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New Information on the Head and Shoulder Girdle of *Canowindra grossi* Thomson, from the Late Devonian Mandagery Sandstone, New South Wales

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ABSTRACT. The head of *Canowindra grossi* is redescribed from newly prepared casts of the holotype. The cheek has a fractionated postorbital series consisting of one large and two small postorbital bones; the lachrymal is small relative to the postorbitals and jugal, and the jugal is elongate. The opercular is deep, and higher than long. The skull table features a parietal shield without differentiated intertemporal, supratemporal or parietal bones. *Canowindra* shares with osteolepids plus eusthenopterids (Osteolepiformes) a large, externally ornamented anocleithrum, and a cheek with bar-like, vertical preopercular and single, large squamosal bone. It differs from these groups in the structure of the postorbital series and skull roof table. *Canowindra* represents an endemic genus which should be regarded as the only member of a taxon equivalent to osteolepids plus eusthenopterids. An amended diagnosis of the genus is given.

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KEYWORDS: Osteichthyes, Osteolepiformes, Devonian, Australia, description, relationships, Porolepiformes, systematics.

Canowindra (Thomson, 1973) was the first crossopterygian genus known only from Australia. Prior to that work only fragmentary bones and scales of *Strepsodus decipiens* (Woodward, 1906) were documented from this country, and that identification has been questioned recently (Long, 1982). *Canowindra* is known from a complete natural mould in a slab of Mandagery Sandstone (Australian Museum F47153) collected in 1956 from a road cutting near the township of Canowindra. Besides the crossopterygian, the slab contains over a hundred well preserved armours of the antiarchs *Bothriolepis* and *Remigolepis*, and a partial armour of the euarthrodire *Groenlandaspis* (Dr A. Ritchie, pers. comm.). A Fammennian age is indicated by correlation with nearby marine intercalations containing brachipod faunas, and also by the abundance of the placoderm *Remigolepis* (Young, 1974; Long, 1983).

The new observations reported here resulted from further preparation of the original natural mould by Dr A. Ritchie and Mr R.K. Jones of the Australian Museum. The new latex cast of the head region reveals important features which could not be described by Thomson, and these are of great importance in discussing the phylogenetic position of the genus. Terminology used herein follows Jarvik (1980).

Description

The head is preserved in dorsal view with the cheeks, opercular bones and part of the pectoral girdle articulated (Figs 1, 2). Overall, the head is broad posteriorly and rather shallow with an acutely pointed snout. Sutures are not distinct on the fronto-ethmoidal shield but can be made out on the parietal shield and cheek. Laterosensory lines are not visible on any part of the head except for obscure pit-lines on the parietals, frontals, squamosals and dentary. Proportions of cranial bones are summarized in Table 1.

Fronto-ethmoidal shield. The fronto-ethmoidal shield reveals little new information. The presence of a large median postrostral (Thomson, 1973: 212) cannot be confirmed. Cracks on the surface suggest a polygonal bone mosaic at the front of the snout, although these do not appear as distinct sutures like the median line separating the frontals (Fr). A pineal foramen (Pin) appears to be present in the posterior

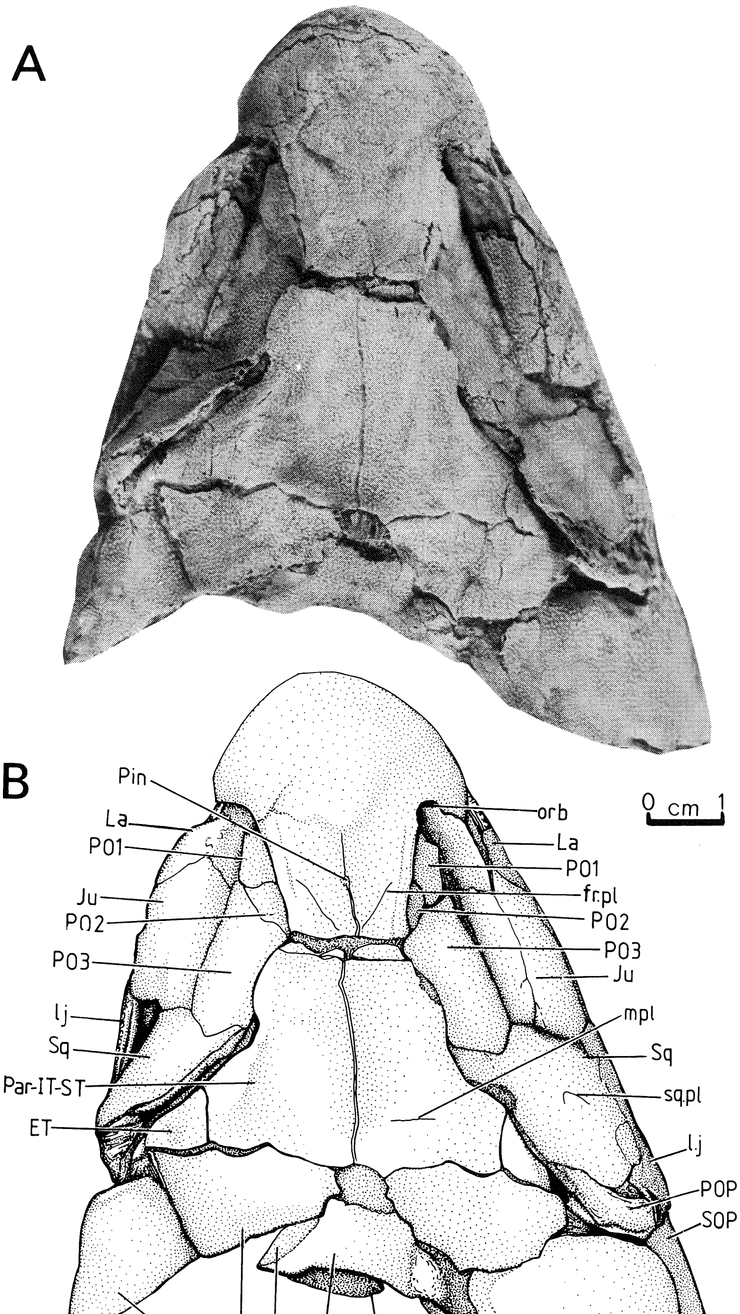

Fig. 1 *Canowindra grossi* Thomson: head of the holotype, Australian Museum F47153, in dorsal view. **A**, photograph; **B**, sketch interpretation. Abbreviations used in all figures: **AC1**, anocleithrum; **ac.pr**, anocleithral process; **Clth**, cleithrum; **ET**, extratemporal; **f.ex**, fenestra exonarina; **fr.pl**, frontal pit-line; **Ju**, jugal; **La**, lachrymal; **L.E**, lateral extrascapular; **l.j**, lower jaw; **Max**, maxilla; **M.E**, median extrascapular; **mpl**, middle pit-line of parietal; **oa.Cl**, area overlapped by cleithrum; **oa.LE**, area of median extrascapular overlapped by lateral extrascapulars; **oa.Pt**, area overlapped by post-temporal; **OP**, opercular; **orb**, orbit; **Par-IT-ST**, parieto-intertemporal-supratemporal; **Pin**, pineal foramen; **PO1, 2, 3**, postorbital bones; **PS**, prespiracular; **PSM**, preoperculosubmandibular; **POP**, preopercular; **PT**, post-temporal; **QJ**, quadratojugal; **SC1**, supracleithrum; **SOP**, subopercular; **Sq, Sq1, 2**, squamosal and accessory squamosals; **sq.pl**, squamosal pit-line.

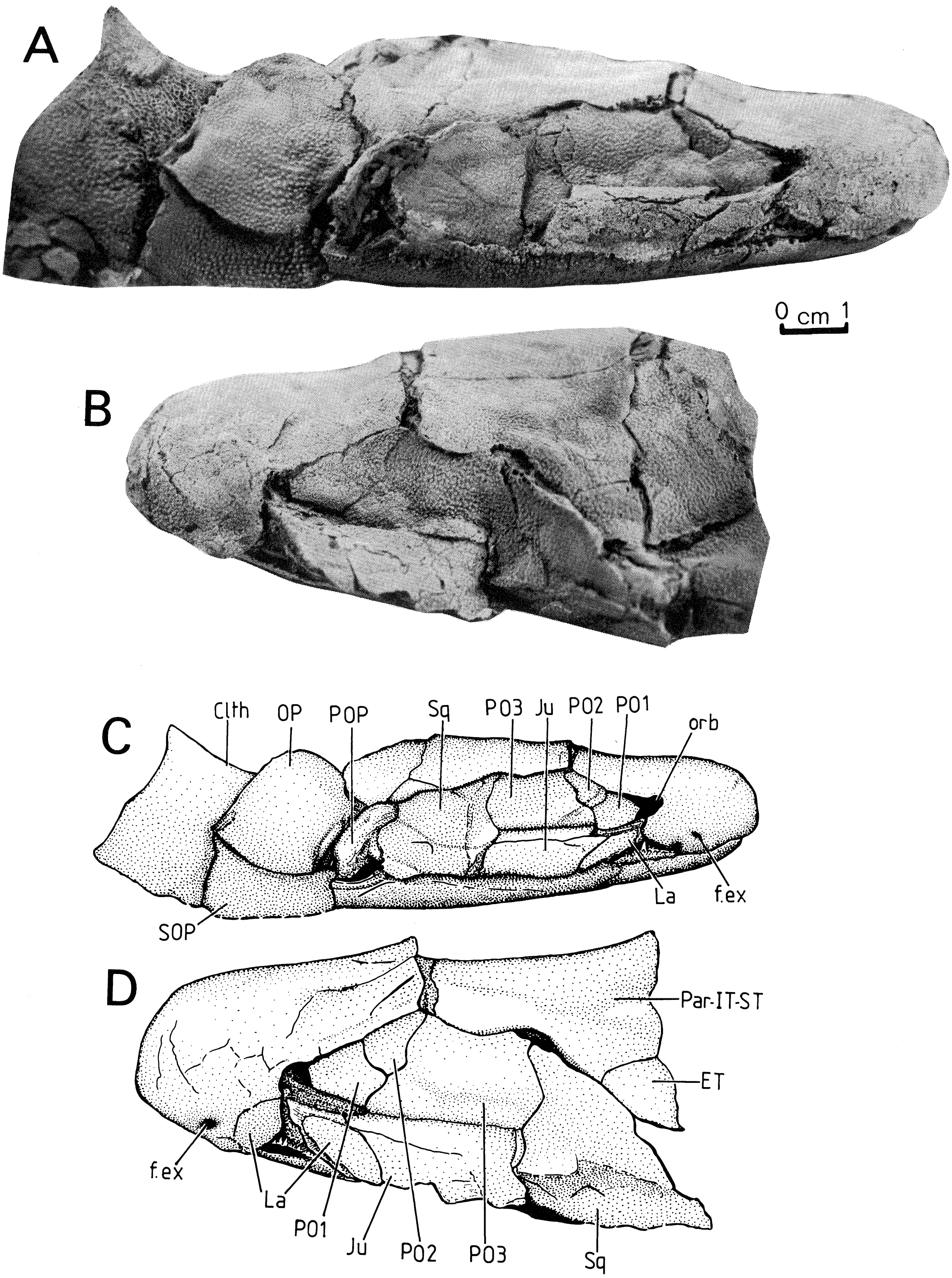

Fig. 2. *Canowindra grossi* Thomson. Interpretation of cheek bones of **A**, **C**, left side; and **B**, **D**, right side of holotype, Australian Mueum F47153. Abbreviations as for Fig. 1.

1.	Length of fronto-ethmoidal shield	40 mm
2.	Breadth of fronto-ethmoidal shield	36.5 mm
3.	Diameter of orbit (r)	4.5 mm
4.	Length of parietal shield	32.5 mm
5.	Breadth of parietal shield	60 mm
6.	Length of lateral extrascapular (1)	17.5 mm
7.	Breadth of lateral extrascapular (1)	27 mm
8.	Median length of median extrascapular	10.5 mm
9.	Breadth of median extrascapular	27 mm
10.	Length of cheek (r)	74 mm
11.	Height of cheek (r)	25 mm
12.	Length of postorbital 1	11.5 mm
13.	Length of postorbital 2	11 mm
14.	Length of postorbital 3	25.5 mm
15.	Length of jugal	36 mm
16.	Length of squamosal	32 mm
17.	Greatest depth of opercular	33 mm
18.	Greatest breadth of opercular	22 mm

Table 1. Cranial measurements of *Canowindra grossi*

third of the shield. Faint lines parallel to the lateral edges of the postorbital region of the shield could be sutures for the dermosphenotics. The frontal pit-lines (fr.pl) are clearly seen, and run posteriorly almost to the rear of the shield. The fenestra exonarina (f.ex) is well defined on both sides as a narrow anteroventrally directed slit. Below each of the small orbits there is a crescentic suture marking the anterior extent of the lachrymal (La).

Parietal shield. As Thomson (1973: 212) observed there are no sutures between the parietal, intertemporal and supratemporal bones of each side, though clear sutures separate the extratemporal bones (ET) from the rest of the shield, and a median suture separates the parietals. Fused parietals and intertemporal bones are known in porolepiforms and actinistians (Andrews, 1973), but fused parietal-intertemporal-supratemporals are unique to *Canowindra*. Unlike osteolepids, which may not show the sutures between these bones because of a cosmine cover (Jarvik, 1948), *Canowindra* has no cosmine. The parietal shield is notably broad, with a breadth/length index of 194. The width of the straight anterior margin is 32% of the posterior margin width. The posterior margin has two distinct notches on each side, one at the suture with the extratemporal bone and the other about midway between this and the midline. Posterior processes are present along the posterior margin at the mesial corners of the lateral extrascapulars, leaving a concave area for the short articulation area of the median extrascapular. The extratemporal bones are slightly narrower than Thomson's figure (1973, Fig. 2) suggests. They are still broader than long and contact the lateral extrascapular for 40% of the breadth of that bone.

Extrascapulars. The lateral extrascapulars (L.Ex) are extremely broad, being 44% as long as broad with irregularly notched anterior margins which contact the parietal shield. The median extrascapular (M.Ex) is also very broad, having a paramedian length one third of the total breadth. It is overlapped laterally by the lateral extrascapulars, as in osteolepiforms. The posterior margin has a strong median embayment.

Cheek. The bones of the cheek are clearly seen on the new cast. The postorbital of Thomson (1973, Fig. 3A) consists of two separate bones divided by a curved suture. As these two bones are present on both sides of the specimen, and laterosensory lines are not easily detected anywhere on the head, it is simpler to accept that this line is a suture dividing small postorbital bones, rather than the infraorbital sensory line canal, as implied by Thomson. The bone posterior to these two small anterior postorbitals occupies the area dorsal to the jugal and directly anterior to the squamosal, and is thus a postorbital bone rather than a prespiracular (Thomson, 1973, Fig 3A). The prespiracular bone occurs only in the cheeks of the porolepiform fishes, where it occupies a position posterior to the postorbital (which is immediately dorsal to the jugal), and dorsal to the squasmosal. It does not contact the jugal in *Porolepis* (Fig. 3C), *Glyptolepis*, *Holoptychius* or *Laccognathus* (Jarvik, 1972; Vorobyeva, 1980), and therefore is most probably a subdivision of the squamosal bone (Thomson, 1973: 219) which may be highly subdivided in some porolepiforms (e.g. *Holoptychius* Jarvik, 1972). In *Canowindra*, the area dorsal to the jugal, anterior to the single large squamosal and posterior to the orbit is therefore occupied by three postorbital bones, viz a large posterior element and two small anterior bones (Fig. 3B).

Each of the two small postorbital bones (PO1, PO2) is approximately half as long as the large subrectangular posterior postorbital. The anterior postorbital (PO1) is almost rhombic with a shorter posterior division, and contacts the other small postorbital at a concave suture. The posterior small postorbital (PO2) tapers posteriorly to an acute point at the junction of the fronto-ethmoidal and parietal shields. The large postorbital (PO3) has relatively straight dorsal and ventral margins, and the anterior margin slopes anteroventrally and is almost straight apart from a small median concavity. The posterior margin is strongly convex.

The jugal (Ju) is clearest on the right cheek, although on both sides the anterior end of the bone is missing. It is unusual in being a slender bone, three times longer than high. It is assumed to have formed the posterior margin of the orbit, as in other rhipidistians.

The lachrymal (La) is imperfectly preserved on both sides. It lies anterior to the jugal, which it meets along a curved suture, thus placing a large portion of the lachrymal ventral to the jugal. The lachrymal extends a short distance anterior to the orbit, and is bordered ventrally by the maxilla.

The squamosal (Sq) is the largest cheek bone, occupying 42% of the total cheek length. As in osteolepiforms it contacts the postorbital and jugal anteriorly, the maxilla and presumably the quadratojugal ventrally, and the preopercular

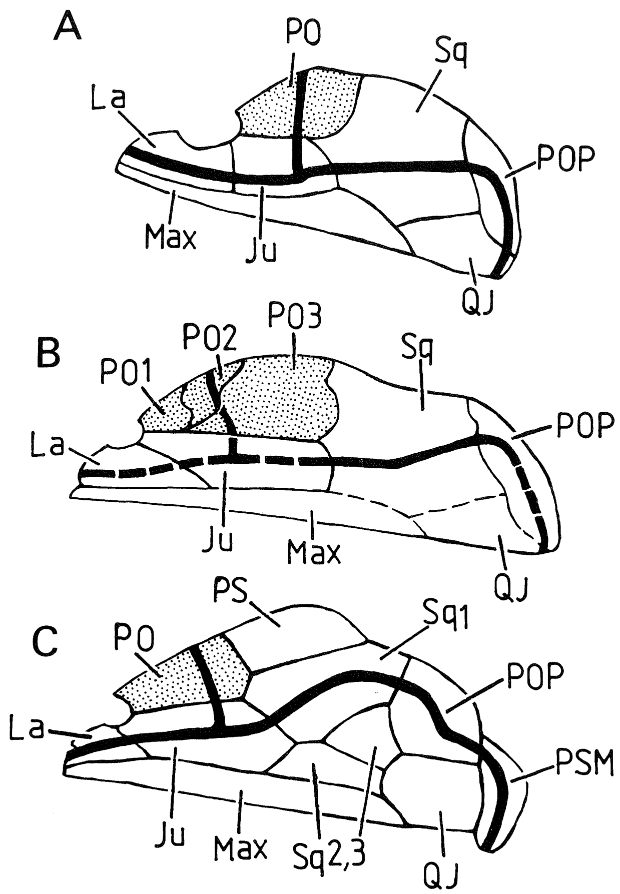

Fig. 3. Rhipidistian cheek bone patterns. **A**, Osteolepiformes (*Eusthenopteron*, after Jarvik, 1980); **B**, *Canowindra grossi*; **C** Porolepiformes (*Porolepis*, after Jarvik, 1972). Postorbital bone or series shaded; sensory-line canals represented by heavy lines. Abbreviations as for Fig. 1.

posteriorly. The anterior margin has two concavities for receiving the convex posterior borders of the jugal and postorbital bones. There is a cuspate squamosal pit-line (sq.pl) visible on the right side located close to a thin depressed line on the bone surface, the preopercular sensory line (pop). The squamosal is approximately two thirds as high as long.

The preopercular (POP) is clear on the right side, firmly attached to the posterior margin of the squamosal. It is a slender bone, three times as long as broad, with a vertical disposition, as in osteolepiforms (Fig. 3A, B).

Although the maxilla cannot be seen on the specimen, it is presumed to have been relatively slender, as Thomson has restored it (Thomson, 1973, Fig. 3A) in order to fit into the available space ventral to the lachrymal, jugal and squamosal bones. The short ventral extent of the preopercular supports this view.

Opercular bones. Only the operculars (OP) and the dorsal region of the subopercular (SOP) is preserved on the specimen. The opercular is much deeper than in Thomson's restoration (1973, Fig. 3A). It is almost one and a half times as deep as broad, extending ventrally from the lateral extrascapular along the complete posterior margin of the cheek. The posterior margin of the opercular is gently convex, the anterior margin relatively straight, and the ventral margin is distinctly convex.

The subopercular has a concave dorsal margin, not a convex one as restored by Thomson. It would appear from the relative position of the lower jaw that the subopercular was not a deep bone, but significantly longer than high.

Lower jaw. There is little new information to add to Thomson's comments. The dentary is slender posteriorly, broadening evenly towards the front, as in osteolepiforms. A posteriorly directed segment of the most posterior infradentary pit-line is present near the articulatory sockets of the mandible.

Pectoral girdle. Thomson (1973: 214) suggested that the cleithrum (Clth) was a double structure, composed of two separate ossifications. It is clear from the new cast that only the dorsal section of this bone is preserved on the right side, the ventral division being folded underneath the specimen. The ventral edge of this bone, as referred to by Thomson, is actually an irregular line caused by breakage of the cleithrum. The pectoral fin seen emerging from this area is partly obscured by the tail squamation of a nearby *Remigolepis*. The dorsal margin of the cleithrum is slightly concave, with a posterodorsal process. The posterior margin of this division of the cleithrum is quite concave.

There is an anocleithrum (ACl) on the left side of the specimen immediately posterior to the cleithrum. It resembles a large scale with a very extensive ventral overlap surface (oa.Cl) and an anteriorly directed anocleithral process (ac.pr; Fig. 4A). The ornamented region of the bone is approximately twice as large as that of the nearby scales, being much the same breadth.

The supracleithrum (Scl) is seen as a small, scale-like bone, anteromesial to the anocleithrum on the left side of the specimen (Fig. 4A). It is slightly larger than the nearby scales and has a broad dorsal overlap flange for the post-temporal bone (oa.PT). In life, only a small part of the supracleithrum was overlain by the opercular.

The post-temporals (PT) are identified as the two subrectangular bones posterior to each of the lateral extrascapulars. The post-temporal is of similar size to the supracleithrum, and contacted a large region of the posterior margin of the lateral extrascapular when articulated in the shoulder girdle (Fig. 4B).

Relationships of *Canowindra*

The unique plexus of characters exhibited by *Canowindra* is not typical of either osteolepiform or porolepiform fishes. Thomson suggested that it was closer to holoptychioids on skull and cheek structure (1973: 216, 217) but was not sure of its affinities. The

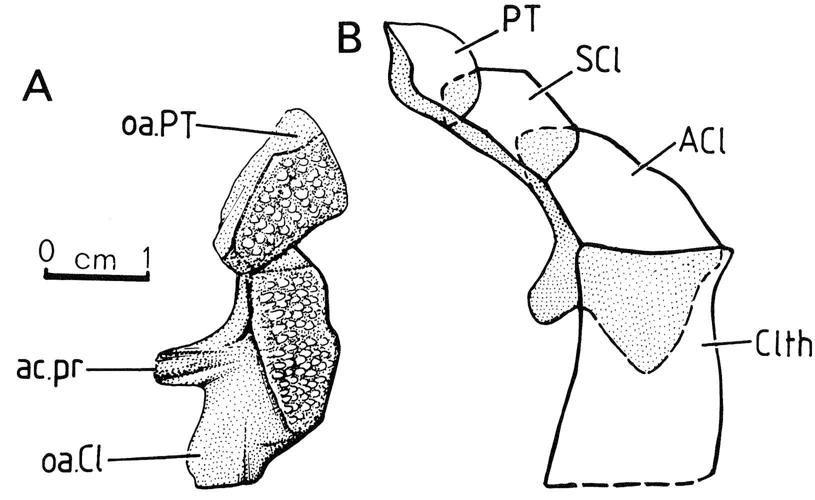

Fig. 4. *Canowindra grossi* Thomson. **A**, two of the dorsal pectoral girdle bones, the anocleithrum (below) and supracleithrum (above); from left side of holotype, Australian Mueum F47153. **B**, attempted reconstruction of the dorsal exoskeletal pectoral girdle bones of *Canowindra*. Overlap areas shaded.

porolepiform features of *Canowindra* are its broad parietal shield with large extratemporal bones and fused parietal-intertemporal bones, and the small orbits. Osteolepiform features of *Canowindra* are: cheek with a large single squamosal and vertical bar-like preopercular, the dermal shoulder girdle with a large, externally ornamented anocleithrum (Long, 1985), a single pair of external nares, median extrascapular overlapped by lateral extrascapulars, and a median boss on the basal surface of the scales. The loss of cosmine in the dermal skeleton and presence of rounded scales would further suggest that the genus is specialized, unlike the primitive members of both porolepiforms and osteolepiforms which bear rhombic scales and have an extensive cosmine cover (Jarvik, 1980). Unique features of *Canowindra* are the fusion of the parietal-intertemporal-supratemporal bones, the subdivision of the postorbital bone in the cheek, and the unusual shape of the median extrascapular.

Characters used to distinguish Osteolepiformes from Porolepiformes which are relevant to *Canowindra* are summarized in Table 2, taken from Jarvik (1972, 1980) and Long (1985). Despite recent suggestions that the osteolepiforms are a paraphyletic group (Rosen *et al.*, 1981), arguments for the monophyly of the group have been advanced (Long, 1985). From this list of characters it can be seen that *Canowindra* shares the following synapomorphies with Osteolepiformes: overall structure of the cheek, shoulder girdle with large anocleithrum. Characters of *Canowindra* in common with porolepiforms, such as the fusion of the intertemporal and parietal bones, and small orbits, can not be shown to be synapomorphies. Actinistia have a similar type of parietal shield to Porolepiformes (Andrews, 1973), and several groups of osteichthyans show that orbit size is a variable feature, such as in the primitive palaeoniscoids *Cheirolepis* and *Moythomasia* (Pearson, 1982), the osteolepiform *Glyptopomus* (Jarvik, 1950) and the dipnoans *Dipnorhynchus* and *Chirodipterus* (Campbell & Barwick, 1982).

Porolepiformes can be shown to be monophyletic by having dendrodont tooth structure (Schultze, 1970). In addition to this character, the presence of a prespiracular plate and preoperculosubmandibular bone may be further synapomorphies of the group. This leaves *Canowindra* to be placed phylogenetically in only one way: as a specialized osteolepiform which differs from all others by the unique pattern of the skull roof, subdivision of the postorbital bone and narrow shape of the jugal bone. Osteolepiform synapomorphies, such as the enlargement of the lachrymal bone and basal scutes at fin origins (Long, 1985), are not seen on *Canowindra*, and may be regarded as synapomorphies of osteolepids and eusthenopterids excluding *Canowindra*. *Canowindra* also differs from these two groups in the shape of the opercular which is a deep bone rather than being squarish or longer than deep. This character could be regarded as plesiomorphic on evidence from the taxonomic distribution of opercular shapes in primitive osteichthyans (Actinopterygii; Pearson, 1982). If cycloidal scales evolved only once within Osteolepiformes, then *Canowindra* could be placed as the sister taxon to eusthenopterids, but this hypothesis would assume that the osteolepiform synapomorphies not seen in *Canowindra* were independently acquired in osteolepids. The parsimonious alternative to this hypothesis is to place *Canowindra* as the sister taxon to osteolepids and eusthenopterids (Osteolepiformes *sensu stricto*) and expand the definition of the group to include *Canowindra*. This assumes that cycloid scales with a median boss on the basal surface evolved

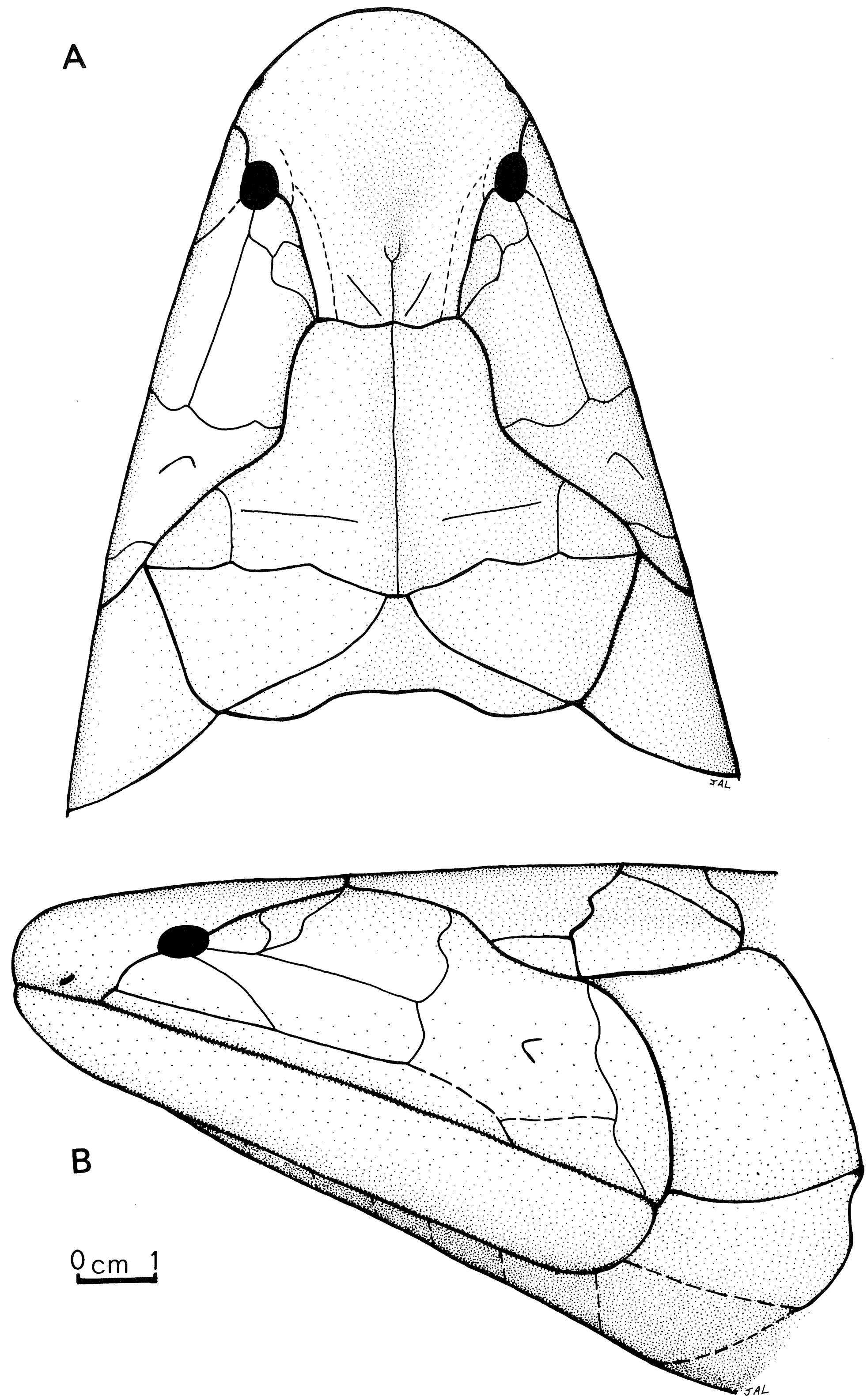

Fig. 5. *Canowindra grossi* Thomson. Attempted restoration of the head in **A**, dorsal and **B**, lateral views. After the holotype, Australian Museum F47153.

	A. Osteolepiformes	B. Porolepiformes	*Canowindra*
1. Parietal shield	Separate parietal, intertemporal and supratemporal bones	Fused parietal and intertemporal bones	Fused parietal, supratemporal and intertemporal bones
2. Parietal shield	Narrow	Broad	B
3. Frontal shield bones	Separate dermosphenotic	Dermosphenotics and frontals fused	?B
4. External nares	One pair	Two pairs	A
5. Orbit size	small-large	small	B
6. Extrascapulars	Median bone is overlapped by lateral bones	Median bone overlaps lateral bones	A
7. Postorbital	Single bone	Single bone	Three bones
8. Squamosal	Single bone	Multiple bones	A
9. Preopercular	Bar-like, verticle	Broad, squarish	A
10. Preoperculosub-mandibular	Absent	Present	A
11. Pectoral girdle	Anocleithrum large externally exposed	Anocleithrum small ?subdermal (Long, 1985)	A
12. Cycloid scales	With median boss on basal surface	Without median boss	A

Table 2. Comparison of character states of Osteolepiformes, Porolepiformes and *Canowindra grossi*

as parallellisms in *Canowindra* and eusthenopterids, as they did for holoptychioids, actinistians and higher dipnoans (Schultze, 1977). *Canowindra* should be placed in its own suborder equal in rank to the Osteolepiformes (Osteolepididae, Lamprotolepididae, Eusthenopteridae, ?Panderichthyidae, ?Rhizodopsidae). However, as there are other newly discovered osteolepiform-like fishes from the Devonian of Australia and Antarctica which share derived features with *Canowindra*, the task of erecting higher taxonomic levels will be postponed until the systematic descriptions of the other new forms are completed.

Formal Systematics

Canowindra grossi Thomson, 1973

Amended diagnosis. A moderately large, fusiform rhipidistian fish. Fronto-ethmoidal shield/ parietal shield ratio 150. Orbits very small. Distance from tip of snout to beginning of first dorsal fin insertion approximately 4 times the combined skull table length; equal to 0.57 times total length of fish. Parietal shield comprises fused parieto-intertemporal-supratemporal bones separated by median suture; broad triangular extratemporals; breadth/length ratio 194. Cheek with single, large, squamosal, bar-like preopercular, and three postorbital bones dorsal to slender jugal. Lower jaw contained 6.8 times in length of fish. Lateral extrascapulars broader than long, almost meeting in midline. Opercular large, deeper than long. Pectoral girdle with large externally exposed anocleithrum, twice the size of scales; cleithrum with straight dorsal edge. Scales round with median boss on basal surface. Dermal bones and scales lack cosmine, ornamented with separate tubercles. Trunk with circular cross-section in front of dorsal fins; tail strongly heterocercal. Basal scutes absent from fin bases.

Holotype. AM F47153 (only specimen), kept in the Australian Museum, Sydney.

Age and occurrence. Upper Devonian Mandagery Sandstone (?Famennian, Long, 1983), collected near Canowindra, New South Wales.

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