

New *Bothriolepis* (Antiarchi: Placodermi) from the Braidwood region, New South Wales, Australia (Middle-Late Devonian)

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Abstract – *Bothriolepis longi* sp. nov., from the Comerong volcanics (Middle-Late Devonian) in the Budawang Range synclinorium near Braidwood (southeastern New South Wales), is the third species of *Bothriolepis* to be formally described from New South Wales. *Bothriolepis longi* resembles species from Victoria, Australia and the Aztec Siltstone, Antarctica (Givetian-Frasnian), and certain unnamed species from the Frasnian of Western Australia. A preliminary phylogenetic analysis considers three possible positions for the new species in a previously published cladogram for species of *Bothriolepis*. A close relationship to several Antarctic species is suggested. Correlation between southeastern Australia and the Aztec sequence of Antarctica is discussed. The Aztec sequence may be younger than previously proposed.

INTRODUCTION

The antiarch *Bothriolepis* has a widespread distribution in Australia, occurring at several localities of Middle-Late Devonian age (Long 1991a; Young 1993). Australian *Bothriolepis* specimens were first studied by E.S. Hills, who described *B. gippslandiensis* from southeastern Victoria (Hills 1929, 1931, 1936). Long (1983) and Long and Werdelin (1986) described these Victorian faunas in greater detail and named several new species. Hills (1932, 1936) also noted the presence of *Bothriolepis* plates in the Upper Devonian of central New South Wales but did not assign these to any species. Subsequently, *Bothriolepis* specimens have been identified from many localities in New South Wales (Figure 1), including Nettleton's Creek, Pambula River, Twofold Bay, Worange Point, Hervey's Range, Jemalong, Canowindra and Grenfell (Young 1993). New species from Grenfell and Canowindra have recently been described by Johanson (1997, 1998).

We describe here a new species of *Bothriolepis* from the western limb of the Budawang Range Synclinorium along a tributary of Nettleton's Creek, east of Braidwood, New South Wales. This is the same locality from which Ritchie (1984) described the phyllolepid placoderm *Placolepis budawangensis*. The Nettleton's Creek assemblage comes from a 75 cm thick siltstone unit, 350 m above the base of the Comerong Volcanics, and 700 m below the contact with the overlying Merrimbula Group (Ritchie 1984). The age has been assumed to be Frasnian (Late Devonian), based on the presence of a Frasnian marine

invertebrate assemblage in the Merrimbula Group near Wog Wog, 8 km north of the Nettleton's Creek locality. A section measured by R.K. Jones at Nettleton's Creek shows the fish assemblage to lie immediately above the highest rhyolite, and 920 m beneath a marine horizon (R.K. Jones pers. comm. 1997). Young (1993) assumed that this marine horizon corresponded to the latest Frasnian maximum transgression on the Devonian sea level curve, but noted there was no meaningful older age constraint on the Nettleton's Creek fauna.

The Nettleton's Creek fish assemblage also includes undescribed rare acanthodians and sarcopterygians. However, the most common remains are the placoderms *Bothriolepis* and *Placolepis*; these occur in similar proportions. The only antiarch, *Bothriolepis longi* sp. nov., shows similarities to Victorian species of *Bothriolepis*, to species from the Frasnian of Western Australia (Gogo Formation and Munabia Sandstone), and to certain species from the Aztec Siltstone fauna of Antarctica. Six zones have been identified within the Aztec Siltstone. However, the ages of its upper and lower boundaries are not well constrained (Young 1993). The material of *Bothriolepis* consists mainly of disarticulated plates, but in several instances closely associated material can be assumed with confidence to have come from the same individual (Figure 2). Morphological details are well preserved, and description of this new species leads to several important conclusions regarding phylogeny and biostratigraphy of the genus in East Gondwana, as discussed below.

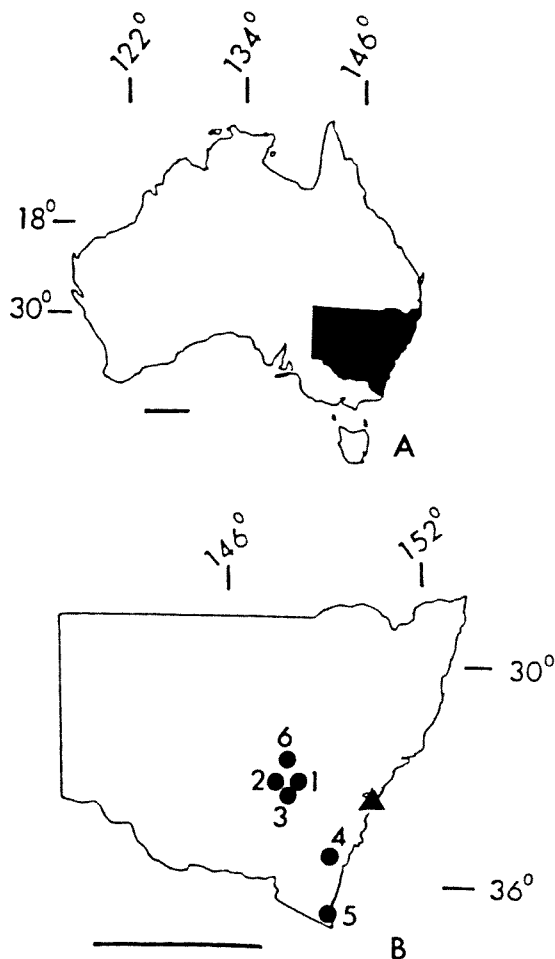


Figure 1 *Bothriolepis* localities of New South Wales (NSW), Australia. A, Australia, with NSW in black; B, NSW, with the following localities: 1, Canowindra; 2, Jemalong; 3, Grenfell; 4, Nettleton's Creek; 5, Pambula River, Twofold Bay, Worange Point; 6, Hervey's Range. Scale bars = 500 km. Triangle = Sydney.

MATERIALS AND METHODS

The Nettleton's Creek material was etched in hydrochloric acid to remove weathered bone. The resulting moulds were cast in blackened rubber latex, then whitened with ammonium chloride sublimate and photographed. Line drawings were made by means of a camera lucida or traced from enlarged photographs. Specimens preserved in part and counterpart are indicated by the suffixes A or B. Specimens are housed at the Australian Museum (AM). Measurements (mm) are given in Tables 1 and 2, and follow Stensiö (1948, figures 1–3). Additionally, measurements of the posterior median dorsal plate are taken from the maximum length and width of the specimen, and on the premedian plate, from the maximum length of the specimen and where the rostral and orbital edges of the plate contact the lateral plate.

SYSTEMATIC PALAEOONTOLOGY

Subclass Placodermi M'Coy, 1848

Order Antiarchi Cope, 1885

Suborder Bothriolepidoidei Miles, 1968

Family Bothriolepididae Cope, 1886

Genus *Bothriolepis* Eichwald, 1840

Bothriolepis longi sp. nov.

Figures 2–9

Bothriolepis sp. Ritchie 1975: 324.

Bothriolepis sp. Long and Turner 1984: 237

Bothriolepis sp. Young 1993: 233, 250.

Material Examined

Holotype

AM F100356A,B, disarticulated specimens preserved as part and counterpart of a head shield, both anterior ventrolateral plates, proximal segment of the right pectoral fin and portion of left, and the left mixilateral (Figure 2), all closely associated and assumed to come from one individual.

Other Material

Head shield specimens, AM F100357A,B, AM F100358A,B, AM F100359A,B, AM F100324A,B, all parts and counterparts, AM F91405, AM F96843, AM F96841, AM F91431, AM F100331, AM F91397, AM F91416 (external); other materials: AM F61764, 61915, 61928A,B; 61929, 91390–91396, 91398–91415, 91417–91430, 91432–91439, 96838–96847, 98649–98653, 100267, 100311–100340, 100341A,B–100347A,B, 100348–100355.

Type Locality and Age

Northern tributary of Nettleton's Creek, northeast of Mongarlowe, east of Braidwood, New South Wales (Ritchie 1984), Givetian or Frasnian in age.

Diagnosis

Medium-sized *Bothriolepis* characterized by subdivided posterior submarginal attachment on the lateral plate and a large posterodorsal groove on interior surface of the submarginal. Preorbital recess semicircular. Large pit present on internal surface of lateral plate. Anterior postorbital processes of otico-occipital depression reduced. Attachment area for prelateral on the lateral plate small, oval and vertically oriented. This attachment is separate from a strong, transverse, shelf-like anterior submarginal attachment. Posterior submarginal attachment on lateral plate extends across spiracular groove, while pre- and postlateral crests of the spiracular groove are continuous around spiracular opening. On internal anterior



Figure 2 *Bothriolepis longi* sp. nov., part and counterpart of holotype. A, AM F100356B; B, AM F100356A. Scale bar = 1.0 cm. Both A and B are to the same scale.

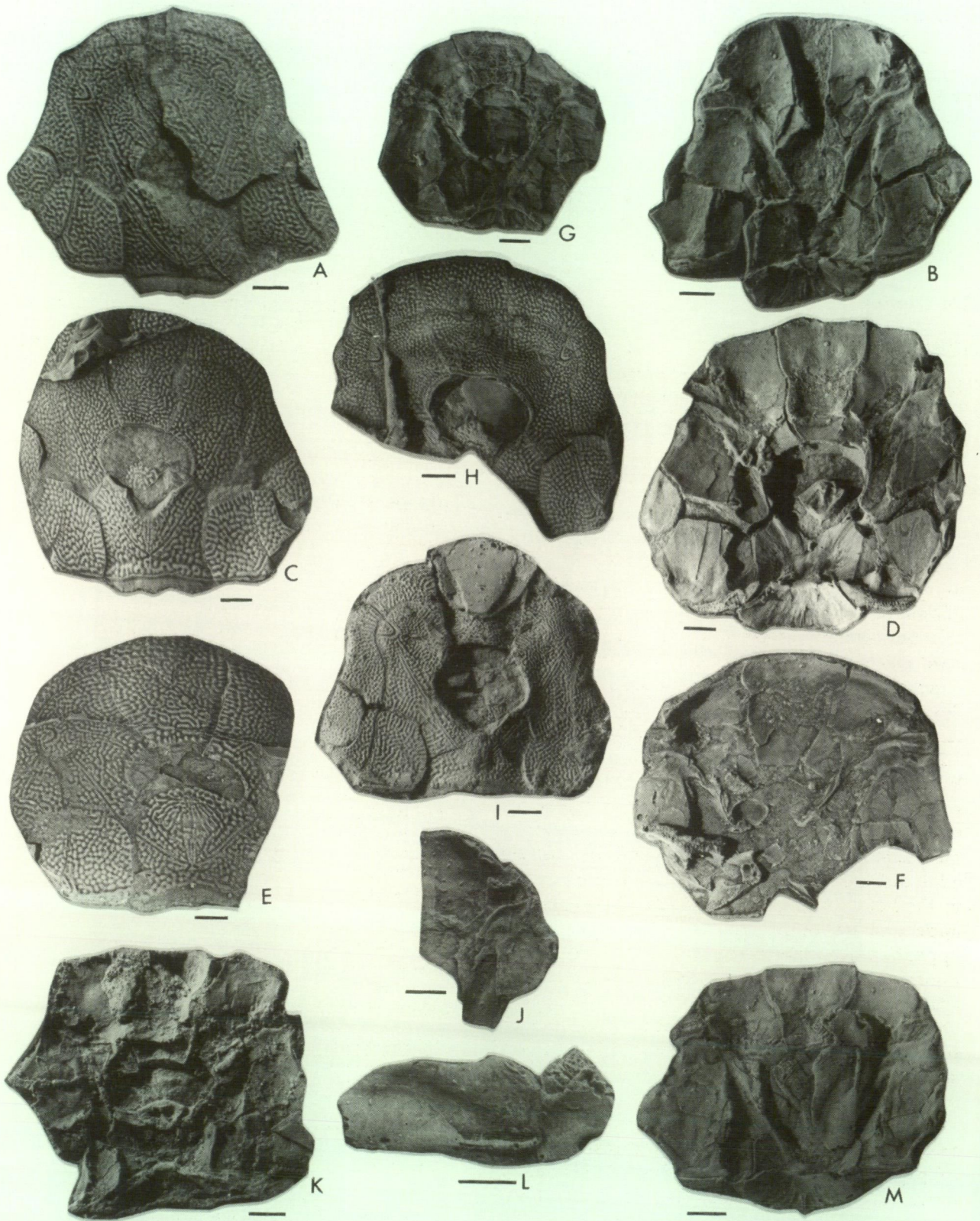


Figure 3 *Bothriolepis longi* sp. nov., head shields. A, AM F100356B, external view; B, AM F100356A, internal view; C, AM F100358A, external view; D, AM F100358B, internal view; E, AM F100357A, external view; F, AM F100357B, internal view; G, AM F91405, internal view; H, AM F100324A, external view; I, AM F96843 external view; J, AM F100331, internal lateral plate; K, AM F96841, internal view; L, AM F91431, detail of internal submarginal and partial external prelateral. M, AM F91431, internal head shield with submarginal and partial suborbital and prelateral plates. Scale bars = 0.5 cm.

median dorsal plate anterior levator fossa broad and shallow, postlevator thickenings low and flat. Median ventral ridge extends into anterior levator fossa, running to anterior margin of plate. Prepectoral corner on anterior ventrolateral plate is poorly developed. On the pectoral fin, Cv_2 and Mm_1 plates contact, preventing overlap of Cv_1 and Mm_2 .

Etymology

For Dr J.A. Long, Western Australian Museum, Perth, for his contributions to the study of *Bothriolepis* and Devonian fishes in general.

Description

Head Shield

Autapomorphies of *Bothriolepis longi* include the presence of multiple posterior submarginal attachments on the lateral plate and the strongly developed groove on the internal surface of the submarginal, the function of which is described below.

The head shield (Figures 2, 3, 4A–C,E, 5) is widest at the postmarginal corners (breadth/length [B/L] average = 1.2, see Table 1). The overall head shield morphology appears variable, with the lateral margin of the lateral plate (L) either more concave or more convex, resulting in narrower or rounder head shield shape. Sensory grooves (ifc_1 , ifc_2) and other features of the external surface are normally developed for the genus (Figure 5C). The orbital fenestra ($fe.orb$) is wider than long (B/L average = 2.21) with average ratio of length of head shield to length of orbital fenestra being 5.25. On the internal surface of the head shield, the anterior postorbital processes of the otico-occipital depression ($pr.po$) in most specimens do not extend beyond the posterior edge of the suborbital fenestra ($fe.sorb$). However, in the holotype (Figures 2, 3A–B), these processes appear to be longer. The preorbital recess (prh) appears semicircular in several specimens (e.g., Figure 3D,K) where the floor of the recess is crushed, but there is no clearly preserved endocast. One specimen (Figure 3H) suggests a pentagonal or trifid preorbital shape on the compressed external surface, but we have assumed this to be an artifact of preservation.

The premedian plate (PrM , Figures 2–5) is longer than wide (average L premedian/B rostral margin of premedian = 1.44), with the orbital margin narrower than the rostral margin. The internal surface is roughened, with internal sutures notched inwards about one-third to one-half the length from the rostral to orbital edges. Ridges and pits on internal surface are absent.

The lateral plate (L, Figures 2–5) on the internal surface possesses a large, open pit (p) with distinct margins, present anteromesial to the spiracular groove (spg). The prelateral plate attachment

Table 1 Head shield plate measurements (in millimetres) for *Bothriolepis longi* sp. nov. Abbreviations: B = breadth; c = circa; L = length; - = missing value.

Head shield	B	L	B/L	
AM F100356B	51	45.5	1.12	
AM F100357A	46	40.5	1.13	
AM F100358A	53	49	1.08	
AM F91431	60.6	40	1.5	
AM F91397	62	45.2	1.37	
AM F100324A	47	45	1.04	
AM F96841	-	44.5	-	
AM F96843	c 55	45	1.2	
		average = 1.2		
Postmarginal plate (PM)				
	B rostral	B orbital	L	B rostral/L
AM F100357A	18.6	8.5	18	1.03
AM F100358A	14.5	7.5	20.4	1.93
AM F91431	16	8.7	13.71	1.16
AM F100324	14	8.5	18.5	1.64
			average = 1.44	
Lateral plate (L)				
	B	L		
AM F100356B	20.25	30		
AM F100358	18.3	26.5		
AM F100357A	c 19.5	27.5		
AM F100324A	14.25	28.3		
AM F96843	15.5	28.1		
AM F91431	16.5	28.5		
Nuchal (Nu)				
	B	L		
AM F100356B	22.2	18.3		
AM F100357A	21	16.1		
AM F100358A	19.2	19.9		
AM F91431	18.45	c 14.25		
AM F91397	21.95	17.8		
AM F96843	c 22.5	18		
AM F100316	c 22	c 16		
Paranuchal plate (PNu)				
	B	L		
AM F100356B	14.5	16.3		
AM F100357A	16.4	15.3		
AM F100358A	16.75	15.4		
AM F91431	17.2	13.2		
AM F91397	16.35	16.2		
AM F96843	17	15.8		
Postpineal plate (PP)				
	B	L		
AM F100357A	8.4	5.9		
AM F100358A	8.9	5.7		
AM F96841	8.8	5		
AM F100317	10.2	6		
Orbital fenestra (Fe.orb)				
	B	L	B/L	
AM F100357A	16.7	5.9	2.8	
AM F100358A	18.2	8.5	2.14	
AM F91431	-	11	-	
AM F100324A	16	9.5	1.68	
AM F96841	19	c 7.5	2.53	
AM F96843	18.25	13.25	1.4	
		average = 2.31		
L head shield / L orbital fenestra				
AM F100357A	6.86			
AM F100358A	5.76			
AM F91431A	3.64			
AM F96841	5.9			
AM F96843	3.4			
AM F100324A	4.73			
	average = 5.05			

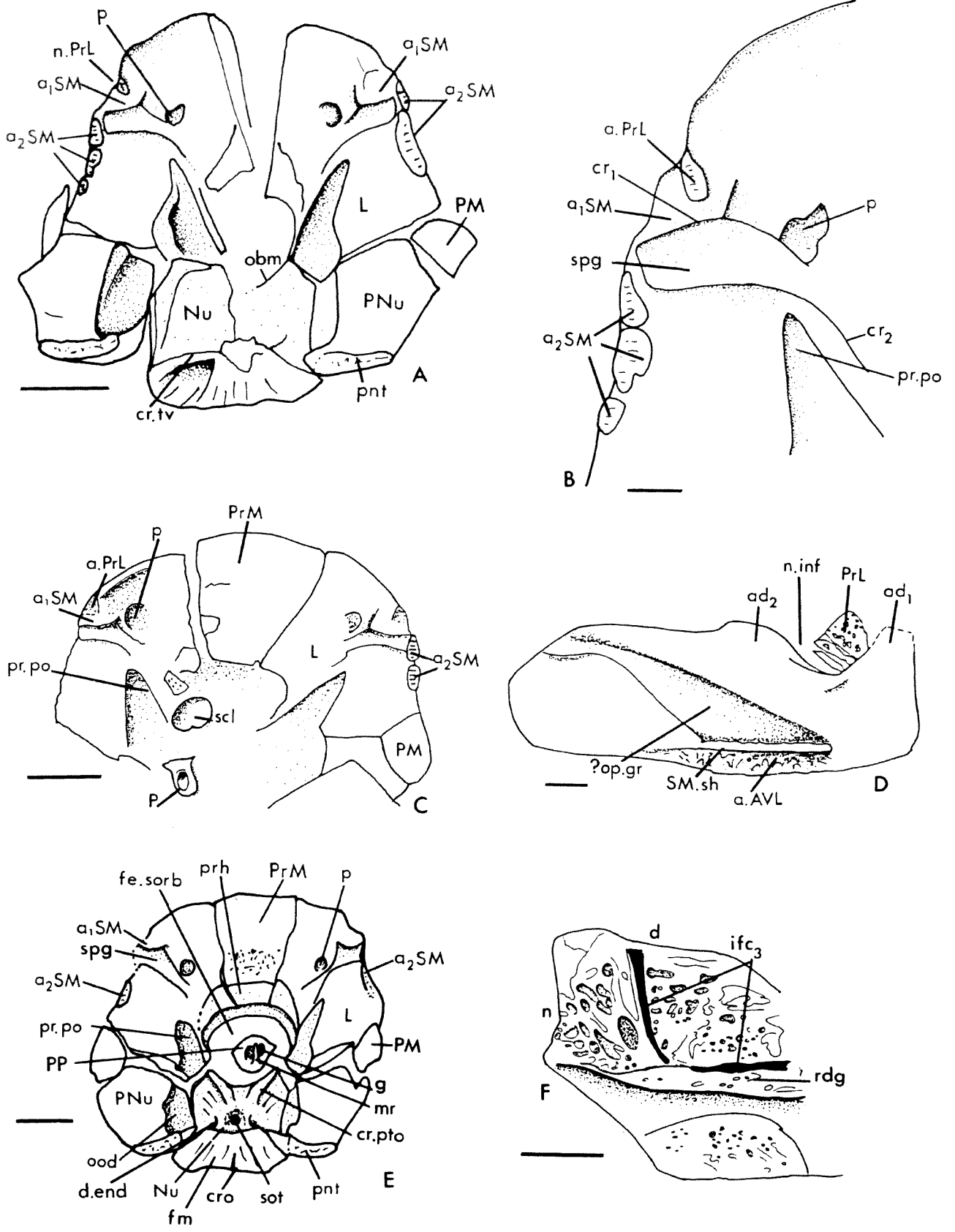


Figure 4 *Bothriolepis longi* sp. nov. A, AM F100356A, internal head shield; B, AM F100356A, detail of right internal lateral plate; C, AM F100357B, internal head shield; D, AM F91431, submarginal; E, AM F100358B, internal head shield; F, AM F91431, suborbital associated with head shield. Scale bars = 1.0 cm.

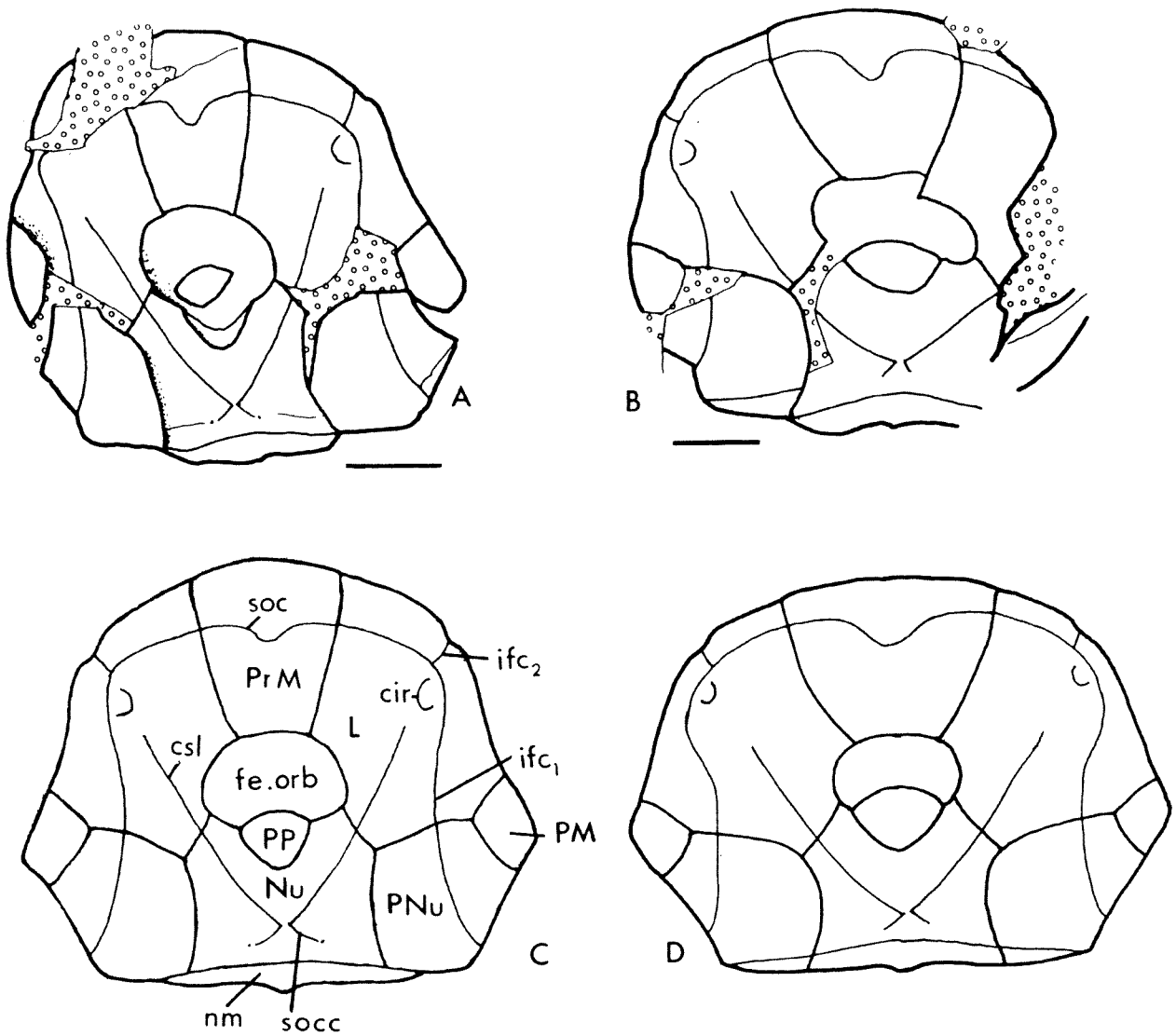


Figure 5 *Bothriolepis longi* sp. nov. A, AM F100358A; B, AM F100357A; C, AM F100358A, reconstruction; D, AM F100357A, reconstruction. Abbreviations are listed in an Appendix. Scale bars = 1.0 cm.

(a.PrL) is small, oval, oriented ventrally inside the prelateral notch (n.PrL). The anterior submarginal attachment (a₁SM) is a transverse, shelf-like area running from the lateral edge of the lateral plate beyond the mesial edge of the prelateral attachment. The posterior edge of the anterior submarginal attachment forms a portion of the prelateral crest (cr₁) of spiracular groove, while the remainder of the anterior crest runs to the margin of the pit on lateral plate. The postlateral crest (cr₂) of the spiracular groove is sharp, angling posteromedially to the anterior postorbital processes. The pre- and postlateral crests of the spiracular groove are continuous around the lateral opening of spiracular groove. The spiracular groove is wide laterally, narrowing towards the anterior tip of the anterior postorbital process. The posterior submarginal attachment (a₂SM) is subdivided into two or three distinct areas, with the anteriormost

area longest, covering the lateral edge of the spiracular groove. The more posterior areas are separated by a distinct notch. A small portion of the prelateral plate (PrL) is preserved on AM F91431 (Figures 3L, 4D), but is insufficient for description.

The pineal (P, Figures 3, 4) possesses a narrow main body, and strongly developed posterolateral corners. The postpineal (PP, Figures 2-5) has a convex anterior border extending slightly into the orbital fenestra. Internally, a strong median ridge (mr) separates two large, deep pits (g).

The nuchal (Nu, Figures 2-5) possesses orbital facets (obm) with a strong posteromesial orientation, and the obtected nuchal (nm) area is wide, about one-third the width of the nuchal. The median occipital crista of the head shield (cro) is distinct, with fine ridges on either side. Insertion areas for levator muscles (fm) are large but shallow. Internally, the transverse nuchal crista (cr.tv) is well

developed; a rounded depression is present in the centre of the large supraotic thickening (sot), the endolymphatic ducts (d.end) are small.

The paranuchal (PNu, Figures 2-5) is longer than wide, with dorsal edges meeting at a sharp corner. The paranuchal trochlea (pnt) are elongate. The postmarginal (PM) is small, roughly triangular, with a well-developed lateral corner, and the widest part either below the midline of the plate or slightly above.

Only one head shield (AM F91431, Figure 3M) has associated cheek and jaw elements. The submarginal (Figures 3L, 4D) on this specimen has a smaller anterior articular process (ad₁), separated by a wide infraspicular notch (n.inf) from a single long, narrow posterior articular process (ad₂). The internal surface of the submarginal has a strong ridge (SM.sh) just above its ventral margin, running antero-posteriorly approximately two-thirds of the way along the submarginal. A similar but less well-developed structure may occur in *Bothriolepis canadensis* (Stensiö 1948, figure 105C). A flattened, roughened area below the submarginal shelf articulated with the ventral trunk shield (a.AVL). A large posterodorsal groove (?op.gr) on the interior surface of submarginal is wider ventrally, narrowing dorsally, running from the submarginal shelf to the posterodorsal corner of the submarginal.

The external surface of the suborbital (SO, Figure 4F) is ornamented dorsally, separated from the unornamented ventral portion by a strong transverse ridge (rdg). A small anterodorsal process is present, separated from the anteroventral corner of the suborbital by a shallow notch (n). The groove for the infraorbital sensory canal (ifc₃) runs very close to the transverse ridge. Denticulation on the ventral margin of the suborbital is absent. The internal surface and lateral margins of the suborbital are not visible.

Trunk Shield

The anterior median dorsal (AMD, Figures 6A-H, 7A,B, 9A,B,D) is longer than broad (B/L index average = 0.86) with weak postlevator processes (pr.pl), but strongly developed lateral (lc) and posterolateral corners (pcl). The postlevator notch (npl) posterior to the postlevator process is weakly developed, the tergal angle (dma) is near the midline of the plate and the dorsal median ridge (dmr) is weakly developed. Internally, the anterior levator fossa (f.retr) is large, broad and shallow. The postlevator thickenings (alr) are low, flat, and bounded anteriorly by low postlevator cristae (cr.pl). The anterior ventral pit of the dorsal wall of the trunk armour (pt₁) is an elongate oval at the confluence of the postlevator cristae. The median ventral ridge (mvr) is weakly developed, and extends anteriorly into the anterior levator fossa, nearly reaching the anteriormost margin of the

Table 2 Trunk shield plate measurements (in millimetres) for *Bothriolepis longi* sp. nov. Abbreviations: B = breadth; c = circa; H = height; L = length; - = missing value.

Anterior ventrolateral plate (AVL)				
	B	L	H lateral lamina	
AM F61929	22	53	15	
AM F100360	27	62	-	
AM F100343	28	52.2	10	
AM F100348	21.5	46.6	10.6	
AM F91411	25.5	48.3	-	
AM F91419	c 29	-	-	
AM F91429	22	46.5	-	
AM F100332	22	56.5	15	
AM F91433	27	58.5	-	
AM F91434	27	47.5	-	
Posterior median dorsal plate (PMD)				
	B	L	B/L	
AM F61928	45	43	1.05	
AM F100353	-	39.1	-	
AM F91430	39	36	1.08	
AM F91438	c 37	c 35	1.06	
AM F96844	41	37.7	1.09	
AM F91428	40	43	0.93	
Anterior median dorsal plate (AMD)				
	B	L	B/L	
AM F91390	23.5	c 34	0.69	
AM F91399	46	50	0.92	
AM F91404	34.75	40.1	0.87	
AM F91414A	38	40.5	0.93	
AM F96839	49	55.5	0.88	
Anterior dorsolateral plate (ADL)				
	B dorsal	L dorsal	B ventral	L ventral
AM F100267	15.5	c 45	9.5	-
AM F100333	13.5	30.9	9.3	33.5
AM F96838	13.5	32	c 10	34
Posterior ventrolateral plate (PVL)				
	B dorsal	L dorsal	B ventral	L ventral
AM F61748D	19.5	32.5	-	51
AM F91409	19.5	39.5	22	54.2
AM F100315	-	38	24.5	59
Posterior ventrolateral plate (PVL) (ctd)				
	L subanal portion/L PVL			
AM F61748D	0.37			
AM F91409	0.39			
AM F100315	0.37			
Median ventral plate (MV)				
	B	L		
AM F100356B	21	26		
AM F100351	15	24		

plate. The median ventral ridge extends posteriorly from the posterior edge of anterior ventral pit, splitting to form the ventral median groove (grm), which continues to the posterior margin of the plate.

The posterior median dorsal (PMD, Figures 6I-K, 6M, 6P, 7C-D, 9B) has strongly developed lateral corners (l); internally, a ventral tuberosity (tb) surrounds the posterior ventral pit (pt₂) which is positioned at approximately two-thirds the length

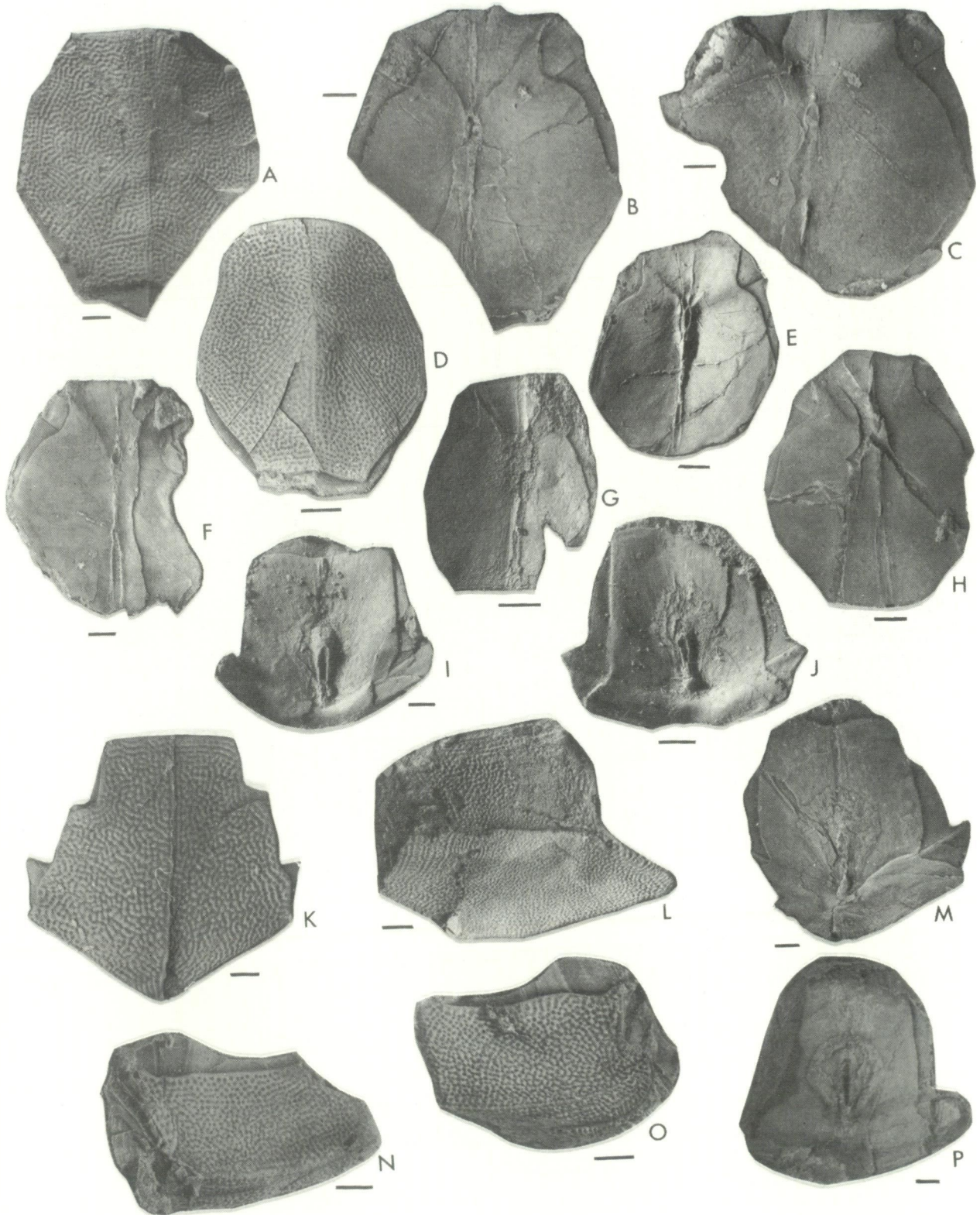


Figure 6 *Bothriolepis longi* sp. nov. A, AM F96840, external AMD; B, AM F96839, internal AMD (counterpart of AM F96840); C, AM F91394, internal AMD; D, AM F91404, external AMD; E, AM F91414, internal AMD; F, AM F100347A, internal AMD; G, AM F91390, internal AMD; H, AM F91399, internal AMD; I, AM F96844, internal PMD; J, AM F91430, internal PMD; K, AM F61928A, external PMD; L, AM F91409, external PVL; M, AM F61928B, internal PMD; N, AM F100333, external ADL; O, AM F91410, external ADL; P, AM F91428, internal PMD. Scale bars = 0.5 cm.

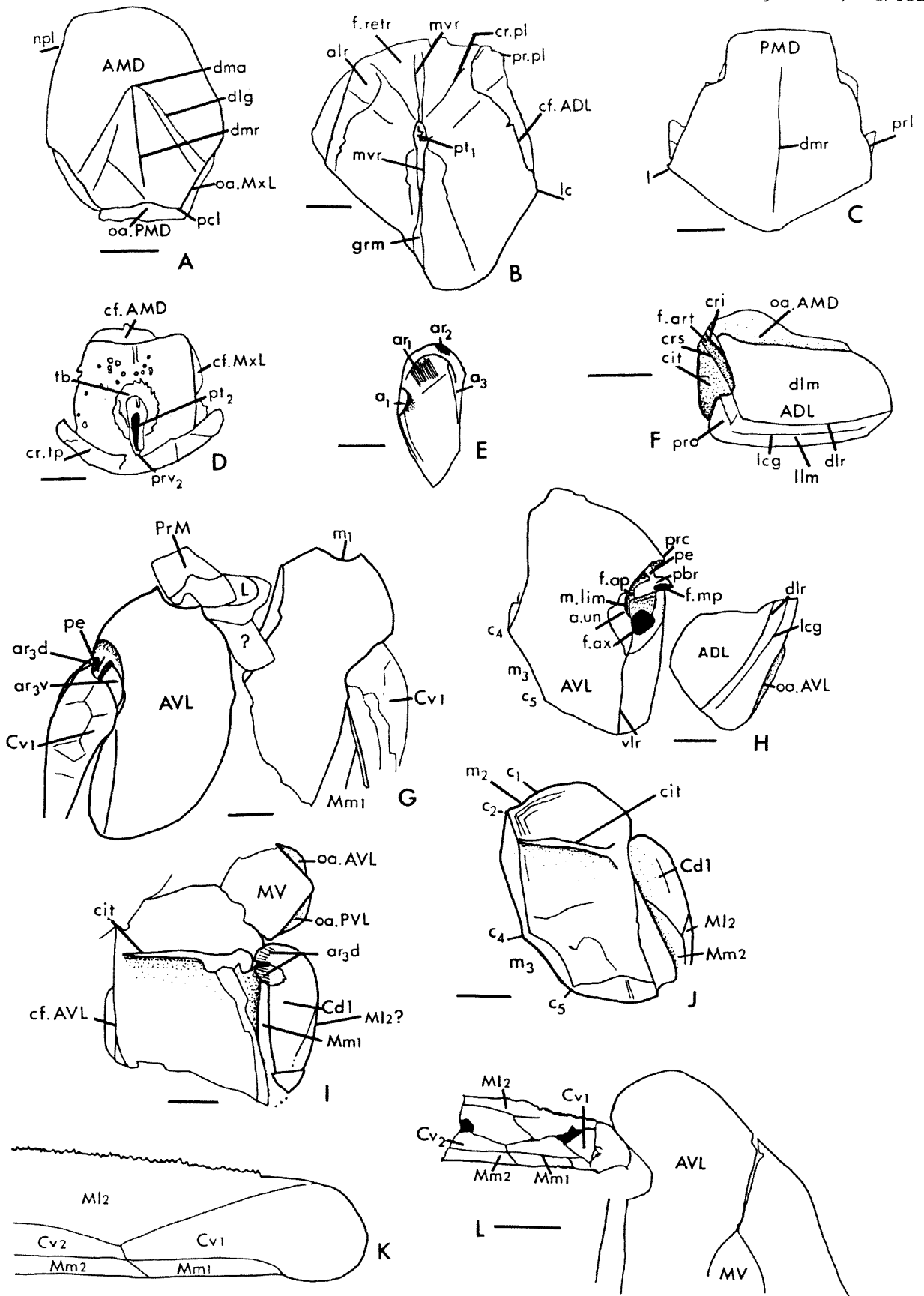


Figure 7 *Bothriolepis longi* sp. nov. A, AM F91404, external AMD; B, AM F96839, internal AMD; C, AM F61928, external PMD; D, AM F96844, internal PMD; E, AM F100321, Cd₁ or Cv₁, internal view; F, AM F100333, anterolateral ADL; G, AM F91436; associated AVLs, external view; H, AM F100343A, external AVL, AM F100344A, external ADL; I, AM F100312 (AVL), AM F100311 (MV); J, AM F91411; K, reconstruction of proximal pectoral fin based on AM F91421; L, AM F91421. Abbreviations are listed in an Appendix. Scale bars = 1.0 cm (A–F) and 0.5 cm (G–J, L).

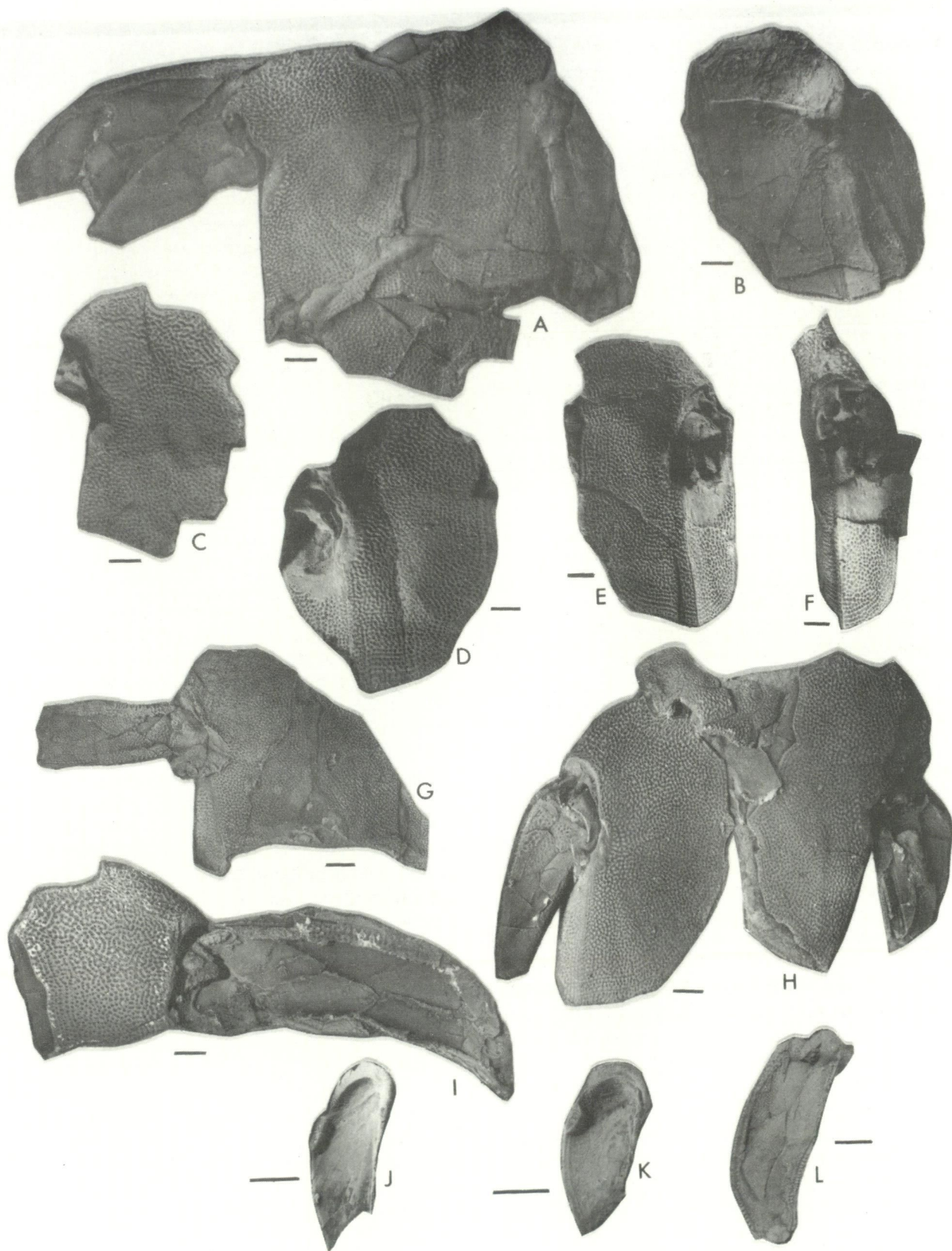


Figure 8 *Bothriolepis longi* sp. nov. A, AM F91434, left and right AVL with attached proximal pectoral fins; B, AM F91411, internal right AVL; C, AM F91419, right AVL, external ventrolateral view; D, AM F61929, right AVL, external ventral view; E, AM F100332, left AVL external lateroventral view; F, AM F100332, left AVL external ventrolateral view; G, AM F91421, left AVL and pectoral fin, external ventral view; H, AM F91436, left and right AVLS and proximal pectoral fins, external ventral view; I, AM F91421, anterior portion of left AVL plus proximal pectoral fin, external ventral view; J, AM F100334, Cd₁ or Cv₁, internal view; K, AM F100321, Cd₁ or Cv₁, internal view; L, AM F100334, proximal portion of pectoral fin preserving Cd₁, Cd₂, ML₂, Mm₂. Scale bars = 0.5 cm except for J-L, where scale bars = 1.0 cm.

of PMD. This pit is connected to a strongly developed *crista transversalis interna posterior* (cr.tp) by a posterior ventral process of the trunk armour (prv₂). The lateral process (prl) is also strongly developed.

The anterior dorsolateral (ADL, Figures 6N–O, 7F) has a strong dorsolateral ridge (dlr) and the lateral lamina is three times as long as wide. The *processus obstans* (pro) is short and rounded, while on the anterior face of the ADL, the *crista transversalis interna anterior* (cit) is large and concave dorsolaterally. The infra-articular crista (cri) and supra-articular crista (crs) are strongly developed, and the articular fossa (f.art) is long and narrow, not expanding laterally.

The ventral lamina of the anterior ventrolateral (AVL, Figures 7G–J, 7L, 8A–I, 9) is widest anteriorly (B/L ratio average = 0.50), narrowing posteriorly. The margin contacting the semilunar plate (m₁) is short, with a straight antero-posterior margin and longer, transverse margin. The various corners of the ventral lamina (c₁₋₅) are distinct. The margin contacting the median ventral plate (m₂) is short, of a typical length for adult *Bothriolepis*. On the lateral lamina of the AVL, the prepectoral corner (prc) is poorly developed, the brachial process (pbr) is helmet-shaped, the protractor area (f.mp) large, triangular, and recessed. The *pars pedalis* (pe) is long, extending from the brachial process mesially or anteromesially, attaching to the AVL well inside the concave articular area for the pectoral fin. The *margo limitans* (m.lim) is sharply developed, and the *fossa articularis pectoralis* (f.ap) is deeply recessed. The axillary foramen (f.ax) is large and rounded, and again of typical size for *Bothriolepis*. A long, narrow unornamented area (a.un) is present on the ventral lamina posteroventral to the brachial process. Internally, a strong *crista transversalis interna anterior* (cit) runs directly transversely.

The posterior ventrolateral (PVL, Figures 6L, 9D) possesses a distinct ventrolateral process (vlp), only slightly curved. The dorsal margin of the lateral lamina rises steeply to the dorsal corner, and the posterior margin is straight. The *crista transversalis interna posterior* (cr.tp) is strong on the ventral lamina, fading on the subanal lamina. The average ratio of the length of the subanal lamina to overall length = 0.37. The mixilateral (MxL) is only well displayed on the holotype (Figure 2). It has a broad dorsal lamina, approximately 2.5 times as broad as ventral lamina height. The median ventral plate (MV, Figures 7I, 9A–B) is approximately 2.4 times long as wide.

Only the proximal section of the pectoral fin is preserved (Figures 7G, 7I–J, 7L, 8A–B, 8G–L, 9A). Measurements on one good example of the dorsal pectoral fin (Figure 8L) give the following L/B ratios: Cd₁, 1.6; Ml₂, 4.2; Mm₂, 2.54. On the proximal

pectoral fin articulation (Figures 7E, 8J–K), the marginal articular area (ar₂) is smooth or striated medially and preserved as a strong ridge. The striated internal articular area (ar₁) is approximately twice as wide as the marginal area. A small, oval thickened area is present laterally for attachment to the opposing plate (a₁). These plates are more elongate than the Cd₁ mentioned above (L/B ratio 2.92 and 2.35), so are assumed to be ventral plates (Cv₁). The Cv₂ and Mm₁ appear to meet at a point on AM F91421 (Figure 7L), excluding overlap between Cv₁ and Mm₂. The plate ornament is nodose to reticulate, while some plates have a stellate pattern.

Remarks

Morphological Variation

There is variation in both morphology and proportions in the available material, but we have assumed for the present that only one species, *Bothriolepis longi*, is represented. The effects of postmortem distortion must be recognized when interpreting proportions of antiarch head and trunk shield plates, and the Nettleton's Creek specimens are both flattened and obliquely distorted. Variation in overall head shield morphology within *B. longi* is exemplified by AM F100356 and AM F100358 (Figure 3A–D) and AM F100357 (Figure 3E,F). In AM F100356 and AM F100358, the head shield is elongate and less rounded anteriorly. The lateral margin of the lateral plate is slightly concave. The orbital fenestra is rounder and the orbital margin of the premedian is more similar in width to the rostral margin (Figure 5C). In AM F100357, the head shield is broader, and the lateral margin of the lateral plate is convex (Figure 5D). The orbital fenestra is more elongate and the rostral margin is distinctly wider than the orbital margin.

The differences between these two morphologies could indicate two closely related species of *Bothriolepis* from Nettleton's Creek, but both types share the large pits on the internal surfaces of the lateral plate, the transverse anterior submarginal attachment, and the multiple posterior submarginal attachments. The last feature is unique to the material, so it is assumed that both head shield types belong to *B. longi*. The differences in proportion may be the result of shearing and distortion in the rocks, and this is clearly evident in the large *Placolepis* plates from the locality (Ritchie 1984, figure 11, A. Ritchie pers. comm. 1997). In this study, qualitative characters such as the nature of the submarginal attachments are preferred to quantitative characters when describing new species.

Bothriolepis longi is thought to be most closely related to the Antarctic taxa *B. macphersoni* and *B. karawaka*, as these taxa possess a strong, transverse

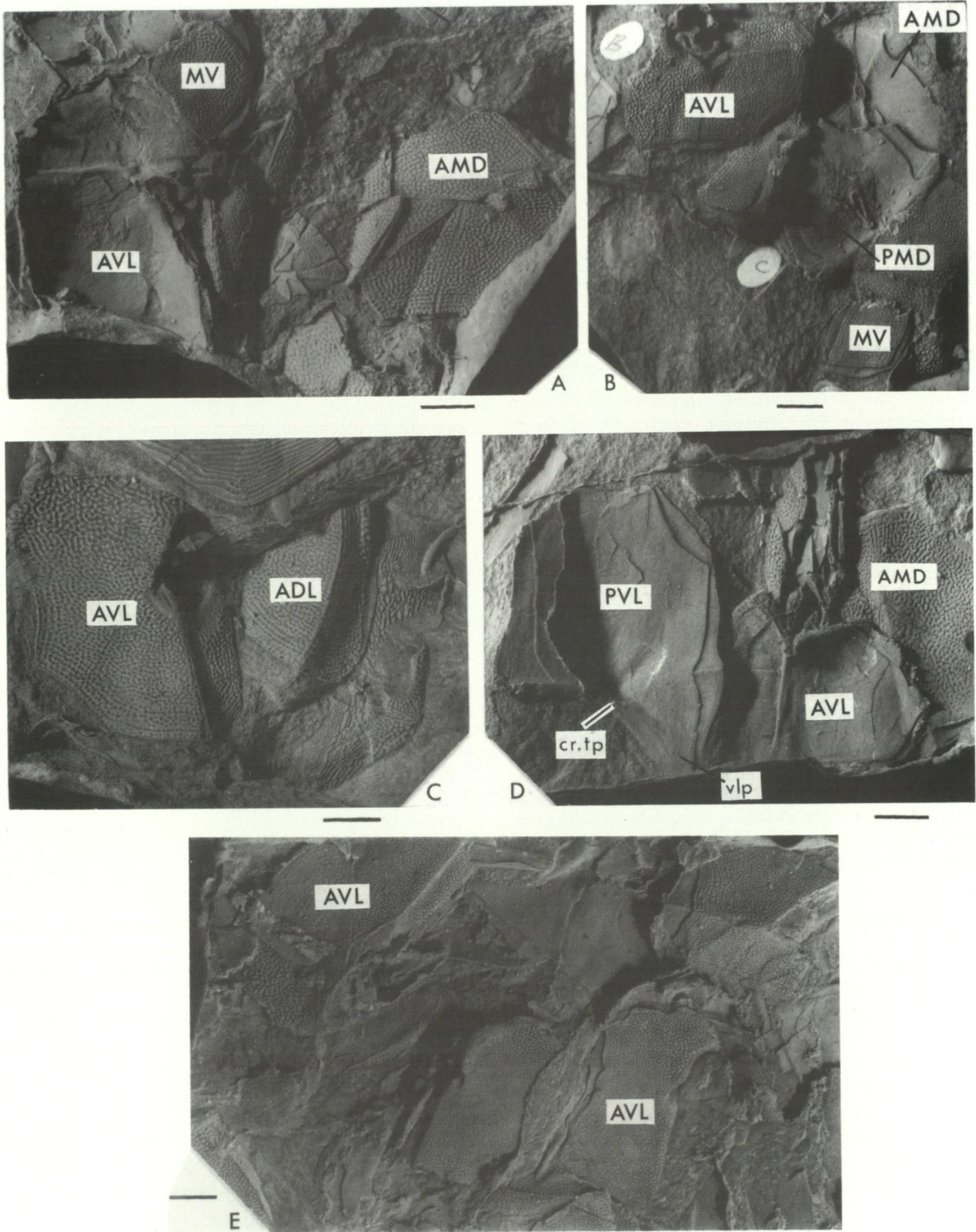


Figure 9 *Bothriolepis longi* sp. nov. A, AM F100312, internal AVL, AM F100311, external MV, AM F100313, external AMD; B, AM F100348, external AVL, AM F100349, internal PMD, AM F100350, internal AMD, AM F100351, external MV; C, AM F100343A, external AVL, AM F100344A, external ADL; D, AM F100346A, internal PVL, AM F100345A, internal AVL, AM F100347A, external AMD; E, AM F91429, left and right external AVL, AM F100352, external AVL. Scale bars = 1.0 cm.

anterior submarginal attachment on the lateral plate, a ventrally oriented prelateral attachment separate from the anterior submarginal attachment, and a transversely oriented *crista transversalis interna anterior*. *B. longi* and *B. karawaka* also share a posterior submarginal attachment that crosses the spiracular opening. However, *B. longi* is similar to several Victorian species (Long 1983, Long and Werdelin 1986) in the possession of a large pit on the internal surface of the lateral plate. These large pits also occur on *B. barretti* and *Bothriolepis* sp. indet. 6 from Antarctica, *Bothriolepis* sp. from the Gogo Formation, Western Australia (Young 1984), the Carnarvon Basin, Western Australia (Munabia Sandstone, Long 1991b), and the Pambula region of New South Wales (Young 1988). *Bothriolepis longi* also shares a semicircular preorbital recess with the Victorian species (among others). This is a plesiomorphic character state for *Bothriolepis* as a whole (Long 1983; Young 1988). *Bothriolepis macphersoni* and *B. karawaka* possess the more derived pentagonal preorbital recess. The phylogenetic relationships of *B. longi* are discussed further below.

Submarginal Articulation and Function

On the submarginal plate of AM F91431 (Figures 3L–M, 4D), there is no indication that the posterior articular process corresponds in length to the articular surface preserved behind the spiracular groove on the lateral plate (right side of Figure 3M). An anterior subdivision of this articulation, lateral to the groove as in the holotype (Figure 4A), cannot be seen in this specimen because of the condition of the preservation. However, assuming it was present, it is difficult to understand how it articulated against the SM, which has a large infrspiracular notch in this position (Figure 4D). With only one submarginal preserved for *Bothriolepis longi*, however, the significance of this is unclear. The function of separate attachment areas on the lateral plate is uncertain, but may indicate the presence of secondary openings connected to the spiracle through the dorsal margin of the gill chamber, as suggested by a distinct notch running between these areas in some examples (Figure 4B–C).

Other features of the submarginal of *Bothriolepis longi* are a flattened, roughened articular area on the middle portion of the ventral surface (Figures 3L–M, 4D), which in *Bothriolepis* sp. from Gogo articulated with an area on the anterior ventrolateral plate of the trunk shield to seal the branchial chamber (Young 1984). The distinct shelf dorsal to this articular area (SM.sh, Figure 4D), delimits the large groove extending to the posterodorsal edge of the submarginal (?op.gr), which may have housed the opercular cartilage as in other placoderms (Young 1986), where it attached to the anterior postorbital process of the

endocranium. However, Young (1986) suggested that in *Bothriolepis* the direct dermal articulation between the submarginal and lateral plates of the head shield indicated that this secondary support was unnecessary, and the opercular cartilage was lost. Furthermore, the groove in *B. longi* is oriented away from the anterior postorbital process of the endocranium, so the contained cartilage could not have articulated against it.

Among other placoderms, the strong ventral shelf on the internal surface of the submarginal in *B. longi* can be compared with that on the submarginal of the arthrodire *Holonema* (Miles 1971, figure 36), while a small groove in *Sherbonaspis hillsi* (Young and Gorter 1981, figure 14) has a similar orientation, as does an elongate groove on the operculum of the lungfish *Uranolophus wyomingensis* (Campbell and Barwick 1987, figure 23). In *Asterolepis scabra* a structure on the internal surface of the submarginal has the opposite orientation (Nilsson 1941, plate 6.1) and is probably not homologous (the contained cartilage attaching to the endocranium). Campbell and Barwick (1987) described the groove in *Uranolophus* as an adductor muscle scar for the opercular, and we also suggest that the groove in *B. longi* may have been for muscle attachment, functioning in movement of the submarginal, to close the gill chamber. This groove was much larger relative to the submarginal than in *Uranolophus*, suggesting powerful muscle action. Rapid closure of the submarginal would forcefully eject water, perhaps to clear sediment from the gill chamber.

DISCUSSION

Phylogenetic Position of Bothriolepis longi

This discussion of the phylogenetic position of *Bothriolepis longi* focuses on relationships to other species from East Gondwana, where direct comparisons of morphological features have been possible. Cladograms for species of *Bothriolepis* have previously been proposed by Long (1983) and Young (1988). A modified version of the cladogram of Young (1988) is reproduced in Figure 10 as a basis for discussion, although a full revision of the phylogeny of *Bothriolepis* species is beyond the scope of this paper. Taxa included in the cladogram, except for *B. longi* and *B. africana* (Long *et al.* 1997), are those from Young (1988). Additional comparisons are made below to *Bothriolepis* spp. from Western Australia, the Pambula region of NSW and from Antarctica. Major clades previously recognized are labelled here A–D for ease of discussion, but none of these should be regarded as strongly supported. Seventeen synapomorphies were proposed on the original cladogram, but only those relevant to this study are considered here (characters 1–12). Three possible phylogenetic

positions for *B. longi* discussed below are indicated by the large stars on this cladogram (Figure 10). Comparisons to Antarctic Aztec Siltstone species are made with reference to the zones proposed by Young (1988) which, from older to younger, are as follows: *askinae*, *kohni*, *portalensis*, *karawaka*, *Pambulaspis*, and *phyllolepid*.

Clade A: *Bothriolepis longi* possesses a large pit on the internal surface of the lateral plate (character 1), the synapomorphy of clade A previously proposed by Young (1988). The species in this clade are entirely Gondwanan, including Victorian species (Long 1983; Long and Werdelin 1986) and *B. barretti* from the *karawaka* zone of the Aztec Siltstone fauna (Young 1988). Other taxa with large lateral pits include *Bothriolepis* spp. from the Canning (Gogo Formation, Young 1984) and Carnarvon (Munabia Sandstone, Long 1991b) Basins, as well as an undescribed species from the Pambula region of New South Wales and *Bothriolepis* sp. indet. 6 from the Aztec fauna (Young 1988). *B. africana* from South Africa (Long *et al.* 1997) and *B. barretti* share a trilobate preorbital recess (character 2), although the lateral corners are more rounded in *B. africana*, and this species lacks a large pit on the internal lateral plate (Long *et al.* 1997). All species of *Bothriolepis* from the Northern Hemisphere (e.g., clades C and D, Figure 10) have smaller or insignificant pits (Stensiö 1948; Miles 1968; Pan *et al.* 1980, 1987).

Bothriolepis longi is believed to possess a semicircular preorbital recess, as do most taxa in clade A. This type of recess, considered to be plesiomorphic for *Bothriolepis* (Long 1983; Young 1988), also occurs in *Bothriolepis* sp. from the Munabia Sandstone, *B. askinae* from the lowermost *askinae* zone of the Aztec Siltstone, and various Northern Hemisphere species (e.g. *Bothriolepis canadensis*). Derived preorbital recess morphologies include trilobate (character 2), pentagonal (character 7) and trifold (character 5, clade C).

Bothriolepis longi differs from other species in clade A in various detailed morphological characters: the postpineal possesses a convex anterior border that extends into the orbital fenestra, but this is less pronounced than in Victorian bothriolepids like *B. cullodenensis* (Long 1983). The anterior postorbital processes of the otico-occipital depression in *B. longi* do not generally extend beyond the anterior edge of the orbital fenestra, as in *B. gippslandiensis* and *B. cullodenensis* (Long and Werdelin 1986). The anterior postorbital processes of the otico-occipital extend beyond the orbital fenestra in most other species of *Bothriolepis*. Additionally, both *B. cullodenensis* (Long and Werdelin 1986) and *B. portalensis* (*portalensis* zone, Young 1988) have a well-developed median ridge on the internal surface of the premedian; this ridge is absent in *B. longi*. The posterior submarginal attachment of *Bothriolepis longi* is

subdivided into two or three separate portions, an autapomorphy for this species, although a similar condition may be present in a juvenile specimen of *B. gippslandiensis* (Long and Werdelin 1986).

Clade B: This clade was proposed by Young (1988) using a single synapomorphy, the point contact between the Cv_1 , Mm_2 , Mm_1 and Cv_2 of the pectoral fin (character 3, Figure 10). This may also be observed for *B. longi*, based on a single specimen, AM F91421 (Figures 7K,L, 8G). *B. gippslandiensis* and *B. karawaka* (*karawaka* and *Pambulaspis* zones, Young 1988) show a longer contact between the Mm_2 and Cv_1 plates. This state also occurs in *B. askinae* (Young 1988), a species that forms a sister group to all other *Bothriolepis* in the cladogram of Young (1988), and in *Monarolepis verrucosa* (Young and Gorter 1981; Young 1988). This suggests that it is a plesiomorphic character for *Bothriolepis*.

Clade D: *Bothriolepis longi* resembles taxa in clade D in possessing a strong transverse, shelf-like anterior submarginal attachment on the internal surface of the lateral plate, just anterior to the spiracular groove (character 4, Figure 10). By comparison, Victorian taxa in clade A and *Bothriolepis* sp. from the Munabia Sandstone possess a short anterior submarginal attachment forming a triangular rather than a shelf-like area. *Bothriolepis* sp. from Gogo (Young 1984) possesses a circular anterior submarginal attachment.

Bothriolepis longi is distinctive in having an oval attachment area for the prelateral plate separate from the anterior submarginal attachment and oriented ventrally within the prelateral notch. Among Antarctic species in clade D, *B. karawaka* and *B. macphersoni* (*Pambulaspis* zone, Young 1988) also have a ventrally-oriented prelateral attachment separate from the anterior submarginal attachment, but this attachment is triangular in shape. In *B. portalensis*, the prelateral attachment is oval and also separate from the anterior submarginal attachment but is directed laterally and can be seen in dorsal view (Young 1988). Other species of *Bothriolepis* have confluent prelateral and anterior submarginal attachments, for example *Bothriolepis* sp. from Gogo and several Northern Hemisphere species (e.g. *B. paradoxa* [Miles 1968]; *B. canadensis* [Stensiö 1948, Young 1988]; *B. cellulosa*, *B. groenlandica* [Stensiö 1948]). These latter species occur in clades B, C, and D.

In *Bothriolepis longi*, the anteriormost part of the posterior submarginal attachment extends forward to cover the lateral edge of the spiracular groove, as in *B. karawaka* (clade D, character 9) and *Bothriolepis* sp. from Gogo. In *B. karawaka* (AM F56334), the attachment covers approximately two-thirds of the groove; the groove is nearly completely covered in *B. longi* and *Bothriolepis* sp. from Gogo. In *B. macphersoni* (clade D), the attachment does not appear to enter the spiracular groove.

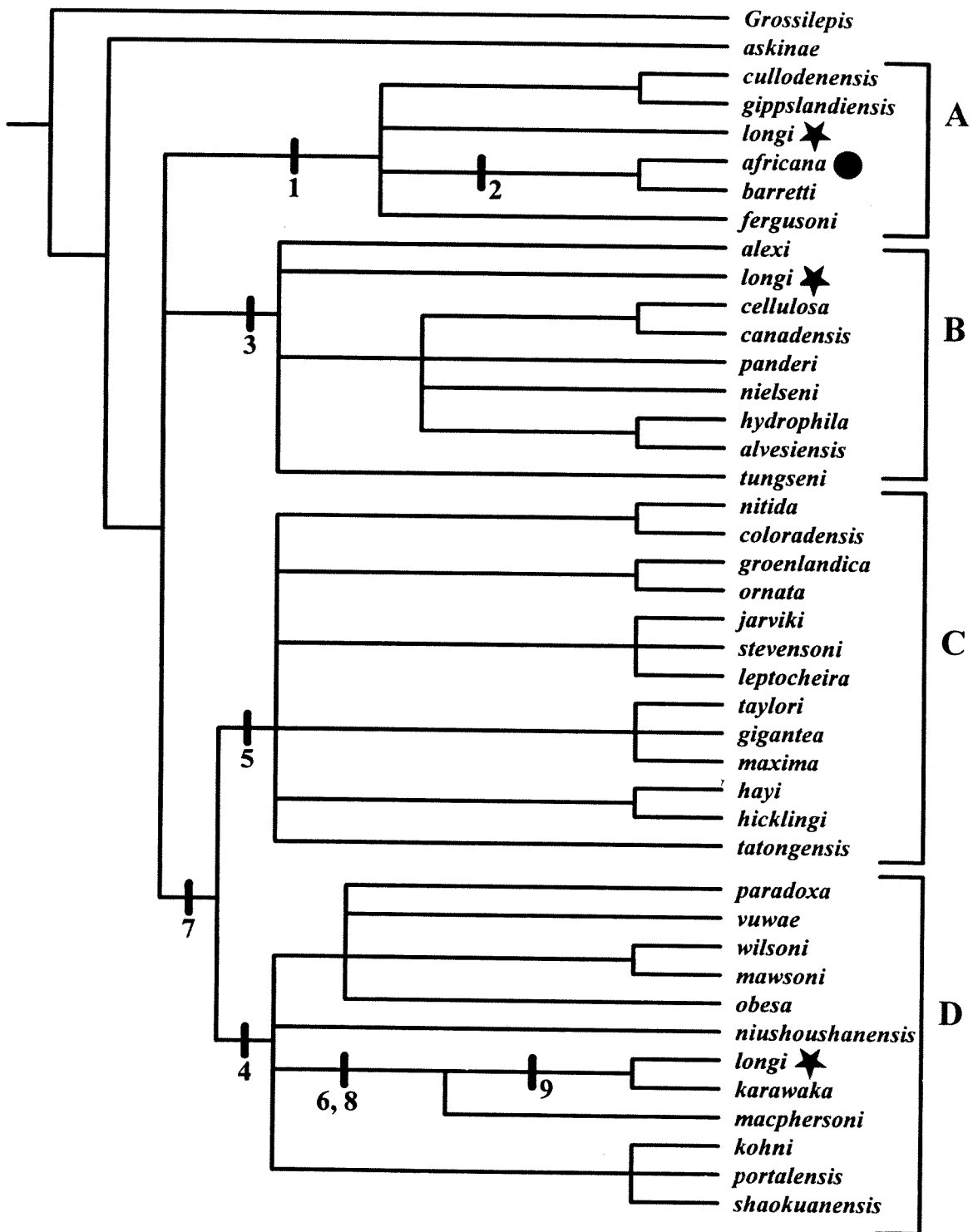


Figure 10 Cladogram adapted from Young (1988) showing phylogenetic relationships of various species of *Bothriolepis*. Clades A-D are discussed in the text. Large stars mark the position of *B. longi* sp. nov., indicating its various positions on the cladogram. Circle marks the position of *B. africana*, a South African species closely related to *B. barretti*. Synapomorphies 1-9 are as follows: 1, enlarged lateral pit (d); 2, trilobate prelateral recess (e, also occurring on *Bothriolepis* sp. from the Harijica fauna, central Australia); 3, point contact between Cv_1 , Cv_2 , Mm_1 and Mm_2 (h); 4, anterior submarginal attachment on lateral plate a transverse ridge (j); 5, trifid preorbital recess (r); 6, *crista transversalis interna* anterior transversely oriented on ventral lamina of AVL (n); 7, pentagonal preorbital recess (i); 8, separate ventrally facing attachment surface for the prelateral on the lateral plate (m); 9, anterior portion of posterior submarginal attachment covers spiracular groove (also present in *Bothriolepis* sp. from the Gogo Formation, Western Australia). Letters in parentheses indicate corresponding characters from Young (1988).

The internal surface of the AVL of *B. longi* has a very strong *crista transversalis interna anterior* that runs transversely and mesially from just below the brachial process to nearly the edge of the AVL, a feature that also occurs in the Antarctic species *B. macphersoni* and *B. karawaka* (character 6). The AVL is not well known in Victorian species and has been figured only for *B. cullodenensis* (Long and Werdelin 1986), where the *crista transversalis interna anterior* is also transverse.

As noted above, a full revision of the phylogeny of *Bothriolepis* species is beyond the scope of this paper, and we have reproduced the cladogram of Figure 10 only as a basis for discussion. We emphasize that none of the major clades is considered to be strongly supported. However, provisionally accepting that the broad framework is valid, the new species *B. longi* can have only one position in this phylogenetic scheme. We suggest that available evidence is best explained by the position in clade D; i.e. we hypothesize that *B. longi* is most closely related to the Antarctic taxa *B. macphersoni* and *B. karawaka*, sharing a combination of three characters: a transverse ridge-like anterior submarginal attachment for the submarginal on the lateral plate (character 4); a ventrally-oriented prelateral attachment on the lateral plate, separate from the anterior submarginal attachment (character 8); *crista transversalis interna anterior* transversely oriented on the ventral lamina of the anterior ventrolateral plate (character 6). *Bothriolepis longi* and *B. karawaka* also share a posterior attachment of the submarginal extending across the spiracular opening (character 9).

The implications of this proposal are that *B. longi* does not belong in clades A or B, either because the morphological evidence is suspect, or because those clades are not monophyletic groups. It was suggested above that character 3 (point contact between plates of proximal pectoral fin) may be a synapomorphy, in which case clade B would be

monophyletic; however, we suggest paraphyly may be the case for clade A, for which the proposed synapomorphy is large lateral pits on the lateral plate. This feature occurs in forms with several different preorbital recess shapes. Assuming large lateral pits also to be primitive for the genus, we can propose that *B. longi* retains two primitive features not relevant to its phylogenetic placement (semicircular preorbital recess; large lateral pits), and otherwise is immediately related to the Antarctic species *B. macphersoni* and *B. karawaka* on the evidence just discussed. A suggested alternative scheme of relationships for some of the better-known taxa within clade D which have been accessible to us for morphological comparison, is given in Figure 11. The main significance of this alternative is that the pentagonal recess (character 7) would emerge as a specialization in its own right, rather than an intermediate condition between simple and trifid recesses as implied by the scheme of Young (1988). Under this interpretation some characters (e.g., character 9) would need to be reassessed as homoplasies, if the pentagonal recess of *B. karawaka* and *B. macphersoni* (and other species where known) is used as a synapomorphy. Another implication of this alternative is that *B. shaokuanensis* Chang, 1963, from South China, is the only species within this clade that does not come from East Gondwana. A second species, *B. niushouhanensis* from North China (Pan *et al.* 1980) was said to have a pentagonal recess (Young 1988: 110), but this is questionable.

BIOSTRATIGRAPHY AND CORRELATION

Comparisons of known *Bothriolepis* species from eastern and western Australia and the Antarctic Aztec Siltstone indicate many morphological similarities that suggest a close biogeographic and biostratigraphic relationship between these areas (see above).

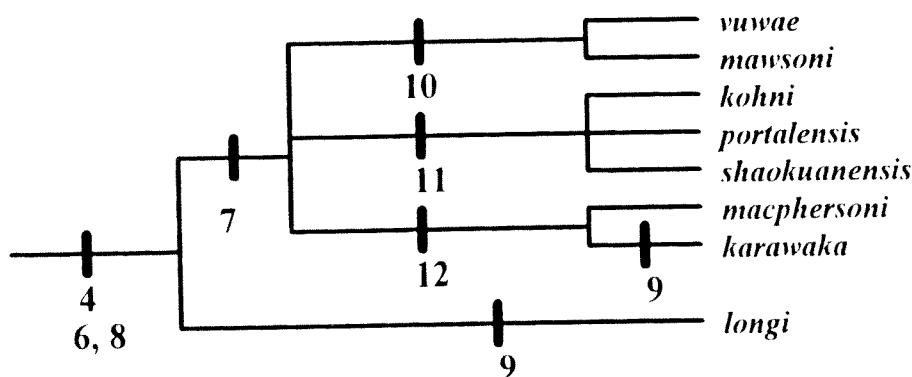


Figure 11 Alternative phylogenetic scheme for clade D of Figure 10. Additional synapomorphies from Young (1988) are as follows: 10, squarish Nu with convex anterior division of the lateral margin and short posterolateral corners (p); 11, elongation of the preorbital region of the skull (l); 12, thickened bone edges on orbital corners of PrM and L plates (o). Letters in parentheses indicate corresponding characters from Young (1988).

However, these characters have a sporadic distribution, both on a phylogenetic scheme (Figures 10, 11), and in relation to stratigraphic position within zonations based on vertebrates (e.g. the Antarctic Aztec sequence). This indicates that the fossil record of *Bothriolepis* species from East Gondwana is still too incomplete to reliably base stratigraphic correlations on specific morphological characters. It is also important to interpret such characters in a phylogenetic framework before they are assigned any biostratigraphic significance. For example, both *B. longi* and *B. askinae* have a simple preorbital recess, but the former occurs in association with the phyllolepid *Placolepis*, in a horizon dated as Frasnian. *Bothriolepis askinae* occurs in presumed older horizons in the Aztec sequence, and phyllolepid is only known in association with other *Bothriolepis* species in the upper parts of the sequence (but see below). The conflicting stratigraphic evidence of this resemblance is consistent with the assumption that it is a symplesiomorphy (see above).

Nevertheless, some new data arising from this study may clarify certain problems of correlation. The vertebrate zonation for the Aztec Siltstone, as developed and elaborated by Young (1988, 1993, 1995) and Long and Young (1995), recognizes six zones, five of which are characterized by antiarch species (*Bothriolepis* spp.) or genera (*Pambulaspis*). However, the upper and lower boundaries of the Aztec sequence are not well constrained (Young 1993). Young (1988) noted that phyllolepid placoderms were present in the majority of Middle-Late Devonian fish assemblages from southeastern Australia containing *Bothriolepis*, but were known only from the uppermost beds of the Aztec sequence. This suggested that the lower Aztec beds, which contain several *Bothriolepis* species associated with the thelodont *Turinina antarctica*, were older than the *Bothriolepis* assemblages of southeastern Australia, none of which are associated with thelodont scales.

Amongst the Middle-Late Devonian macro-vertebrate faunas of southeastern Australia there are at least two assemblages which are reasonably well known, and apparently lack phyllolepid: the *Wuttagoonaspis* fauna of western NSW (Ritchie 1973), and the Hatchery Creek fauna of the Burrinjuck area (Young and Gorter 1981). Both of these also contain turiniid thelodonts. In the Carnarvon Basin thelodonts occur in the ?late Givetian-early Frasnian Gneudna Formation (Turner and Dring 1981), associated in this case with remains of *Bothriolepis* (J.A. Long pers. comm. 1997, 1998). It might be assumed therefore that this association is older than the lower occurrence of phyllolepid, but phyllolepid has not yet been recorded from any locality in the Devonian of Western Australia.

In the Antarctic Aztec sequence, phyllolepid is common only in the upper horizons (e.g. Long and Young 1995, figure 2), but further collecting by J.A. Long has demonstrated that they occur lower in the sequence than originally assessed by Young (1988). Phyllolepid is recorded from 'fish hotel site B' in the Cook Mountains, associated with the sharks *Aztecodus*, *Anareodus* and *Portalodus* (Long and Young 1995: 299). This assemblage is assigned to the *karawaka* zone (Long and Young 1995, figure 2). Possible phyllolepid fragments have also been identified with turiniid thelodonts in the lowermost beds of sections in the Lashly Range (J.A. Long, pers. comm. 1997), but this association needs to be confirmed with better material.

For the present, the range of phyllolepid is confirmed to extend downward through the next two zones beneath the 'phyllolepid zone' originally recognized by Young (1988). Generic assignment of this Antarctic phyllolepid is uncertain, and it has not yet been described; previously the material was provisionally attributed to *Austrophyllolepis* (Young 1993, 1995), but validity of this genus has now been questioned (A. Ritchie, pers. comm. 1996).

Bothriolepis longi occurs in the Nettleton's Creek fauna, where the phyllolepid placoderm *Placolepis budawangensis* is also abundantly represented. This fauna was assigned an early Frasnian age by Ritchie (1984). Long (1984, figure 27) and Young (1987, figure 5) proposed that *Placolepis* was a relatively primitive phyllolepid. Similarly, *B. longi*, as described above, exhibits a range of primitive morphological features for the genus, but with some evidence of close relationship to species from the *karawaka* zone of the Aztec sequence. As noted above, this zone is the lowest in the Aztec sequence where phyllolepid is confirmed. Using this evidence for correlation implies either that the Nettleton's Creek fauna is somewhat older than previously assessed, or alternatively that the Aztec sequence is younger than its most recent age assignment (early-mid Givetian on the chart of Young 1995). We have no evidence to resolve these alternatives at present, but taxonomic study of phyllolepid from the many localities in southeastern Australia and Antarctica, whence they remain undescribed, should help clarify an older age limit to the appearance of this group.

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APPENDIX

Abbreviations Used

ADL	anterior dorsolateral plate	d	dorsal margin of SO
AMD	anterior median dorsal plate	d.end	endolymphatic ducts
AVL	anterior ventrolateral plate	dlg	oblique dorsal sensory line groove
a ₁	area on lateral margin of proximal pectoral fin plate for articulation with opposing plate	dln	dorsal lamina of ADL
a ₃	thickened area on the proximal plate of the pectoral fin for attachment to opposing plate	dlr	dorsolateral ridge of trunk shield
a ₁ SM	anterior attachment area for SM	dma	tergal angle of AMD
a ₂ SM	posterior attachment area for SM	dmr	dorsomedial ridge of trunk shield
a.AVL	attachment for AVL on SM	f.ap	<i>fossa articularis pectoralis</i>
ad _{1,2}	anterior and posterior articular processes on SM	f.art	articular fossa
alr	postlevator thickening of AMD	f.ax	axillary foramen
a.PrL	attachment area for PrL	fe.orb	orbital fenestra
ar ₁	internal articular area on proximal plate of pectoral fin	fe.sorb	suborbital fenestra
ar ₂	marginal articular area on proximal plate of pectoral fin	fm	insertion fossa for levator muscles
ar ₃ d	external articular area of Cd ₁	f.mp	protractor area of brachial process
ar ₃ v	external articular area of Cv ₁	f.retr	levator fossa of AMD
a.un	unornamented area on AVL	g	pit on PP
Cd ₁	dorsal central plate of pectoral fin	grm	ventral median groove on internal wall of trunk shield
Cv _{1,2}	ventral central plates of pectoral fin	head	head shield
c _{1,2,4,5}	corners between margins of AVL	ifc ₁	principal section of infraorbital sensory line
cf.ADL	area overlapping ADL on AMD	ifc ₂	branch of infraorbital sensory line on L
cf.AMD	area overlapping AMD on PMD	ifc ₃	branch of infraorbital sensory line on SO
cf.AVL	area overlapping AVL on opposite AVL	L	lateral plate
cf.MxL	area overlapping MxL on PMD	l	lateral corner of PMD
cir	semicircular pitline groove	lc	lateral corner of AMD
cit	<i>crista transversalis interna anterior</i>	lcg	main lateral line groove
cr _{1,2}	prelateral, postlateral crista of spiracular groove	llm	lateral lamina of ADL
cri	infraarticular crista of ADL	ML ₂	lateral marginal plate 2
cro	median occipital crista of Nu	Mm _{1,2}	mesial marginal plate 1, 2
cr.pl	postlevator crista on AMD	MV	median ventral plate
cr.pto	postorbital crista of head shield	m _{1,2,4,5}	margins of AVL
crs	supra-articular crista of ADL	m ₃	margin of AVL overlapping MV
cr.tp	<i>crista transversalis interna posterior</i>	m.lim	<i>margo limitans</i>
cr.tv	transverse nuchal crista of Nu	mr	median ridge of PP
csl	central sensory line groove	mvr	median ventral ridge
		MxL	mixilateral plate
		Nu	nuchal
		n	notch separating anterior processes on SO
		n.inf	infraspicular notch
		nm	obtected nuchal area of head shield
		npl	postlevator notch

n.Prl	prelateral notch	pr.pl	postlevator process
oa.AMD	area on ADL overlapped by AMD	pr.po	anterior postorbital process
oa.AVL	area on MV overlapped by AVL	prv ₂	posterior ventral process of dorsal wall of trunk armour
oa.MxL	area on AMD overlapped by MxL	pt ₁	anterior ventral pit of dorsal wall of trunk armour
oa.PMD	area on AMD overlapped by PMD	pt ₂	posterior ventral pit of dorsal wall of trunk armour
oa.PVL	area on MV overlapped by PVL	PVL	posterior ventrolateral plate
obm	orbital facet of Nu	rdg	ridge separating ornamented from biting portion of SM
ood	otico-occipital depression of head shield	SM	submarginal plate
?op.gr	opercular cartilage groove on internal surface of SM	SO	suborbital plate
P	pineal plate	SM.sh	shelf on internal surface of submarginal plate
PM	postmarginal plate	scl	sclerotic ossicle
PMD	posterior median dorsal plate	soc	anterior section of supraorbital sensory line on PrM
PNu	paranuchal plate	socc	supraoccipital cross-commissural pitline groove.
PP	postpineal plate	sot	supraotic thickening
PrL	prelateral plate	spg	spiracular groove
PrM	premedian plate	tb	ventral tuberosity on internal surface of AMD or PMD
p	pit on internal surface of L plate	vlp	ventrolateral process of PVL
pbr	brachial process	vlr	ventrolateral ridge
pcl	posterolateral corner of AMD		
pe	<i>pars pedalis</i>		
pnt	paranuchal trochlea		
prc	prepectoral corner		
prh	preorbital recess		
prl	lateral process on PMD		
pro	<i>processus obstans</i>		