	9		1			1		4		1
Acanthodii indet. tooth						1				
Acanthodii indet. scales	3				4	1		7		1
PLACODERMI					-					
?brindabellaspid	x	x	x	x				x	x	
romundinid	x	x	x	x		x	x	xx	x	
palaeacanthaspid	?	x	x	x		x	?	xx	x	
?petalichthyid			x							
acanthothoracid other								x		
PALAEONISCOID					-	-	-	-	-	-
Terenolepis turnerae	x	x	x	x						

this region; the samples described here are from other sites, as listed in Table 2. A small microvertebrate fauna has previously been recorded (Turner 1993) from an older stratum (Pridoli, *eosteinhornensis* CZ) of the Cookeys Plains Formation; that fauna comprises scales of thelodont *Turinia* sp. and ischnacanthidid acanthodian *Gomphonchus*? *turnerae* (Burrow 2001), and was collected near Meloola, about 30 km W of sample sites C864 and C865. There is a gradational boundary between the Cookeys Plains Formation and the overlying Yarrabandai Formation (a fine-grained, laminated sandstone of early Lochkovian age) when contact is exposed (Sherwin *et al.* 2000). Although C923-5 and C937 map out in undifferentiated Siluro-Devonian deposits in Fig. 1, the grid references for the localities (Table 2) place them in limestone lenses of the Cookeys Plains Formation at North Gunning (cf. Sherwin *et al.* 2000: 72). Similarly, although C864-5 map out in the Yarrabandai Formation, because the samples are limestones they are presumed to have derived from another Formation. The composition of the gnathostome fauna indicates these samples, and also C866-7 (which map out in the Cookeys Plains Formation), could rather derive from the Connemarra Formation, Trundle Group, which overlies the Derriwong Group.

ABBREVIATIONS

CZ	Conodont Zone;
GI N	Institute of Geology, Vilnius;
IVPP	Institute of Vertebrate Palaeontology, Beijing;
MMMC	Collection of the Geological Survey of New South Wales (GSNSW);
NNM	Nationaal Natuurhistorisch Museum, Leiden;
UALVP	University of Alberta Vertebrate Paleontology Laboratory, Edmonton, Alberta.

SYSTEMATICS

Class ACANTHODII Owen, 1846
Family CLIMATIIDAE Berg, 1940

Genus *Nostolepis* Pander, 1856

TYPE SPECIES. — *Nostolepis striata* Pander, 1856.

HOLOTYPE. — Scale figured by Pander (1856: pl. 6, fig. 7) from the Late Silurian (Pridoli) Ohesaare Formation, Saaremaa, Estonia.

Nostolepis lacrima Valiukevicius, 1994

HOLOTYPE. — Scale GI N 30-1604 (Valiukevičius 1994: pl. XIX, fig. 10) from outcrop 775, layer 47, Lochkovian Urum Beds, Tareya River, Taimyr, Russia.

DIAGNOSIS (after Valiukevičius 1994). — Scales up to 0.6 mm long and 0.3 mm wide; four or five regularly-spaced sub-parallel ridges extending up to half the length of the crown; posterior part of crown narrows to a sharp point; neck low to moderate height; base smaller than crown and weakly convex; crown formed of two to four growth zones filled with simple mesodentine, without any wide canals; numerous lacunae in the embryonic growth zone; abundant fine bone cell cavities in the base.

MATERIAL EXAMINED (Table 1). — Eight scales from sample C923 including figured specimen MMMC2551 (Fig. 4A, B), 24 scales from C925 including figured specimens MMMC02555-7 (Fig. 2A-D, H), one scale from Y4, possibly one scale from C920.

DESCRIPTION

Morphology (Figs 2A-D; 4A, B)

The scales are relatively small, ranging from 0.2-0.4 mm wide and 0.3-0.4 mm long. Scale crowns are simple, with a rounded anterior margin bearing three to five short, sharp ridges which usually rise up directly from the base; on some scales the crown and base are separated by a short neck anteriorly. The ridges are evenly spaced and aligned radially relative to the posterior corner of the crown. The crown plane is horizontal, being smooth behind the ridges and with smooth, sharp postero-lateral edges. Most of the scales have an asymmetrical crown. The base is moderately swollen, with its maximum depth slightly forward of centre; a sharp rim often delineates the base/neck junction.

Histology (Fig. 2H)

The crown is quite shallow, and the base/crown junction is almost flat. Four growth zones form the crown. Poor preservation and remineralization have destroyed/obscured fine histological structures including dentine tubules and bone cell lacunae (if any); no durodentine or wide vascular canals are discernible.

REMARKS

Morphologically, the scales closely resemble the type material (Valiukevičius 1994: pl. XIX, figs 8-11) from the Uryum beds (mid-Lochkovian, spanning the equivalent of the *eurekaensis-delta* Conodont zones: Valiukevičius 2000: fig. 9) of Taimyr, northern Russia. The taxon has otherwise only been recorded from a borehole in the Timan-Pechora region of northern Russia (Valiukevičius 1994). The Australian scales resemble the type material in having a relatively flat-topped base and lacking vascular canals and durodentine (Valiukevičius 1994: fig. 64.3-6). However, Valiukevičius (1994) also described them as having a base filled with small bone cell cavities. Bases of the Australian scales are also filled with small "spots" which are possibly equivalent to these structures; however, they could have resulted from remineralization of the fibres penetrating the base rather than infilling of bone cell cavities (Fig. 2H). Scales with a comparable morphology have also been reported from the Windellama Limestone (*delta* CZ: Parkes *in* Basden *et al.* 2000: fig. 5.1-6: "*Nostolepis* sp. nov.") and the Garra Formation (*pesavis* CZ: Burrow *in* Basden *et al.* 2000; Burrow 2002: "Ischnacanthidae? nov. gen. et sp."; *Garralepis simplex*), both also in New South Wales, as well as from the Martins Well Limestone (*pesavis*?/*sulcatus* CZ), Broken River region, north Queensland (Turner *et al.* 2000: table 1: "*Gomphonchus*? n. sp. 1"; Burrow 2000, 2002: "Ischnacanthidae? nov. gen. et sp."; *Garralepis simplex*). Histological structure of the scales from the latter two strata differs from the *Nostolepis*-type (*sensu* Gross 1947) in having durodentine extensively developed in the upper centre of the crown growth zones, and in having numerous bundles of Sharpey's fibres layered through the base; unlike the scales of *N. lacrima*, the anterior crown margin on scales of *Garralepis simplex* is not separated from the base by a marked neck/base rim. The histological structure of the Windellama Limestone scales is not known.

Nostolepis? spp. indet.

MATERIAL EXAMINED (Table 1). — Two flank scales including figured scale MMMC02558

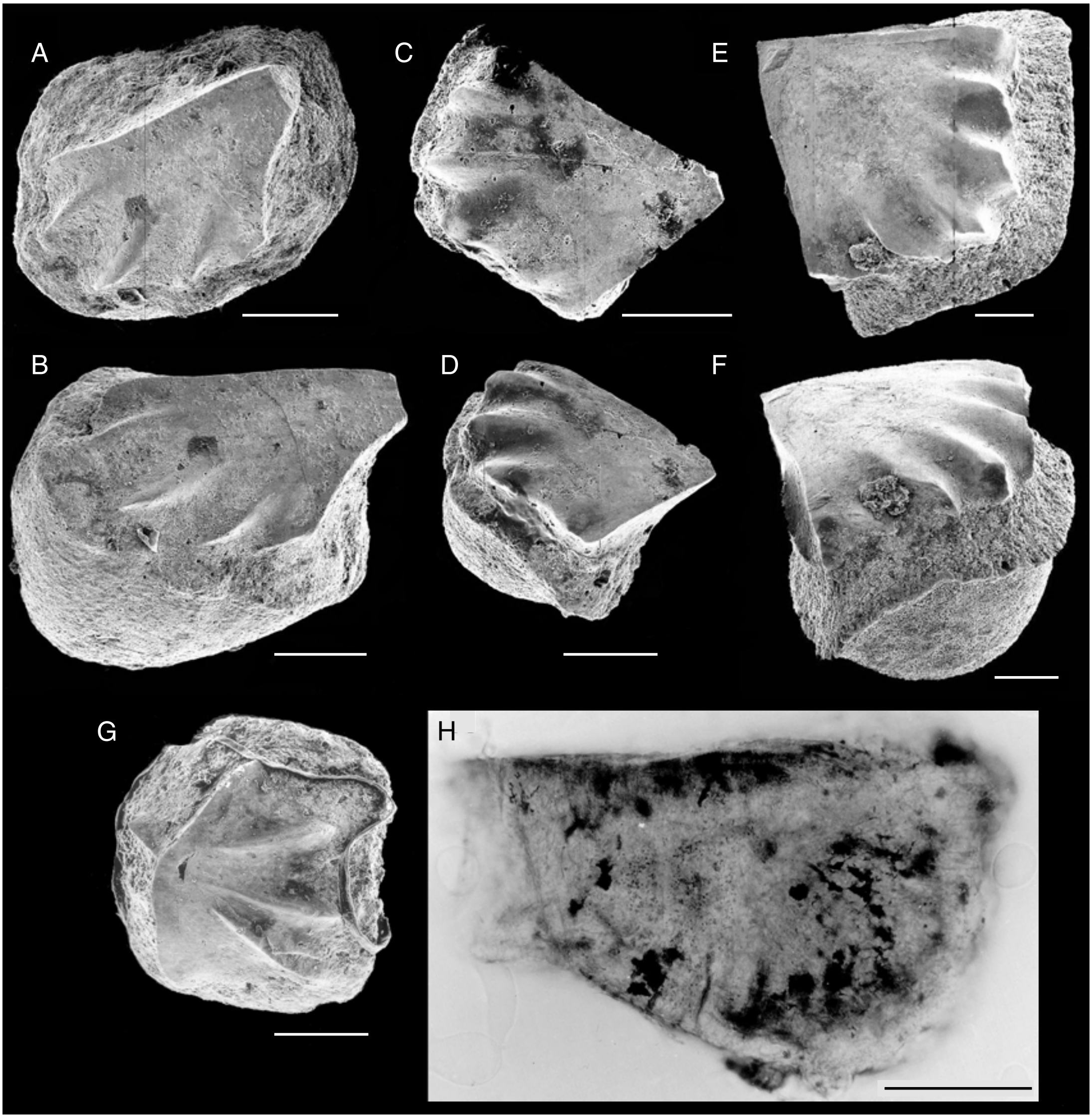

FIG. 2. — Acanthodian scales from sample C925, Cookeys Plains Formation (early Lochkovian), central New South Wales, Australia; **A**-**D**, **H**, *Nostolepis lacrima* Valiukevicius, 1994; **A**, **B**, specimen MMMC02555; **A**, crown view; **B**, antero-lateral view; **C**, **D**, specimen MMMC02556; **C**, crown view; **D**, lateral view; **H**, vertical longitudinal ground thin section MMMC02557; remineralization has obscured histological details; **E**-**G**, *Nostolepis* sp.; **E**, **F**, specimen MMMC02558; **E**, crown view; **F**, antero-lateral view; **G**, ?branchial scale MMMC02559 in crown view. Anterior of scale faces to left in A-D, and to right in E-H. Scale bars: 0.1 mm.

(Fig. 2E, F), a possible branchial scale MMMC02559 (Fig. 2G), one "*N. applicata*"-type scale and one tooth whorl MMMC02560 (Fig. 3A, B) from sample C925; one flank scale and one "*N. applicata*"-type scale MMMC02552 (Fig. 4C, D) from C923.

DESCRIPTION AND REMARKS

Flank scales (Fig. 2E, F)

These two scales are twice as big as those assigned to *N. lacrima*. MMMC02558 is 0.7 mm wide, with a horizontal crown, five short anterior crown ridges which are radially directed relative to the posterior corner, and a short diagonal ledge on each postero-lateral vertical face of the crown. Except for this ledge and their larger size, the scales are morphologically similar to those of *N. lacrima*; however, they also resemble scales which have been assigned to several other taxa including "*Gomphonchus* cf. *hoppei*" from the Lochkovian of Ellesmere Island (Vieth 1980: pl. 8, fig. 9) and *Nostolepis taimyrica* from the Pragian-Emsian of Tareya, Russia (Valiukevičius 1994: pl. XVIII, fig. 5a, b). Scales of this general shape have traditionally (although perhaps not correctly!) been assigned to *Nostolepis*. Because there are so few scales, their histological structure was not determined.

?Branchial scale (Fig. 2G)
Scale MMMC02559 has a crown which is smaller than the base, with three ridges extending almost to the weakly curved posterior edge, from the centre of which a single ridge extends down towards the base/neck rim. This scale type resembles flank scales of "*Nostolepis*" *guangxiensis* Wang, 1992 but differs in lacking a flat horizontal crown plane with a sharp posterior corner. Scales of this type are found in the branchial region of one of the enigmatic fish – specimen UALVP42273 – from the Lower Devonian MOTH site in the Northwest Territories, Canada (pers. obs.; G. Hanke pers. comm. 2000), and are likely to be a morphotype common to several different species.

*"*N. applicata*"-type scale (Fig. 4C, D)*
Scale MMMC02552 is 0.7 mm long and 0.4-0.5 mm wide, with a flat base having an irregularly polygonal outline. The ornament comprises separate areal growth zones stacked against each other like petals, most of which have broken off. Vieth (1980: pl. 4, figs 6-17) erected a new taxon *Nostolepis applicata* for scales with this general form from the Lochkovian Red Canyon River Formation Member A, Ellesmere Island, Arctic Canada. However, scales with this form have been recognized as a morphotype found in several different species, rather than being a biological taxon: e.g., the "tessera-like head platelets" of *Nostolepis linleyensis* Miller & Märss, 1999 (Miller & Märss 1999: pl. 5, figs 2-5) and some of the coronate plates and stellate tessera of *Nostolepis striata* (Gross 1971: pls 2, 3).

Tooth whorl (Fig. 3A, B)
This element is very small, being 0.4 mm wide and 0.3 mm long. Its base is slightly concave antero-posteriorly with a curved anterior and a straight posterior edge. The two teeth are extremely worn and flattened, with a shallow groove visible between them on the upper surface of the bone base. The teeth are presumed to have had larger central cusps, flanked by smaller cusps on the posterior tooth, which have all worn down to stubs. There is no indication of an enameloid surface on the teeth. The element, though smaller, shorter and more worn-down, resembles a tooth whorl of *Nostolepis striata* (Gross 1971: pl. 3, fig. 32a-c).

?Family CLIMATIIDAE

"*Nostolepis*" *guangxiensis* Wang, 1992

HOLOTYPE. — Scale IVPP V9745.1 (Wang 1992: pl. I, fig. 3a, b) from the Ertang Formation (early Emsian), Wuxuan County, Guangxi, China.

MATERIAL EXAMINED (Table 1). — Four scales in sample C937.

DESCRIPTION

The scales (not figured) are 0.6-0.8 mm wide and long, with a flat crown bearing about five short, regularly-spaced ridges along the anterior margin; posterior margins of the crown are straight and smooth. The crown is smaller than the base; short diagonal ridges radiate down the lateral faces of the crown from its posterior corner. The base is moderately swollen.

REMARKS

The type scales of *"Nostolepis" guangxiensis* are from the Lower Devonian Ertang Formation of

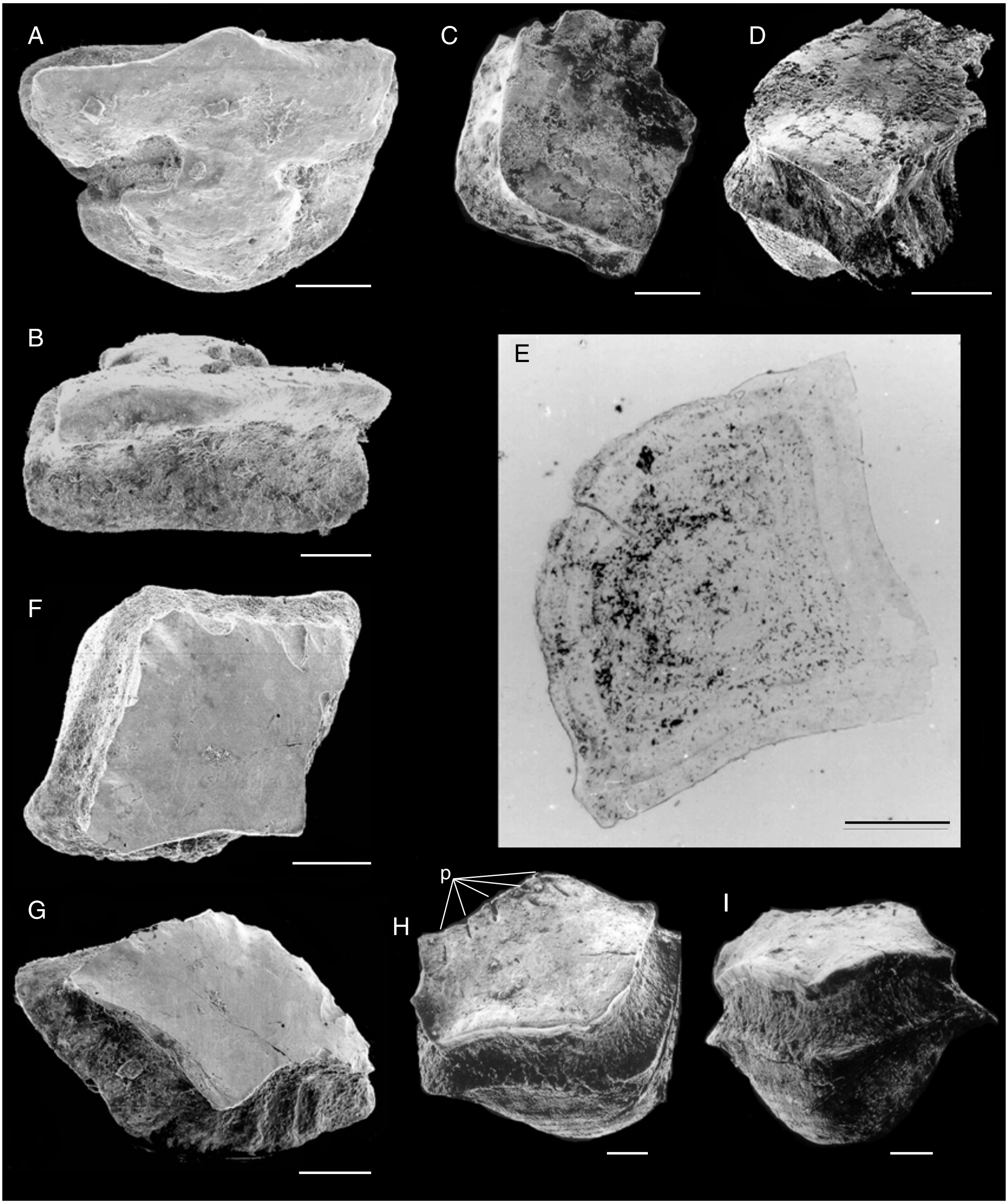

FIG. 3. — Acanthodian tooth and scales from sample C925, Cookeys Plains Formation (early Lochkovian), central New South Wales, Australia; **A**, **B**, *Nostolepis* sp. tooth whorl MMMC02560 in occlusal (lingual edge at top) and posterior and lingual views; **C**, **D**, *Gomphonchus sandelensis* (Pander, 1856) scale MMMC02561 in crown and lateral views, with anterior edge to the left (crown riddled with hyphal borings); **E**, *Trundlelepis* sp., horizontal ground thin section of scale crown MMMC02562, anterior edge to left; **F**, **G**, *Gomphonchoporus hoppei* (Gross, 1947) scale MMMC02563 in crown and posterior views, anterior edge at top; **H**, **I**, *Radioporacanthodes porosus* (Brotzen, 1934) *s.s.* scale MMMC02564 in antero-crown and anterior views. Abbreviation: **p**, pore rows. Scale bars: 0.1 mm.

Guangxi, China (Wang 1992: pl. 1, figs 3-5). Burrow (1997, 2001, 2002) described scales of this form from numerous eastern Australian localities of late Lochkovian-early Emsian age. The scales from C937 fit the most common morphotype of scales found in the Connemarra Formation (late Lochkovian-early Pragian), central New South Wales (Burrow 1997, 2001, 2002; Burrow *in* Basden *et al.* 2000).

Family ISCHNACANTHIDAE Woodward, 1891

Genus *Gomphonchus* Gross, 1971

TYPE SPECIES. — *Gomphodus sandelensis* Pander, 1856.

Gomphonchus sandelensis (Pander, 1856)

SYNTYPES. — Scales figured by Pander (1856: pl. 6, figs 15-17) from the Late Silurian (Pridoli) Ohesaare Formation, Saaremaa, Estonia. These types have been lost.

MATERIAL EXAMINED (Table 1). — Four scales in sample C923, 13 scales in C925 including figured specimen MMMC02561 (Fig. 3C, D) and two scales in C937.

DESCRIPTION (FIG. 3C, D)

The scales are about 0.4 mm wide and long. The crown is horizontal, forming a smooth surface without ridges; some scales have a shallow medial sulcus on the anterior crown edge. The posterior part of the crown extends behind the base. The neck is of medium height, concave all round, and with vertical "buttresses" posteriorly. The base/neck rim is sharp, and the base bulges slightly forward of the crown. The base is convex, resembling a rounded, upturned pyramid which flattens out towards the base/neck rim, and is always smaller in area than the crown.

REMARKS

G. sandelensis is widespread throughout northern Europe, being recorded from Upper Silurian (Ludlow) through Lower Devonian (Emsian) strata of the Baltic countries, Byelorussia, Ukraine, the Central Devonian Field, Timan-Pechora and Taimyr in Russia (e.g., Valiukevičius 1999, 2000), southern Great Britain (Vergoossen 1999a, 2000) and Spain (Mader 1983), and also from Arctic Canada (Vieth 1980) and possibly Greenland (Blom 1999). Vergoossen (1999a, b, 2000) delved into the difficulties of *Gomphonchus* taxonomy, erecting several new species and resurrecting one old species; the scales described herein are deemed to be *G. sandelensis* s.s.

Family PORACANTHODIDAE Vergoossen, 1999

Genus *Radioporacanthodes* Vergoossen, 1999

TYPE SPECIES. — *Poracanthodes porosus* Brotzen, 1934.

Radioporacanthodes porosus (Brotzen, 1934)

HOLOTYPE. — Scale figured by Brotzen (1934: pl. 3, fig. 2) from a Lower Devonian erratic boulder (Bey. 36), lowlands of north Germany. Type material appears to be lost.

DIAGNOSIS (summarized from Vergoossen 1999b). — Average to large porosiform scales; rhombic horizontal crown that is longer than wide, a round or angular anterior crown edge which is smooth or with 12 or more short radial ribs, and a medial sulcus; pore canal system developed in posterior half of crown, with up to six subparallel rows of pores; deep neck; deep, concave base.

MATERIAL EXAMINED (Table 1). — One scale in sample C864, four scales including MMMC02553 (Fig. 4E, F) in C923 and three scales including MMMC02564 (Fig. 3H, I) in C925.

DESCRIPTION (FIGS 3H, I; 4E, F)

The scales are mostly relatively large, being up to 1.0 mm wide. The crown has a smooth anterior margin with a medial sulcus. None of the scales are preserved whole, with most having the posterior crown broken off. MMMC02564 (Fig. 3H, I) has six radial canals running back from the centre of the crown, parallel to the broken edges of the postero-lateral sides. The neck is deeply concave all round, with a sharp rim separating it from the deep, rounded base. The smaller scale MMMC02553 (Fig. 4E, F) is much flatter, with a smooth crown having a medial sulcus on the

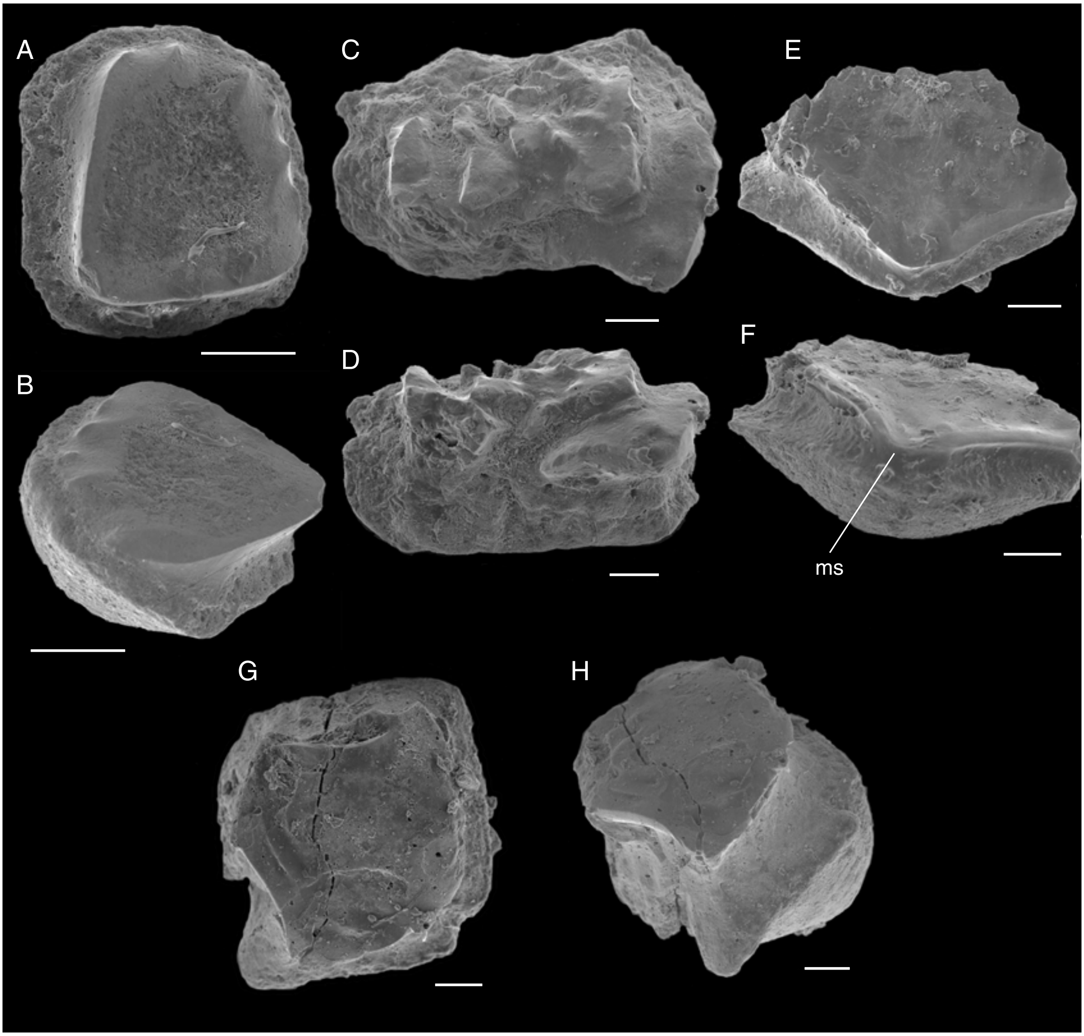

FIG. 4. — Acanthodian scales from sample C923, Cookeys Plains Formation (early Lochkovian), central New South Wales, Australia; **A**, **B**, *Nostolepis lacrima* Valiukevicius, 1994 scale MMMC02551 in crown (anterior edge to right) and lateral (anterior edge to left) views; **C**, **D**, *Nostolepis* sp. scale of "*N. applicata*"-type MMMC02552 in crown and lateral views (presumed anterior edge to left); **E**, **F**, *Gomphonchoporus hoppei* (Gross, 1947) scale MMMC02553 in crown (anterior edge at bottom) and anterior views; **G**, **H**, *Trundlelepis* sp. scale MMMC02554 in crown and lateral views (anterior edge to right). Abbreviation: **ms**, median sulcus. Scale bars: 0.1 mm.

anterior edge. Although the posterior crown has broken off, thus removing evidence of crown pores, the openings of six radial canals are visible high on the posterior neck.

REMARKS

The taxon *R. porosus* s.s. has been recorded from Pridoli-Lochkovian deposits in the Baltic, northern Germany, Great Britain (Vergoossen 1999b) and possibly Arctic Canada (Burrow *et al.* 1999) and Greenland (Blom 1999). Vergoossen (1999b) revised the taxonomy of the poracanthodidid acanthodians, excluding many of the poracanthodidid variants which have been assigned to "*Poracanthodes porosus*" over the years (e.g., those listed by Lehman 1937; Märss 1986; Valiukevičius

1998). The Australian scales conform to the smooth-crowned diagnostic type for *R. porosus* s.s.; some resemble a specimen from the Cape Phillips Formation (Late Silurian, Pridoli), Cornwallis Island, Arctic Canada which Burrow *et al.* (1999: fig. 6C) assigned to *Poracanthodes* sp. cf. *P. porosus*. Although MMMC02553 has a low neck and base, which would exclude it from *R. porosus* s.s. by Vergoossen's (1999b) diagnostic criteria, it is presumed such dorso-ventrally flattened scales are a rarer, non-typical scale form as has been noted in other taxa (e.g., *Trundlelepis cervicostulata* Burrow, 1997).

Genus *Gomphonchoporus* Vergoossen, 1999

TYPE SPECIES. — *Gomphodus hoppei* Gross, 1947.

Gomphonchoporus hoppei (Gross, 1947)

HOLOTYPE. — Scale f 449 figured by Gross (1947: pl. 24, fig. 7) from a Late Silurian erratic boulder, north Germany. Vergoossen (1999b: pl. 4, figs 42-44) erected a neotype NNM 423034, from a Pridoli-aged erratic, Oosterhaule, northern Netherlands.

MATERIAL EXAMINED (Table 1). — Two scales in sample C864, three scales including figured specimen MMMC02563 (Fig. 3F, G) in C925, and two scales in Y4.

DESCRIPTION (FIG. 3F, G)

These scales are up to 0.8 mm wide, relatively shallow, and wider than long. MMMC02563 (Fig. 3F, G) has numerous short, weak ridges along the anterior crown margin. The posterior part of the crown has broken off, creating concave postero-lateral edges (Fig. 3G), with no evidence preserved of a radial pore canal system. The neck is concave all round with "buttresses" on the posterior faces; the rounded base is shallow.

REMARKS

Vergoossen (1999b) erected the poracanthodidid genus *Gomphonchoporus* for scales which Gross (1947) had assigned to the ischnacanthidid genus *Gomphonchus*. Gross' type material was from northern German erratic limestones (Pridoli), and the taxon has been recorded from Pridoli-Lochkovian deposits of the Baltic, northern Europe and Great Britain (Valiukevičius 1998; Vergoossen 2000); Vergoossen (1999b) proposed a neotype (associated with a full range of variants) deriving from a Pridoli erratic collected from Oosterhaule, northern Netherlands. *Gomphonchoporus hoppei* has a relatively wide variety of scale forms, with some of the variants (particularly when poorly preserved) appearing indistinguishable to scales from *R. porosus*. Difficulty in separating scales of these taxa applies to Baltic samples comprising thousands of scales, as observed by Gross (1971) and Vergoossen (1999b), as well as to the small samples studied here.

?Family PORACANTHODIDAE

Genus *Trundlelepis* Burrow, 1997

TYPE SPECIES. — *Trundlelepis cervicostulata* Burrow, 1997.

HOLOTYPE. — Scale MMMC02239 (Burrow 1997: pl. 3, fig. 11) from the Lochkovian-Pragian (*pesavis-sulcatus* CZ) Connemarra Formation, near the Troffs railway station, central New South Wales.

Trundlelepis sp.

MATERIAL EXAMINED (Table 1). — Nine scales in sample C864, one scale in C866, one scale MMMC02554 (Fig. 4G, H) in C923, three scales and one ground thin section MMMC02562 (Fig. 3E) in C925, and one scale in Y4.

DESCRIPTION

Morphology (Fig. 4G, H)

The scales are relatively large, being up to 1.0 mm wide and long, with a horizontal crown bearing regularly-spaced ridges along the anterior edge; the ridges are placed radially relative to the posterior corner of the crown. Some scale crowns (not figured) have denticulated postero-lateral edges. The neck is deep and concave all round, with vertical buttresses on the posterior face, and most scales have a large convex base which bulges forward of the crown. Scale MMMC02554 has a diagonal ridge, or accessory growth zone, leading down and forwards from the posterior limit of the crown.

Histology (Fig. 3E)
The histological structure of the scale sectioned is of typical *Gomphonchus*-type, with finely-branching dentine tubules filling the crown.

REMARKS
The scales resemble the most common morphotype in the original material of *T. cervicostulata* Burrow, 1997 from the Connemarra Formation (late Lochkovian-early Pragian) in this region of central New South Wales. However, some of the scales have accessory growth zones off the postero-lateral edges of the crown (Fig. 4G, H) which are a distinguishing feature, in combination with radial canals, of scales of *Gomphonchoporus* Vergoossen, 1999. Such accessory growth zones are noted on scale variants of many Early Devonian taxa – e.g., *Nostolepis taimyrica* Valiukevicius, 1994 (Pragian-Emsian), *N. athleta* Valiukevicius, 1994 (Lochkovian-Pragian) and *N. tcherkasovae* Valiukevicius, 1994 (Lochkovian) from Tareya, Russia (Valiukevičius 1994: pl. XVIII, fig. 5; pl. XIX, fig. 14; pl. XX, fig. 4 respectively) – and also on scales of *Nostolepis halli* Blom, 1999 (Blom 1999: fig. 29A, B, D, E) from the Late Silurian (Pridoli) Chester Bjerg Formation, Hall Land, north Greenland. The scales described here also resemble scales from Lochkovian deposits of Arctic Canada which Vieth (1980: pl. 6, fig. 15) assigned to *Gomphonchus* cf. *hoppei*. Once again, the small number of scales in the assemblages studied here, and the probability of similar forms occuring within the morphological range of several taxa, preclude a definite taxonomic assignment. Perhaps the scales are from a biological taxon showing scale characters which are transitional between the older, more cosmopolitan species and the younger endemic species.

ACANTHODII indet.

Sixteen acanthodian scales and one tooth fragment (Table 1) were incompletely or poorly preserved, and not assignable to a higher taxon.

TABLE 2. — Grid references for sample localities.

C864	Trundle	1:50000 sheet	GR 558000E6363100N
C865	"	"	GR 557300E6363300N
C866	"	"	GR 562300E6365000N
C867	"	"	GR 562400E6364800N
Y4	Bogan Gate	1:50000 sheet	GR 562900E6345600N
C924	"	"	GR 583000E6341600N
C923	"	"	GR 582700E6341800N
C925	"	"	GR 583700E6342500N
C937	"	"	GR 583700E6342400N
C920	"	"	GR 588700E6350100N

OTHER VERTEBRATES IN THE FAUNAL ASSEMBLAGES

Placoderm scales and dermal bone fragments are relatively common in most of the samples, and include forms similar or identical to some found in middle to upper Lochkovian strata of the Garra and Connemarra formations (Basden *et al.* 2000; Burrow 1996; Burrow & Turner 1998). The morphotypes found in the samples investigated here (Table 1) are designated as romundinid (Figs 5A-F; 6I), palaeacanthaspid (Fig. ?6G, H), ?brindabellaspid (Figs 5G; 6E, F; equivalent to the "protobrindabellaspid" scale type *sensu* Burrow & Turner 1998), other acanthothoracid and ?petalichthyid (Fig. 6C, D), and are being further investigated in conjunction with dermal plate material from the Connemarra Formation.
Scale and dermal bone fragments of the palaeoniscoid actinopterygian *Terenolepis turnerae* Burrow, 1995 are the only other vertebrate remains found in the samples, and these are only in C864-7 (Table 1; Fig. 6A, B).

AGE AND SIGNIFICANCE OF THE FAUNA
Most of the acanthodian taxa in the samples have a relatively long stratigraphic range. *Nostolepis lacrima* is the only taxon with a short known range, spanning the *eurekaensis-delta* zones of the early to middle Lochkovian, indicating samples C923 and C925 are of this age. The value of the other acanthodians is more biogeographical than biostratigraphic, with many of the taxa being widely and abundantly distributed throughout

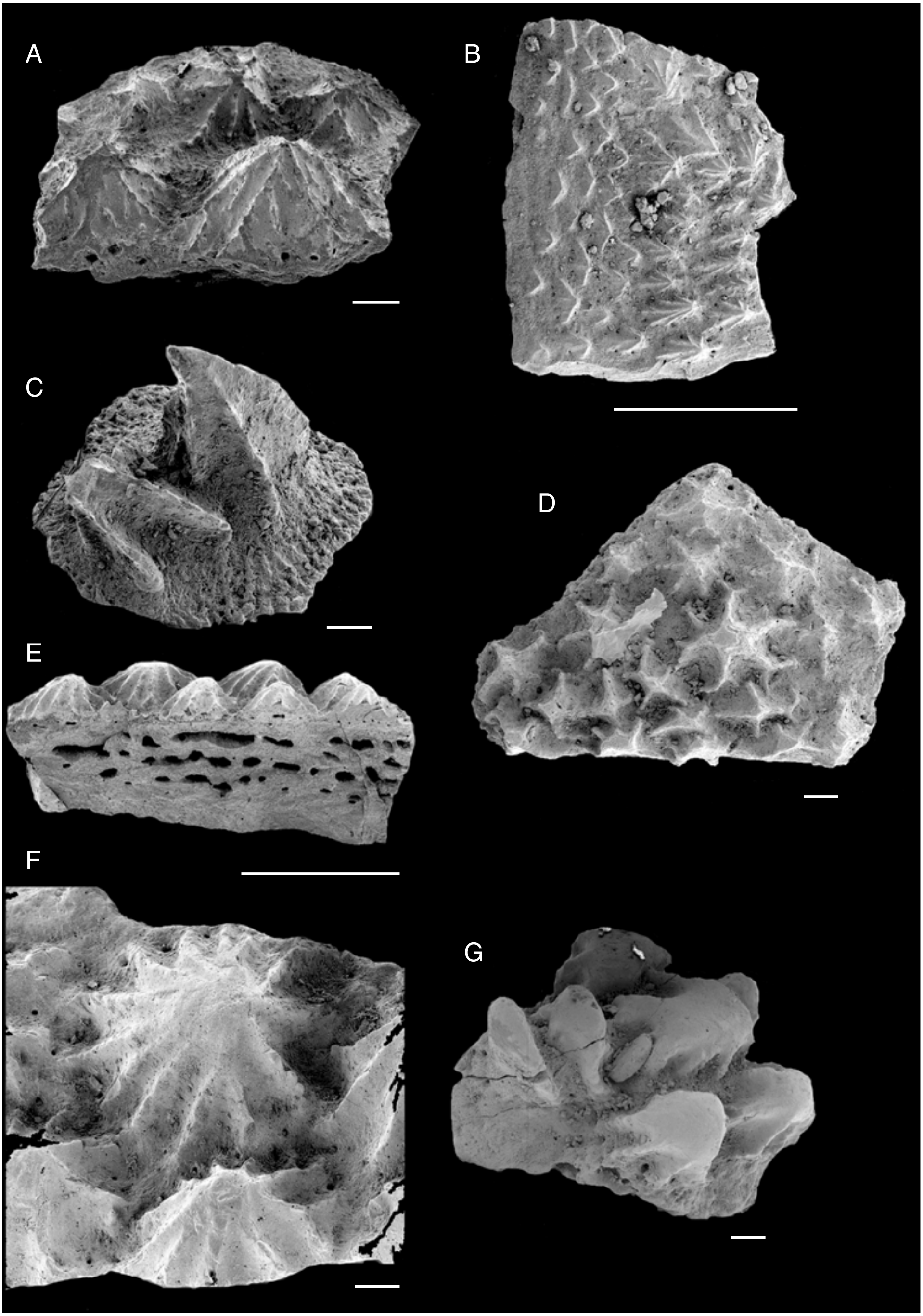

FIG. 5. — Placoderm scales from sample C925, Cookeys Plains Formation (early Lochkovian), central New South Wales, Australia; **A**, romundinid dermal bone fragment with thin base, MMMC02628; **B**, romundinid dermal plate fragment MMMC02629 showing edge ornament; **C**, romundinid scale MMMC02630, latero-crown view; **D**, romundinid scale MMMC02631, crown view; **E**, **F**, romundinid dermal plate fragment MMMC02632, showing thick cross-section, and close-up of ornament tubercles; **G**, ?brindabellaspid scale MMMC02633. Scale bars: A, C, D, F, G, 0.1 mm; B, E, 1.0 mm.

Late Silurian and Early Devonian northern European deposits.

While the ?brindabellaspid and palaeacanthaspid placoderms are also found in younger deposits, the romundinid type has previously been recorded only from the mid-Lochkovian (*delta*? CZ; Parkes *in* Basden *et al.* 2000: fig. 3.7, 14) in Australia. Elsewhere, macro- and microremains of *Romundina* Ørvig, 1975 have been collected from Lochkovian strata in the Canadian arctic region (Blieck & Cloutier 2000; Goujet 2001; Turner & Burrow 1997) and the Roberts Mountains Formation, Nevada (Parkes 1995). As *Terenolepis turnerae* is found in C864-7, the fauna in these samples is probably youngest – the taxon has been recorded previously only in late Lochkovian (*pesavis* CZ) limestones of the type stratum, the Connemarra Formation (Burrow 1995a) and the MUNG section, Garra Limestone (Hocking *in* Basden *et al.* 2000). Of course, the alternative is that *Terenolepis* appears earlier than has been recorded. However, this taxon is also missing from the *woschmidti-delta* CZ vertebrate microfaunas from Windellama Limestone (Parkes 1995). The latter fauna otherwise shows a similar suite of taxa, with acanthodians (Parkes 1995: fig. 34.1-6, 9-10, 12-14), including *Nostolepis* sp., *Gomphonchus*? sp., a ?ischnacanthid denticulated plate plus tooth whorl, and a poracanthodidid dentition cone (latter two *sensu* Burrow 1995b), and acanthothoracid placoderms (Parkes 1995: fig. 26.1-15).

For the GSNSW samples, the overlapping stratigraphic ranges of the vertebrates indicate a probable *delta* CZ level for samples C864-7. As the Yarrabandai Formation, which overlies the Cookeys Plains Formation, is dated as early Lochkovian (Sherwin *et al.* 2000), the vertebrate-based age for the samples indicates they are too young to be from the Cookeys Plains Formation. The dating rather indicates that these samples are probably from the lowermost strata of the Connemarra Formation, which has previously been dated as late Lochkovian (*pesavis* CZ) to middle Pragian (Sherwin 1996). Based on the presence of *N. lacrima* and the absence of *T. turnerae*, the relatively rich samples C923 and C925, and also C924 and C937 which were collected nearby, are probably from the *eurekaensis* CZ in the Cookeys Plains Formation.

Through the Siluro-Devonian of Australia, the changes in acanthodian faunas, in particular, mirror changes in conodont faunas: namely, an affinity with Chinese assemblages in the early Late Silurian; with circum-Arctic assemblages by the Late Silurian; and then increasing provinciality through the Early Devonian. The identification of this new Australian vertebrate fauna, which includes acanthodian and placoderm taxa with circum-Arctic affinities, accords with the relatively cosmopolitan aspect of many invertebrate faunas during the latest Silurian to earliest Devonian in Australia (Pickett *et al.* 2000; Talent *et al.* 2000). Early Devonian fish microfaunas from Saudi Arabia show a comparable assemblage of acanthothoracid and acanthodian scales (Lelièvre *et al.* 1994), although these faunas have not yet been described in detail. Macadie (1998) described vertebrate microfaunas from the Early Devonian (?Pragian) of New Zealand; their composition compares more closely with Pragian-early Emsian faunas of south-eastern Australia. Despite the sparseness of the new Australian fauna, it has proven valuable in further elucidating the stratigraphy of this region of New South Wales, and could also help with worldwide biogeographical analyses.

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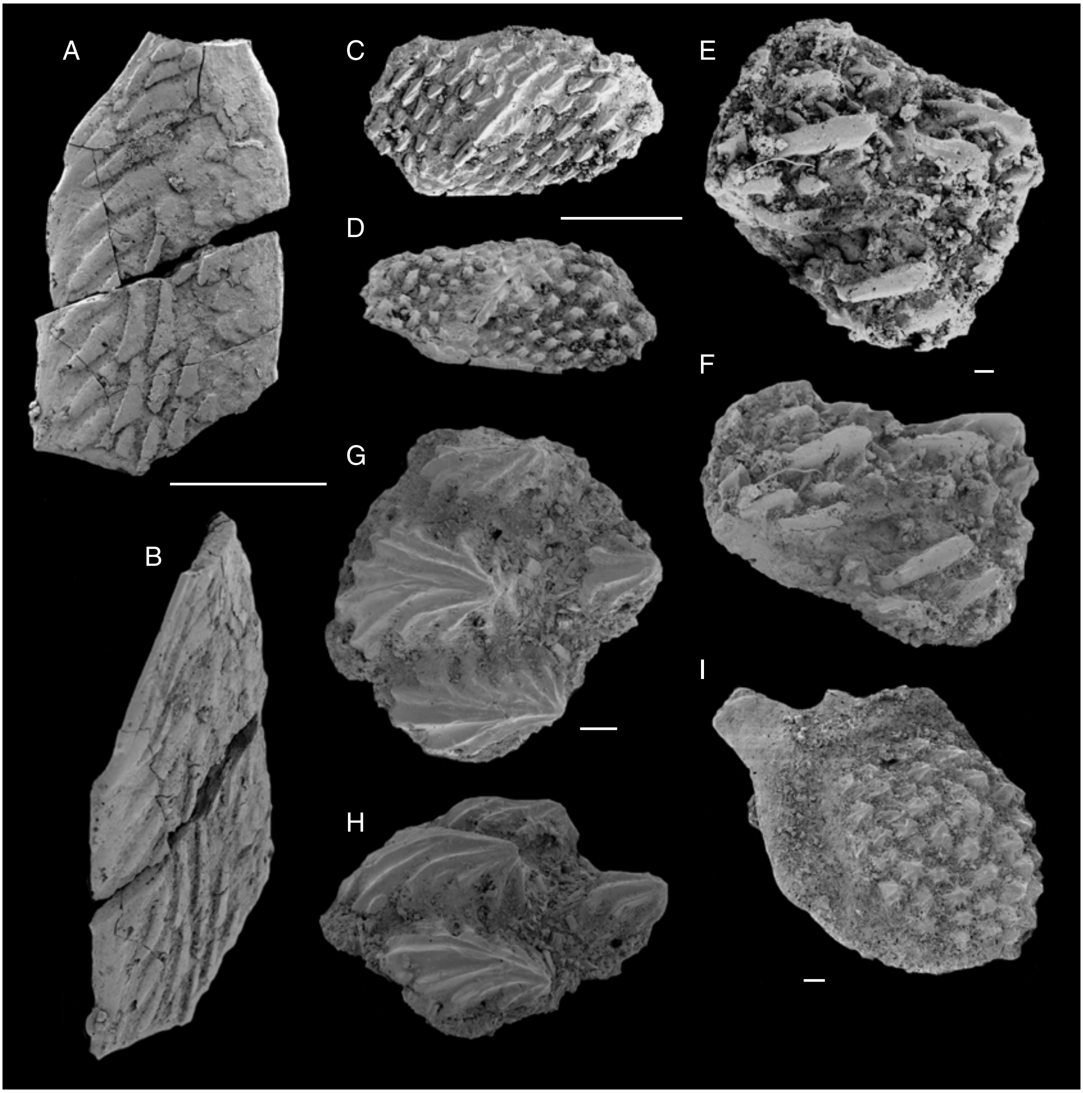

FIG. 6. — Placoderm and palaeoniscoid scales from sample C866, middle Lochkovian (?*delta* CZ) ?Connemarra Formation, central New South Wales, Australia; **A**, **B**, broken scale MMMC02623 from *Terenolepis turnerae* Burrow, 1995, in crown and antero-crown view (anterior edge to right); **C**, **D**, ?petalichthyid scale MMMC02624, in crown and postero-crown view; **E**, **F**, ?brindabellaspid scale MMMC02625, in crown and antero-crown view; **G**, **H**, ?palaeacanthaspid scale MMMC02626, in crown and lateral view (anterior to left); **I**, ?romundinid scale MMMC02627 in crown view. Scale bars: A-D, 1.0 mm; E-I, 0.1 mm.

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