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The Upper Devonian Fish *Bothriolepis* (Placodermi: Antiarchi) from near Canowindra, New South Wales, Australia

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ABSTRACT. The Upper Devonian fish fauna from near Canowindra, New South Wales, occurs on a single bedding plane, and represents the remains of one Devonian palaeocommunity. Over 3000 fish have been collected, predominantly the antiarchs *Remigolepis walkeri* Johanson, 1997a, and *Bothriolepis yeungae* n.sp. The nature of the preservation of the Canowindra fauna suggests these fish became isolated in an ephemeral pool of water that subsequently dried within a relatively short space of time. This event occurred in a non-reproductive period, which, along with predation in the temporary pool, accounts for the lower number of juvenile antiarchs preserved in the fauna. Thus, a mass mortality population profile can have fewer juveniles than might be expected. The hypothesis that a single species of *Bothriolepis* is present in the Canowindra fauna is based on the consistent presence of a trifid preorbital recess on the internal headshield and separation of a reduced anterior process of the submarginal plate from the posterior process by a wide, open notch. Principal Components Analysis (PCA) based on head and trunkshield plate measurement shows no separation of *Bothriolepis* individuals into distinct clusters and is consistent with this hypothesis. A wide range of plate shape variation can thus occur within a species of *Bothriolepis*, and caution should be used when separating species on this basis in the future.

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In 1993, Alex Ritchie (Australian Museum) collected approximately 3000 fish from a single layer within the Upper Devonian Mandagery Sandstone, at a site approximately 10 km southwest of Canowindra, along the road to Gooloogong (Fig. 1). The recovery of these fish from a single bedding plane suggests these fish lived and died together, representing the remains of a palaeocommunity. Thus, the Canowindra fauna provides an opportunity to describe the nature and structure of an Upper Devonian fish community, although it must be remembered that the total community has not been preserved. The crowding of fish on the layer suggests a mass mortality during dry conditions. Additionally, the large number of well-preserved specimens of *Bothriolepis* present allows for a determination of the range of variation in head and trunkshield plate proportions that could be expected within a single species.
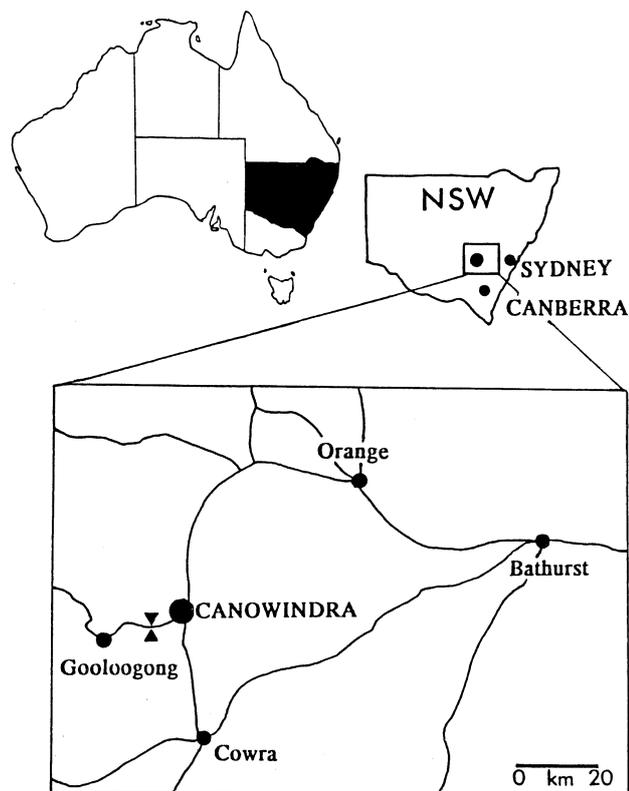
Figure 1. Map showing locality of Canowindra fauna, Mandagery Sandstone. From Johanson & Ahlberg, 1997.

The fauna is dominated by the antiarchs *Bothriolepis yeungae* n.sp. and *Remigolepis walkeri* Johanson, 1997a, and less commonly, the euarthrodire *Groenlandaspis* Heintz, 1932. Sarcopterygians are rare, including the canowindrid *Canowindra grossi* Thomson, 1973, the tristichopterids *Mandageria fairfaxi* Johanson & Ahlberg, 1997, and *Cabonnichthys loomesi* Ahlberg & Johanson, 1997, the rhizodontid *Gooloogongia loomesi* Johanson & Ahlberg, 1998, and two specimens of the dipnoan *Soederberghia* Lehman, 1959. No other vertebrates (e.g., tetrapods), plants or invertebrates have thus far been observed.

In 1993, nearly 195 rock slabs of varying sizes were collected from the Canowindra locality, but attempts to record the sequence of rocks as they were removed from the layer were largely unsuccessful. The counterpart of the collected fish layer remains *in situ*, preserving the original positions of these rock slabs and the fish on them. Due to time limitations, sedimentological features of the rocks above and below the fish layer were not recorded. This layer was completely covered to prevent vandalism, and is not currently available for examination (but will be uncovered in the future).

Nevertheless, information regarding various aspects of the preservation of the fish can be obtained from separate slabs and extrapolated to the fauna as a whole. Information as to the demise of the fauna can be garnered by considering the taphonomic aspects of the fauna, including events or processes occurring both before and after death (Behrensmeyer & Kidwell, 1985; Wilson, 1984, 1996). Population profiles of the antiarchs can indicate the relative abundances of juveniles and adults in the community, and can be compared to profiles expected when death is either catastrophic or attritional (e.g., Wilson, 1988). Differences in population profiles are also of interest, and can be used to speculate on timing of reproduction, growth rates, and prevalence of predation.

More than 1300 individuals of *Bothriolepis* from Canowindra have been noted to date, and, when preserved, a trifid preorbital recess and a reduced anterior process of the submarginal are consistently present. The first character is present in several species of *Bothriolepis*, while the second character appears to be unique to this species. In combination, they suggest that one species of *Bothriolepis* is present at Canowindra. This hypothesis is tested by performing a Principal Components Analysis (PCA) on head and trunkshield measurements on the individuals in this fauna.

Materials and methods

The Canowindra fauna is preserved as three-dimensional natural moulds filled with hardened sandstone casts, preserving the external and internal surfaces of the dorsal head and trunkshield plates, respectively. Latex casts were taken of both surfaces, whitened with ammonium chloride, and photographed. Labelled line drawings were made from these photographs or using a camera lucida. Measurements used in the PCA were taken from the maximum length and width of plates in the midline of the head and trunkshield (see Abbreviations, below) and from the orbital fenestra. Ratios given in the descriptive section are taken from the average of these measurements.

Specimens in the Canowindra fauna have been flattened and distorted to a certain degree. The degree of distortion was determined with the assistance of Dr D. Durney, School of Earth Sciences, Macquarie University. Latexes of the larger rock slabs (preserving a large number of individuals) were photographed, and the head and trunkshield outlines of *Bothriolepis* were drawn on overlying tracing paper. An image of these outlines and their relative orientations were taken and entered into a computer application developed by D. Durney. Using this, the distortion of these outlines from the ellipse was determined, and the amount and direction of shear affecting the specimens on the slab calculated. The amount of distortion was equivalent on the 8 slabs tested and was minimal (approximately 2–5%, as indicated by the appearance of the specimens themselves). The general direction of shear can be determined on each slab, but relating these to one another and to direction of cleavage in the rock will have to wait until the Canowindra site is reexcavated and the position of these slabs determined.

If a specimen lies exactly along the axes of the direction of cleavage, distortion can make them narrow and long (Fig. 3B) or short and broad (Fig. 3D), with no apparent

angular distortion (G.C. Young, pers. comm.). This could result in misleading impression of the degree of distortion in the fauna, but this would only occur in those specimens lying exactly along the axes of distortion. These would surely be very low in number relative to all other specimens not lying exactly along these axes (e.g., Fig. 4C). Because of this, and because overall distortion does not appear to be substantial, measurements can be confidently taken and used in a PCA without further correction.

Australian Museum specimen registration numbers are prefixed "AM F". Figures in the present work are referred to using the abbreviation Fig. or Figs., reference to other figures is indicated by use of lower case—fig. or figs.

Principal Components Analysis

Seventy-seven better preserved specimens of *Bothriolepis* were identified in the Canowindra fauna and measurements taken from midline plates as described above. Lateral plates were often crushed post mortem so that measurements could not be confidently and consistently made. Measurements were taken with a vernier caliper to the nearest 0.05 or 0.1 mm, and subjected to a PCA to test the initial hypothesis (Ho) that a single species of *Bothriolepis* is present at Canowindra. Clusters of individuals can be recognised visually through ordination of the results of the PCA, where the position of individuals is plotted using the components as the X and Y axes (Abbott *et al.*, 1985).

The effects of individual size must be removed from the data set before the PCA, because variation in shape is of taxonomic interest (e.g., Ciochon, 1993: 60). The majority of *Bothriolepis* individuals measured in this analysis were relatively large, with a range in head + trunkshield length from 76.6 to 190 mm, and a mean of 123.1 mm. Larger specimens were chosen for measurement as these were the best preserved and easiest to prepare for casting and study. Smaller specimens were very difficult to prepare (e.g., Fig. 6E,F), so that plate measurements could not be confidently taken.

Various methods for size removal have been suggested, with little agreement on the best method. A summary of these methods was provided by Reist (1985). Several address allometry, or unequal changes in shape during ontogeny. The morphology of juvenile *Bothriolepis* differs in many respects from adults (Stensiö, 1948; Werdelin & Long, 1986), and these differences would affect the results of this analysis, which is concerned with taxonomic rather than ontogenetic variation. However, because larger specimens of *Bothriolepis* were measured, allometric effects may not be substantial. To test this, measurements taken for *Bothriolepis* from Canowindra were regressed against the total head+trunkshield length in a simple linear regression (Sokal & Rohlf, 1981; Zar, 1996), where a slope other than one indicates allometry (e.g., Werdelin & Long, 1986). It is important to note that the regression method used is a Model I regression, requiring that the independent variable be error-free (Sokal & Rohlf, 1981). A Model II regression does not have this requirement, but can be controversial (e.g., Sokal & Rohlf, 1981: 550). Because the measurement of head and trunkshield length

(independent variable X) was simple to consistently and confidently take from specimen to specimen, it is assumed to be error-free, and a Model I regression is used below.

The statistical program "Datadesk" was used in this and all subsequent analyses. All variables were log transformed to standardise variances. The null hypothesis was Ho: regression slope equals 1 (isometric change). The results of the regression (Appendix) indicated that the null hypothesis could only be accepted for four variables. In all others, allometry was indicated.

Thus, the choice of method to remove the effects of size before PCA must account for this allometry. One method not highly criticised by Reist (1985) is regression, such that the shape variate is represented by the deviation of each observed data point from the regression line describing the size relationship of the two variables. A predicted value is read from the regression line such that the observed point minus the predicted gives the shape variate (Reist, 1985).

Results of the Principal Components Analysis

The use of simple line regression to remove size appears to have had the desired results. To test the efficacy of size removal, Reist (1985) suggested regressing the transformed data against X: if the slope of the regression line is 0, then no relationship is present between the variables. Thus, the shape variate (Y) is independent of size (X), and size has been removed from the original variables. In this analysis, regressing transformed variables against size resulted in slopes of 0 for all variables. These shape variables were used in the PCA below.

The results of the PCA are shown graphically in Fig. 2A–C, with the first three Principal Components as the axes. A wide range of variation is shown by the distributions of various specimens on the graphs, and although certain specimens lie on the outer margins of this distribution, no grouping of individuals into distinct clusters is apparent. This suggests that variation in head and trunkshield plate shape is not sufficient to separate *Bothriolepis* from Canowindra into more than one species. This is consistent with the original hypothesis, that a single species of *Bothriolepis* is present in the fauna, and more importantly indicates that a certain range of variation in quantitative measurements can be expected within populations.

A similar result was obtained by Trinajstic (1995) for arthrodires from the Gogo Formation (Frasnian, Western Australia). Statistical analyses indicated that individuals assigned to two separate genera were in fact part of a continuous variation and thus should be part of the same species. These results demonstrate the care that should be taken when attempting to discriminate species on the basis of plate proportions. Besides the usual problems (distortion, breakage, etc.), consideration of only a small sample of individuals may indicate differences that would disappear as more individuals are sampled. Therefore, species diagnoses should stress qualitative characters. Quantitative characters may be included in the description, but the potential problems inherent in these characters should be recognised.
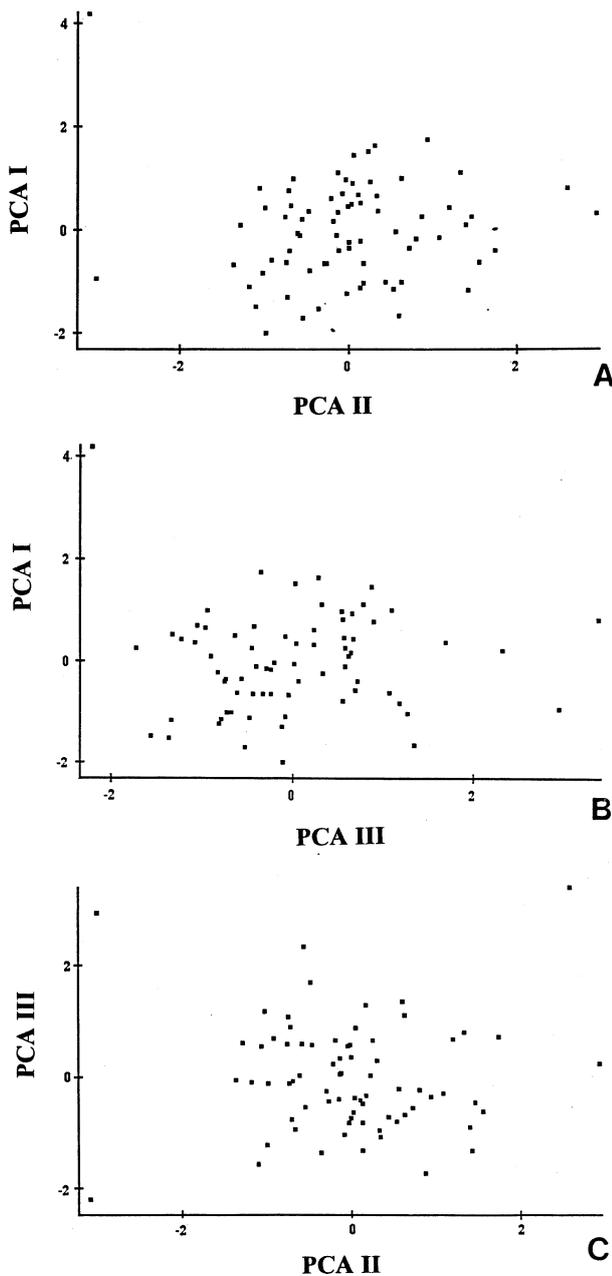
Figure 2. A, scattergrams of PCA axes I versus II. B, scattergram of PCA axes I versus III. C, scattergram of PCA axes III versus II. Dots indicate position of each of 77 specimens of *Bothriolepis yeungae* relative to these axes. Note that there is no separation of these individuals into different clusters, indicating that variation in plate measurements is not sufficient to differentiate more than one species of *Bothriolepis* at Canowindra.

Systematic palaeontology

Subclass Placodermi McCoy, 1848
Order Antiarchi Cope, 1885
Suborder Bothriolepidoidei Miles, 1968
Family Bothriolepidae Cope, 1886
Genus *Bothriolepis* Eichwald, 1840

Bothriolepis yeungae n.sp.

Figs. 3–10, 11C,J, 13–18

Bothriolepis sp. Conolly, 1965: 56.
Bothriolepis sp. Gilbert-Tomlinson, 1965: 208.
Bothriolepis sp. Long, 1982: 66.
Bothriolepis sp. Young, 1993: 251.
Bothriolepis sp. Johanson & Ahlberg, 1997: 39.
Bothriolepis sp. Ahlberg & Johanson, 1997: 653.
Bothriolepis sp. Johanson, 1997a: 213.
*Bothriolepis* sp. Johanson, 1997b: 201.

Holotype. AM F.101247, external head and trunkshield, left pectoral fin in dorsal view (Figs. 3A, 10G).

Other material. AM F.99692, AM F.100838–844, AM F.100885–904, AM F.101232–273, 101275–277, AM F.101608, AM F.101609, AM F.102397–399, AM F.105479–540, representing internal and external views of the head and trunkshield as well as disarticulated plates. Proportions given below are taken from specimens used in PCA, including (AM F.101247 and 105479–540). Measurements available from the author upon request.

Locality and horizon. 10 km SW of Canowindra, NSW, Australia, along the road to Gooloogong (33°35'56"S 148°33'59" E). The fossil fish layer is located within the Mandagery Sandstone (Upper Devonian).

Etymology. The species is named after Monica Yeung, Gondwana Dreaming Pty Ltd, Canberra, for her invaluable contributions to the Canowindra project.

Diagnosis. Differs from all other *Bothriolepis* in possessing a reduced anterior process of the submarginal, separated from the posterior process of the submarginal by a wide, open notch. Characterised by: Preorbital recess trifid. Oval attachment area for prelateral on the lateral plate small, laterally oriented, separated from a strongly developed, horizontal anterior submarginal attachment on the lateral plate. Posterior submarginal attachment on lateral plate ending at posterior margin of spiracular groove. Pineal plate with reduced posterolateral corners. Postlevator cristae of anterior median dorsal plate sharply defined and short, often dissociated from the postlevator thickenings and situated in the levator fossa. *Crista transversalis interna anterior* on anterior ventrolateral plate obliquely oriented. Cv2 and Mm1 plates do not overlap on mesial margin of pectoral fin.
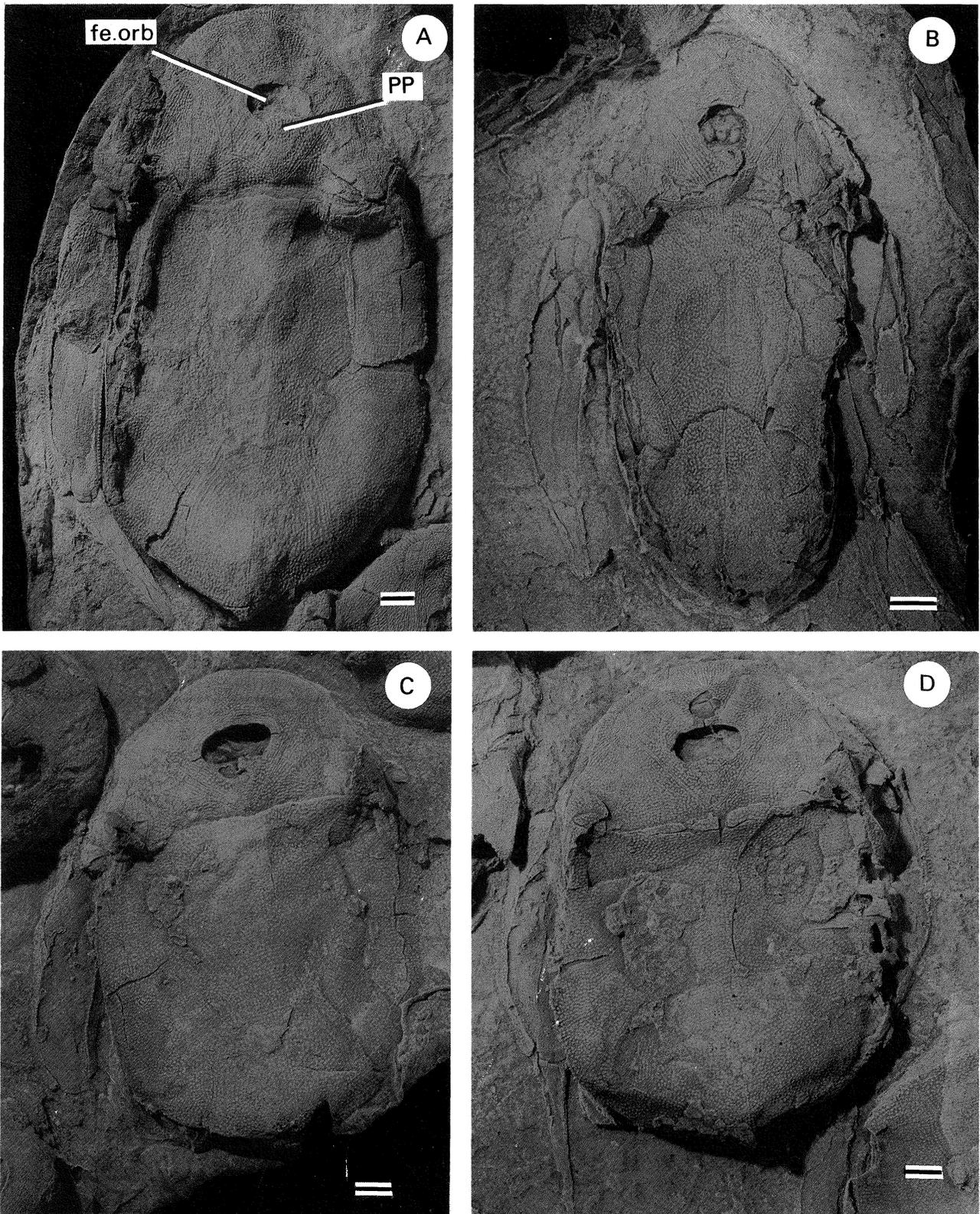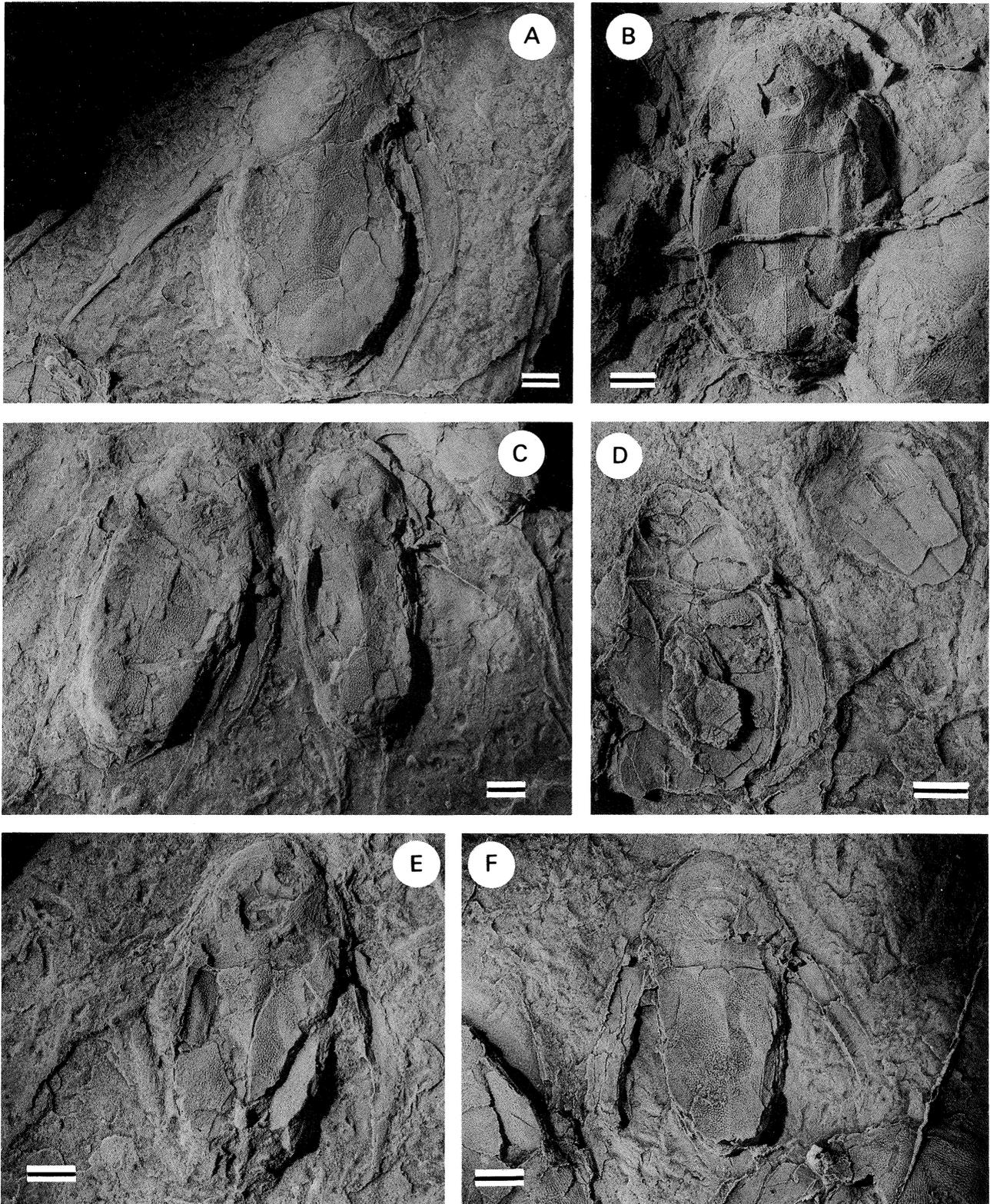
Figure 3. *Bothriolepis yeungae* n.sp. A, AM F.101247, holotype; B, AM F.100901; C, AM F.101271; D, AM F.101272; all dorsal view of head and trunkshield. Scale = 1 cm.
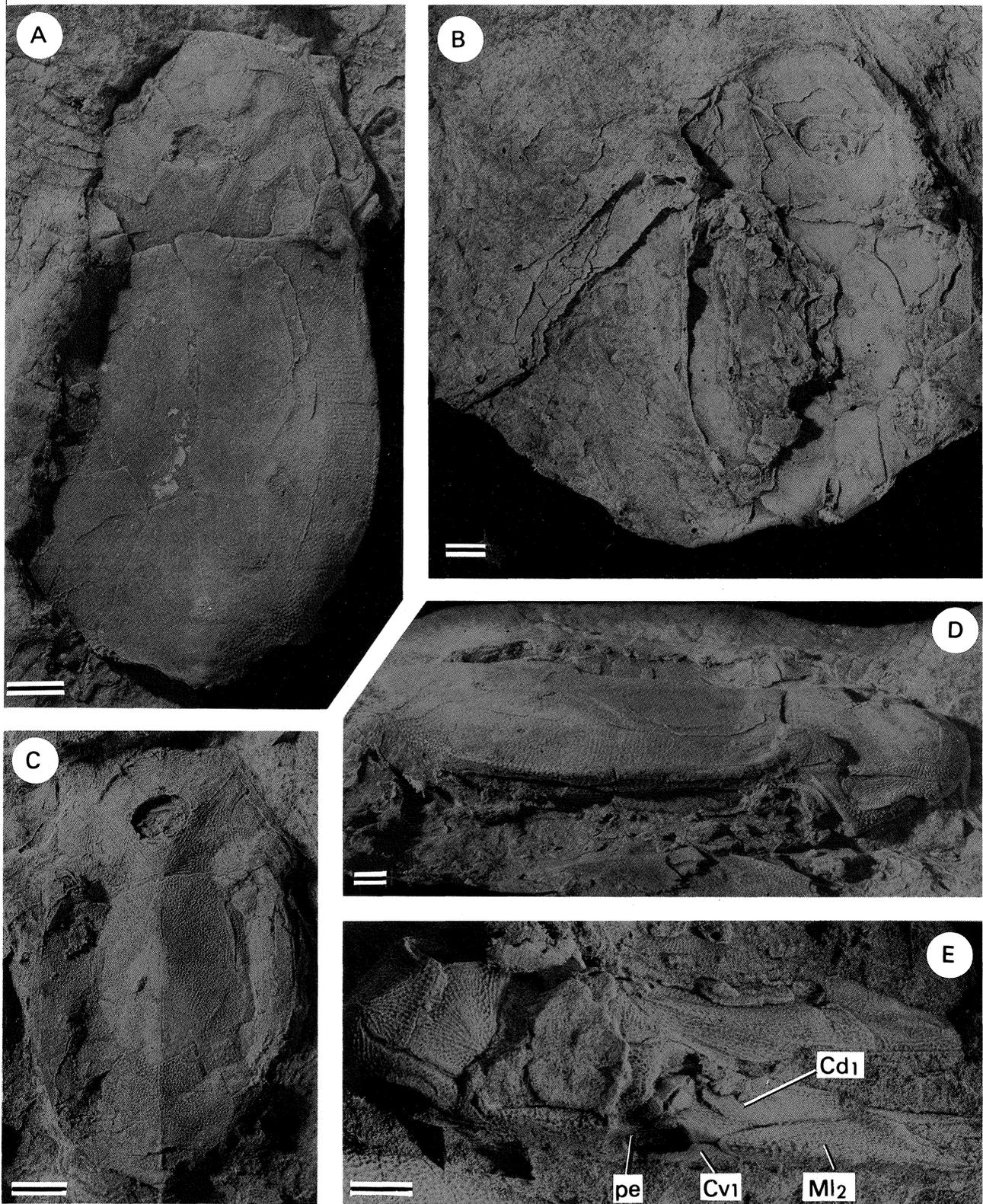
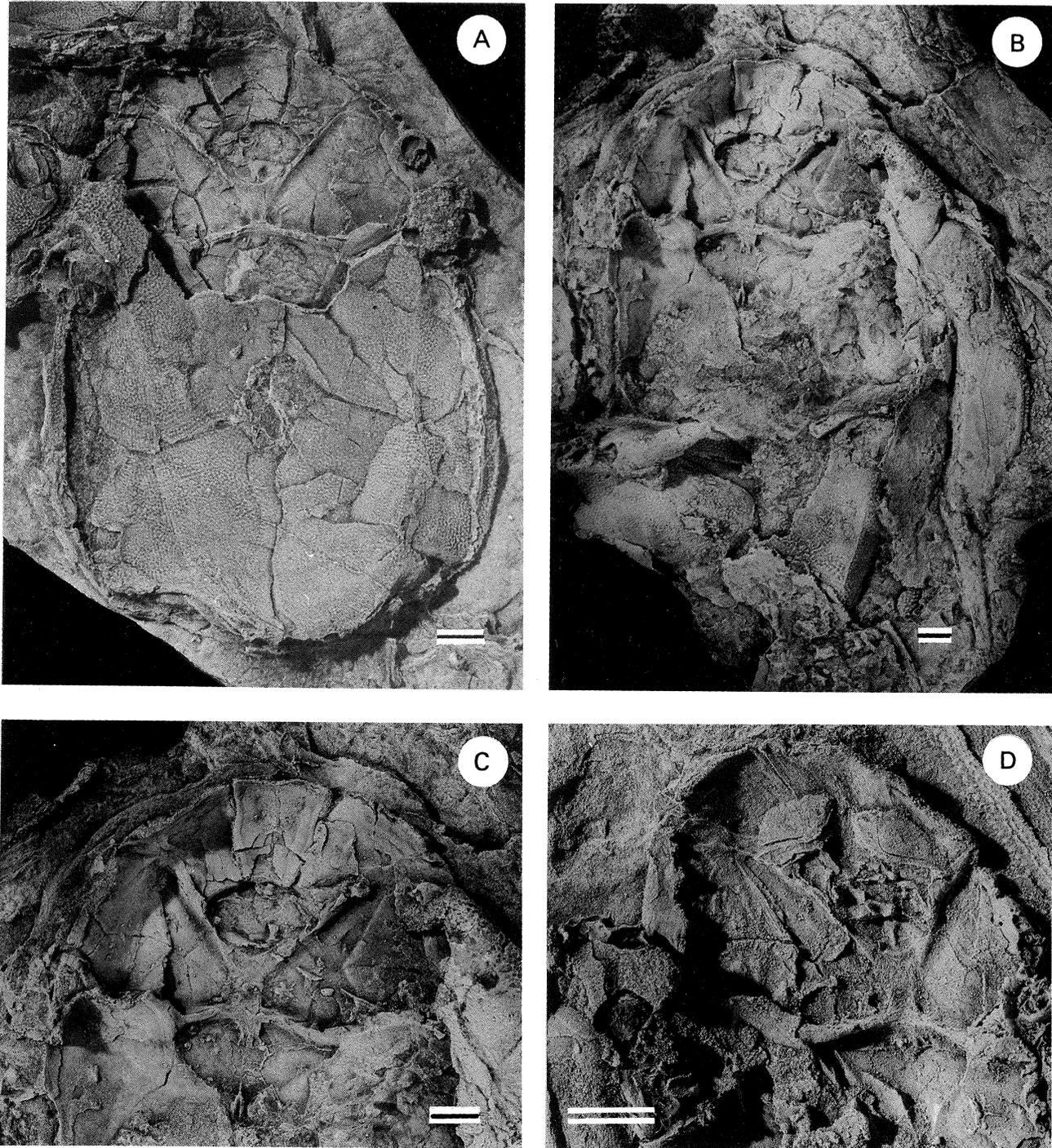**Figure 4**. *Bothriolepis yeungae* n.sp. A, AM F.100891, dorsal view of head and trunkshield; B, AM F.100901, ventral or internal view of head and trunkshield; C, AM F.101241, dorsal view of head and trunkshield; D, AM F.100891, lateral view of head and trunkshield and partial pectoral fin; E, AM F.101250, lateral view of head and trunkshield with proximal plates of pectoral fin. Scale = 1 cm.
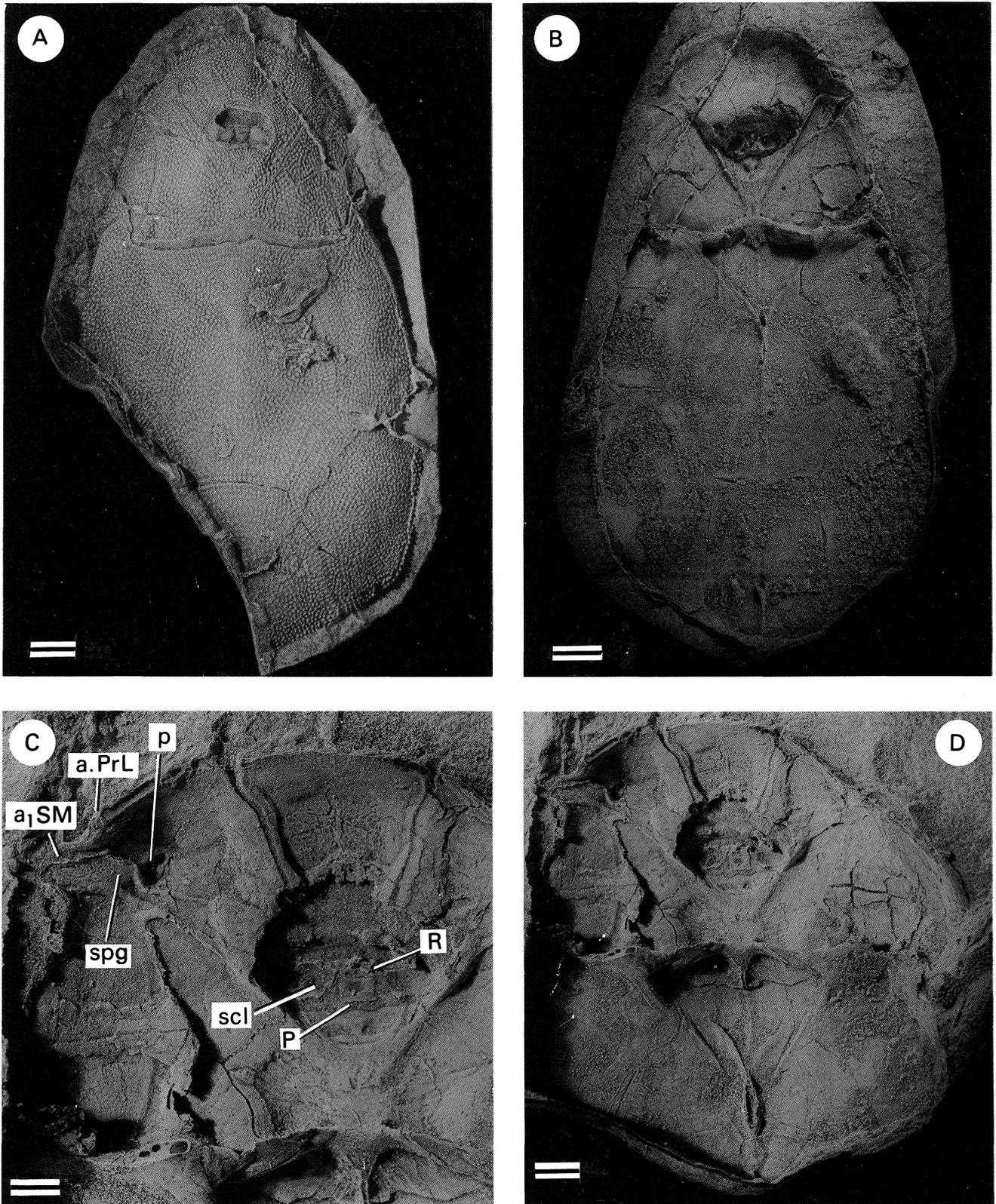
Figure 5. *Bothriolepis yeungae* n.sp. A, AM F.100802a, dorsal view of head and trunkshield; B, AM F.100802b, ventral or internal view of head and trunkshield, counterpart of Fig. 5A; C, AM F.100843, closeup of internal view of headshield; D, AM F.100843, internal view of headshield and anterior portion of AMD. Scale = 1 cm.

Figure 6. *Bothriolepis yeungae* n.sp., smaller individuals. A, AM F.101608; B, AM F.101243; C, AM F.101276, AM F.101277, all dorsal view of head and trunkshield; D, AM F.101274, AM F.101275 (PMD), internal view; E, AM F.102397; F, AM F.101240, both dorsal view of head and trunkshield, including pectoral fins (also Fig. 6A). Scale = 1 cm.

Figure 7. *Bothriolepis yeungae* n.sp. A, AM F.100893, ventral view of external trunkshield and internal view of headshield; B, AM F.101234, internal view of headshield, partial internal view of trunkshield; C, AM F.101234, closeup of internal view of headshield; D, AM F.100842, internal view of headshield with external view of suborbitals. Scale = 1 cm.

Remarks. Despite criticisms of quantitative measurements above, the diagnosis illustrates the difficulty in finding a large number of unique qualitative characters to diagnose species of *Bothriolepis*. However, the unusually low anterior process of the submarginal and the wide notch between this and the posterior submarginal process are present on all individuals of *Bothriolepis* from the Canowindra type locality.

A large number of specimens of *Bothriolepis* are available for examination, and the majority are well preserved (although flattened) with articulated plates in the head and trunkshield. The majority of specimens are

preserved in life position. Although this appears to be an ideal situation for species description and comparison, it is in fact limiting. Views of the internal surface of the head and trunkshield are present, but less common. The pectoral fin is most frequently preserved attached to the trunkshield so that the articular area on the anterior ventrolateral plate is not generally visible. Flattening of specimens means the medial wall of the pectoral fin is rarely visible, as are the plates comprising the lateral lamina of the trunkshield. These problems were also apparent in description of *Remigolepis walkeri* from Canowindra (Johanson, 1997a).

Description

Headshield (Figs. 3–11). The premedian (PrM, Fig. 10E,H) is longer than wide (mean L/W ratio = 1.04), with the rostral margin wider than the orbital (mean ratio = 2.10). Internally, the lateral margins kink slightly inwards just below the rostral margin. An elongate roughened area is present along the midline of the internal surface of the premedian, in the anterior half of this plate.

The orbital fenestra (fe.orb, Fig. 3A) is wider than long (mean L/W = 0.55). Internally (Fig. 10A,B,D), the suborbital fenestra (fe.sorb) is smaller than the orbital fenestra (Fig. 5B). The preorbital recess (prh) is trifid, with three well-developed extensions (Figs. 4B, 7A–C, 8E, 9A–C, 9E). The borders of the otico-occipital depression (ood, Fig. 10A,B,D) are sharply defined by the paramarginal crista (cr.pm), and the anterior postorbital processes (pr.po) extend well beyond the anterior margin of the suborbital fenestra. The postorbital cristae (cr.pto) are well developed and extend onto the internal surface of the nuchal plate.

The pineal plate (P) is small and roughly rectangular (Fig. 5C), with reduced posterolateral corners. The pit on the internal surface of the pineal is deep, occupying most of this surface. The rostral plate (R) comprises a long, rectangular base, with a thin protrusion extending anteriorly from the midpoint of the base. This protrusion separates the nasal openings so that the rostral has the shape of an inverted "T". Large, rounded sclerotic ossicles (scl) are present, but usually broken. The postpineal (PP, Fig. 3A) is wider than long (mean L/W ratio = 0.83) with a rounded anterior margin that extends only slightly anteriorly into the orbital fenestra (Figs. 3A,D, 10A,B,G,H). Internally, a median ridge (mr, Fig. 10B) separates two large, rounded pits (g) that dominate the internal surface of the postpineal.

The lateral plate (L, Fig. 10D,E) was not measured due to damage along its lateral margin. Internally, a moderately large, shallow pit (p) is positioned just anterior to the narrowest part of the spiracular groove (Fig. 5C). The spiracular groove (spg) is long and shallow. It is widest at the lateral margin of the headshield, narrows abruptly at the pit, then widens gently again. The medial portion of the spiracular groove extends well beyond the anterior postorbital process, and appears to abut against the lateral protrusion of the preorbital recess. The anterior and posterior crests (cr1, cr2, Fig. 10A) of the spiracular groove do not fade medially, but are sharply developed along their entire extent. The anterior attachment for the submarginal

(a1SM) is best preserved on AM F.100843 (Fig. 5C), where it is a strongly developed, transverse structure, bordering the anterior crest of the spiracular groove. At the mesial end of the anterior attachment, the anterior spiracular crest bends posteriorly towards the preorbital recess. The anterior submarginal attachment is separated from the more anterior prelateral attachment (a.PrL, Fig. 5C), which is small, oval-shaped and oriented laterally or posterolaterally. The posterior attachment for the submarginal (a2SM) is a single, elongate structure (Fig. 8C), widest anteriorly, narrowing posteriorly. The attachment extends from the midpoint of the postmarginal plate (PM, Fig. 8C) to the posterior spiracular crest, but does not extend anteriorly across the spiracular groove. The prelateral plate (Pr.L, Fig. 9D) is small and rounded, with a deeply incised sensory groove externally. No infraprelateral (e.g., Young, 1984: fig. 1) was observed.

Because the headshield is frequently preserved in articulation with the trunkshield, the paranuchal trochlea (pnt) on the internal surface of the paranuchal plate (PNu, Fig. 10B) is rarely observed. However, on AM F.101270 (Fig. 8C), these trochlea are elongate and narrow, extending the length of the paranuchal along the transverse nuchal crista. They are widest medially, narrowing concavely to a point mesially and laterally.

The mean L/W ratio of the nuchal plate (Nu, Fig. 10A) is 0.73. Externally, the endolymphatic ducts (d.end) are small, rounded openings. Internally, the endolymphatic ducts are still small, positioned on either side of the large supraotic thickening (sot). The majority of the surface of the supraotic thickening is covered by a moderately deep pit. The transverse nuchal crista (cr.tv) is well developed. Posterior to this, the median occipital crest of the headshield (cro, Fig. 10B) is well developed and sometimes divided, so that there are paired insertion areas for the levator muscles (fm). The lateral insertion areas dominate this area, and in one large specimen, AM F.100843 (Fig. 5C), these are very deep, but this may be related to the size of the individual or less flattening of the specimen. The postmarginal plate is roughly diamond-shaped. The widest lateral point (and the widest part of the headshield) is approximately in the middle of the postmarginal.

The submarginal plate (SM, Figs. 4A,D, 8, 9, 10B–G, 11C) is preserved on a small number of specimens, both in internal and external view. The lateral margins of the headshield were often not well preserved, being either flattened, damaged or difficult to prepare. Thus, the number of describable submarginal plates is low relative to the large number of individuals of *Bothriolepis yeungae* preserved in the fauna. Only one specimen thus far (AM F.100891, Fig. 4A,D) clearly shows the submarginal in external view. Six others (Figs. 8A,B,D,E, 9A–C,E) preserve the internal view. Although the number of preserved plates is low, they show an unusual morphology, as described below.

The submarginal plate is long, low anteriorly and high posteriorly. In external view the plate has a teardrop appearance, with a blunt anterior edge where it contacts the prelateral. The posterior submarginal attachment (ad2, Figs. 9B, 10C,D) is a raised, elongate, oblique area, situated

at approximately one-third the plate length. Anterior to this the plate lowers dramatically, marking the position of a wide, open notch (N, Fig. 10C) between the posterior and anterior (ad1) articular processes of the submarginal (Figs. 8A,B, 9A,B, 10A–C, 11C). The latter process is low, and well separated from the posterior process by the wide notch. This morphology is not believed to be due to damage because it is present in all those specimens where the submarginal is preserved (e.g., Fig. 9A,B,E). Furthermore, on AM F.100904 (Figs. 8A,B, 10B,C), the anterior portion of the submarginal rests on or nearly on the anterior submarginal attachment of the lateral plate, so that very little if any is missing. A large, roughened oval surface is present along the ventral margin of the submarginal (a.AVL, Fig. 10C), representing the contact area between the submarginal and the anterior ventrolateral plate. A comparison of this submarginal to those figured for other species of *Bothriolepis* and the antiarch *Nawagiaspis wadeae* Young, 1990, and a reconstruction of the internal surface of the headshield is presented in Fig. 11J.

The suborbital plates (SO) are preserved in life position in external (Figs. 7D, 10A, 13A) and internal views (Fig. 13D). The overall shape is rectangular with more prominent posterolateral corners. The lateral margin is somewhat concave down to this latter corner. The suborbital pair meet dorsomesially, becoming separated ventrally due to the oblique mesial margins of the plates. The ventral margin of the suborbital, best preserved on AM F.101232 (Fig. 13A), appears to be smooth, lacking denticulation. The ventral third of the suborbital is unornamented, and separated from the ornamented portion by a strongly developed ridge (r, Fig. 10A) running to the anterodorsal corner. The sensory canal (ifc3) runs ventrally from near the mesial margin of the dorsal edge, just offset from the midline of the plate, then bends laterally at the strongly developed ridge. The canal runs to the lateral edge of the suborbital, widening near this edge.

The only specimen thus far preserving the internal surface of the suborbital is AM F.100803 (Fig. 13D). This surface is dominated by a strong transverse ridge (tr) which begins near the dorsomesial margin, extends ventrally for a short distance, then curves to continue laterally to the edge of the plate. This ridge is located in approximately the centre of the plate and varies in height along its length, being highest in the middle and becoming lower laterally. The lateral third of the ridge is very low and appears closely applied to the surface of the suborbital. This morphology is similar to that described for *Bothriolepis* sp. from Gogo (Young, 1984) and *B. canadensis* (Stensiö, 1948).

Remnants of the anterior portion of the S-shaped infragnathals (Ifg, Fig. 13D) are preserved at the ventral margin of the internal surface of the suborbital, as curved structures wider laterally, narrowing to a point medially. There appears to be a second surface below and confluent with that just described. The now-flattened space between these two surfaces represents the groove along the ventral surface of the infragnathal, as described for *Bothriolepis* sp. from Western Australia (Young, 1984). The posterior portion of the infragnathal is missing, due to breakage at what would have been the thinnest part of the S-shaped infragnathal.

Sensory lines on the external surface of the headshield (ifc1, ifc2, cir, csl, socc, Fig. 10E,F,H) are similar to those found in other species of *Bothriolepis*.

Trunkshield (Figs. 3–10, 13–17). The mean L/W ratio of the anterior median dorsal (AMD) is 1.03. Externally (Fig. 10E–H), the highest point of the trunkshield is the dorsal median ridge (dmr, Fig. 10H) which runs from just anterior to the middle portion of the AMD (dma, the tergal angle, Fig. 10E) to the posterior margin of the posterior median dorsal. The posterior oblique dorsal sensory line groove (dlg2) runs posterolaterally across the AMD and mixilateral plates (MxL) from the tergal angle. Internally (Figs. 5B,D, 8A, 9A, 14F, 15C–F, 16B,E, 17F,G), the postlevator thickenings (alr, Fig. 17F) are low and oblique, grading gently into the surrounding plate. The postlevator crista (cr.pl) are sharp and high, and are separated from the anterior margins of the postlevator thickenings, extending instead into the posterior portion of the levator fossa (f.retr). The posterior levator processes (pr.pl) are moderately developed. The median ventral ridge (mvr) extends anteriorly from the anterior ventral pit of the dorsal wall of the trunkshield (pt1) into the shallow, triangular levator fossa, the latter being more strongly developed on some specimens (Fig. 5D) than others (Figs. 14F, 15C–F). This is not considered to be an important taxonomic difference and may be related to the overall size of the individual. The anterior ventral pit is located at the confluence of the postlevator cristae, and is long, open and narrow. The postlevator cristae issue from the midpoint of the pit (Figs. 5B, 15C), or from its anterior edge (Figs. 5D, 14F). The median ventral ridge extends posteriorly from this pit, splitting to form a median walled groove (grm, Fig. 17G) at approximately one-half the length of the AMD, which then fades before the posterior margin of this plate. Overlap areas for the ADL (cf.ADL, Fig. 17F) are moderately wide, as in other species of *Bothriolepis*.

The posterior median dorsal (PMD) is bell-shaped externally, with well-developed lateral corners and a small, triangular posteriormost corner (pa, Figs. 3A, 10G, 17B,E). Internally (e.g., Fig. 14C,D,G), the median groove (grm, Fig. 17B) continues posteriorly from the AMD, but lacks the thin walls of this groove, and is instead more like a linear depression stretching to the posterior ventral pit (pt2). At the posterior margin of the PMD, the *crista transversalis interna posterior* (cr.tp) forms a strongly developed, rounded ridge that continues onto the mixilateral plate. The posterior marginal area (pma, Fig. 17E), between the posteriormost margin and the *crista transversalis interna posterior* is narrow laterally and wider medially. The posterior ventral pit sits just anterior to the *crista transversalis interna posterior*, connected by a short, low ridge, the posterior ventral process (prv2). In some specimens (Fig. 14C,F), the posterior ventral pit is covered and so more like a high ridge. A faint ventral tuberosity (tb, Fig. 17B,E) surrounds the posterior ventral pit. Lateral to the *crista transversalis interna posterior* and following the line of this ridge are the lateral processes (prl). The anterior and lateral overlapping areas of the PMD (cf.AMD, cf.MxL) are wide.

The dorsal lamina of the anterior dorsolateral plate (ADL) is preserved on most specimens, but the lateral lamina is usually flattened and hidden from view. On AM F.101276 (Fig. 13C) and AM F.101277 (Fig. 13F), the ADL is less crushed, and the anterolateral surface can be seen (Fig. 13F). The *processus obstans* (pro, Figs. 10F,H, 13F) is very large and rounded, which can also be seen in dorsal view, where it articulates with the postmarginal and paranuchal (Fig. 5A). The main lateral line groove (lcg, Fig. 13F) runs across the middle of the *processus obstans* where it turns upward to cross on to the headshield. The ornamented angle (pnoa) is elongate and strongly developed. Below this, the two crests defining the articular fossa, the supra- and infraarticular cristae (crs, cri), are also strongly developed, and the articular fossa (f.art) contacting the paranuchal trochlea is deep and concave. The *crista transversalis interna anterior* (cit) is the dominant feature of the anterior articular area, being large and triangular with a rounded posterior margin. The overlap area for the AMD (oa.AMD, Fig. 13F) is widest anteriorly, where the AMD possesses small lateral extensions. It then appears to narrow posteriorly.

Several anterior ventrolateral plates (AVL) are preserved, showing internal and external surfaces. The ventral lamina is preserved (Fig. 13A,B), but the lateral surface is rarely seen, again due to flattening (e.g., AM F.100891, Figs. 4D, 10F). On the latter specimen, the lateral lamina is not visible in its entirety, but the following features can be noted. The lamina is narrow above the area of pectoral fin attachment, and the anterodorsal corner appears to be low, although the lateral lamina of the AVL may have slipped under the ventral margin of the ADL. The prepectoral corner (prc) is not present on this specimen (Fig. 4A), but a small corner is visible on others (Fig. 13A). The AVL continues anteriorly from this point as a narrow elongation overlapped by the submarginal.

As noted above, articulation of the pectoral fin to the AVL obscures certain features of the fin attachment on the AVL, for example, the *margo limitans* and the *fossa articularis pectoralis*. However, on AM F.100891 (Figs. 4D, 10F), the brachial process (pbr, Fig. 10F) is visible, being large, rectangular, with a large funnel pit (fp). The process faces posteriorly or slightly posterolaterally. This is also observed on AM F.100886 (Fig. 16D), where the anterior dorsal and ventral muscle insertions (a.sup, a.inf) are visible. These are positioned above and below the funnel pit and are elongate, curved and deep. The *pars pedalis* (pe, Fig. 4E) is short and extends horizontally. The axillary foramen (f.ax, Fig. 14H) behind the brachial process is not visible externally (e.g., Fig. 4D), again due to the attachment of the pectoral fin. However, one specimen (Fig. 14E,H) preserves an AVL with an articulated pectoral fin. The lateral lamina of this AVL is mostly absent, but a small portion is preserved near the anterior part of the pectoral fin. In internal view, a large, elongate opening is visible in this portion of the lateral lamina, representing the axillary foramen (cf. Young & Zhang, 1992: fig. 8A). This foramen is surrounded anteriorly by a wide, raised ridge. Part of the medial opening of the pectoral fin is visible, and some type of

material is visible at this opening. This may be a portion of the endoskeletal unit inside the fin (Stensiö, 1948, 1969), or it may simply be sediment infill.

The anterolateral corner of the subcephalic division of the ventral lamina of the AVL (c.al, Fig. 17A) is distinct, and the anterior margin contacting the semilunar plate is long (ml, Fig. 14A). Other overlapping areas (cf. AVL, cf. MV, cf. PVL, Fig. 17A) are visible on the internal surface of the plate and are wide and well developed. The *crista transversalis interna anterior* (cit, Fig. 17A,D) is developed as a high, thin ridge running at an oblique angle across two-thirds the width of the anterior portion of the plate.

The dorsal lamina (dlm, Fig. 17C) of the mixilateral plate is nearly twice as wide as the height of the lateral lamina (Figs. 13G, 15G). The overlap surface for the PMD (oa.PMD, Fig. 17C) is wider posteriorly, narrowing anteriorly. The overlap surface for the ADL (oa.ADL) is arrow-shaped, with the dorsal portion being narrower than the lateral portion. On the lateral lamina, the overlap for the posterior ventrolateral (oa.PVL) is very narrow anteriorly, widening rapidly posteriorly until it occupies the majority of the lamina. The overlap area ends at this point, and posterior to this is a relatively wide, triangular posteroventral ornamental angle of the mixilateral (cu). The main lateral line groove (lcg) runs across the midline of the ornamented portion of the lateral lamina and is thus relatively widely separated from the dorsolateral ridge of the trunk armour (dlr) anteriorly, but rises towards this ridge posteriorly. Here, the lateral line groove curves ventrally to meet and run posterior to the dorsalmost margin of the PVL overlap area.

The lateral lamina of the posterior ventrolateral (PVL) is not well preserved, but the ventral lamina can be observed in some specimens (Fig. 13A,B). The ventral lamina is broadest anteriorly, beginning to narrow just at its posterior half. The lamina narrows sharply at this point to the posterior margin, which is small and slightly rounded. The median ventral plate (MV) is visible in AM F.101232 and AM F.101261 (Fig. 13A,B), where it is moderately large relative to the surrounding plates, as in most species of *Bothriolepis*.

Pectoral fins. The pectoral fins are frequently found articulated to the AVL and often fully adducted to the trunkshield so that their medial face is not visible. As well, the fins are frequently crushed or broken. The fin itself is long, extending beyond the posterior margin of the trunkshield (Figs. 3, 6A,C). The fin is hinged distally, and the distal portion of the pectoral fin is approximately one-third the length of the proximal portion. The lateral marginal plate 2 (Ml2, Figs. 4E, 17A,D) is the dominant plate of the proximal pectoral fin, wrapping around the lateral margin of the fin and extending on to the ventral surface. The lateral margin is sharp, not rounded, and is lined with a series of small protrusions (Fig. 3A).

The two most proximal plates dorsally (Cd1) and ventrally (Cv1) articulate with the brachial process on the AVL (Fig. 4E). The articular areas of these plates are narrow, elongate areas (ar3d, ar3v, Figs. 10F, 13B), separated from the rest of the ornamented plate by a thin,

unornamented section. On AM F.100886 (Figs. 16C, 17D), the internal articular area of Cv1 can be seen as a roughened, striated surface (ar1v). The Cd1 and Cv1 articulate closely with the brachial process (e.g., Fig. 4E), although the plates themselves are separated anterolaterally around the *pars pedalis* (pe) by a narrow, U-shaped area. This area is wider than the *pars pedalis*, suggesting that the fin could move dorsal and ventral relative to the trunkshield to some degree (Young & Zhang, 1992). Just posterior to this area, the Cd1 and Cv1 articulate for a very short distance, then are separated by the Ml2, which comes to a rounded point in this area.

AM F.101249 and AM F.100900 preserve the pectoral fin in internal view (Fig. 14B,H), and show that Cd1, Cv1 and the mesial marginal plate 1 (Mm1) formed a rounded proximal opening of the pectoral fin. This opening is intimately associated with the axillary foramen although the posterior extent of this foramen is not known.

In contrast to the sharp lateral margin, the mesial face of the pectoral fin forms a low, flat wall that allows the fin to be held flat against the trunkshield when fully adducted (Fig. 14H). The Mm1 is elongate, forming a narrow lip to separate Cd1 and Cv1 (Fig. 14B). The Mm1 extends posteriorly to contact the Mm2, which wraps around from the dorsal surface. The Mm1 is only approximately two-thirds as long as the Mm2. The overlap relationship between the mesial and ventral plates of the fin is a potentially important taxonomic character for *Bothriolepis*, but unfortunately only visible on one specimen of *B. yeungae* to date (Fig. 14B). On this specimen, the Mm1 overlaps the anterior margin of the Mm2, which is slightly concave. A small portion of the Cv1 and Cv2 plates are visible just below these mesial marginal plates, and all four appear to meet at a cross-shaped junction just dorsal and to the left of the line marking Cv1 in Fig. 14B. Therefore, these four plates all contact another at a point, such that the Cv2 and Mm1 do not overlap. Other more distal plates of the pectoral fin (Cd2, Cd4, Cd5, Ml4, Ml5, T, Figs. 10G, 17D), are as in other species of *Bothriolepis*.

Posterior body and fins. The body of *Bothriolepis yeungae* posterior to the trunkshield is very rarely preserved in the Canowindra fauna, and was probably not scale-covered. By contrast, the post-trunkshield body of *Remigolepis walkeri* was scale-covered, and is very commonly preserved (Johanson, 1997a). One specimen of *B. yeungae* (AM F.105545) preserves the external mould of a long, elongate body (approximately 1.2 times the length of the head and trunkshield) in dorsal view, but little additional morphological information can be obtained. No scale impressions are preserved on this specimen, and there is no indication of dorsal or caudal fins. Otherwise, rare patches of faint lepidotrichia-like elements have been observed in the Canowindra fauna, and may belong to *B. yeungae* (A. Ritchie, pers. comm.), but do not occur in clear association with specimens of *Bothriolepis*. Trunk scales also appear to be absent in *B. canadensis* (Stensiö, 1948), but are strongly developed in the Victorian species *B. gippslandiensis*, *B. cullodenensis* and *B. fergusoni* (Long, 1983; Long & Werdelin, 1986), particularly the ventrolateral scales.

Since the morphology of the caudal fin cannot be interpreted from the specimen discussed above, the reconstruction of *Bothriolepis yeungae* presented in Fig. 18 is based on *B. canadensis* (Stensiö, 1948). A lateral reconstruction is not presented due to flattening and crushing of specimens.

Comparisons to other species of *Bothriolepis*

Bothriolepis yeungae is characterised by the presence of a submarginal in which the low anterior process is well separated from the more typical posterior process by a wide, rounded notch (Fig. 11C). This appears to be unique within *Bothriolepis*, however, it should be noted that no disarticulated submarginal plates have been observed for *B. yeungae*, so that the specimen shown in Fig. 11C is not shown strictly in mesial view. Other plates in Fig. 11 are seen in direct lateral or mesial view, but this is not felt to be an overwhelming problem when comparing these to *B. yeungae*. In other species of *Bothriolepis* (Fig. 11A,D–I) and antiarchs like *Nawagiaspis* (Fig. 11B), the anterior process of the submarginal is raised and more similar in height to the posterior, while the notch between the processes is smaller and more closed. Exceptions to this are *B. cullodenensis* (Long & Werdelin, 1986: fig. 5D), *B. cullodenensis* (Long & Werdelin, 1986: fig. 11A; Fig. 11I) and one specimen of *B. canadensis* (Stensiö, 1948: fig. 105B; Fig. 11D) in which the anterior submarginal process is also reduced in height. However, the submarginal in front of the notch is very short, relative to the more elongate process in *B. yeungae* (Figs. 10B,C, 11C). Additionally in *B. cullodenensis*, there is a long, roughened area extending posteroventrally from the anterior submarginal process which Young & Zhang (1992: 459) suggest may have held cartilage attaching to the anterior postorbital processes of the braincase, as in other placoderms. In *Bothriolepis*, attachment between the submarginal and lateral plates is direct, and this cartilage is usually absent (Young, 1986). In fact, Young & Zhang (1992) imply that the anterior submarginal process may have been absent in *B. cullodenensis*, a plesiomorphic condition for *Bothriolepis* and unlike the condition in *B. yeungae*. As well, no roughened area for cartilage attachment is present on the internal submarginals of *B. yeungae* (Figs. 8A,B,D,E, 9A–C,E).

Relatively few synapomorphies designating clades of species within *Bothriolepis* have been identified, and these have tended to be more inclusive clades, containing several species. Thus, relationships of species within these clades have been less well elucidated. The most recent attempts to summarise the phylogenetic relationships of various species of *Bothriolepis* were made by Long (1983) and Young (1988; Fig. 12). In the former, the structure of the cladogram was based on changes in the shape of the preorbital recess of the headshield, from a plesiomorphic semicircular form through to a derived trifid recess. Young (1988) expanded on this, providing additional synapomorphies for a group characterised by a pentagonal preorbital recess, including the presence of a strong, transverse anterior submarginal attachment on the lateral plate, separated from the attachment for the prelateral plate.
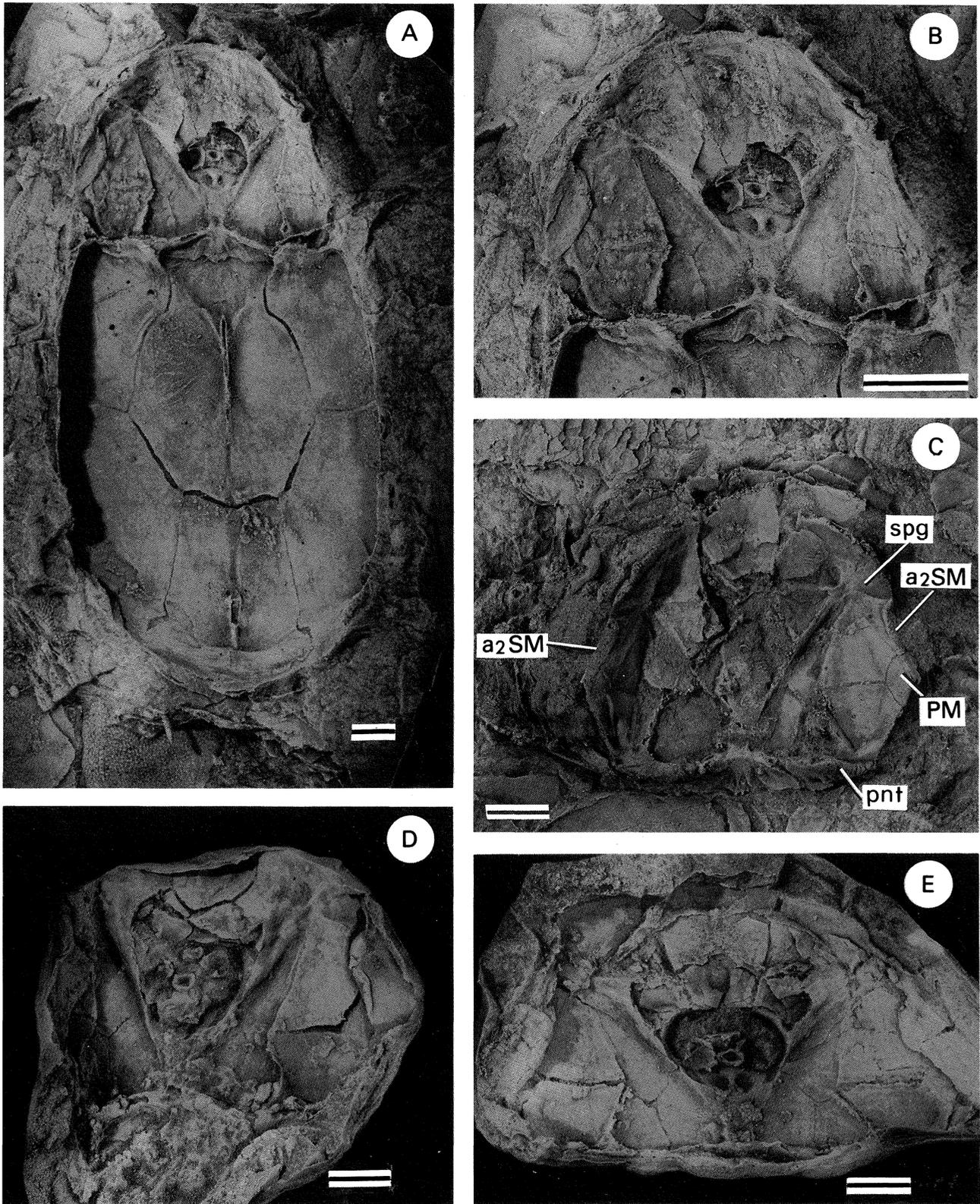
Figure 8. *Bothriolepis yeungae* n.sp. A, AM F.100904, internal view of head and trunkshield; B, AM F.100904, closeup of internal view of headshield; C, AM F.101270; D, AM F.100894; E, AM F.100888; C–E, internal view of headshield. Scale = 1 cm.
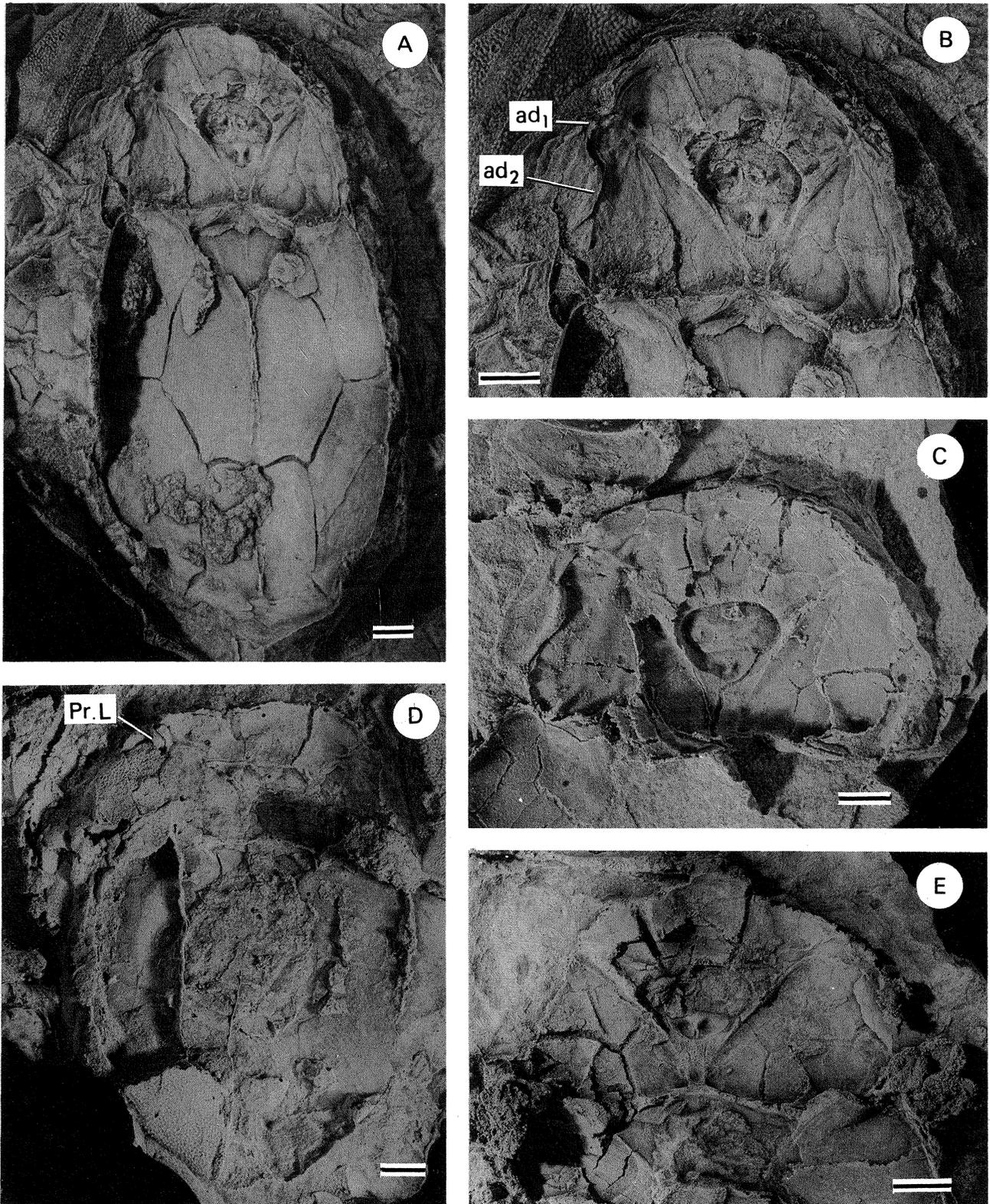
Figure 9. *Bothriolepis yeungae* n.sp. A, AM F.102398, internal view of head and trunkshield; B, AM F.102398, closeup of internal view of headshield; C, AM F.100844, internal view of headshield; D, AM F.100899, internal view of head and trunkshield; E, AM F.101273, internal view of headshield. Scale = 1 cm.
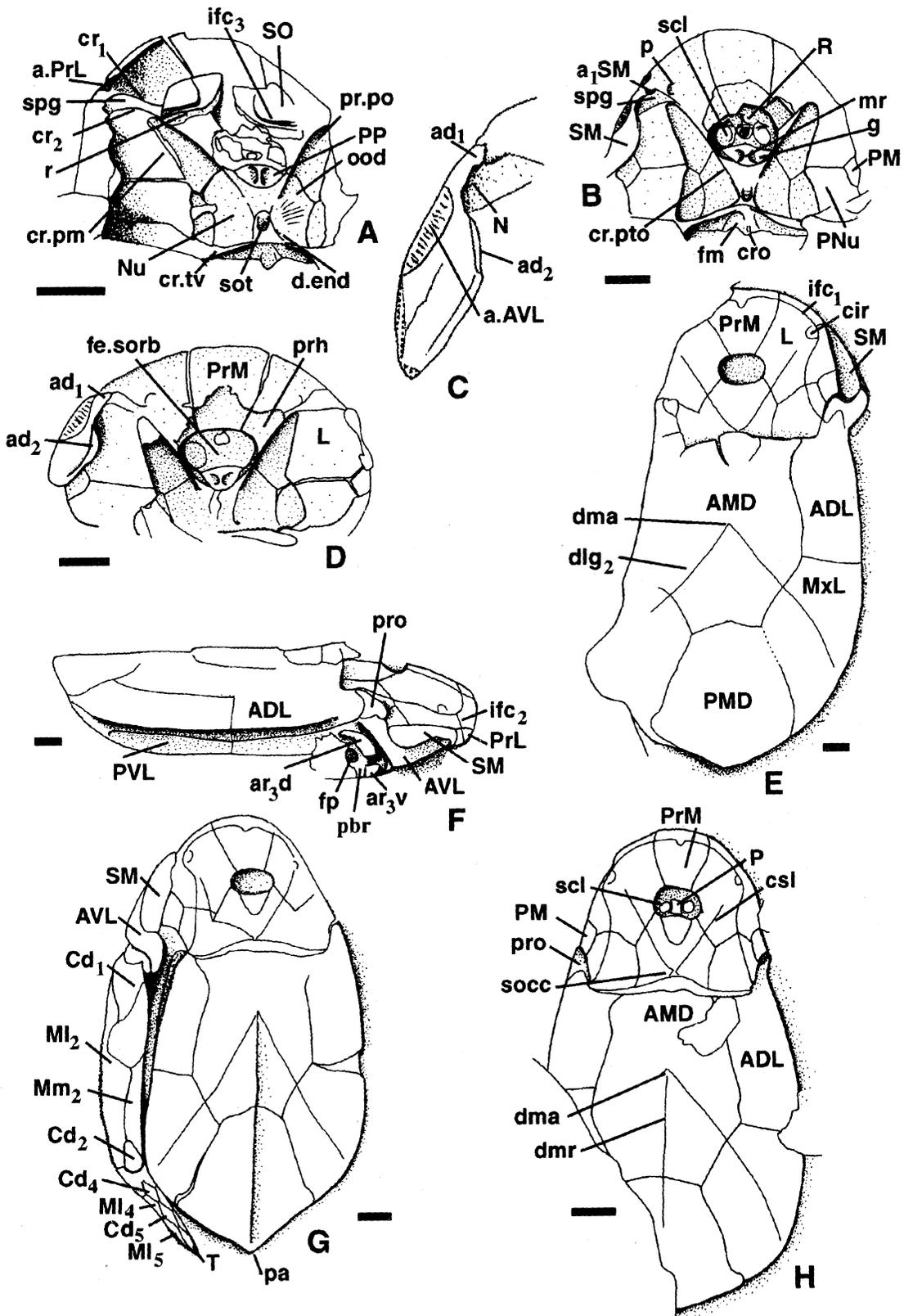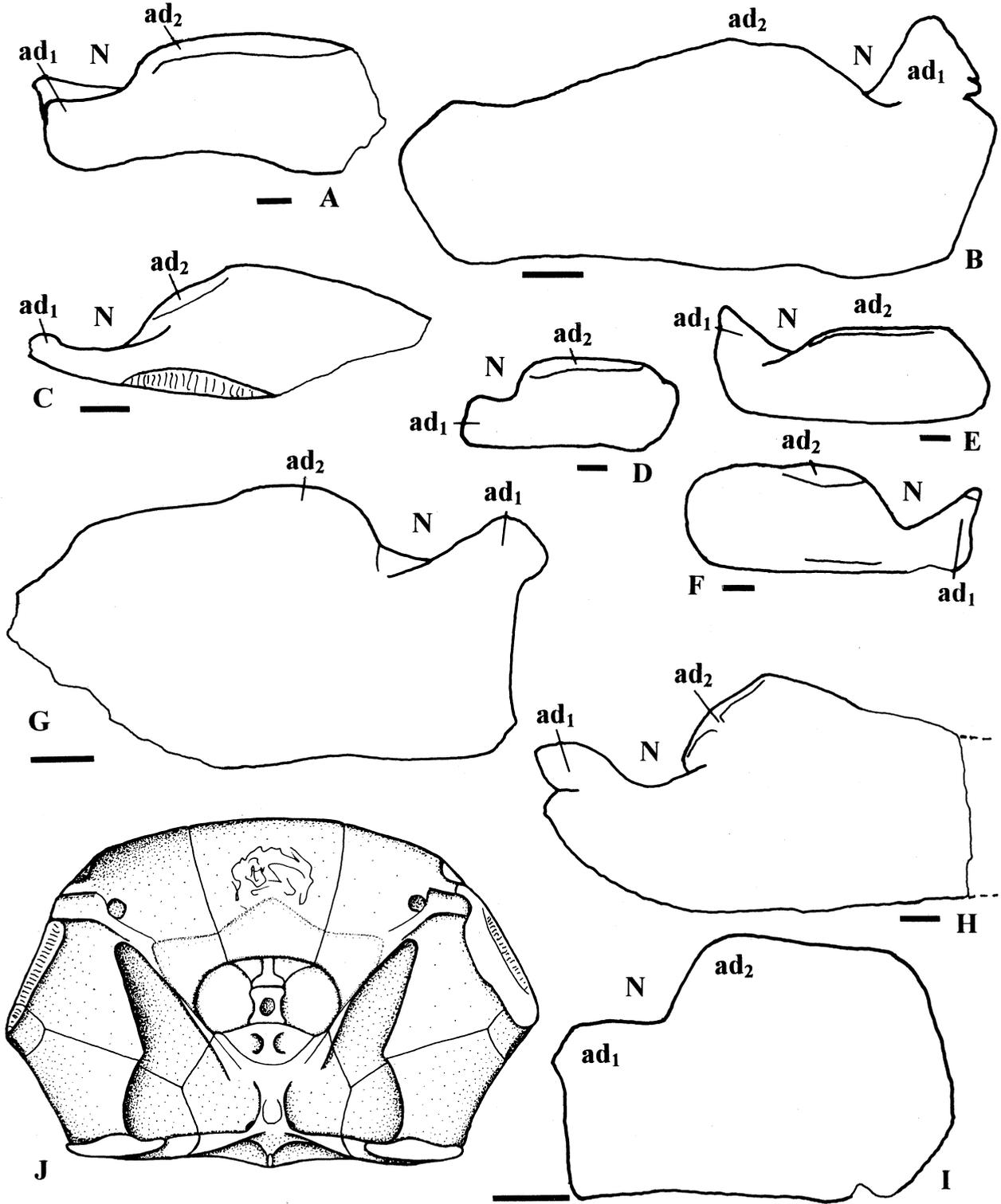
Figure 10. *Bothriolepis yeungae* n.sp. A, AM F.100842, internal view of headshield with suborbital plates; B, AM F.100904, internal headshield; C, AM F.100904, detail of right submarginal plate; D, AM F.100844, internal view of headshield; E,F, AM F.100891; G, AM F.101247; H, AM F.100802a, all dorsal view of head and trunkshield, except F, lateral view. Scale = 1 cm.

Figure 11. A–I, outlines of submarginals of various species of *Bothriolepis*, and of *Nawagiaspis*. A, *Bothriolepis canadensis*: Stensiö, 1948; B, *Nawagiaspis wadeae*: Young, 1990; C, *Bothriolepis yeungae* n.sp. Note that while other submarginals are shown in lateral view, that of *Bothriolepis yeungae* n.sp. is seen in a slightly oblique view, as preserved attached to the headshield (see text for further discussion); D,E, *Bothriolepis canadensis*: Stensiö, 1948; F, *Bothriolepis obruschewi*: Karatajute-Talimaa, 1966; G, *Bothriolepis* sp. from the Gogo Formation, Western Australia (Young, 1984); H, *Bothriolepis macphersoni*: Young, 1988; Young & Zhang, 1992; I, *Bothriolepis cullodenensis*: Long & Werdelin, 1986; J, *Bothriolepis yeungae* n.sp. Reconstruction of internal headshield, slightly flattened to show attachment of submarginal plate.
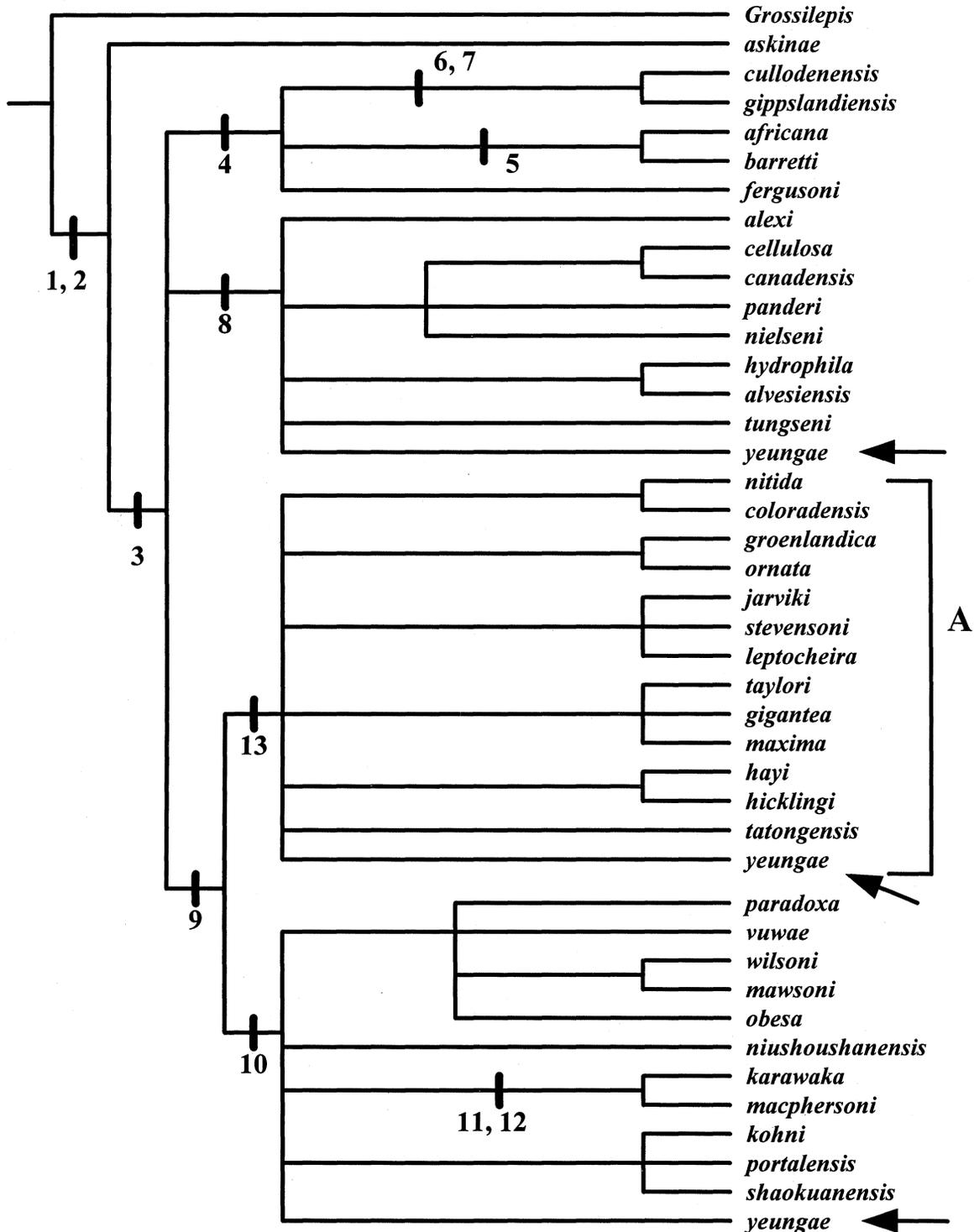
Figure 12. Cladogram of *Bothriolepis*, adapted from Young (1988: fig. 68). Note multiple position of *B. yeungae* on this cladogram, denoted by arrows. Synapomorphies are as follows (letters in brackets indicate characters designated by Young [1988]): 1—reticulate ornament in juveniles and adults (a); 2—AMD in adults broadest across lateral corners, and MxL broadest through its dorsal corner (b); 3—lateral corners on AMD appear early in ontogeny (c); 4—enlarged lateral pit (d); 5—trilobate prelateral recess (e); 6—trunk armour with pronounced median dorsal crest (f); 7—short, deep, SM plate (g); 8—point contact between Cv1, Cv2, Mm1 and Mm2 (h); 9—pentagonal preorbital recess (i); 10—anterior submarginal attachment on lateral plate a transverse ridge (j, modified from Young, 1988); 11—separate ventrally facing attachment surface for the prelateral on the lateral plate (m); 12—*crista transversalis interna anterior* transversely oriented on ventral lamina of AVL (n); 13—trifid preorbital recess (r).
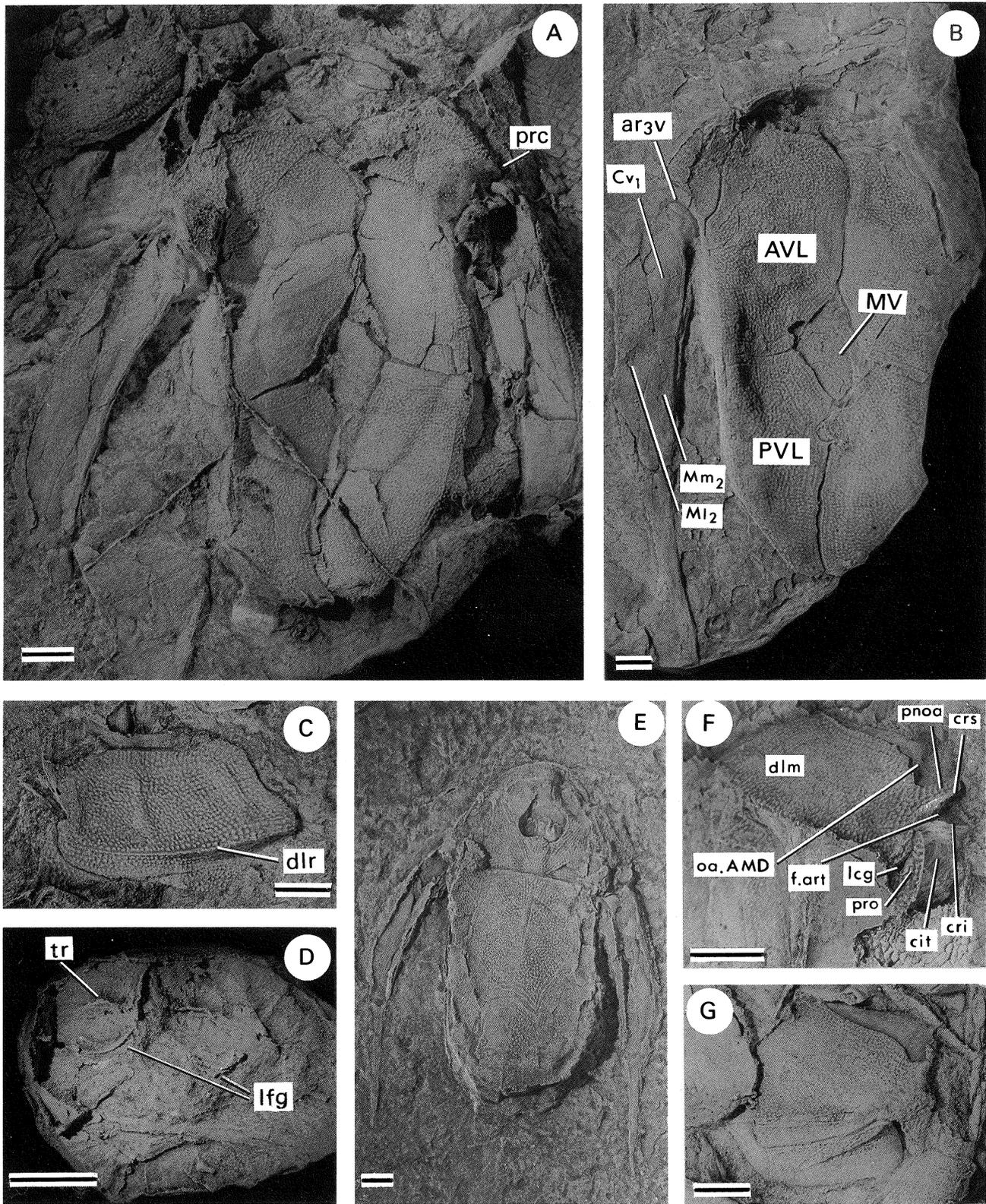
Figure 13. A, AM F.101232; B, AM F.101261; A,B, both ventral view of trunkshield and pectoral fin; C, AM F.101276, dorsolateral view of ADL; D, AM F.100803, internal view of suborbital plates; E, AM F.102399, dorsal view of head, trunkshield and pectoral fin; F, AM F.101277, anterolateral view of ADL; G, AM F.100841, lateral view of mixilateral plate. Scale = 1 cm.
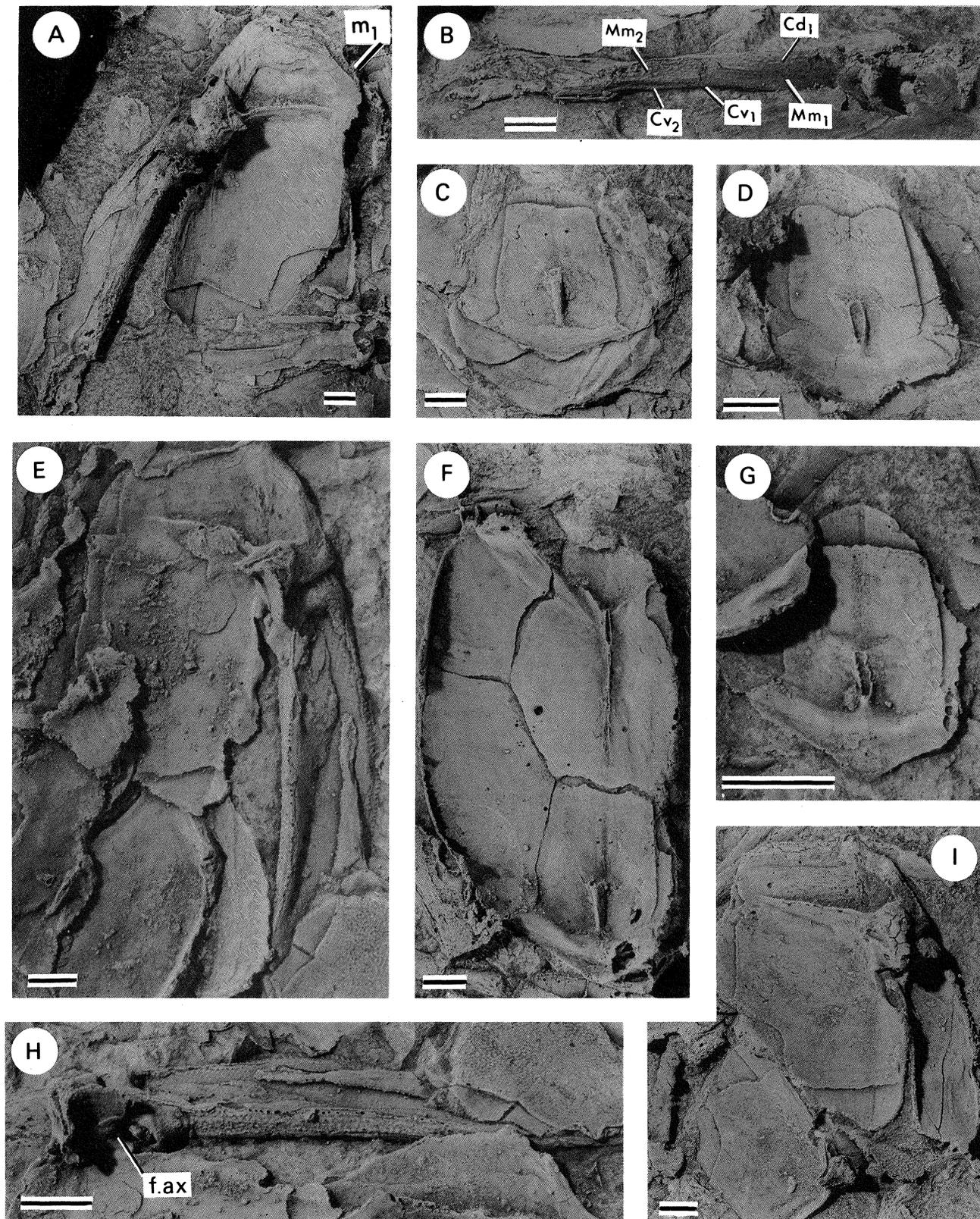
Figure 14. *Bothriolepis yeungae* n.sp. A, AM F.101249, internal view of AVL with partial pectoral fin; B, AM F.101249, closeup of medial pectoral fin; C, AM F.100838, internal view of PMD; D, AM F.100839, internal view of PMD; E, AM F.100900, internal view of AVL with partial pectoral fin; F, AM F.100898, internal view of partial trunkshield; G, AM F.101855, internal view of PMD; H, AM F.100900, closeup of medial pectoral fin and part of internal pectoral fin attachment; I, AM F.100840, internal view of AVL with partial pectoral fin.
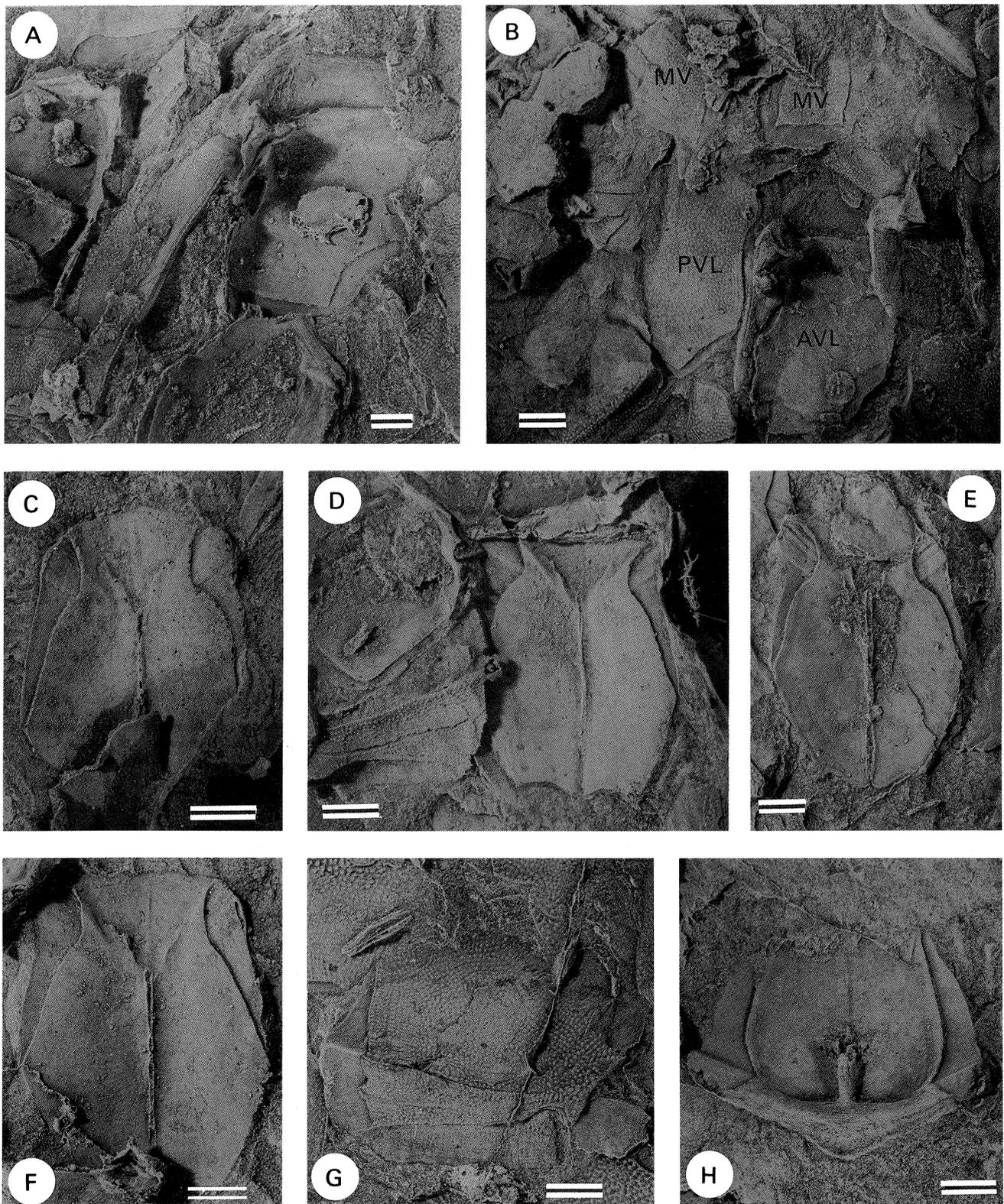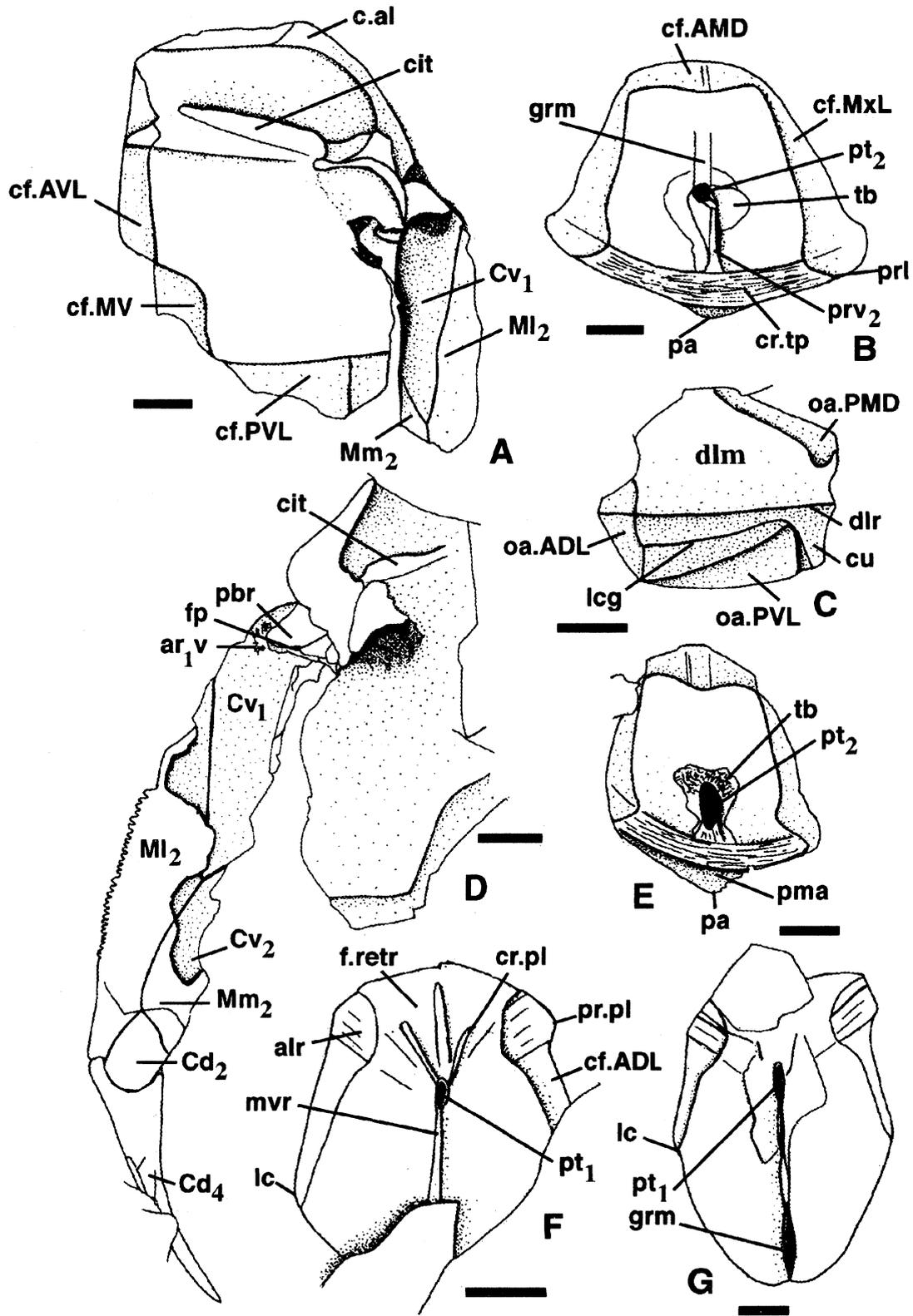
Figure 15. *Bothriolepis yeungae* n.sp. A, AM F.101609, internal view of AVL with partial pectoral fin; B, AM F.101251, internal AVL, AM F.101252, AM F.101253, external MVs; C, AM F.101241, internal view of AMD; D, AM F.101246, internal view of AMD; E, AM F.101244, internal view of AMD; F, AM F.101245, internal view of AMD; G, AM F.101255, external dorsolateral view of MxL; H, AM F.101256, internal view of PMD.
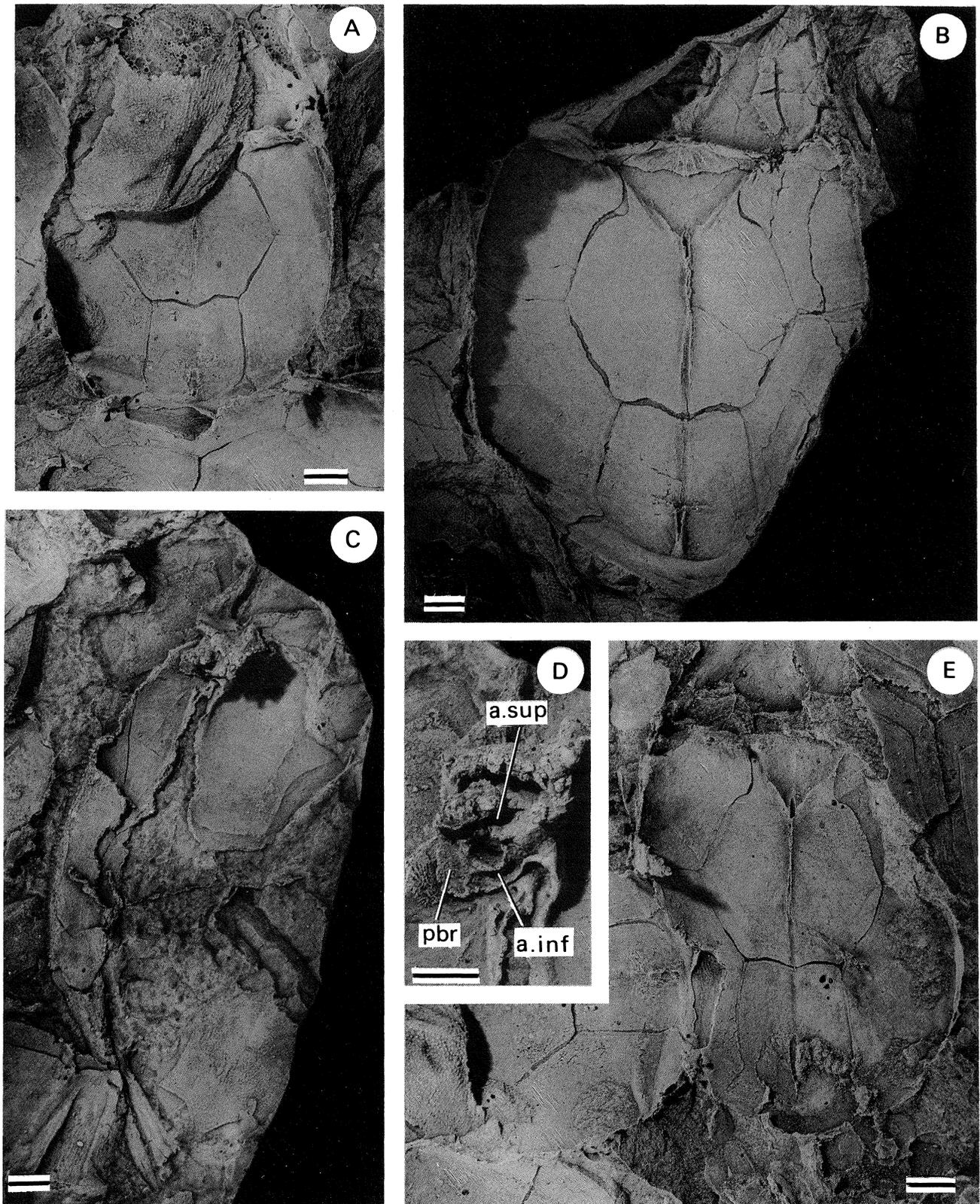
Figure 16. *Bothriolepis yeungae* n.sp. A, AM F.100897, internal view of trunkshield; B, AM F.101233, internal view of trunkshield and partial headshield; C, AM F.100886, internal view of AVL with pectoral fin; D, AM F.100886, closeup of brachial process; E, AM F.100896, internal view of trunkshield. Scale = 1 cm.

Figure 17. *Bothriolepis yeungae* n.sp. A, AM F.100840, internal view of AVL with pectoral fin; B, AM F.100838, internal view of PMD; C, AM F.100841, lateral view of mixilateral plate; D, AM F.100886, internal view of AVL with pectoral fin; E, AM F.100839, internal view of PMD; F, AM F.101241, internal view of AMD; G, AM F.100244, internal view of AMD. Scale = 1 cm.
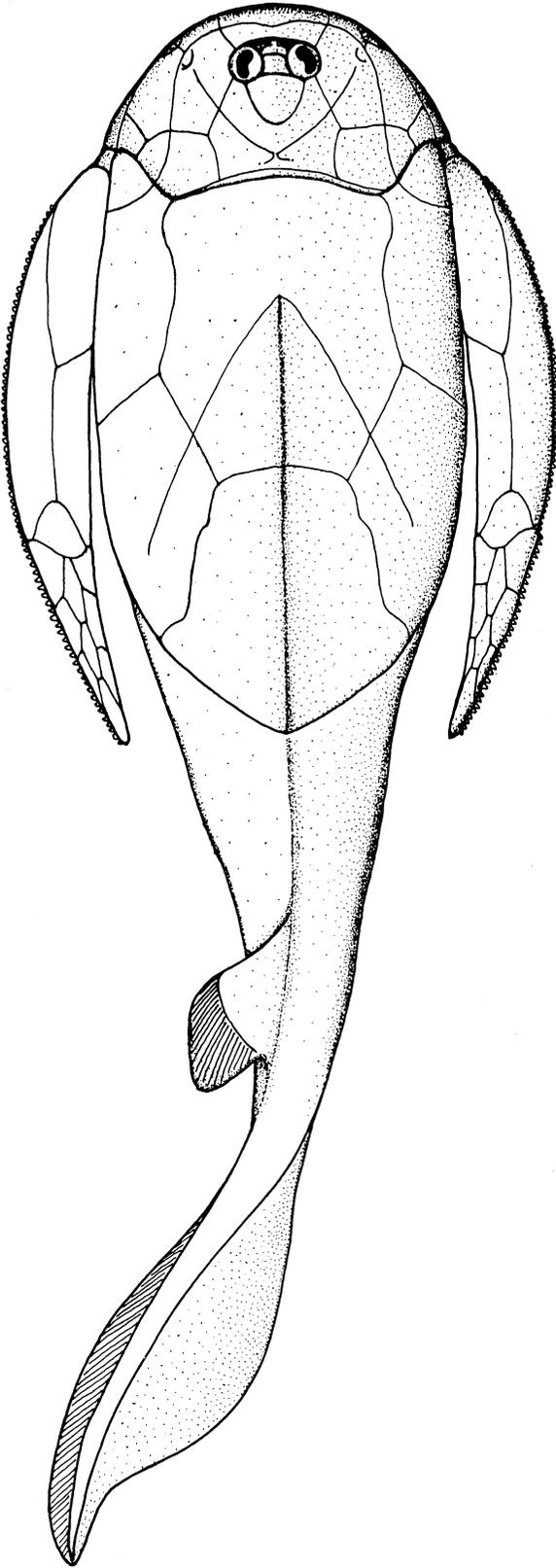
Figure 18. *Bothriolepis yeungae* n.sp. Reconstruction in dorsal view, based on specimens in Fig. 3; caudal fin morphology from *Bothriolepis canadensis* (Stensiö, 1948).

This also characterises *B. yeungae* (Fig. 12, character 10), although *B. yeungae* differs from these species in possessing a trifid preorbital recess.

In Young's cladogram, the trifid preorbital recess was a synapomorphy of a clade consisting of Northern Hemisphere taxa (clade A, Fig. 12, character 13). Among these, *Bothriolepis yeungae* is separated from taxa like *B. leptocheira* and *B. gigantea* (Miles, 1968) in possessing the strongly developed transverse anterior submarginal attachment and well-developed crests of the spiracular groove. These taxa, as well as *B. hayi*, lack the small pit on the internal surface of the lateral plate present in *B. yeungae*. *Bothriolepis maxima* (Stensiö, 1948: fig. 233) possesses a very small pit, but a weaker and more oblique anterior submarginal attachment, and what appears to be continuous anterior and posterior attachments for the submarginal around the spiracular groove. Additionally, the pit on the internal surface of the AMD is very large in *B. maxima* (Stensiö, 1948: fig. 238), and the pit on the internal surface of the PMD is distinctly anteriorly placed, as in *B. jarvki* (Stensiö, 1948: fig. 305). In *B. hicklingi*, the pit on the internal lateral plate is said to be broad and shallow (Miles, 1968: 108), although this is not visible on certain specimens (Miles, 1968, pl. 36, figs. 5, 10). Additionally, the PMD plate is unusual in possessing a large open pit on the internal surface, not connected to the *crista transversalis interna posterior* by a ridge. In *B. nitida* (Stensiö, 1948: 395), the ornament is very coarse, and the terminal segment of the pectoral fin is striated, appearing to lack the polygonal plates more characteristic of *Bothriolepis*.

The trifid recess type also occurs in *B. grenfellensis* from the Grenfell region of NSW (Johanson, 1997b), *Bothriolepis* sp. from the Jemalong fauna from Forbes, NSW, and *Bothriolepis* sp. from Gogo, Western Australia. However, *B. grenfellensis* lacks the separate, transverse anterior attachment for the submarginal seen in *B. yeungae*, instead possessing a small, oval attachment separated from the prelateral attachment by only a narrow groove. The anterior attachment for the submarginal in *Bothriolepis* from Gogo (Young, 1984) is more rounded still.

Within the groups possessing a semicircular recess, one clade is characterised by a point contact between Cv1, Cv2, Mm1 and Mm2, preventing overlap between the Cv2 and Mm1 plates (Young, 1988; Fig. 12, character 8), including taxa from Euramerica and South China. The pectoral fin of *B. yeungae* also shows this point contact, but differs from all species in this clade in the possession of a trifid preorbital recess.

The different synapomorphies from the cladogram of Young (1988) possessed by *B. yeungae* indicate that some of these must instead be homoplastic for *Bothriolepis*. Long *et al.* (1997: 266) imply that the morphology of the preorbital recess is the most important character in distinguishing clades of *Bothriolepis* species. However, all characters in a phylogenetic analysis should *a priori* be given equal weight, and difficulties in placing *B. yeungae* into clades recognised by Young (1988; see Johanson & Young, in press, for problems placing *Bothriolepis* from Nettleton's Creek, NSW) indicate that

certain morphological characters contradict phylogenies suggested by preorbital recess morphology. No attempt is made at this point to reanalyse the phylogenetic relationships of *Bothriolepis*, which will require a considerable and painstaking search for the qualitative characters necessary.

Therefore, it is presently difficult to identify the closest relatives of *Bothriolepis yeungae*. Of particular interest in this regard will be the morphology of *Bothriolepis* sp. from the nearby Jemalong fauna, placed in the same macrovertebrate zone as the Canowindra fauna by Young (1993). The *Bothriolepis* in each fauna have a trifid preorbital recess; as well, *Bothriolepis* occurs in association with *Remigolepis* and the dipnoan *Soederberghia* in both faunas. These comparisons will be part of a future work on the Jemalong fauna.

Palaeoecology of the Canowindra fauna

Certain observations that can be made with regards to the Canowindra fauna provide evidence as to the life and death of these fish, including: (*a*) the recovery of the fauna from a single bedding plane in the Mandagery Sandstone, with fish lying side by side rather than on top of one another; (*b*) the large number of fish crowded together on the rock slabs (Fig. 19B,C); (*c*) the excellent preservation of the fish (e.g., Fig. 3); (*d*) the preservation of the fish predominantly in life position, with dorsal surfaces upward.

The first observation indicates that the Canowindra fauna represents the remains of a Devonian palaeocommunity including fish that lived, interacted and died together. Time averaging (Walker & Bambach, 1971; Fürsich & Aberhan, 1990; Kidwell & Flessa, 1995; Olszewski & West, 1997), where plants and animals from different time periods can become concentrated or collected by biological or physical agents, is not believed responsible. Fürsich & Aberhan (1990) list various ways to recognise a time-averaged fauna, including evidence of physical transport of skeletal elements (e.g., disarticulation), or differences in preservation quality among the skeletal elements. The latter indicates that individuals from different times with different taphonomic histories have become mixed; neither this nor disarticulation is characteristic of the Canowindra fauna.

Additionally, individuals from different time periods can be accumulated by the winnowing of sediments, or if overall sedimentation rates are low. However, it is assumed that this type of accumulation would result in a thicker layer of fossils (e.g., a bone bed), which again, is not characteristic of the Canowindra fauna. Thus, the layer of fish in the Canowindra fauna comprises individuals living together and subsequently dying together during one restricted time period.

The second observation, crowding of a large number of fish on the rock slabs, is compatible with three scenarios: (*a*) loss of water habitat during dry conditions, forcing the fish to occupy a shrinking pool of water; (*b*) a mass kill of fish in water; (*c*) attritional death of fish in water, with subsequent accumulation and collection of individuals. The last scenario requires fish to die over an interval of time, potentially years, which contradicts the suggestion above that the Canowindra fish lived together and died within a short period. As well, accumulation of these individuals would require transport, which generally leads to disarticulation of skeletal elements or overturning of individuals. Disarticulation can be affected by degree of decay, where skin and flesh could hold bones, plates and scales together over some distance. Susceptibility to overturning can be influenced by morphology, where the flat-bottomed antiarchs may be more stable during transport. However, an example of physical agents collecting and overturning antiarchs may be seen in the assemblage of very large *Remigolepis* from near Eden, NSW. Here, several specimens (with fully articulated head and trunkshields) are closely spaced and almost entirely on their sides (pers. obs.). Additionally, the accumulation of over 3000 fish in the Canowindra fauna would require transport of individuals from over a wider area. It seems doubtful that so many fish could be transported over greater distances without a proportionately greater number being overturned or disarticulated in the process. In fact, the only distinct disarticulation of fish in the Canowindra fauna is associated with the larger sarcopterygian fishes (see below), and so occurred within the fauna, rather than by transport. Therefore, death by attrition is considered unlikely for the fish of the Canowindra fauna.

In the second scenario, the Canowindra fauna would result from a mass kill of fish in water. Causes of this type of mortality include volcanic activity, influx of toxins, algal blooms, change in water temperature, etc. (reviewed by Zinmeister [1998]). However, this type of death in the water column is believed to result in some degree of decay, disarticulation, transport of skeletal elements, non-life orientations of fish and a thicker layer of fish, none of which is observed in the Canowindra fauna. These are described in more detail below.

Fish dying in water can either float, sink to the substrate or sink to the substrate and be subsequently refloated. Schäfer (1972) noted that under similar water conditions, some fish will float due to gases created by decay, while others will decay entirely at the sediment surface. Schäfer (1972) related this to the size of the body cavity relative to the mass of the fish, and the amount of food present in the stomach upon death. Fish with relatively smaller body cavities result in smaller quantities of gas produced in decay, making the fish less likely to float after death. It is difficult to determine variables like these in fossil fishes, and it is assumed here that the dominant factor in determining whether fish float or sink is water temperature, and the effect water temperature has on rates of decay and production of body gases.

If these temperatures were higher (above 16°C; Elder & Smith, 1988), decay would be greater, and gases produced would tend to cause the fish to float. Decay and water movement would result in skeletal material becoming disarticulated and spread across a wide area (Schäfer, 1972; Elder & Smith, 1988). This water movement need not be strong. Decay and disarticulation were observed for the antiarch *Pterichthyodes* (Achanarras
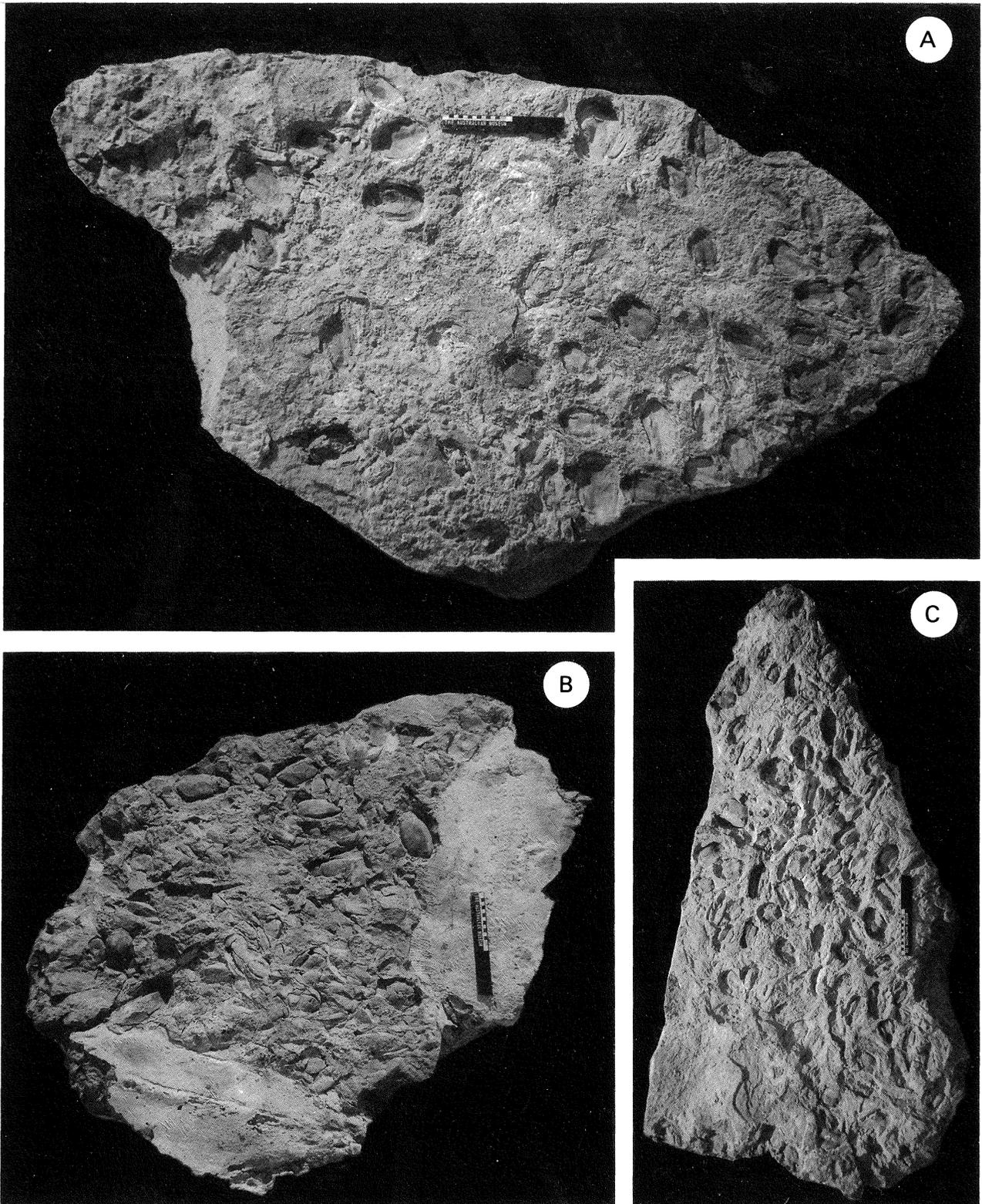
Figure 19. A–C, rock slabs showing dorsal or upper layer of Canowindra fauna, and distribution of fishes on each slab. Fishes are preserved as external moulds with occasional internal cast. The majority of the fishes belong to *Remigolepis walkeri* and *Bothriolepis yeungae*. In B, two large *Mandageria fairfaxi* are preserved, along with disarticulated antiarch plates. Scale in centimetres.

fish bed, Scotland), where dorsal head and trunkshield plates were displaced relative to ventral plates due to movement by weak water currents (Trewin, 1986). Trewin & Davidson (1996) described similar preservation for the acanthodians *Climatius* and *Ischnacanthus* from the Tillywhandland fish bed (Lower Old Red Sandstone, Scotland). This is not characteristic of the Canowindra fauna, where the majority of placoderm and sarcopterygians are well preserved and little disarticulated, including scales (e.g., Figs. 3–10, 13A,B,G,E; also Ahlberg & Johanson, 1997; Johanson, 1997a; Johanson & Ahlberg, 1997). Disarticulation of some antiarchs does occur at Canowindra (Figs. 13C,D,F,G, 14, 15), but this is usually associated with the presence of the larger sarcopterygians (Fig. 19B), as discussed further below. Thus, the Canowindra fauna does not appear to be the result of a mass mortality of fish in warmer waters.

Alternatively, Elder & Smith (1988) noted that in colder water (15°C or lower), fish will sink to the bottom and generally lie intact for an extended period of time, especially if cold or anaerobic conditions preclude the presence of scavengers. Fish will thus be well preserved (as is the Canowindra fauna), particularly if burial is rapid. However, it is assumed that upon dying, fish lose the ability to maintain life orientation as they sink. Counts of individual Canowindra *Bothriolepis* and *Remigolepis* in life (dorsal surface visible, e.g., Fig. 3) *vs* non-life orientation (side or ventral surfaces visible) were made on three randomly selected rock slabs (n = 196 antiarchs). The majority (177 or 91%) of individuals are in life orientation, while 11 are facing down and 8 are on their side.

This life orientation may suggest that the fish from Canowindra did not sink for any substantial distance after death, and so did not die in the water column. But again, the dorsal or life orientation of the majority of the antiarchs may be due to their morphology, with flat ventral and rounded dorsal head and trunkshield surfaces. Antiarchs are also believed to have lived near the sediment surface, especially *Remigolepis* (Stensiö, 1931; Johanson, 1997a), which may result in a preferred dorsal orientation. This result may therefore be somewhat equivocal, although most sarcopterygians with a fusiform body shape are also found in life orientation in the Canowindra fauna (Thomson, 1973; Ahlberg & Johanson, 1997; Johanson & Ahlberg, 1997).

Thus, it is possible that the fish of the Canowindra fauna died as the result of a mass mortality in colder water, sank to the bottom and were well preserved. However, it would be expected that these sinking fish would land on top of one another to some degree, and form a thicker layer on the substrate. Again, this is not observed in the Canowindra fauna, where fish predominantly lie side by side along the bedding plane (e.g., Fig. 19).

The overwhelming absence of disarticulation, decomposition, and the dominant preservation of individuals in life orientation side by side in a single layer along the bedding plane suggest the fish of the Canowindra fauna did not die and decompose in water, nor were individuals transported or collected by moving water. This is consistent with the hypothesis that the Canowindra fauna died in

place, with the crowding of the fish occurring prior to death rather than afterwards. The most parsimonious explanation for these observations, particularly the crowding before death, is that the fish became trapped in an ephemeral or temporary pool of water which subsequently dried. Thus, the first scenario listed above is the hypothesis that is followed in discussions below.

Some disarticulation of fish is present in the fauna (Fig. 19B), as seen on a rock slab containing two large individuals of the sarcopterygian *Mandageria fairfaxi*. Between these are scattered and disarticulated antiarch plates. Sarcopterygians had the capacity to breathe air through external and internal nostrils (choanae), and would be able to survive longer in a drying pool. The antiarchs lack this ability and would die before the sarcopterygians. As the *M. fairfaxi* individuals moved, they would disturb these antiarchs and disarticulate their plates. Of interest is the observation that several individuals of *M. fairfaxi* have been noted in the Canowindra fauna, but to date, the rock slab just discussed is the only one where disarticulated antiarchs are noticeably present. If the sarcopterygians could survive longer, more disarticulated and overturned antiarchs would be expected as the sarcopterygians moved through the diminished pool of water. However, by the time oxygen is depleted from the pool, conditions would be so harsh (increased temperature, increased toxicity) that the movement of the sarcopterygians would be minimal, perhaps involving only tail movements in an attempt to aerate remaining water.

Lack of postmortem disarticulation and transport also suggest that the burial was gentle, although the fish could also have become trapped to some degree in drying sediment. Lack of advanced decomposition suggests this burial happened relatively soon after death, or that some degree of mummification occurred during dry conditions (e.g., Weigelt, 1989). The sarcopterygians are collapsed postcranially, suggesting some postmortem decay and flattening of the softer parts of the body. However, decay does not appear to have continued to the point where developing gases caused the body to explode and rupture (e.g., as in *Scaumenacia curta* from the Escuminac Formation, Canada; Parent & Cloutier, 1996). The head and trunkshields of the antiarchs also show no indication of this, and the scale-covered portions of *Remigolepis* are flattened, but not exploded (Johanson, 1997a). Absence of disarticulation could also indicate lack of scavenging. This also suggests burial occurred relatively soon after death.

Burial by a relatively low energy physical agent may also be indicated by the apparent absence of a strong or distinct orientation of fish on individual rock slabs (e.g., Fig. 19), since this agent would tend to reorient individuals in its direction of movement. Additionally, fish may orient themselves side by side in a drying pool of water prior to death, in order to maximise available space (G.C. Young, pers. comm., also Weigelt, 1989), and so would be aligned, but potentially facing opposite directions along this line. Information regarding this orientation is preserved on the individual rock slabs collected, but it is believed that the initial observation of a more random orientation of

individual fish would be best investigated and tested when the *in situ* counterpart of the collected Canowindra fauna is uncovered and available for study. In this way, the orientation of individuals throughout the fauna can be determined.

The above discussion suggests that the fish of the Canowindra fauna died as the result of a single event, that is, isolation of the fish in an ever decreasing pool of water during drier conditions. In this sense (single event, death of a large number of individuals living at the same time), the term "mass mortality" can be applied. Subsequent burial was rapid, but did not transport or disarticulate the fish. The fauna was not subsequently reworked or redeposited. Further analysis of the environment of burial must await a full sedimentological analysis of the rock above and below the fauna, including sedimentological structures. Additional comment on the environment in which the Canowindra fishes lived is deferred until the environment of burial is established. Marine invertebrates have not been discovered in the Canowindra fauna, but taxa like *Bothriolepis* lived in both definite marine (Gogo Formation, Western Australia, e.g., Long, 1995) and freshwater (Catskill Formation, USA, Daeschler *et al.*, 1994) environments. Some recent workers have suggested that many Devonian environments traditionally thought to have fluvial are in fact marine, but evidence based on strontium ratios (Schmidz *et al.*, 1991) of skeletal elements collected from these environments has been equivocal (reviewed by Janvier, 1996). Therefore, care must be taken in the interpretation of the Canowindra environment, based on a future full sedimentological analysis.

Faunal characteristics

A large number of fish have been collected from Canowindra (n = 3033), a sample which represents the original Devonian community. Certain fishes known from other Australian Upper Devonian deposits are absent from Canowindra (phyllolepids, acanthodians, porolepiform sarcopterygians; see Young [1993] for review of these faunas). It is possible that these missing fish groups were present, but not yet collected. For example, these could have been separated from the other Canowindra fishes in distinct pools. This could occur as fish school in different parts of the original habitat, becoming isolated in these areas as the habitat shrinks.

However, the Canowindra fauna shows a greater diversity than fish assemblages described, for example, by Trewin (1986), Wilson (1996) and Trewin & Davidson (1996), the second being dominated by paracanthopterygian fishes and the first and third by acanthodians. Therefore, a reasonable representation of the original Canowindra fish community may have already been collected. It is important to be aware that fossil deposits will always be biased relative to the living assemblage. For example, Smith *et al.* (1988) compared Recent to Early Cainozoic fish faunas and found that floodplain deposits of the latter age preserve only 10–20% of the fish species

expected (also G.C. Young, pers. comm.), due to biological and physical destruction of smaller, more delicate fish. Predation certainly could have affected the fish preserved in the Canowindra fauna, but this is believed to have predominantly affected smaller antiarchs (see below), rather than other taxa. Unfortunately, coprolites (perhaps preserving missing fish taxa, e.g., acanthodian fin spines or scales) have not been observed at Canowindra. It is always difficult to evaluate negative evidence (i.e., absence of taxa), so until additional collecting indicates the presence of other types of fishes, the Canowindra assemblage will be considered indicative of the original community, particularly with regards to *Bothriolepis* and *Remigolepis*, whose population profiles at Canowindra are discussed below.

The most abundant fishes, in counts of all 195 rock slabs examined as of 1997, are the antiarchs *Bothriolepis yeungae* (n = 1379 individuals) and *Remigolepis walkeri* (n = 1555). Less common are the euarthrodire *Groenlandaspis* (n = 48) and the sarcopterygians. The number of sarcopterygians in the fauna is low (n = 51 individuals), but they are relatively taxonomically diverse (see pp. 315–316), compared to the antiarchs.

The non-dipnoan sarcopterygians have strongly developed jaws and dentitions, suggesting they were the predators in the fauna, preying predominantly on the placoderms. Caudal fin morphology suggests the sarcopterygians were unsteady rather than steady swimmers (Webb, 1982; Johanson & Ahlberg, 1997; Ahlberg & Johanson, 1997). As unsteady swimmers, these sarcopterygians waited, accelerating and attacking prey as it passed. The caudal fins were also small relative to overall length, and would not have generated a strong accelerating thrust. In contrast, steady swimmers include fishes like the tuna, which swim constantly in search of prey. It may seem unusual that all predators in the Canowindra fauna were unsteady swimmers, but this appears characteristic of many Devonian sarcopterygians (Belles-Illes, 1992).

In contrast, both *Bothriolepis* and *Remigolepis* possess ventral mouths with small, weak lower jaws (Stensiö, 1931, 1948; Johanson, 1997a), suggesting that these fishes were bottom feeders, taking small particles from the sediment surface, or perhaps ingesting and processing the sediment itself for food (Denison, 1941; Weems *et al.*, 1981). However, Johanson (1997a) noted that *Bothriolepis* and *Remigolepis* show differences in jaw structure and inferred musculature as well as in pectoral and more posterior fin morphology, suggesting differences in swimming ability and feeding. *Bothriolepis* is thought to be a more able and manoeuvrable swimmer based on its relatively longer tail and pectoral fins, with the capacity to extend and use its pectoral fins to generate lift and potentially feed within the water column. *Remigolepis* was thought to have been a poorer swimmer with shorter caudal and pectoral fins relative to length (with a reduced capacity for generating lift), and was likely restricted to the bottom. The pectoral fins could also be adducted or swung away from the body in both *Bothriolepis* and *Remigolepis*, perhaps to discourage predation through some type of threat display.

Population characteristics

Size-frequency distributions for *Remigolepis walkeri* and *Bothriolepis yeungae* (Fig. 20) indicate that the Canowindra fauna preserves fewer small individuals, particularly of *Remigolepis*. These size-frequency distributions are based on length (head + trunkshield) measurements taken from specimens on all available (i.e., prepared and latexed) rock slabs, for a total of 343 individuals (n = 233 for *Bothriolepis yeungae* and n = 110 for *Remigolepis walkeri*). This total includes length measurements of the smaller specimens noted above to be too difficult to adequately prepare for individual plate measurements for PCA (Fig. 6). The measurements included a smaller proportion of *Remigolepis* specimens relative to *Bothriolepis*, due to its relatively lower proportion on the slabs prepared, latexed and available for measurement in this analysis (as opposed to counts of individuals from all collected [but often unprepared] rock slabs). The slabs prepared and suitable for measurement were chosen randomly as work on the fauna progressed over the previous three to four years, and thus the specimens measured represent a random sample of both antiarchs.

The size-frequency distributions for both antiarchs are skewed (Fig. 20), *Remigolepis walkeri* towards larger individuals (g1 = –0.36615; kurtosis g2 = 0.68463), and *Bothriolepis yeungae* towards smaller individuals (g1 = 0.42355; kurtosis g2 = 0.55012). Size acts as a proxy for age of the individual in these histograms. Ages of fish can often be determined from skeletal elements such as otoliths and scales (Wootton, 1990), but otoliths are not preserved in the natural moulds present in the Canowindra fauna. Scales are not preserved for *B. yeungae*, while the concentric ridges or circuli needed to determine age are not preserved on the scales of *R. walkeri* (Johanson, 1997a: fig. 18). Growth patterns may be represented on the internal trunkshield of *R. walkeri* (see below), but it would be very difficult to use these to assign absolute ages to these individuals, since these do not necessarily represent yearly growth increments.

Wilson (1984, 1996) commented on the type size-frequency distribution or profile expected in a mass or catastrophic mortality of fish, the effect of which is to sample a living population in a short period of time (Wilson, 1984). Thus, the mass mortality profile would include distinct year-classes or cohorts (fish born at the same time [Wootton, 1990]), represented by multiple peaks in the size-frequency distribution (also Sheldon, 1965; Cummins *et al.*, 1986). Peaks in the size-frequency distribution should also be more distinct for younger individuals, since growth slows in older fish and these peaks become less distinct (Wilson, 1984).

The profiles of *Bothriolepis* and *Remigolepis* possibly show these presumed age classes (Fig. 20, indicated by the arrows), although these are certainly less distinct than in some living fish populations (e.g., Wootton, 1990). However, the size-frequency distributions of *Bothriolepis* and *Remigolepis* do not show distinct peaks for smaller or younger individuals, and in fact,
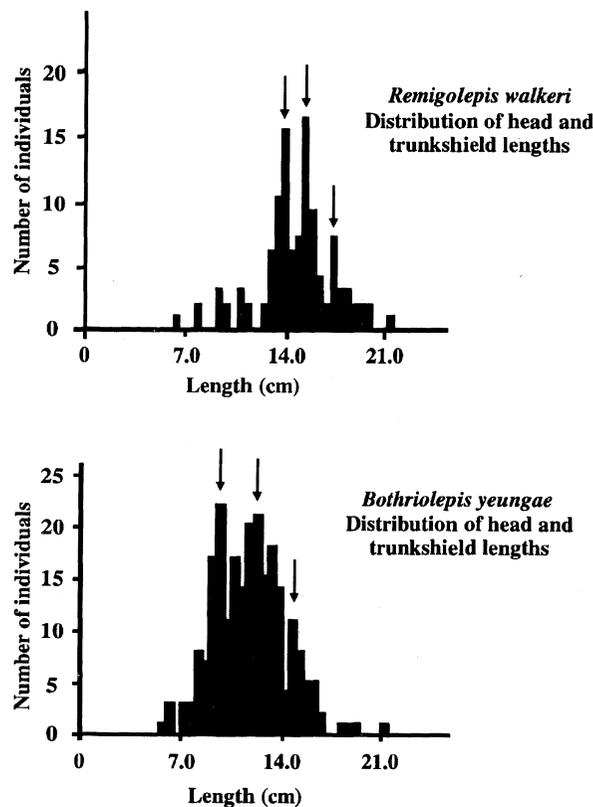
Figure 20. Size-frequency distributions of *Remigolepis walkeri* and *Bothriolepis yeungae*.

specimens of length 5–10 cm make only up 27% of the measured sample of *Bothriolepis yeungae*, while smaller specimens are very rare in the profile of *Remigolepis walkeri* (only 0.06% of the sample). Individuals under 7 cm appear to be rare for both taxa (Fig. 20), and very small juvenile specimens (e.g., similar in size to *Bothriolepis askinae* from the Aztec Siltstone, Antarctica [Young, 1988]) are missing from both population profiles.

The absence of smaller individuals in size-frequency distributions has been reviewed by Cummins *et al.* (1986) and Olszewski & West (1997), including both physical and biological factors. Smith *et al.* (1988) suggest predation by larger fishes on smaller fishes trapped in temporary ponds commonly biases the composition of fish assemblages from Cainozoic floodplain deposits. Predation by the sarcopterygians in the Canowindra fauna could certainly have been important in removing smaller individuals from the fauna. It is assumed that larger antiarchs in the Canowindra fauna would more readily avoid predation. Cummins *et al.* (1986) focus more on bias caused by physical factors such as breakage, dissolution, and abrasion, which can be linked to active transport or movement of the individuals. This can also remove smaller individuals entirely, but it is believed that the Canowindra fauna was little affected by these types of physical processes, as discussed in previous sections.

Another reason why smaller individuals could appear absent from a fauna is sampling bias. Smaller specimens may be overlooked during collection, however, the Canowindra fauna was removed *en masse* by a heavy earth mover, rather than by individual collectors. Smaller specimens can be more difficult to recognise on a crowded rock slab, but this bias is not believed to be large. Additionally, one rock slab preserves smaller individuals of *Bothriolepis yeungae* (but only three smaller fish of *Remigolepis walkeri*, one less than 10 cm), perhaps representing a pool separated from the main Canowindra fauna. If additional rocks from such areas were available for collection, more small fish might be recorded. However, this suggestion remains speculative until more of the fish layer is collected and the presence of these separate pools established. Overall, bias during collection is assumed to be negligible.

Although predation could be a dominant factor in removal of smaller individuals from the Canowindra fauna, the near complete absence of smaller specimens of *Remigolepis* needs to be considered. One possibility may be relatively higher growth rates in *Remigolepis*. *Bothriolepis* and *Remigolepis* plates grow by addition to the outer margins (Stensiö, 1948; Graham-Smith, 1978). On the internal surface of *Remigolepis* plates, concentric lines are visible, separating bands of uneven width (Johanson, 1997a: fig. 15a,b), with wider increments indicating increased growth and narrower indicating reduced growth. These bands can also be observed on East Greenland species of *Remigolepis* (e.g., Stensiö, 1931: pls 7.3, 9.2, 13.1) and less certainly on species from North China (Pan *et al.*, 1987: pl. 16.A1, 18.3, 8.4). Interestingly, on the East Greenland plates, the bands are more equal in size, being wider on some plates (Stensiö, 1931: pl. 7.3) and narrower on others (Stensiö, 1931: pls 9.2, 13.1).

Spacing between growth lines on scales and otoliths of fish is linked to environmental conditions (e.g., Wootton, 1990), whether favourable (wider) or not (narrower). However, the wider bands on trunkshield plates of *Remigolepis walkeri* from Canowindra may be linked to rapid spurts of growth rather than changing environmental conditions as these increments are not observed on plates of *Bothriolepis yeungae* (e.g., Figs. 14–16). The growth spurts may indicate that *Remigolepis* increased rapidly rather than gradually in size. This comparison would be stronger if *B. yeungae* possessed evenly spaced bands on the internal surface of the plates, indicating continuous or more gradual growth. Conversely, gradual growth in if *B. yeungae* may be indicated by the absence of growth lines, if these themselves indicate some type of change or alteration of growth rates.

Another factor to be considered is timing of reproduction. Reproduction in fishes is widely variable among living species and is influenced by environmental factors, food availability for parent and offspring, and presence of predators (Wootton, 1990: 161). The near absence of smaller individuals of *Remigolepis* might suggest differences in timing of reproduction relative to *Bothriolepis*. This might be expected, as these antiarchs numerically dominate the fauna; having different time spawning times would lessen pressure on resources.

Alternatively, the composition of the Canowindra fauna suggests that the mass mortality event resulting in its demise could have occurred during a non-reproductive period for both *Bothriolepis* and *Remigolepis*. Fishes of the same species tend to aggregate when spawning, which was clearly the case in the fauna studied by Wilson (1996), where one species of paracanthopterygian fish dominated the fauna (1700 specimens) to the near exclusion of the other two present (69 osmerids and 2 osteoglossids). Wilson (1996) described the diversity in this fauna as being low, and considered that this might be due to an aggregation of spawning species in a pool of shallow water during a high-water event. The Canowindra fauna differs from this in having a higher taxonomic diversity, and two numerically dominant species, *Bothriolepis* and *Remigolepis*, rather than just one. Even if the antiarchs offset their times of reproduction, as discussed above, it seems unusual that two genera would be present in such large numbers, which would result in increased pressure on various resources and reduce potential success of the reproducing species. This is consistent with the suggestion that lack of juveniles from the Canowindra fauna was due to the mass mortality event occurring during a non-reproductive period. Wilson (1996) was further able to suggest that the fishes in the Joffre Bridge fauna aggregated to spawn because he was able to recognise breeding tubercles (on the males). No such structures have been observed at Canowindra, and further, it is presently impossible to distinguish males from females in the fauna.

Conclusions

The Canowindra fauna, representing the remains of a single Upper Devonian palaeocommunity, is believed to have been trapped in an isolated and ephemeral pool of water that shrank over a restricted period of time during dry conditions. Absence of smaller (younger) individuals of *Bothriolepis yeungae* and *Remigolepis walkeri* appears due to the timing of the mass mortality relative to timing of reproduction of these antiarchs. The smallest specimens would be fish spawned in a previous reproductive season, however, predation on smaller individuals (e.g., Smith *et al.*, 1988) could also have occurred while the temporary pool was drying, removing many of these from the fauna. The absence of small specimens of *Remigolepis* relative to *Bothriolepis* is more difficult to explain, and may be due to differences in growth rates. Reaching large adult size may have had an ecological advantage (in both feeding and avoiding predation) for *Remigolepis*. The term "mass mortality" is applied to the Canowindra fauna, with death occurring over a restricted (but not instantaneous) period of time, affecting individuals living together during this time. Absence of smaller individuals of *Bothriolepis* and *Remigolepis* at Canowindra indicates that population profiles produced by a mass mortality can be affected by biological factors occurring before death, as well as taphonomic factors after death (e.g., Cummins *et al.*, 1986; Smith *et al.*, 1988) and should be interpreted with care.

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Abbreviations used in text and figures for *Bothriolepis yeungae*

ad1, ad2	anterior, posterior attachment on the SM for the lateral plate
a.inf	ventral muscle insertion on brachial process
alr	postlevator thickening of AMD
a.AVL	articular area on SM for AVL
a.PrL	attachment area for prelateral
ar3d	external articular area of Cd1
ar1v	internal articular area of Cv1
ar3v	external articular area of Cv1
a.sup	anterior dorsal muscle insertion on brachial process
a1SM	anterior attachment area for submarginal
a2SM	posterior attachment area for submarginal
ADL	anterior dorsolateral plate
AMD	anterior median dorsal plate
AVL	anterior ventrolateral plate
c.al	anterolateral corner of subcephalic division of ventral lamina of AVL
cf.ADL	area overlapping ADL
cf.AMD	area overlapping AMD
cf.AVL	area overlapping AVL
cf.MV	area overlapping MV
cf.MxL	area overlapping MxL
cf.PVL	area overlapping PVL
cir	semicircular pit-line groove
cit	*crista transversalis interna anterior*

cr1, 2 anterior, posterior crista of spiracular groove
cri infraarticular crista of ADL
cro median occipital crista of Nuchal
cr.pl postlevator crista of the AMD
cr.pm paramarginal crista of the headshield
cr.pto postorbital crista of the headshield
crs supraarticular crista of ADL
cr.tp *crista transversalis interna posterior*
cr.tv transverse nuchal crista of Nuchal
csl central sensory line groove
cu posteroventral ornamented corner of MxL
Cd1 dorsal central plate 1
Cd2 dorsal central plate 2
Cd4 dorsal central plate 4
Cd5 dorsal central plate 5
Cv1 ventral central plate 1
Cv2 ventral central plate 2
d.end endolymphatic duct
dlm dorsal lamina
dlr dorsolateral ridge of trunk armour
dlg2 posterior oblique sensory line groove
dma tergal angle
dmr dorsal median ridge of trunk-armour
f.art smooth articular fossa of ADL
f.ax axillary foramen
fe.orb orbital fenestra
fe.sorb suborbital fenestra
fm insertion fossa for levator muscles on Nuchal
fp funnel pit of brachial process
f.retr levator fossa of AMD
g pit on internal PP
grm ventral median groove on dorsal wall of trunk armour
ifc1 principal section of infraorbital sensory line on headshield
ifc2 branch of infraorbital sensory line diverging on L
ifc3 branch of infraorbital sensory line on SO
Ifg infragnathal
lc lateral corner of AMD
lcg main lateral line groove
L lateral plate
L AMD length of AMD
L PMD length of PMD
L NU length of Nu
LPM length of PM
L PP length of PP
L ORBFEN length of orbital fenestra
LORBM PM length of orbital margin of PM
L ROSTM PM length of rostral (anterior) margin of PM
Ml2 lateral marginal plate 2
Ml4 lateral marginal plate 4
Ml5 lateral marginal plate 5
Mm1 mesial marginal plate 1
Mm2 mesial marginal plate 2
MxL mixilateral plate
MV median ventral plate

m1 anterior lamina of AVL contacting SM plate
mr median ridge of PP
mvr median ventral ridge
N notch between ad1 and ad2 on SM
Nu nuchal
oa. ADL area overlapped by ADL
oa. AMD area overlapped by AMD
oa. PMD area overlapped by PMD
oa. PVL area overlapped by PVL
ood otico-occipital depression of headshield
p pit on internal surface of lateral plate
pa posterior corner of PMD
pbr brachial process of AVL
pe *pars pedalis* of brachial process
pma posterior marginal area of PMD
pnoa postnuchal ornamented angle of ADL
pnt paranuchal trochlea
prc prepectoral corner of AVL
prl lateral process of PMD
prh preorbital recess
pro *processus obstans*
pr.pl postlevator process
pr.po anterior postorbital process
prv2 posterior ventral process of dorsal wall of trunk armour
pt1 anterior ventral pit of dorsal wall of trunk armour
pt2 posterior ventral pit of dorsal wall of trunk armour
P pineal plate
PM postmarginal plate
PMD posterior median dorsal plate
PNu paranuchal plate
PP postpineal plate
Pr.L prelateral plate
PrM premedian plate
PVL posterior ventrolateral plate
r ridge separating ornamented and unornamented (oral) portions of the SO
R rostral plate
scl sclerotic ossicle
spg spiracular groove
socc supraoccipital cross-commissural pitline groove
sot supraotic thickening
SM submarginal
SO suborbital plate
tb ventral tuberosity on internal surface of AMD or PMD
tr transverse ridge running along internal surface of SO
T terminal plate of pectoral fin
W AMD width of AMD
W NU width of Nu
W PMD width of PMD
W PP width of PPW ORBFEN length of orbital fenestra

Appendix

Model I regression for *Bothriolepis yeungae*. Independent variable is head plus trunkshield length; dependent variables are as below. All variables log transformed to standardise variances. W, width; L, length. Null hypothesis Ho: b = 1; df = 77–2 = 75; t-test: t = b–1/standard error; $t_{[0.05, 75]}$ = 1.665 (approximately).

dependent	a (constant)	b (slope)	standard	t variable	error
W PMD	-0.132664	0.844759	0.09334	1.662 *	accept Ho
L PMD	-0.245285	0.888829	0.760	1.4627 *	accept
W AMD	0.039971	0.751069	0.0825	3.0173 **	reject
L AMD	-0.427343	0.981729	0.05428	0.3371 *	accept
W NU	-0.123761	0.70291	0.12021	2.47166 **	reject
L NU	-0.413476	0.77724	0.0838	2.658 ***	reject
W PP	-0.216405	0.561688	0.08238	5.3237 ***	reject
L PP	-0.73940	0.772064	0.0985	2.31401 *	reject
W ORBFEN	0.151456	0.4904343	0.0948	5.375 ***	reject
L ORBFEN	-0.455043	0.651	0.0948	3.68 ***	reject
LORBM PM	0.455615	0.240687	0.1599	4.7867 ***	reject
L ROSTM PM	-0.2350	0.7179	0.1162	2.4276 **	reject
LPM	-0.9458	1.06105	0.0763	0.8 *	accept