Early Devonian arthrodire remains (Placodermi, ?Holonematidae) from the Burrinjuck area, New South Wales, Australia

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ABSTRACT

A new taxon, *Bimbianga burrinjuckensis* n. gen., n. sp., is erected for a small collection of acid-prepared bones from the Early Devonian (Emsian) limestones of the Burrinjuck area showing affinity with the holonematid arthrodires, a widespread brachythoracid family in the Middle-Late Devonian. The skull is represented by nuchal and paranuchal plates of holonematid shape, the nuchal overlapped by both paranuchal and central plates. Suborbital and submarginal plates show various primitive features not seen in other holonematids. Other brachythoracid submarginal plates from Burrinjuck are illustrated for comparison. The trunk armour of the new taxon is represented only by a single elongate median dorsal plate. Comparisons are made with the genus *Holonema* Newberry, 1889 from the Middle-Late Devonian of Europe, Russia, and the Middle East, and the best preserved material from the Gogo Formation, Western Australia. *Bimbianga* n. gen. is interpreted as more primitive than other holonematids in the shape of the paranuchal and suborbital plates, and the posterior angle on the median dorsal, and would be the oldest known representative of the family, although material from Khush-Yeilagh, Iran, may be of similar age.

KEY WORDS
Vertebrata,
Placodermi,
Arthrodira,
Devonian,
Australia,
new genus,
new species.

RÉSUMÉ

Restes d'arthrodires du Dévonien inférieur (Placodermi, ?Holonematidae) de la région de Burrinjuck, Nouvelles Galles du Sud, Australie.

Un nouveau taxon, *Bimbianga burrinjuckensis* n. gen., n. sp., est créé pour un petit nombre d'os préparés à l'acide. Il est daté du Dévonien inférieur (Emsien) et provient des calcaires de la région de Burrinjuck. Il présente des affinités avec les arthrodires holonématides, une famille de brachythoracides du Dévonien moyen et supérieur. Le crâne est représenté par des plaques nuchales et paranuchales de forme holonématide, la nuchale est recouverte à la fois par les plaques paranuchales et centrales. Les plaques suborbitaires et submarginales possèdent des caractères primitifs inconnus chez les autres holonématides. Pour comparaison des plaques submarginales d'autres brachythoracides de la même région sont présentées. La cuirasse thoracique de *Bimbianga burrinjuckensis* n. gen., n. sp. n'est connue que par la seule plaque médiane dorsale. Des comparaisons sont proposées avec les différentes espèces du genre *Holonema* Newberry, 1889 du Dévonien moyen et supérieur d'Europe, de Russie et du Moyen-Orient, ainsi qu'avec les spécimens parfaitement conservés de la Formation Gogo (Australie de l'Ouest). *Bimbianga* n. gen. est interprêté comme étant plus primitif que les autres holonématides par la forme des plaques paranuchales et suborbitaires et par l'angulation postérieure de la plaque médiane dorsale. En outre, il serait le plus ancien représentant de la famille, bien que les spécimens de Khush-Yeilagh (Iran) soient peut-être de même âge.

MOTS CLÉS
Vertebrata,
Placodermi,
Arthrodira,
Dévonien,
Australie,
nouveau genre,
nouvelle espèce.

INTRODUCTION

The first placoderm fish remains recorded from Australia were described by McCoy (1876) as "*Asterolepis ornata* var. *australis*" from the Early Devonian limestones near Buchan in eastern Victoria (Fig. 1). Etheridge (1906) reported a fossil lungfish skull from similar limestones along the Murrumbidgee River in New South Wales, now the site of Burrinjuck Dam and Reservoir. Chapman (1916) described a second placoderm specimen from Buchan, an almost complete arthrodire skull interpreted by Hills (1936) as belonging to the European genus *Coccosteus* Miller, 1841, for which Stensiö (1945) erected the new genus *Buchanosteus*. White (1952) described additional material of *Buchanosteus* from Burrinjuck, and assigned associated material to two new arthrodire genera (*Williamsaspis* White, 1952; *Taemasosteus* White, 1952). Material collected by the British Museum (Natural History) expeditions to southeastern Australia in 1955 and 1963 was described by White & Toombs (1972) and White (1978). Systematic collecting from the Burrinjuck area over the last 30 years has built up a substantial body of vertebrate macroremains from this area, housed in the Earth & Marine Sciences Department, Australian National University, Canberra. Young (1979, 1981, 2004a, b), Long (1984), Findlay (1996), Young *et al.* (2001) and Mark-Kurik & Young (2003) have documented additional arthrodire material. Arthrodires were clearly the most diverse group in the fauna, and globally they were the most diverse and successful subgroup of the class Placodermi, with some 170 genera (Carr 1995). Most arthrodires belong to the Brachythoraci, a major subgroup represented in the Late Devonian by giant forms like *Titanichthys* Newberry, 1885 and *Dunkleosteus* Lehman, 1956, which exceeded 6 m in length.

Middle Devonian representatives of the Arthrodira include such "generalised" forms as *Coccosteus* from the Old Red Sandstone of Scotland (e.g. Miles & Westoll 1968). However, already highly specialised were several Middle Devonian lineages, such as very large arthrodires (*Homostius* Asmuss, 1856 and *Heterostius* Asmuss, 1856) from the Baltic Province (Heintz 1930, 1934), and the recently described long snouted *Carolowilhelmina* Mark-Kurik & Carls, 2002 from Spain. Members of the family Homostiidae have now been documented from the Early Devonian (Emsian) of Morocco (Lelièvre 1984a) and Australia (Young 2004b). Another widely distributed arthrodire group is the family Holonematidae, represented on all continents except South America and Antarctica, in rocks of Eifelian or younger age. The best known form is the acid-prepared *Holonema westolli* Miles, 1971 from the marine Gogo Formation of Western Australia.

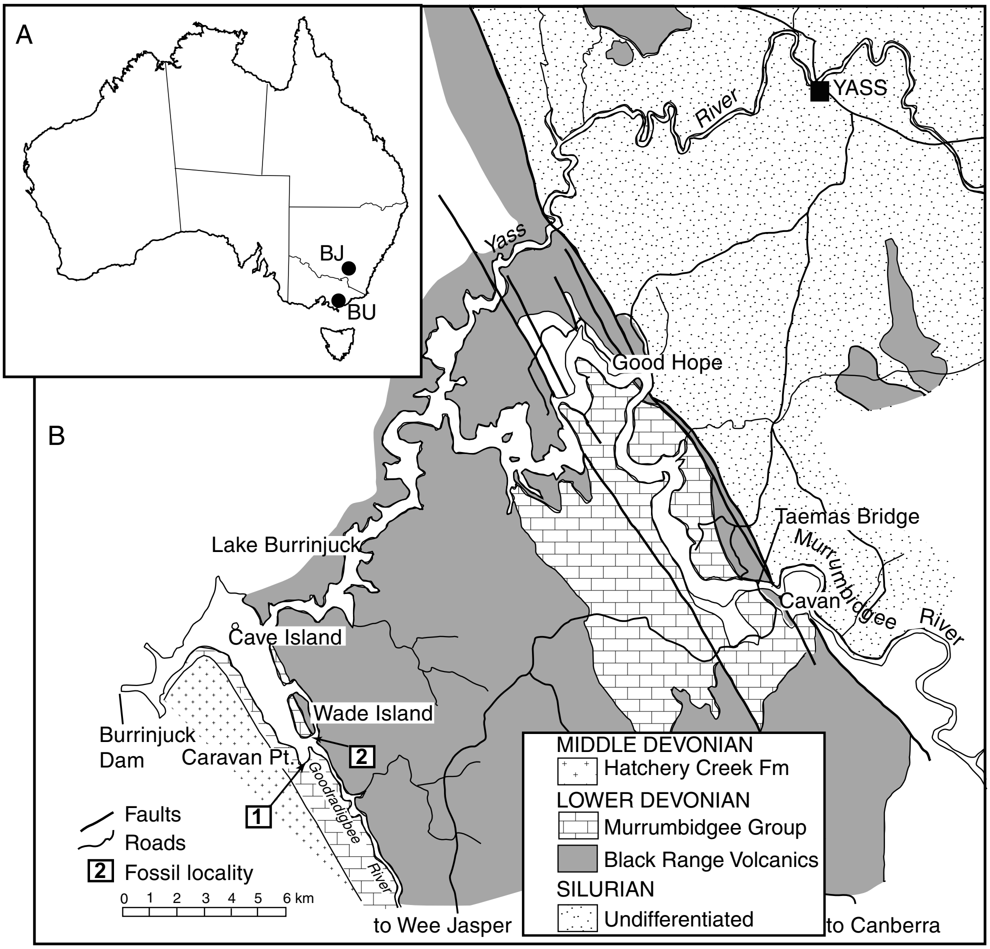

FIG. 1. — **A**, two main vertebrate-producing localities from Early Devonian (Pragian-Emsian) limestones in southeastern Australia: **BJ**, Burrinjuck, New South Wales, **BU**, Buchan, Victoria; **B**, general geology of the Taemas-Wee Jasper region at Lake Burrinjuck, showing the two localities producing fish remains described in this paper.

This paper records some acid-prepared remains of isolated bones from marine limestones of the Burrinjuck area, New South Wales, which are provisionally interpreted as belonging to an early representative of the family Holonematidae. If correctly assigned, they extend the range of this group back into the Early Devonian (early Emsian). The Burrinjuck fauna includes several other placoderm groups: petalichthyids and acanthothoracids (Young 1978, 1980, 1985; Long & Young 1988), and also ptyctodontids. Osteichthyans are best represented by lungfishes (Campbell & Barwick 1982a, b, 1984, 1985, 1999, 2000; Campbell *et al.* 2000). Less common are acanthodians (Long 1986; Lindley 2000, 2002a), actinopterygians (Schultze 1968; Basden *et al.* 2000a; Basden & Young 2001), onychodontids (Ørvig 1969; Lindley 2002b), and thelodont agnathans (Basden 1999). The stratigraphic occurrence of elements of the fauna has been reviewed by Basden *et al.* (2000b), Lindley (2002a, b), and Young (2004c). Currently some 40 vertebrate taxa are recognised, making the Burrinjuck fauna comparable in diversity to the early Frasnian Gogo fish fauna from Western Australia.

The new material described here, like the homostiid *Cavanosteus* Young, 2004b, is apparently restricted to the lower parts of the Burrinjuck limestone sequence. This may be facies related, with these fishes being more common in inshore environments – the lower strata of the Murrumbidgee Group (e.g. Cavan Bluff Formation) have been interpreted as shallow subtidal to intertidal deposits, whereas the higher levels (e.g. *Receptaculites* Limestone Member and above) may represent deeper shelf environments (see Chatterton 1973; Johnston 1993).

ABBREVIATIONS

Repositories

ANU V	GCY collection, Earth & Marine Sciences Dept., Australian National University, Canberra;
BM P	Natural History Museum, London (NHM).

Placoderm dermal bones

ADL	anterior dorsolateral plate;
AL	anterior lateral plate;
Ce	central plate;
M	marginal plate;
MD	median dorsal plate;
Nu	nuchal plate;
PDL	posterior dorsolateral plate;
PNu	paranuchal plate;
PSO	postsuborbital plate;
SM	submarginal plate;
SO	suborbital plate.

SYSTEMATICS

Class PLACODERMI McCoy, 1848
Order ARTHRODIRA Woodward, 1891
Suborder BRACHYTHORACI Gross, 1932

Family ?HOLONEMATIDAE Obruchev, 1932

REMARKS

The diagnosis of this family by Miles (1971: 204) was based on armour proportions (head shield greater than two thirds the length of the median dorsal plate; preorbital plate more than 25% of skull roof length), and tooth plate morphology (anterior supragnathal greatly reduced, posterior supragnathal and infragnathal with pipe-like ornamentation). These characters are not available in the isolated bones described below. Denison (1978: 60) characterised the family as having a "long or very long" trunk armour, which "retains a contact between its lateral and ventral parts behind the pectoral fenestrae even when the latter are lengthened". Ten genera were included in the family, but two of these (*Groenlandaspis* Heintz, 1932; *Tiaraspis* Gross, 1962) are now generally viewed as phlyctaeniids rather than brachythoracids. Apart from *Holonema*, the remaining taxa (*Belemnacanthus* Eastman, 1898; *Deirosteus* Wells, 1942; *Deveonema* Kulczycki, 1957; *Gyroplacosteus* Obruchev, 1932; *Megaloplax* Obruchev, 1932; *Rhenonema* Obruchev, 1964; *Tropidosteus* Gross, 1933; *Artesonema* Lelièvre & Goujet, 1986; *Tropinema* Nessov & Mark-Kurik, 1999) are poorly known forms based on isolated large trunk armour plates. Most are of Frasnian age, but *Belemnacanthus* is Eifelian, and *Rhenonema* and *Tropinema* are Givetian. *Holonema* was described from the Eifelian of Spain by Lelièvre *et al.* (1990), and several Middle Devonian genera (*Belemnacanthus*, *Rhenonema*, *Tropidosteus*, *Tropinema*) are distinguished by dorsal crests or processes on the MD plate (Denison 1978: fig. 43; Nessov & Mark-Kurik 1999).

Denison's (1978: 60) characterisation of the family stated "dermal bones variously ornamented", but in relation to the poorly known *Tropidosteus* he said (1978: 65): "Because of the absence of ridged ornament the reference of this genus to the Holonematidae is uncertain". The other holonematids generally have ridged ornament, but the ornament in *Gyroplacosteus* and *Megaloplax* is partly tuberculate, and some taxa are only represented by a few isolated tuberculate bones or fragments (e.g. *Deveonema*, *Artesonema*). However *Holonema* species are known from the Eifelian with entirely tuberculate ornament (Otto 1998), and tubercles are well developed on some bones of *H. westolli* (Miles 1971). The poorly known genus *Aspidichthys*, characterised by a dermal ornament of large tubercles, has been questionably assigned to the Holonematidae (Schultze 1971; Denison 1978: 103). Gardiner (1994) cited this genus as one of the latest holonematids (Frasnian). However I agree with Miles (1971) that assignment to the family is not warranted without further information on the morphology of *Aspidichthys*. The earliest definite members of the family so far known are from the Eifelian of Europe (Lelièvre *et al.* 1990; Otto 1998; Mark-Kurik 2000) and the ?Emsian-Eifelian of Iran (Blieck *et al.* 1980; see Discussion below).

Otto (1998) described a new species *Holonema bruehni* from the Eifelian of Germany, but excluded the character of ridged ornament from Denison's (1978) family diagnosis, because the dermal bones of his species had tuberculate ornament, the assumed primitive placoderm condition. The material described below belongs to a brachythoracid of uncertain position, also with tuberculate ornament rather than the typical ridged ornament of holonematids. Accepting Otto's revised family diagnosis, the new taxon is provisionally interpreted as an early member of the family Holonematidae, differing from other holonematids in a range of primitive characters. More complete remains are needed before this assessment can be confirmed.

Genus *Bimbianga* n. gen.

ETYMOLOGY. — The generic name comes from the Aboriginal word "*bimbiang*" (spear shield) listed by Mathews (1904: 304) in the vocabulary for the local Ngunnawal tribe, which occupied an area including the Goodradigbee valley.

Bimbianga burrinjuckensis n. sp.

(Figs 2; 3A, B; 5)

"holonematid nov." – Young, Long & Turner 1993: 246.

ETYMOLOGY. — The specific name derives from Lake Burrinjuck (Fig. 1).

MATERIAL EXAMINED. — ANU V158 (holotype; Nu plate); ANU V160 (PNu plate); ANU V144 (SO plate); ANU V1826 (SM plate); ANU V1834 (MD plate).

LOCALITY AND HORIZON. — ANU V144 and V158 are recorded from the "*Spirifer yassensis*" Limestone Member of the Taemas Limestone, Murrumbidgee Group, Wee Jasper, presumably from the southern shore of Goodradigbee Inlet, Lake Burrinjuck, the best and most thoroughly collected locality (locality 1, Fig. 1B). ANU V168, V1826, and V1834 are recorded from the Cavan Bluff Limestone, exposed on the shore of Lake Burrinjuck at the southern end of Wade Island (2, Fig. 1B).

DIAGNOSIS. — A presumed holonematid arthrodire with tubercular dermal ornament. Nuchal plate transversely arched posteriorly, and flattened anteriorly, with concave longitudinal profile, a convex posterior margin, and similar length to breadth. Anterolateral angle of nuchal forms a projecting process, overlapped behind by a mesial process of the paranuchal, and in front by the central plate. Paired infranuchal pits separated by strong infranuchal ridge. Paranuchal plate slightly longer than broad, with an ornamented postnuchal process, and mesial overlapping process fitting a notch in the nuchal plate. Lateral line sensory groove dividing the ornamented area of the paranuchal into triangular lateral and mesial parts of similar area. Central plate probably with external posterolateral process overlapping anterior nuchal margin, and internal posterior process occupying a deep posterior pit on the contact face of the nuchal. Suborbital plate ovate, with central ossification centre, shallow anterior orbital notch, acute angle between suborbital and postorbital branches of infraorbital sensory groove, and postsuborbital sensory groove not developed. Submarginal plate ovate, with short longitudinal keel over ossification centre. Median dorsal plate flat, relatively elongate (estimated breadth/length index 57), with posterior median angle, and low ventral keel continuous from rounded posterior process to anterior region of bone. Keel with anterior and posterior median grooves developed. Other bones of trunk armour unknown. Dermal ornament of crowded tubercles, sometimes aligned in short meandering rows in a concentric pattern.

REMARKS

The included nuchal (Nu) plate (Fig. 2A, C) is readily distinguished from the trapezoidal Nu of all other brachythoracids described so far from the Burrinjuck arthrodire fauna. Its distinct anterolateral notch, and the corresponding process on the referred paranuchal (PNu) plate, are evidence that these isolated bones come from the same taxon. These structures do not occur in previously described Burrinjuck arthrodire taxa. However the PNu lacks several holonematid characters shown by other members of the family, so this association remains provisional.

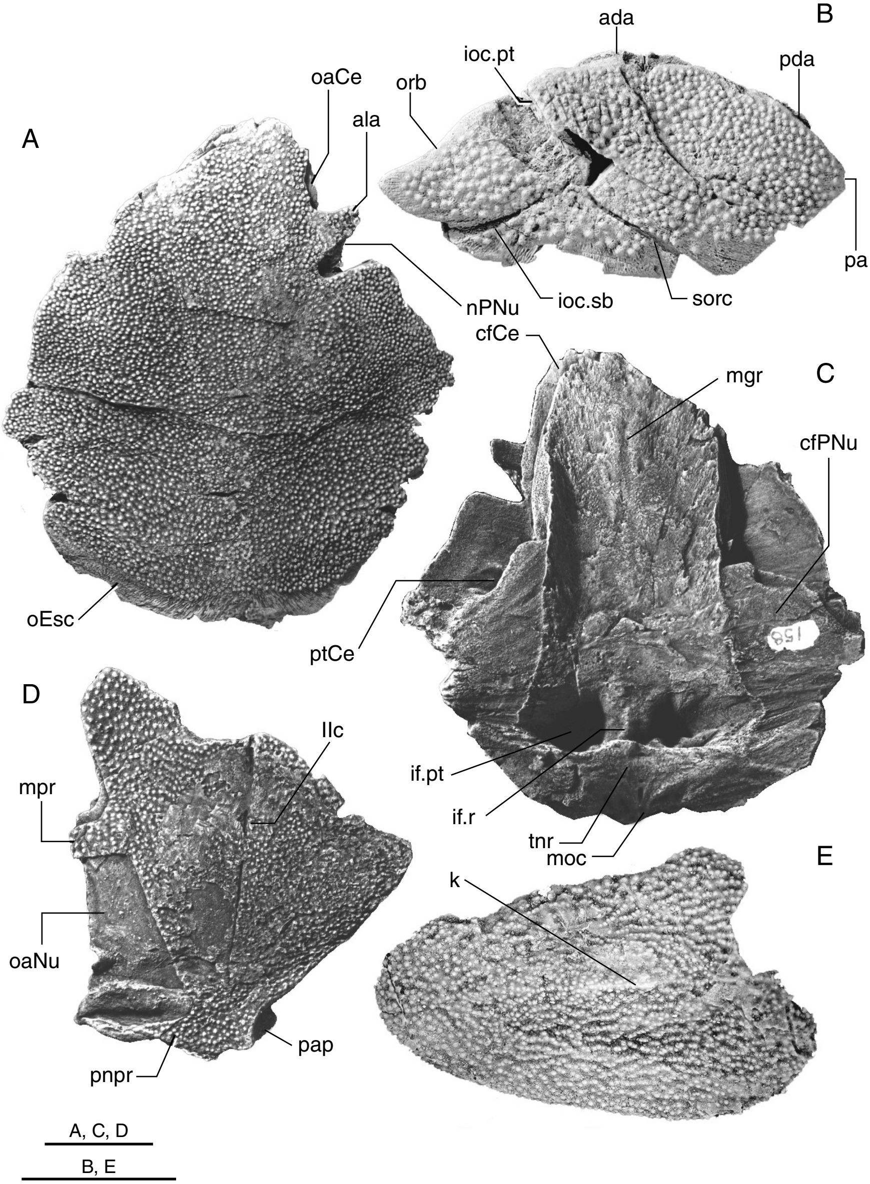

FIG. 2. — *Bimbianga burrinjuckensis* n. gen., n. sp.; **A**, **C**, holotype (ANU V158), an incomplete nuchal plate from the skull in dorsal (**A**) and ventral (**C**) views; **B**, ANU V144, a left suborbital plate in external view; **D**, ANU V160, a right paranuchal plate in external view; **E**, ANU V1826, a probable right submarginal plate in external view. All specimens whitened with ammonium chloride for photography. Abbreviations: **ada**, anterior dorsal angle of suborbital plate; **ala**, anterolateral angle of Nu plate; **cfCe**, area overlapping central plate; **cfPNu**, area overlapping paranuchal plate; **ioc.pt**, postorbital section of infraorbital sensory canal groove; **ioc.sb**, suborbital section of infraorbital sensory groove; **if.r**, infranuchal ridge; **if.pt**, infranuchal pit; **k**, keel; **llc**, main lateral line sensory canal; **mgr**, median ventral groove on Nu plate; **moc**, median occipital crest on Nu plate; **mpr**, mesial process of paranuchal plate; **nPNu**, notch for mesial process of paranuchal plate; **oaCe**, area overlapped by central plate; **oaNu**, area overlapped by nuchal plate; **oEsc**, area loosely overlapped by extrascapular plate; **orb**, orbital notch; **pa**, posterior angle of suborbital plate; **pap**, para-articular process; **pda**, posterior dorsal angle of suborbital plate; **pnpr**, postnuchal process on paranuchal plate; **ptCe**, pit for internal posterior process of central plate; **sorc**, supraoral sensory canal groove; **tnr**, transverse nuchal ridge or thickening. Scale bars: 20 mm.

The remaining isolated bones are provisionally included because they also differ from other arthrodire remains so far documented from the Burrinjuck fauna, and show evidence for holonematid affinity as follows: elongate proportions, low keel and process, tubercles aligned in rows (MD plate); ovate to sub-triangular shape, with shallow orbital notch (SO plate); ovate, with tubercles aligned in rows and partly fused to form ridges (SM plate). More than one closely related holonematid taxon could be represented in this small collection of isolated bones. The most distinctive example with recognisable characters of the family Holonematidae (ANU V158) is selected as holotype.

DESCRIPTION

ANU V158 (Fig. 2A, C) is an isolated nuchal (Nu) plate from an arthrodire skull probably 25-30 cm long. This bone evidently had a narrow anterior, and convex posterior margin, and rounded to subtriangular shape, and is thus readily distinguished from the trapezoidal Nu of other brachythoracids in the Burrinjuck arthrodire fauna in which this bone has been described. The anterior margin is irregular and incomplete. The anterolateral margin displays a distinct notch (nPNu, Fig. 2A) for a process of the PNu plate. A small embayment of the PNu into the Nu is seen also on the left side of the holotype of *Antineosteus* Lelièvre, 1984a (Lelièvre 1984a: fig. 1). In ANU V158 another process in front formed an angle (ala) which overlapped the PNu. A small anterior overlap, presumably for the Ce plate (oaCe, Fig. 2A), is also seen in *Holonema radiatum* Obruchev, 1932, and *H. westolli* (Fig. 3C, E). The left anterolateral margin of ANU V158 is less complete, but indicates that the bone was not completely symmetrical, with the anterolateral process less pronounced on that side (ala, Fig. 3B). A marked unornamented zone on the posterior margin (oEsc) is where the extrascapular plates fitted closely into the nuchal gap between the skull roof and trunk armour, as is well shown in the articulated *Holonema* specimen from Spain described by Lelièvre *et al.* (1990: pl. 1A). ANU V158 is transversely arched with a bulbous rounded median dorsal convexity posteriorly, and flattened anteriorly. The angle between left and right laminae of the bone was measured at 152° at the posterior margin. The longitudinal profile resembles that figured for *H. westolli* by Miles (1971: fig. 29C), except for a distinct concavity between the bulbous posterior and flattened anterior parts of the bone.

The visceral surface of ANU V158 shows deep paired infranuchal pits, and a strongly developed infranuchal ridge (if.pt, if.r, Fig. 2C). This bone differs from forms such as the Early Devonian homostiid *Antineosteus* in having a strongly developed transverse nuchal thickening (tnr). This structure is also developed on the Nu of *Holonema* (e.g. Miles 1971: fig. 27C, D), but entire skulls in posterior view show that most of the thickening along the posterior skull margin was under the PNu plates, in support of the dermal neck-joint (Miles 1971: fig. 3; Lelièvre *et al.* 1990: fig. 4A). In ANU V158 the Nu plate is some 15 mm thick at the posterior margin, with a median occipital crest (moc, Fig. 2C), and an anterior median groove (mgr), as in *Holonema*. Unlike *H. westolli* there is no paired posterior median process. The contact face for the Ce plate is more complete on the right side (cfCe), where it extends forward as a narrow strip, turning mesially at the anterior end to indicate that this approximates the natural margin of the bone. It seems that the (unknown) Ce plate probably had an internal posterior process passing between the PNu and the overlapping Nu, as indicated by pits at the posterior end of its contact face (ptCe, Fig. 2C). On the right side, this deep pit extends back inside the bone some 15 mm. The contact face for the Ce plate is shown as more strongly developed on the Nu of *H. radiatum* compared to *H. westolli* (Fig. 3D, F). In the *Holonema* specimen from Spain these pits have a more posterior position, and closely resemble their development in ANU V158 (labelled as "anterior ridge" by Lelièvre *et al.* 1990: fig. 3B). It is also noteworthy that in that specimen, and the restoration of *H. radiatum* by Miles (1971: fig. 117A), the infranuchal pits are distinctly paired, as described

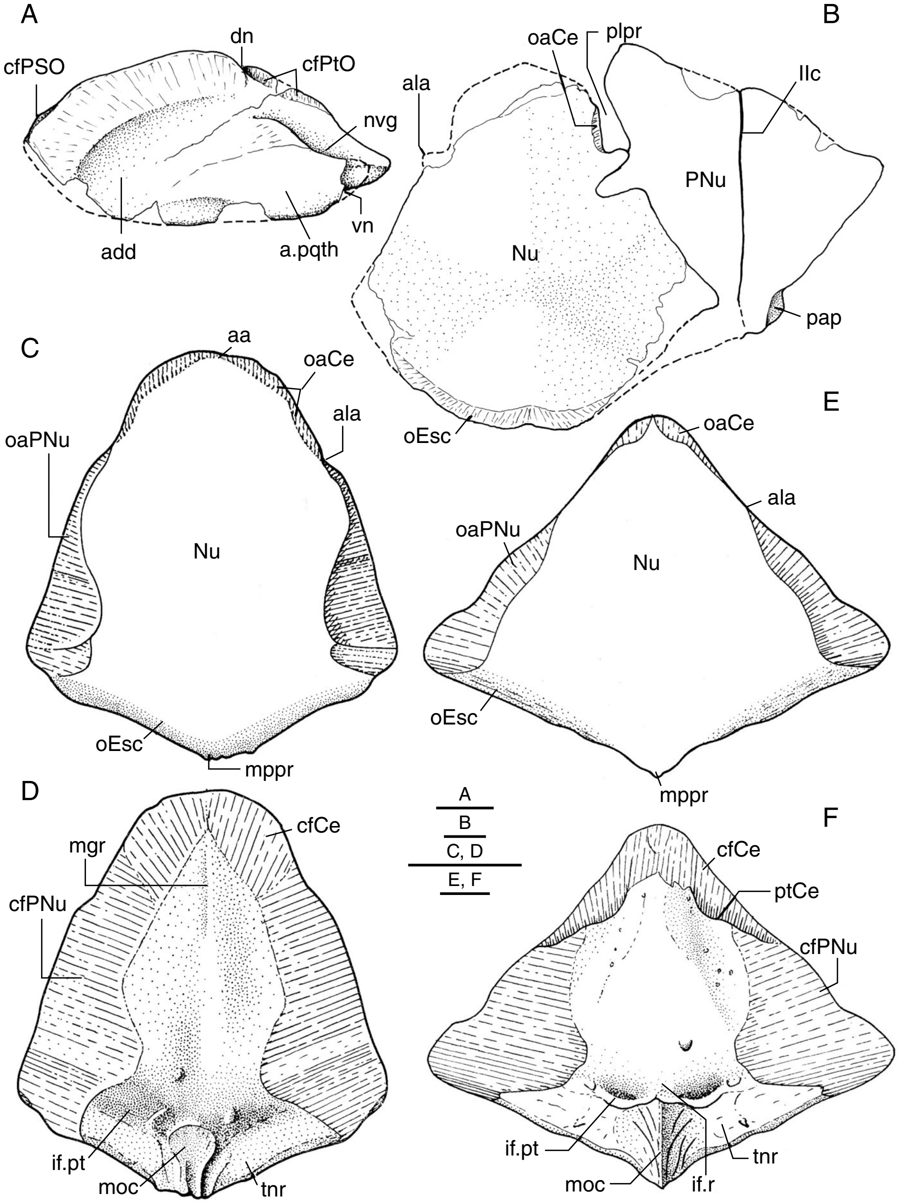

FIG. 3. — **A**, **B**, *Bimbianga burrinjuckensis* n. gen., n. sp.; **A**, internal surface of a left suborbital plate, based on ANU V144; **B**, restoration of the Nu/PNu plates of the skull, based on ANU V158, V160 (alternative interpretations of the lateral angle on the Nu plate shown); **C**, **D**, *Holonema westolli* Miles, 1971, restored Nu plate in external (**C**) and internal (**D**) views; **E**, **F**, *H. radiatum* Obruchev, 1932, restored Nu plate in external (**E**) and internal (**F**) views (C-F modified from Miles 1971: figs 27, 117). Abbreviations: **aa**, anterior angle of Nu plate; **add**, depression for adductor mandibulae muscle; **ala**, anterolateral angle of Nu plate; **a.pqth**, anterior thickening for palatoquadrate attachment; **cfCe**, area overlapping Ce plate; **cfPNu**, area overlapping paranuchal plate; **cfPSO**, area overlapping postsuborbital plate; **cfPtO**, area overlapping postorbital plate; **dn**, dorsal notch; **if.r**, infranuchal ridge; **if.pt**, infranuchal pit; **llc**, main lateral line sensory canal; **mgr**, median ventral groove on Nu plate; **moc**, median occipital crest on Nu plate; **mppr**, posterior median process of Nu plate; **Nu**, nuchal plate; **nvg**, neurovascular groove inside suborbital plate; **oaCe**, area overlapped by central plate; **oaPNu**, area overlapped by paranuchal plate; **oEsc**, area loosely overlapped by extrascapular plate; **pap**, para-articular process; **plpr**, space for posterolateral process of Ce plate; **PNu**, paranuchal plate; **ptCe**, pit for internal posterior process of central plate; **tnr**, transverse nuchal ridge or thickening; **vn**, ventral notch. Scale bars: 10 mm.

here for *Bimbianga* n. gen., whereas in *H. westolli* the infranuchal ridge is much reduced, so that the infranuchal pits are combined in a continuous "transverse fossa" (Miles 1971: fig. 27C, D).

Miles (1971: 204) characterised the Nu plate for the genus *Holonema* as follows: posterior margin markedly convex; well developed median posterior process; nuchal thickening well developed. ANU V158 is incomplete anteriorly, and lacks the extremities of the lateral corners. However the preserved lateral and posterior margins show clearly that it had a strongly convex posterior margin. In overall shape it more closely resembles the Nu of *Holonema westolli* rather than *H. radiatum*, the latter being represented as somewhat broader than long with strong lateral angles (Miles 1971: figs 27, 117). However shape of the Nu is variable in both species, with strong lateral angles developed in some examples of *H. westolli* (Miles 1971: fig. 28), whilst the specimen from the Eifelian of Spain referred to *H. radiatum* has a more oblong Nu plate (Lelièvre *et al.* 1990: fig. 3A, B). In ANU V158 the strength of posterolateral and lateral angles is uncertain, but they were probably not too pronounced given the orientation of the complete sections of the bone margins (Fig. 2A, C). As restored (Fig. 3B) this bone was probably approximately as long as broad, as in *H. westolli*, where three figured Nu plates (Miles 1971: figs 27, 28), have breadth/length indices of about 90, 98, and 107.

In summary, the narrow anterior and convex posterior margins of ANU V158 indicate holonematid affinity. It has shorter proportions than the Nu of other brachythoracids described from the Burrinjuck arthrodire fauna, which have generally more elongate Nu plates, of trapezoidal shape. The Nu of *Taemasosteus* is about 1.2 times as long as broad (White 1978), and in *Arenipiscis* Young, 1981 it is broadest at the level of the posterior margin, which is deeply concave. The Nu/PNu plates are markedly elongate in several large brachythoracids (e.g. *Homostius*; *Tityosteus* Gross, 1960), and elongation of the posterior part of the skull roof has been used as a defining feature of the Homostiidae (character 11 in the phylogeny of Lelièvre 1995). The brachythoracids *Exutaspis* Liu & Wang, 1981 and *Jiuchengia* Wang & Wang, 1983 from China have markedly convex posterior skull margins, but again the Nu is more elongate, with trapezoid shape.

The referred right PNu plate (Fig. 2D) has a maximum length of 75 mm and breadth of 69 mm, and shows a mesial process (mpr) that corresponds well to the notch (nPNu) in the lateral margin of the holotype, and forms the anterior border of a relatively short overlap area for the Nu plate (oaNu). Anteriorly the fit is not close, apparently to accommodate a posterolateral process of the Ce plate. The PNu probably also came from a somewhat smaller individual than the Nu, and was collected from lower in the sequence. However, like the holotype, it is less elongate than the PNu of other arthrodires described from the Burrinjuck fauna, so is provisionally assumed to belong to the same form. ANU V160 is less well preserved, and somewhat flattened due to shearing within the limestone. The external surface is damaged in the central part, but the ornament is clear anteriorly. Neither pitlines nor the endolymphatic opening can be discerned on the abraded surface. The lateral line groove (llc) has a straight anterolateral orientation, dividing the ornamented area into triangular lateral and mesial parts of similar area. This is rather different from the PNu of *H. westolli*, where the sensory groove has a marked lateral position, with most of the ornamented surface of the bone on its mesial side. This seems to be characteristic of the genus, and is also seen in the entirely tuberculate PNu of *H. bruehni* (Otto 1998: fig. 1C). On the other hand, a more lateral position for the sensory groove is also seen in the ridged buchanosteid *Uralosteus* (Mark-Kurik & Young 2003: fig. 2D). The short broad MD, and high and narrow AL and ADL plates of *Uralosteus* show that it is not a holonematid.

A small ornamented postnuchal process is preserved in ANU V160 (pnpr, Fig. 2D) but its posterior margin is missing. In typical *Holonema* it is only slightly developed or absent. The complete posterior lateral margin shows a small para-articular process projecting only a little laterally (in

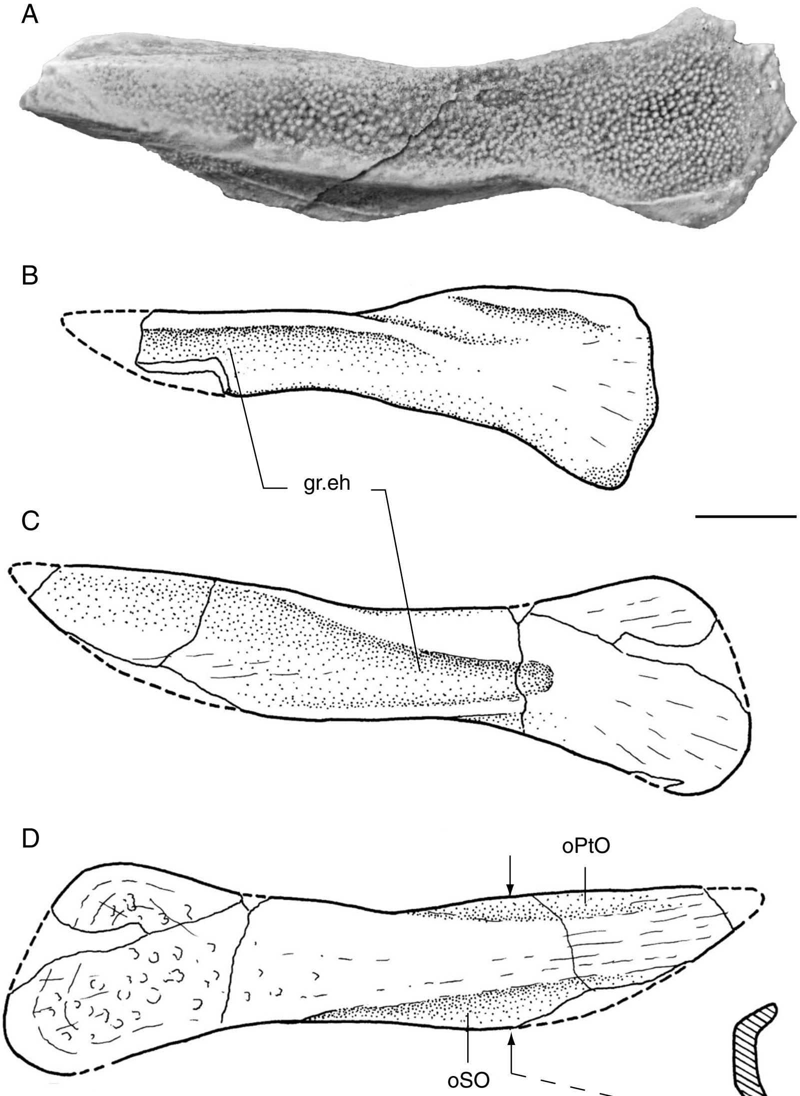

FIG. 4. — Several submarginal plates of brachythoracid arthrodires from the Burrinjuck fauna, probably belonging to *Taemasosteus* or related forms; **A**, ANU V72 (Bloomfield Limestone Member, Wee Jasper), incomplete left submarginal plate (SM) in lateral view (whitened with ammonium chloride); **B**, BMP 50361, internal view of an incomplete right SM assigned to *Taemasosteus novaustrocambricus* by White (1978: fig. 86), locality HAT 63/10/1, *Spirifer yassensis* Limestone Member, Taemas; **C**, **D**, BMP 50471 (identified in NHM register as "?SM of ?dinichthyid"), a nearly complete right SM in internal (**C**) and external (**D**) views, with transverse section at the level indicated, locality HAT 63/50/1, *Receptaculites* Limestone Member, Taemas. Abbreviations: **gr.eh**, groove for epihyal or opercular cartilage inside submarginal plate; **oSO**, area loosely overlapped by suborbital plate; **oPtO**, area loosely overlapped by postorbital plate. Scale bar: 20 mm.

H. westolli it is larger, but with similar orientation and shape; Miles 1971: fig. 3A). The posterior bone margin is incomplete, and only the upper lateral margin of the articular fossa for the neck-joint is preserved. This seems to project further posteriorly than the ventral margin of the fossa, but otherwise its shape is uncertain. In both *H. westolli* and *H. radiatum* the fossa is distinctly higher laterally, reducing to a mesial rounded point (e.g. Miles 1971: fig. 3; Lelièvre *et al.* 1981: fig. 15; 1990: fig. 4). However in *H. bruehni* both the fossa and condyle for the neck-joint are more rounded (Otto 1998: fig. 2E, F), so its proportions are not a reliable holonematid character.

The previously described PNu plates all have a much deeper configuration than ANU V160 as preserved, but this is probably due to postmortem distortion (ANU V158 is normally developed in this respect). The crushed visceral surface of the PNu has little relief, and shows a poorly preserved paranuchal crista, a thickening along the posterolateral margin, and a narrow contact face for the M plate behind the point where the lateral line sensory groove passes off the anterolateral margin. There is an indistinct contact face for the Ce plate beneath the anterior angle of the bone. Given the difference in overall shape, this bone shows expected differences to the visceral surface of the PNu in *H. westolli* (Miles 1971: fig. 29B).

An attempted reconstruction of the posterior skull region, assuming the Nu and PNu represent the same taxon, is compared with the Nu plate of *Holonema westolli* and *H. radiatum* in Figure 3. The two bones are certainly not from the same individual, and given the variation in Nu shape in *H. westolli* (Miles 1971: figs 27, 28), a close fit would not be expected. However significant resemblances may be the development of overlaps onto the Nu by the PNu behind a distinct anterolateral angle, and by the Ce plate in front of this angle. These features are well developed in both *H. westolli* and *H. radiatum* (Fig. 3C, E).

Miles (1971: 119) noted that the posterior process on the Ce plate is proportionately much longer in *Holonema* than in any other arthrodire. In this new material there is an anterior gap between the Nu and PNu for this process (plpr, Fig. 3B), with a small overlap onto the Nu (oaCe, Fig. 2A).

One left suborbital (SO) plate is provisionally referred to this new taxon. ANU V144 (Fig. 2B) is 60 mm long (incomplete posteroventrally), with a maximum 30 mm depth in the middle of the plate. The shape is ovate, with more angularity than the similarly proportioned SO of *Antineosteus* (Lelièvre 1984a: fig. 13), but less than the typical triangular shape of the SO in *Holonema*, best represented in *H. westolli* (Miles 1971: fig. 33). As in that form the ossification centre is centrally placed on the bone, and a little closer to the anterior end. The ornament is of crowded tubercles showing no alignment (coarser tuberculation occurs on the SO plate in some other brachythoracids). Tubercles are absent from a smooth zone around the orbital (orb) and (partly broken) ventral margins, presumably where the bone was more deeply embedded in the skin. Like *H. westolli*, the orbital notch (orb, Fig. 2B) is very shallow, but unlike it the notch is much closer to the anterior end, rather than in the middle of the dorsal margin. In *H. westolli* the infraorbital sensory canal groove runs in an anteroventral direction from behind the orbital notch to the anteroventral corner of the SO (Miles 1971: fig. 32A). In ANU V144 the dorsal (postorbital) part of this groove is directed anteriorly, as shown by a short section preserved at the dorsal margin (ioc.pt, Fig. 2B). The central part of the groove is mainly missing where the bone is broken. The ventral (suborbital) part of the infraorbital groove (ioc.sb) passed anteroventrally off the bone, forming a distinct notch (vn, Fig. 3A). Another sensory canal groove passing posteriorly off the ventral margin is the supraoral groove of other forms (sorc, Fig. 2B). A connection with the infraorbital sensory groove may have been present, but is not preserved.

There is no sign of the postsuborbital sensory groove, which crosses from the PSO plate towards the ossification centre of the SO in *H. westolli*. In a SO plate from the Frasnian of Iran referred to *H.* cf. *radiatum* this groove is more strongly developed, and joins the supraorbital sensory groove just before it connects to the infraorbital sensory groove (Lelièvre *et al.* 1981: fig. 16). The SO plate in *Rhenonema* and *H. bruehni* is rather different (Miles 1971: fig. 126; Otto 1998: fig. 1A, B), with three unconnected sensory grooves, and the orbital notch possibly situated even farther posteriorly than in *H. westolli*. Otto (1998) considered the PSO to be fused with the SO in *H. bruehni*, but his sensory groove evidence is doubtful (the postsuborbital sensory line may develop as short intermittent grooves on *Buchanosteus*; Young 1979: pl. 3A). The interpreted "posterior" margin of the SO in *H. bruehni* may be broken, but its unornamented external edge suggests otherwise (Otto 1998: fig. 1A). Its shape invites comparison with the truncated anterior margin of the SO in *Goodradigbeeon* and *Taemasosteus* (White 1978: figs 30, 88). This bone is difficult to interpret, and bears little resemblance to the SO described here.

A right SO plate from Khush-Yeilagh, Iran, assigned to *Holonema* sp., and of possible Emsian age (see below), is markedly triangular, also with a high posterior position for the orbital notch, and shows a separate postsuborbital sensory groove (Blieck *et al.* 1980: fig. 4C), both possible resemblances to *H. bruehni*.

The angular configuration of the infraorbital sensory groove in ANU V144 is similar to the SO plate figured by Long (1984) from Buchan, Victoria, which may represent a closely related taxon. Lelièvre (1995) identified two characters of the sensory groove pattern of the SO for phylogenetic analysis: connection between the supraorbital and infraorbital sensory lines (character 47), and the angle between the suborbital and postorbital branches of the infraorbital groove (character 53). The inflection in the infraorbital sensory groove in this new SO plate is presumably related to the anterior position of the orbit. The fact that the infraorbital groove has a similar angular configuration in several other apparently distantly related brachythoracids like *Goodradigbeeon*, *Taemasosteus*, or *Atlantidosteus* Lelièvre, 1984b (see White 1978: figs 30, 88; Lelièvre 1984b: fig. 2A; Young 2003a: figs 2A, 3A, 4A) suggests that this is a symplesiomorphy.

The dorsal margin of the SO in ANU V144 has a narrow overlap area visible laterally in the middle part (ada, Fig. 2B), and another forming the posterodorsal angle (pda). The whole margin is grooved as far back as the posterior angle (pa). The posterior section of this grooved margin presumably represents the connection to the missing postsuborbital plate (cfPSO, Fig. 3A). The distinct ventral notch (vn), where the suborbital part of the infraorbital groove (ioc.sb) passes off the ventral margin, corresponds internally with a deep groove (nvg, Fig. 3A) passing back in just the same position as the "neurovascular groove" on the SO of *H. westolli*. Beneath is a similar thickening for the palatoquadrate attachment (a.pqth), which has a broken anterior end, and thus could have been more pointed than in *H. westolli*. A depressed area behind (add) corresponds to the adductor depression for the adductor mandibulae muscle in *H. westolli*. A dorsal notch (dn) divides the dorsal margin into an anterior part which overlapped (cfPtO), and a posterior part which underlapped, the lateral edge of the skull. This is in contrast to the SO of *Antineosteus*, where the entire dorsal margin was apparently overlapped by the skull roof (Lelièvre 1984a: fig. 13A).

ANU V1826 (Fig. 2E) is another small ovate plate (55 mm long; maximum height 35 mm), in this case lacking sensory grooves. It is gently convex about a longitudinal axis that carries a short keel 8 mm long in the centre of the plate (k), marking the presumed ossification centre. The plate is incompletely preserved, but it is not a symmetrical bone. The ventral part (as oriented in Fig. 2E) in transverse section is more convex than the dorsal part, which is flat to gently concave, thus eliminating its identification as a dorsal scute or small median plate behind the armour. For a paired bone of this size and shape, a holonematid submarginal (SM) plate from the cheek seems the most likely interpretation. The complete convex margin is interpreted as ventral, and the rounded end can be interpreted as the posterior margin (of a right SM), which compares well in both shape and size with the left SM of *H. westolli* illustrated by Miles (1971: fig. 41).

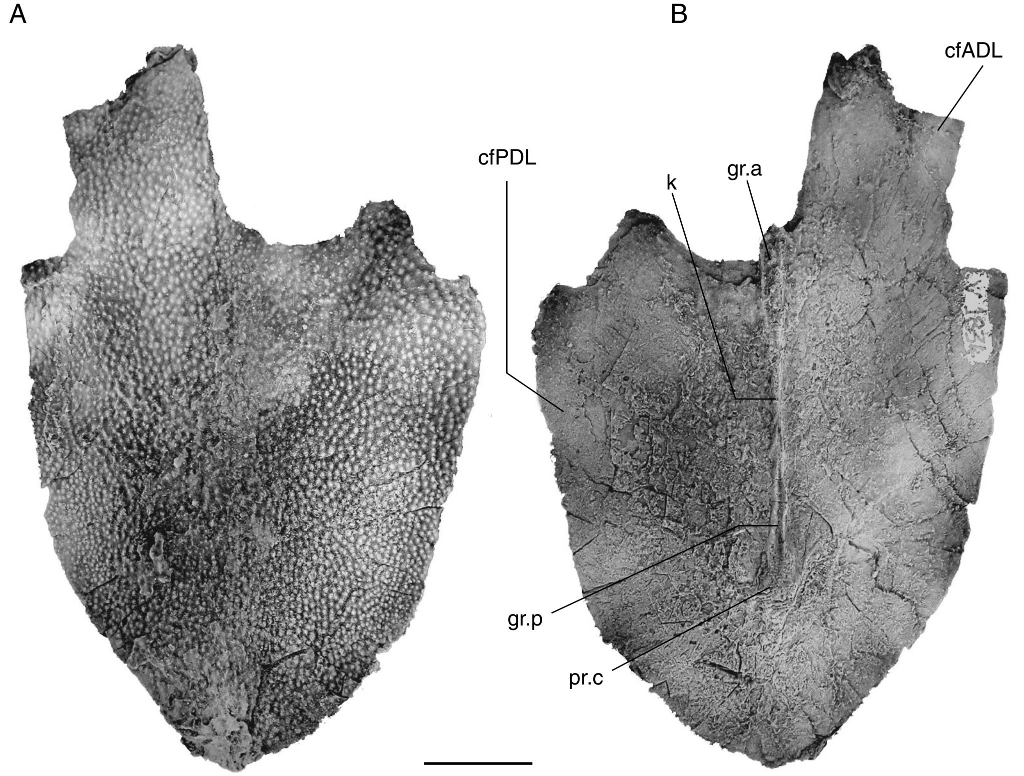

FIG. 5. — *Bimbianga burrinjuckensis* n. gen., n. sp., incomplete median dorsal plate (ANU V1834) in external (**A**) and internal (**B**) views. Specimen whitened with ammonium chloride for photography. Abbreviations: **cfADL**, area overlapping anterior dorsolateral plate; **cfPDL**, area overlapping posterior dorsolateral plate; **gr.a**, anterior groove on ventral keel; **gr.p**, posterior groove on ventral keel; **k**, ventral keel of median dorsal plate; **pr.c**, posterior thickening on ventral keel. Scale bar: 20 mm.

In *Holonema* the SM has its narrow end oriented posteriorly (Miles 1971: fig. 55). In the other arthrodires from Burrinjuck in which the SM is known, it is a more elongate bone situated above, rather than behind, the SO (e.g. Young *et al.* 2001: fig. 1), and with the narrow end to the anterior (Fig. 4). Within brachythoracids, an elongate SM situated above the SO is an advanced condition, by comparison with arthrodire outgroups (e.g. actinolepids, phlyctaeniids), which have a larger SM plate behind the SO. Unlike holonematids, in these groups the narrow end of the SM is also to the anterior.

In ANU V1826 the main differences to the SM of *H. westolli* are the very different ridged ornament, and a central longitudinal groove over the ossification centre in that form. In contrast, the ornament of ANU V1826 shows short meandering alignments of tubercles forming a partly concentric pattern of intervening ridges (Fig. 2E), which is closely similar to finer areas of ornament on the median dorsal plate described next. It also compares well with the aligned tubercular ornament on both the skull roof and trunk armour plates of juvenile *H. westolli* (e.g. Miles 1971: figs 17, 24, 76, 77). The inner surface of ANU V1826 is gently concave, showing no significant features apart from the centrally placed ossification centre, again as in *H. westolli* (Miles 1971: fig. 42). There is no sign of a small ridge or keel as described by Otto (1998: fig. 7P, Q) in a possible SM plate of *H. bruehni*.

ANU V1834 (Fig. 5) is a flat and relatively elongate median dorsal (MD) plate (maximum width

86 mm; preserved length 136 mm). An estimated total length of about 150 mm would give a breadth/length index of about 57. This MD is again very different from the short, broad, transversely arched brachythoracid MD plates commonly encountered in the Burrinjuck sequence (e.g. White 1978: figs 94, 95). Nevertheless ANU V1834 is considerably less elongate than in *H. westolli* (breadth/length index 31 in the holotype; Miles 1971: 155), whereas *Maideria* from the Givetian of Morocco has a MD with a breadth/length index of about 50 (Lelièvre 1995: fig. 11A, B). *H. westolli* differs from *Maideria*, and the new MD described here, in having a truncated posterior margin, which never shows a posterior median angle or process (Miles 1971: 155). Since the entire anterior end of ANU V1834 is broken, proportions can only be generally estimated from the features of the ventral surface (Fig. 5B). The keel is very low, with a maximum depth of only 2-3 mm. Unlike *H. westolli*, it is continuous to the anterior preserved margin (k, Fig. 5B). Posteriorly it is expanded as a rounded process (pr.c) 7-8 mm high, which carries a narrow groove in front (gr.p), giving way to the thin-edged middle part of the keel. About 25 mm from the preserved anterior end the keel broadens, and carries a broader, shallow median groove (gr.a). In *Holonema* the structure of the visceral surface of the MD plate is variably developed, with a reduced groove and anterior thickening in *H. westolli*, two separate expanded grooves and an articular crest in *H.* cf. *radiatum* from Iran (Lelièvre *et al.* 1981: figs 18, 19), and a continuous groove extending to the anterior margin in the specimen of *H. radiatum* from Spain (Lelièvre *et al.* 1990: fig. 6). In *H. bruehni* the MD has an indistinct median groove in front of an expanded boss (Otto 1998: fig. 2C, D). The anterior expanded groove in ANU V1834 (gr.a, Fig. 5B) is a point of difference to the similarly shaped MD of *Maideria* from the Givetian of Morocco (Lelièvre 1995: fig. 11B). Contact faces are very indistinct, and the relative lengths of posterior and anterior faces for overlapping the PDL and ADL are not clearly demonstrated (cfADL, cfPDL, Fig. 5B).

The ornament of ANU V1834 (Fig. 5A) varies a little across the bone, with spaced coarser tubercles in meandering rows anteriorly (about seven per cm), becoming finer posteriorly (about nine per cm). As noted above, the ornament resembles that of the SM plate (Fig. 2E).

DISCUSSION

BIOSTRATIGRAPHY

The isolated specimens described above may prove to represent more than one taxon, when better material becomes available. However, taken together, the material provides some evidence for the presence of an Early Devonian holonematid in the Burrinjuck arthrodire fauna. Previously, the earliest representatives of the family Holonematidae are specimens assigned to *Holonema* sp. from the Emsian-Eifelian of Iran (Blieck *et al.* 1980), the Eifelian *H. radiatum* from Spain (Lelièvre *et al.* 1990) and Germany (Otto 1998), and undescribed species of *Holonema* from the Eifelian of the Baltic sequence in Estonia and Latvia (Mark-Kurik 2000).

There has been some uncertainty about the age of the Iranian occurrence, in the Khush-Yeilagh Formation. It was referred to the Eifelian by Blieck *et al.* (1980), but a slightly higher conodont assemblage suggested an older Emsian age to Hamdi & Janvier (1981). This would give the Khush-Yeilagh fish assemblage the earliest known records for a range of placoderm and osteichthyan groups, including the holonematids (Lelièvre *et al.* 1993). Alternatively, Dastanpour (1996: 163) argued for a much younger (Frasnian) age using spores, which is seriously discrepant with the evidence of the other groups, including a brachiopod-trilobite assemblage of Givetian age above the conodont level (P. Janvier pers. comm.). Here it is noted that one specimen of an incomplete right AL plate figured by Blieck *et al.* (1980: pl. 1, fig. 13), showing distinctive ridged ornament, is not dissimilar to the corresponding part of the AL plate of *Errolosteus* Young, 1981 from the Emsian of Burrinjuck

(Young 1981: fig. 12A). *Uralosteus* Mark-Kurik & Young, 2003 has a shorter and higher AL plate, and *Holonema* a much lower and longer AL, but the Iranian specimen is incomplete posteriorly, so its total length is unknown. Associated "coccosteomorphs" in the Iranian assemblage include some specimens suggestive of buchanosteids (e.g. Blieck *et al.* 1980: pl. 13, fig. 6), so this provisional placoderm evidence would also support an older (?Emsian) age.

Conodont dating of the Burrinjuck sequence at Wee Jasper (Mawson *et al.* 1992) identified the Pragian-Emsian boundary to lie in the Cavan Bluff Limestone, the lowermost formation of the Murrumbidgee Group, which has yielded some of the material described above, the remainder coming from the overlying *Spirifer yassensis* Limestone Member of the Taemas Limestone. As summarised by Young (2004c: fig. 2), other evidence suggests that the conodont zone alignments of several constituent members of the Taemas Limestone shown by Basden *et al.* (2000b: fig. 2) need to be revised downwards. Lindley (2002a: 275) noted that the occurrence of the index species (*Chalcidophyllum recessum*) of Coral Fauna D (Garrett & Wright 1989) in the Currajong Limestone Member, which overlies the *Spirifer yassensis* Limestone Member, indicates that the Currajong should be aligned with the *dehiscens*, rather than the *perbonus*, conodont zone. Above the Currajong, the Bloomfield Limestone Member may also have lower beds of *dehiscens* rather than the *perbonus* conodont zone age (Basden 2001: table 2.1), and the Warroo Limestone Member contains *perbonus* conodont zone elements (Nicoll *in* Lindley 2002b). On this evidence the material assigned above to *Bimbianga* n. gen. is probably restricted to the *dehiscens* conodont zone, the lowermost zone of the Emsian stage of the Early Devonian.

From the lower part of the Baltic sequence two undescribed species of *Holonema* are recorded. As summarised by Mark-Kurik (2000: 313), the older taxon ("*Holonema* sp. A") occurs in the lower Vadja Member of the Narva Formation, and has fine tuberculate ornament, comparable with *H. bruehni* Otto, 1998 from the Brandenberg Group, Saureland, Germany (*australis* – lower *kockelianus* conodont zone). In the overlying Kernave Member of the Narva Formation is another species ("*Holonema* sp. B") with typical ridged ornament, and close to the specimen referred to *H. radiatum* from the Eifelian (mid-upper *costatus* conodont zone) of Spain described by Lelièvre *et al.* (1990). Thus the genotype for the family Holonematidae, of which the type species *Holonema rugosum* (Claypole, 1883) comes from the Givetian-Frasnian of north America, is demonstrated from the early Eifelian of Europe by one or more species showing typical development of the dermal armour, and differing mainly in dermal ornamentation. The material from Khush-Yeilagh, Iran, if correctly assigned to the genus, and correctly dated as Early Devonian, would indicate that tuberculated and ridged holonematids diverged in pre-Emsian times.

Holonema is widely represented in Middle-Upper Devonian strata in the Northern Hemisphere, including many localities interpreted as "non-marine" deposits (see below). In Australia *Holonema* was erroneously recorded from the Upper Devonian of Victoria by Hills (1929), but the material later proved to belong to a phyllolepid placoderm. Western Australian occurrences (in the Munabia Sandstone, Gneuda and Gogo formations; Miles 1971; Long 1991; Long & Trinajstic 2000) are of Givetian-Frasnian age. The only older possible holonematid material so far recorded from Australia is the new taxon *Bimbianga burrinjuckensis* n. gen., n. sp. described above.

BIOGEOGRAPHY

Holonematids are common and diverse in the Middle-Late Devonian of North America, Europe, and Russia (e.g. Schultze 1971: fig. 6). *Holonema* is also recorded from various Late Devonian localities in North Africa and the Middle East, representing the northern Gondwana margin (e.g. Morocco, Afghanistan, Iran, Turkey; Lehman 1977; Lelièvre *et al.* 1993). In Europe and North America this taxon occurs in facies assessed as both typical marine, and marginal to "nonmarine" (e.g. Denison

1956, 1968). The terms "invertebrate-dominated" and "vertebrate-dominated" of Blieck *et al.* (1989; also Otto 1998: 133) are very appropriate for these two assemblage types. *H. westolli* from the Gogo fauna is clearly a marine species, but typical ridged ornament of *Holonema* type has not been identified so far in extensive Early-Middle Devonian "vertebrate dominated" assemblages in Australia (Young & Turner 2000; Young & Goujet 2003). However, wuttagoonaspid, bulbocanthid, and phyllolepid placoderms also have ridged ornament, so it is possible that fragmentary remains have not yet been recognised. Also noteworthy is the fact that *Holonema* has never been recorded from China, even though fishes in both of the facies assemblages just discussed are well-documented throughout the Chinese Devonian (Zhu 2000). Given these observations, it might be suggested that *Bimbianga* n. gen., as a primitive sister-group to other holonematids, indicates a Gondwanan origin for the group, and subsequent dispersal into, and Middle Devonian diversification within the Northern Hemisphere, consistent with evidence from some other groups (Young 2003b). However the occurrence in the Khush-Yeilagh Formation of Iran, assumed also to represent the northern Gondwana margin, is inconsistent with this scenario, but its age and fauna await full documentation. The same applies to other poorly known Early-Late Devonian occurrences from adjacent regions (e.g. Saudi Arabia, Qatar, Morocco). Full documentation of these assemblages is crucial to the question of Gondwana-Laurussia interconnections of fish faunas during the Early-Middle Devonian (Young 2003b).

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