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Devonian fish remains from the Munabia Sandstone, Carnarvon Basin, Western Australia

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Abstract

Fish fossils have been recovered from two horizons at the base of the Munabia Sandstone, near the type section of Williambury Station. The fauna contains the antiarch *Bothriolepis* sp., the arthrodire *Holonema* sp., and an indeterminate osteolepidid crossopterygian. The presence of *Holonema* (Eifelian-Frasnian) with *Bothriolepis* (Givetian-Famennian), as well as microfossil dates from the underlying conformable Gneudna Formation (Early Frasnian), suggests a Frasnian age for the base of the Munabia Sandstone. Conodonts suggest that the top of the Munabia Sandstone is of Lower Famennian age.

Introduction

The Munabia Sandstone outcrops over a distance of almost 90 km from Mt. Sandiman homestead in the south to just north of Williambury Station as part of a linear belt of Devonian rocks at the base of the Carnarvon Basin sedimentary succession (Figure 1). The type section occurs about 8 km southeast of Williambury Station where it conformably overlies the lower Frasnian carbonates of the Gneudna Formation and underlies the coarser conglomerates of the Willaradie Formation (Condon 1954, 1965, Hocking *et al.* 1987). Although Condon (1965) favoured a marine depositional environment for the Munabia Sandstone and Willaradie Formation, Moors (1981) reported that only the base of the Munabia Sandstone was marine, the majority of the sequence representing distal fan to braided stream deposits, with minor marine incursions. The overlying Willaradie Formation is part of this depositional event, representing proximal alluvial fan deposits. None of the previous field studies of the Munabia Sandstone had found any body fossils, although trace fossils are common in the lower (marine) horizons, and the age of the unit was based entirely on extrapolation from the underlying Gneudna Formation, itself well-dated from marine invertebrates and palynomorphs (Seddon 1969, Dring 1980, Playford and Dring 1981). The Gneudna Formation has also yielded the world's youngest turiniid thelodont scales (Turner and Dring 1981). Recent studies of Gneudna Formation microfossils confirm the earlier age assessment of lower Frasnian (Balme 1988). Age determination of the top of the Munabia Sandstone from conodonts in a thin limestone intercalation gives a probable lower Famennian age (Dr. R. Nicoll, pers. comm.), indicating the unit straddles the Frasnian-Famennian boundary.

In August 1988 a field party from the Museum of Western Australia and the Geology Department, University of Western Australia, discovered remains of fossil fishes in two horizons near the base of the Munabia Sandstone (Figure 2), as well as many fish fossils

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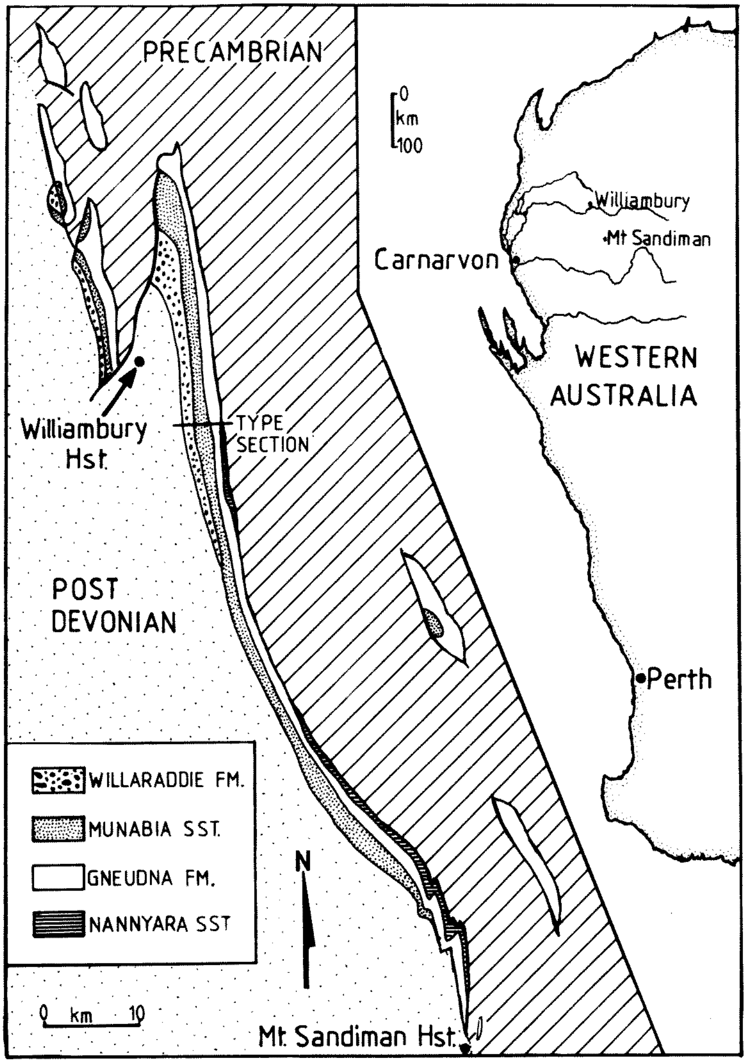

Figure 1. Locality map showing the Devonian formations of the Carnarvon Basin and location of type sections for the Gneudna Formation and Munabia Sandstone, where the fossils were found.

from the Gneudna Formation. The Munabia Sandstone fishes are preserved as natural moulds with no traces of bone preserved. The material is studied by latex casts. For convenience, and in convention with other workers (e.g. Young 1988) plate names are abbreviated in the text, and all abbreviations are listed at the end of the paper. Similarly the words "length, breadth and height" are abbreviated in the text as L, B and H respectively. Measurements taken are from points designated in Miles (1968). Indices are

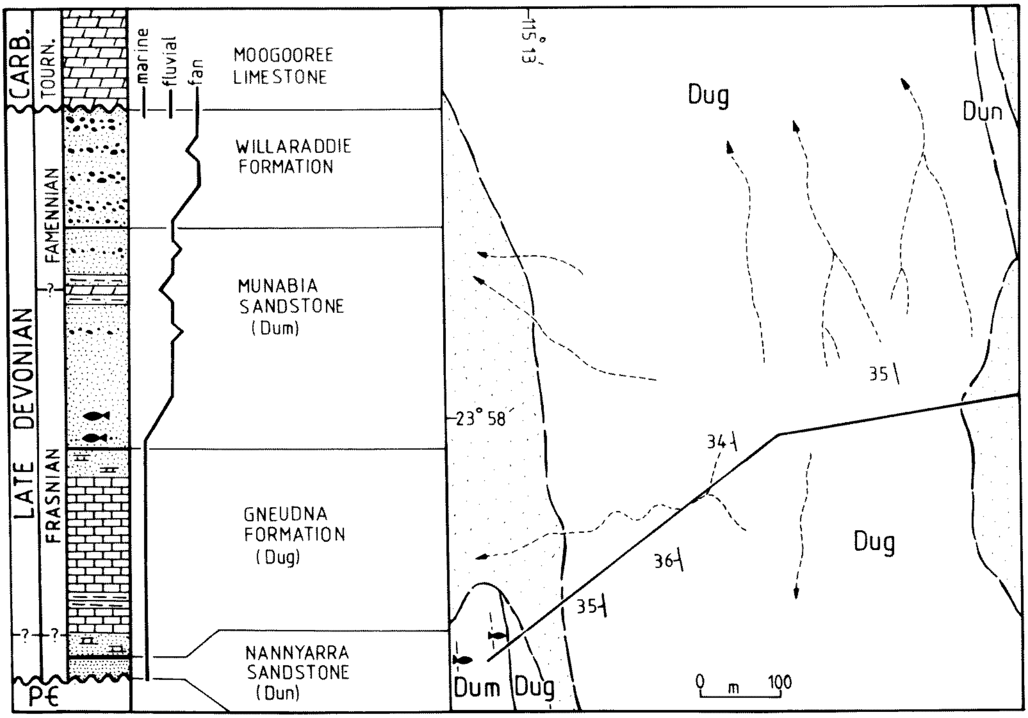

Figure 2. Detailed locality map showing the position of the two fish-bearing horizons in plan view, in the type section area and in the generalized stratographic column (as fish symbols). Geology after Dring (1980) and Moors (1981).

expressed as the ratio of two linear measurements multiplied by 100 (e.g. L/B index = L/B x 100). The specimens are housed in the palaeontological collections of the Western Australian Museum (prefix WAM).

Stratigraphic position of the fish fossils

The fossils were discovered about 1 km north of the type section of the Munabia Sandstone, immediately above the type section for the Gneudna Formation (Figures 1, 2). The lowermost fossil horizon, about 30 metres from the base of the unit, represents a lag accumulation of claygall pebbles with broken fish plates. The abundance of trace fossils from near this horizon is suggestive of marine deposition (Moors 1981). The fish plates from this lag horizon are all broken fragments, dominantly of *Bothriolepis* sp., indicative of high energy deposition. A single osteolepidid scale was also found in this horizon. Both *Bothriolepis* and osteolepidids are known from marine and continental deposits (Gardiner and Miles 1975).

The second fossiliferous horizon is about 90-100 metres from the base of the unit. The fossils come from clean white-reddish sandstones and brownish-silty sandstones, which according to the criteria of Moors (1981) could represent either marine or continental deposition. The fauna contains *Bothriolepis* sp. and the arthrodire *Holonema* sp., a fish known predominantly from marine deposits (Miles 1971; Denison 1978). The fish material from this horizon was deposited as complete isolated plates indicating a lower energy of deposition than for the lower fossil horizon.

Systematics

Class Placodermi

Order Antiarcha

Family Bothriolepididae

Genus *Bothriolepis* Eichwald 1840

Type species

Bothriolepis ornata Eichwald 1840. Upper Devonian of the Leningrad region, U.S.S.R.

Bothriolepis sp.

Figures 3 A-D, F, 4

Material

WAM 87.8.1, a complete external mould of the left ADL plate; WAM 87.8.2, imperfect external mould of a PVL plate; WAM 87.8.3, external mould of proximal bone of pectoral appendage; WAM 87.8.4, internal mould of an AMD plate; 87.8.5, internal mould of a L plate.

Description

The material is assumed to belong to one species, because the external ornament on plate fragments in the lower horizon is similar to that of more complete plates from the upper horizon.

The headshield is represented by a single L plate in visceral view (Figure 3B). It is almost complete save for damaged rostral (rm) and posterior margins, but can easily be restored to full shape (Figure 4B). It has a B/L index of 82, and is of regular bothriolepidoid morphology showing clearly the large orbital notch (orb), depression for the anterior postorbital process of the endocranium (pr. apo), the transverse lateral groove (tig) bound by two cristae (cr 1, cr 2) and a moderately large lateral pit (p). The latter feature is characteristic of certain *Bothriolepis* species from Victoria and Antarctica, although in those species it is much larger (Long 1983, Long and Werdelin 1986; Young 1988). The preorbital recess (prh) is of the simple semilunar type. The anterior (a.ar.SM) and posterior (p.ar.SM) articulations for the submarginal plate are normally developed (Young 1984)

The trunkshield is represented by an almost complete ADL plate, an imperfect PVL plate and an imperfect AMD plate. These all suggest that the armour was deeper than in *B. canadensis* (Stensiö 1948), being low-vaulted with an estimated trunkshield breadth comparable to *B. canadensis* relative to its length.

The left ADL plate (Figures 3C, 4A) lacks only the dorsal overlap area and the posterior margin. It is 48 mm long and 30 mm deep. The dorsal lamina (dlam) has a weakly concave external dorsal margin (dem) and an apparently strongly convex

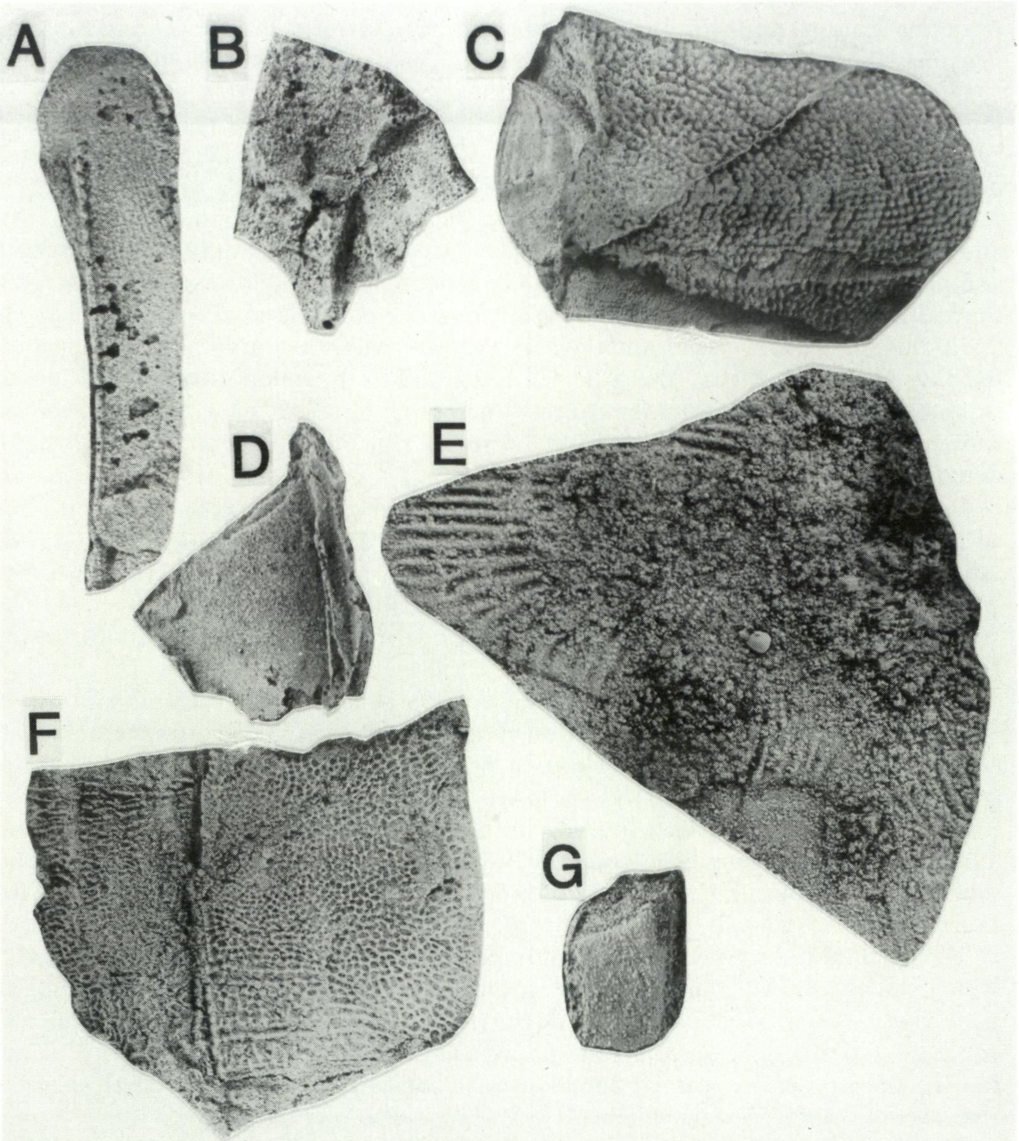

Figure 3. Fish fossils from the Munabia Sandstone. All are latex casts whitened with ammonium chloride. A-D, F. *Bothriolepis* sp. A, part of proximal segment of the right pectoral appendage, WAM 87.8.3. (x2). B, left L plate in visceral view. WAM 87.8.5. (x2). C, left ADL plate in dorsolateral view, WAM 87.8.1. (x1.5). D, visceral view of imperfect AMD plate, WAM 87.8.4. (x2). F, imperfect left PVL plate in ventrolateral view, WAM 87.8.2. (x1.5). E, *Holonema* sp., part of AMV plate in ventral view. WAM 87.8.6. (x1.5). G, osteolepidid scale in external view, WAM 87.8.7. (x3).

posterior margin (pm), although the dorsal division is not complete. The postnuchal ornamental angle (pnoa) is not accentuated as in some species (e.g. *B. maxima,* Gross 1948, in Stensiö 1948). The dorsal lamina is deepest anteriorly and is just over twice as long as its midline breadth. The dorsolateral ridge (dlr) is weakly defined, not developed as a prominent keel, and is gently curved throughout its length. The lateral lamina (llam) is almost triangular in form, being very deep posteriorly and narrow anteriorly. It is 17 mm deep at the posterior margin and 40 mm long. The external ventral margin (vem), and the ventral margin (vm) are quite straight. The processus obstans (pro) is quite short and blunt, not projecting far anteriorly. The articular area of the plate is developed as normal for the genus except that the *crista transversalis interna anterior* (cit) has an additional small transverse ventral ridge (tvr) ventral to its junction with the overlap area for the AVL (l.oa.AVL). The articular fossa (arf) is bounded dorsally by a thiçk supra-articular crista (crs) and ventrally by a narrower infra-articular crista (cri). A weak transverse ridge (ri) is developed in the lower half of the *crista transversalis interna anterior.*

The PVL plate (Figures 3F, 4C) is imperfectly preserved showing the external surface of its anterior half. The ventral lamina (v. lam) is 22.5 mm at its widest, meeting the lateral lamina (l.lam) along a well-defined ventrolateral ridge (vir). The lateral lamina has a maximum breadth of 15 mm, although the dorsal margin is poorly preserved. The overlap surfaces for the AVL plate (v.ao.AVL, l.oa.AVL) are developed as normal for the genus.

The AMD plate (Figure 3D) is represented only by a fragment showing part of the visceral surface, with a very small portion of the external surface visible on the latex cast. It indicates that the AMD was of regular proportions. The dorsal surface shows the median dorsal ridge developed as a sharp keel, although, because of the small size of the plate, this character may be a juvenile feature, as recorded for other species (Stensiö 1948, Werdelin and Long 1986, Long 1990). The visceral surface shows a well-developed median ventral ridge, but the region of the ventral pit is not sufficiently preserved for description.

The pectoral fin is represented by an imperfect proximal segment (Figures 3A, 4D) which shows a mesial ridge (cr. dm) on the CD1 plate that is abraded and lacking denticulations, a weak mesial thickening (mt) and the anconeal area at the proximal end of the bone (ard), all of which are developed as normal for the genus. Sutures dividing individual plates of the pectoral appendage are not seen, but its overall length suggests that part of the MM2 plate (Figure 4D, MM2?) is also preserved.

The dermal ornament of the dorsal and lateral laminae is best known on the ADL plate, and the PVL plate shows that of the ventral lamina. The dorsal lamina has closely packed tubercles, some with weakly interconnecting ridges, and is quite similar to that of mature *Bothriolepis gippslandiensis* from Victoria (Long and Werdelin 1986, figure 4A, B). On the lateral lamina the tubercles have a more rectangular disposition, forming almost transverse alignments between the dorsolateral ridge and the lateral line canal groove. Close to the ventral margin of the ADL plate the tubercles are more widely

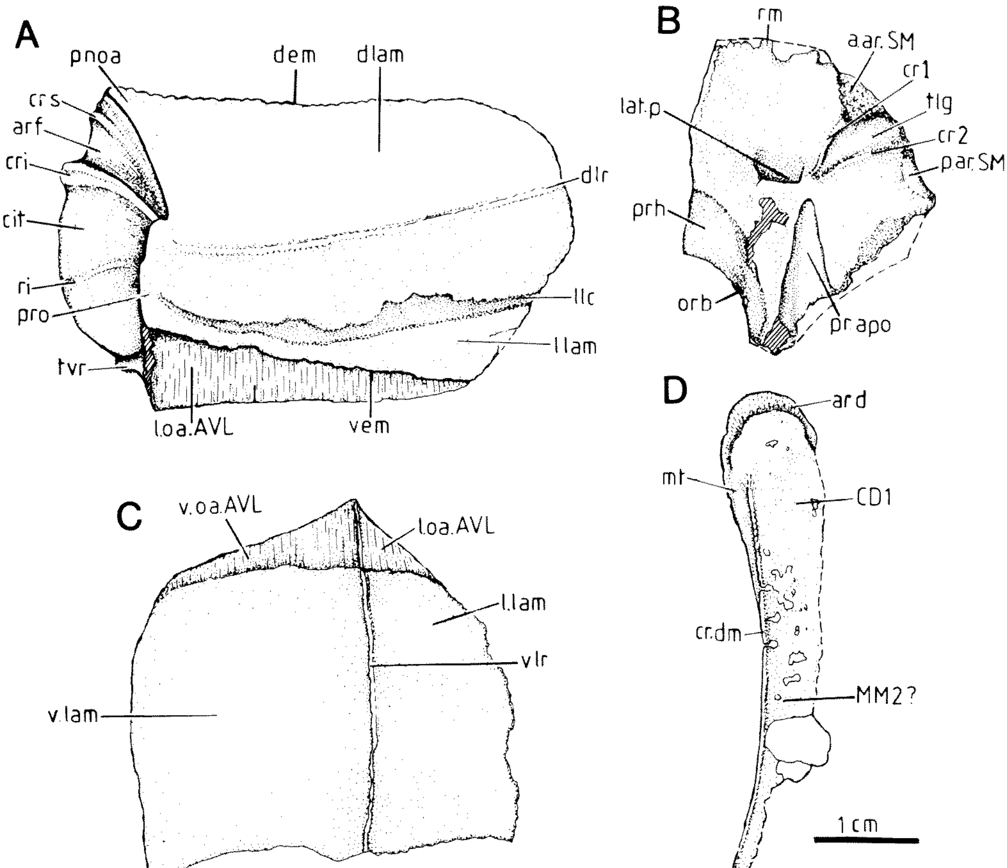

Figure 4. *Bothriolepis* sp. from the Munabia Sandstone. A, left ADL plate in dorsolateral view, WAM 87.8.1. B, left lateral plate in visceral view. WAM 87.8.5. C, imperfect left PVL plate in ventrolateral view, WAM 87.8.2. D, part of proximal segment of pectoral fin in dorsal view, WAM 87.8.3.

spaced and the ornament gives way to a reticulate network of thick ridges. The ventral lamina has an ornament almost entirely of thin reticulated ridges forming a pattern of small equally-sized enclosures, with some ridges developed parrallel to and near the plate margins.

Order Arthrodira

Family Holonematidae

Genus *Holonema* Newberry 1889

Type species

Holonema rugosum (Claypole 1883), Middle-Upper Devonian of North America.

Holonema sp.
(Figures 3E, 5A)

Material

WAM 87.8.6, an impression of the external surface of the right half of the AMV plate.

Description

The specimen is identified as *Holonema* by the ornamentation of bony ridges bearing small tubercles (as distinct from *Deirosteus* and other genera allied to *Holonema,* Miles 1971; Denison 1978), and by the shape of the AMV plate which is characteristic for holonematids (Figure 5). Aside from ornament, the presence of a ventral sensory-line canal on the AMV distinguishes it from that of *Groenlandaspis* (Ritchie 1975). The plate is comparable in size with that of *H. westolli* from the Frasnian Gogo Formation, if restored to full size it would be approximately 10 cm in breadth (Figure 5A). It shows conspicuous overlap surfaces for the AVL plates (Figure 5, oa.AVL) and a posterior overlap surface presumably for the PMV plate (oa. PMV). Although the PMV is overlapped by the AMV in *Holonema westolli* and most other arthrodires, the reverse condition may occur occcasionally (e.g. *Dicksonosteus,* Goujet 1984, figure 64), and there is generally much variation exhibited in the extent of contact between median ventral plates in the sample of arthrodires from the Gogo Formation in the collections of the Western Australian Museum. The overlap area for the interolateral plate is not seen in ventral view on *H. westolli* (WAM 90.12.137), and similarly there is no trace of this on the Munabia Sandstone plate. The ossification centre of the plate is not clearly defined. A short sensory-line canal groove runs towards the centre of the plate (vsl) just anterior to an indentation (ind) in the external lateral margin. The posteroventral corner (plc) is sharply pointed, unlike the anterolateral corner (alc) which is rounded. In all of these features the plate closely agrees with that in *Holonema westolli.*

Subclass Osteichthyes
Order Osteolepiformes
Family Osteolepididae
osteolepidid gen. indet.
(Figure 3G)

Material

One scale, preserved as an impression in external view, WAM 87.8.7.

Description

The scale is a typical osteolepidid type, distinguished from the rhombic scales of porolepiforms by the lack of pores. It is rectangular with a well-marked groove around the external, presumably cosmine-covered surface. It is thick, and the overlap area for neighbouring dorsal and anterior scales are short. There is no large dorsal peg as in some Australian forms like *Beelarongia* (Long 1987).

Such scales are commonly found in deposits of both marine and continental facies, especially during the Middle and early Late Devonian (Jarvik 1950, 1985; Janvier and

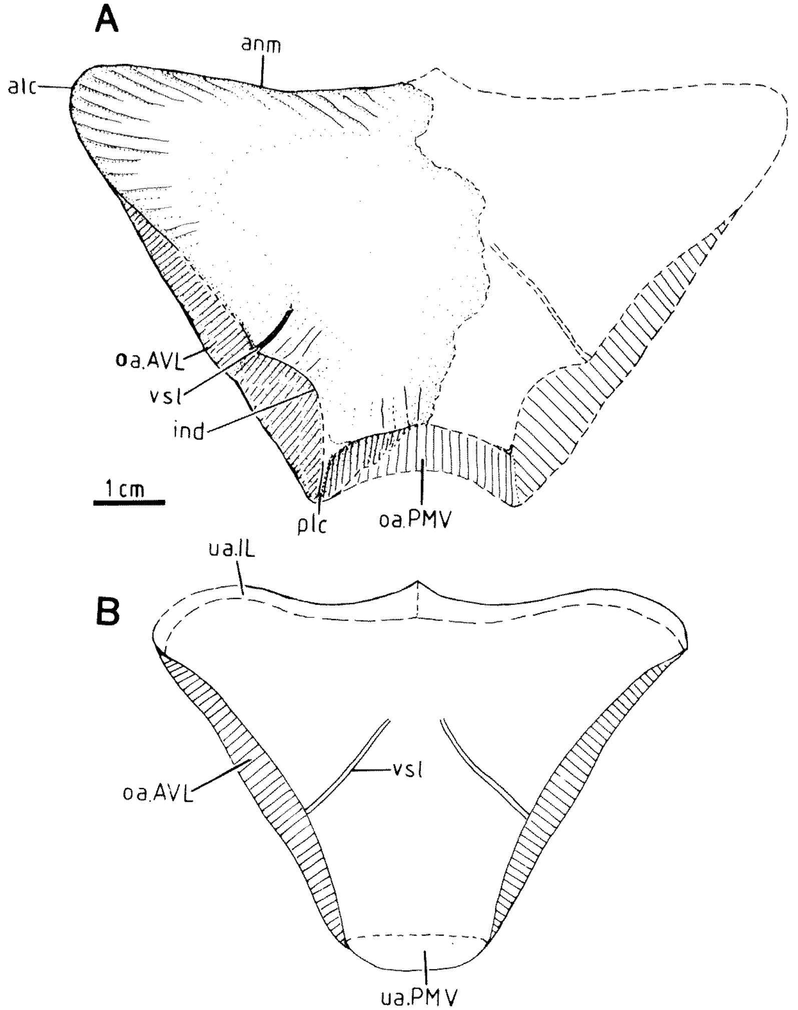

Figure 5. A, *Holonema* sp., AMV plate in ventral view, with missing areas restored (WAM 87.8.6; see Figure 3E for scale). B, the AMV plate of *Holonema westolli* from the Frasnian Gogo Formation (after Miles 1971, Figure 65 and WAM 90.12.137).

Martin 1979). By the Famennian most osteolepiforms had developed cycloid scales, except for the megalichthyids, but these have relatively thinner scales than in more primitive osteolepidids. The Munabia Sandstone osteolepidid scale is indistinguishable from those of the Gogo Formation osteolepiform *Gogonasus*, (based on WAM 86.9.661) but confident identifications cannot be made from scales alone.

The age of the Munabia Sandstone

The most age-diagnostic fish taxa identified from this assemblage are *Bothriolepis* and *Holonema. Bothriolepis* is restricted to the late Middle Devonian (Givetian) and Late Devonian in Europe, North America and the eastern U.S.S.R. (henceforth collectively referred to the Palaeozoic province of Euramerica, *sensu* Young 1981), but occurs in the Middle Devonian of China (P'an Jiang 1981), Antarctica and probably Australia (Young 1974, 1988). "*Bothriolepis*" from the Middle Devonian (?Eifelian) Hatchery Creek Conglomerate in New South Wales (Young and Gorter 1981) has since been referred to the new genus *Monarolepis* (Young 1988), but is a closely related form to *Bothriolepis* and *Briagalepis* (Long *et al.* 1990). Perhaps the oldest occurrences of *Bothriolepis* in Australia are now placed as possibly Late Givetian (Tatong, Victoria; Long and Werdelin 1986; Amadeus Basin, Young 1985).

Holonema has an age range of Middle Devonian -Frasnian in Euramerica and has been reported in association with *Bothriolepis* from several localities (e.g. Antalya Nappe, Turkey, Janvier 1983). However it is known from only one other site in Australia — the early Frasnian Gogo Formation. The occurrence of these two forms together in Western Australia is consistent with an early Frasnian age, indicated by the invertebrate and microfossil ages given for the underlying Gneudna Formation (late Givetian to earliest Frasnian). The base of the unit interfingers with the marine Gneudna Formation and there is no field evidence for assuming that the Munabia Sandstone is not conformable with the Gneuda Formation.

The uppermost section of the Munabia Sandstone has yielded some conodonts from a limy horizon within the sandstone (interval 24 of section CB93, Bureau of Mineral Resources unpublished report GEOL 79:034, by R.S. Nicoll). Nicoll identified *Polygnathus communis communis* and *Icriodus cornutus,* indicating the upper horizons of the unit may be of early Famennian age. Thus from both contact relationships with the Gneudna Formation and biostratigraphic assessment of fish and conodonts, the Munabia Sandstone is most likely to be early-middle Frasnian at the base, ranging into early Famennian in its youngest horizons. The maximum thickness for the unit is 555 metres at the type section (Hocking *et al.* 1987) and near where both the fish and conodonts were found. It would seem therefore that the Munabia Sandstone was deposited continuously over a time range of approximately 7-10 million years.

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Abbreviations used in text and figures

a.ar.SM	anterior articulation area for submarginal plate
ADL	anterior dorsolateral plate
alc	anterolateral corner
AMD	anterior median dorsal plate
anm	anterior margin of plate
ard	anconeal area of central dorsal plate 1
arf	articular fossa of anterior dorsolateral plate
AVL	anterior ventrolateral plate
CD1	central dorsal plate 1 of pectoral appendage
cit	crista transversalis interna anterior
cr1,2	cristae defining transverse lateral groove
cr.dm	mesial ridge on dorsal margin of pectoral appendage
cri	infra-articular crista of anterior dorsolateral plate
crs	supra-articular crista of anterior dorsolateral plate
dem	dorsal external margin of plate
dlam	dorsal lamina of plate
dlr	dorsolateral ridge of trunkshield
ind	indentation in plate margin
L	lateral plate
lat.p	lateral pit of lateral plate
llam	lateral lamina of plate
l.oa.AVL	overlap area for anterior ventrolateral plate
MM2?	suggested mesial marginal 2 plate
mt	mesial thickening on pectoral appendage
oa.AVL	overlap surface for anterior ventrolateral plate
oa.PMV	overlap surface for posterior median ventral plate
orb	orbital notch
p.ar.SM	posterior overlap area for submarginal plate
plc	posterolateral corner of plate
pnoa	postnuchal ornamental angle
pr.apo	groove for anterior postorbital process of endocranium
prh	preorbital recess
pro	processus obstans
PVL	posterior ventrolateral plate
ri	ridge
rm	rostral margin
tvr	transverse ventral ridge on anterior dorsolateral plate
ua.IL	area underlapped by interolateral plate
ua.PMV	area underlapped by posterior median ventral plate
v.lam	ventral lamina of plate
vlr	ventrolateral ridge of trunkshield
v.oa.AVL	ventral overlap surface for anterior ventrolateral plate
vsl	ventral sensory-line canal groove.

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