

NEW BOTHRIOLEPID FISH FROM THE LATE DEVONIAN OF VICTORIA, AUSTRALIA

by J. A. LONG

ABSTRACT. *Bothriolepis gippslandiensis* Hills and four new species (*B. cullodenensis*, *B. fergusonii*, *B. bindareei*, and *B. warreni*) are defined, and synoptic descriptions of their atypical features given. Bothriolepid faunas of Victoria permit biostratigraphic correlation between the Cerberean Volcanics (Taggerty) and the dominantly sedimentary Mt. Howitt Province (Mt. Howitt, Freestone Creek). Radiometric dates, palynological evidence, and the absence of *Remigolepis*, a characteristic Famennian form in the faunas of New South Wales, indicates a Frasnian age for the Victorian faunas. Interrelationships of antiarchs suggest that the bothriolepidoids and asterolepidoids are sister groups. The presence of large lateral pits on the headshield, cristate short armour, ventrolateral scales on the tail, and a primitive pectoral appendage place the Victorian species *B. gippslandiensis*, *B. cullodenensis*, and possibly *B. fergusonii* as the sister group to most other bothriolepids. A revised classification of antiarchs is proposed which places the sinolepids in the new suborder, Sinolepidoidei. The suborder Bothriolepidoidei contains two families: Bothriolepididae Miles and the new family Dianolepididae.

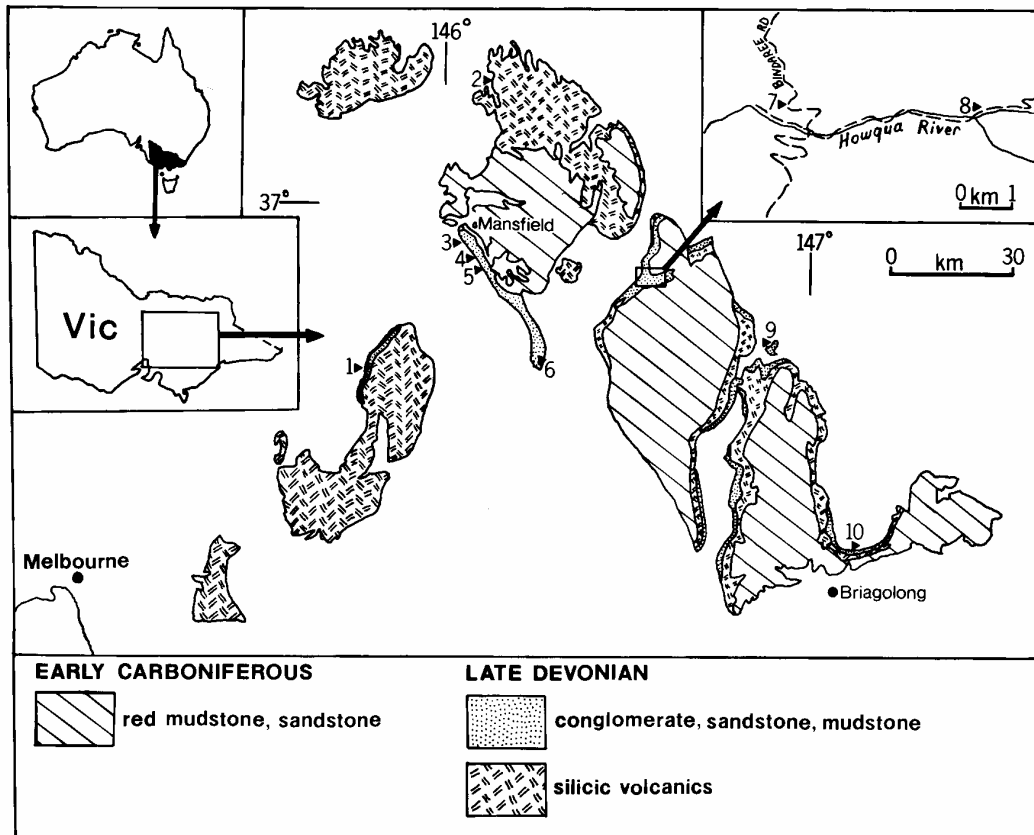
THE aberrant antiarch *Bothriolepis* is known from over fifty described species of nearly world-wide distribution. New finds of *Bothriolepis* in Victoria show that some species differ significantly from the standard bothriolepid morphology which has been well documented by several workers (Stensiö 1931, 1948; Miles 1968; Karatajute-Talimaa 1966; Denison 1941, 1951). The published record of antiarchs in Australia is scant compared to the amount of collected material. Hills first recorded *Bothriolepis* in Australia in 1929 and subsequently published a series of papers updating descriptions and records of Late Devonian fish faunas (Hills 1929, 1931, 1932, 1936, 1958, 1959). Gilbert-Tomlinson (1968) described fragmentary remains of *Bothriolepis* from the Amadeus Basin, central Australia, but was unable to make a specific determination in this case. Gardiner and Miles (1976) record the genus from the marine carbonates of the Gogo Formation, West Australia, and Young (in Ferguson *et al.* 1979) briefly described bothriolepids from near Eden, New South Wales. Young and Gorter (1981) described a new *Bothriolepis* from the Middle Devonian near Canberra.

This paper outlines the geological settings and phylogenetic significance of the new species of *Bothriolepis* from the Late Devonian of Victoria. Lengthy systematic descriptions, necessary for biostratigraphic use, will be published separately in the Memoirs of the National Museum of Victoria. Synoptic descriptions are given in the species definitions with unusual morphological features described briefly in the subsequent section.

Specimens prefixed with NMV are housed in the palaeontological collections of the National Museum of Victoria, those preceded by MUGD are kept in the Geology Department of Melbourne University.

LOCALITIES AND FAUNAL LISTS

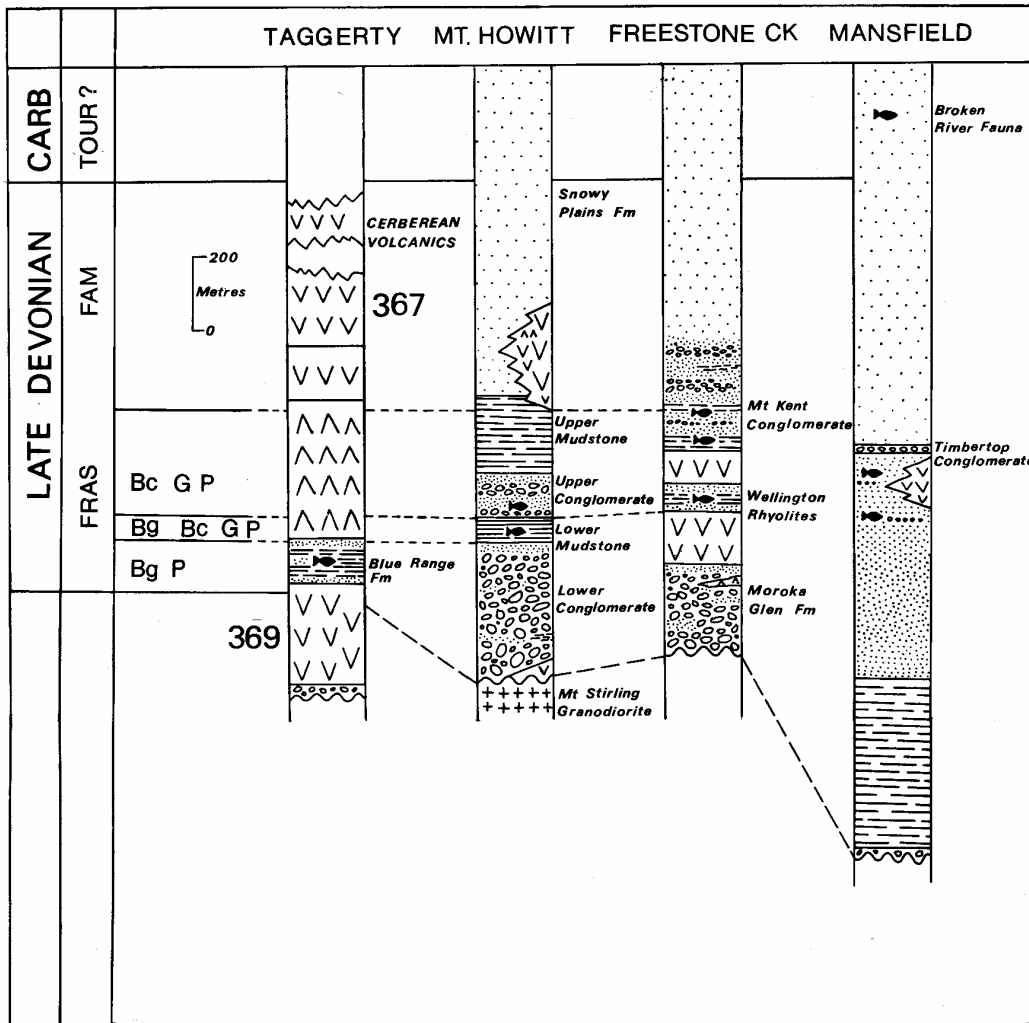
Text-fig. 1 shows a map of the major Late Devonian fish localities in Victoria. The Mt. Howitt Spur fish site was discovered in the early 1970s and subsequent excavations have yielded hundreds of well preserved, entire fish. The deposit comprises finely varved black anaerobic shales with minor silts and sands indicative of a lacustrine environment (Marsden 1976; Long 1982). The Bindaree Road site was discovered in 1980 and is situated stratigraphically above the main fish beds at Mt. Howitt. This site is of great interest in being geologically younger than the Mt. Howitt fossiliferous shales while containing a fauna identical to that of the Freestone Creek sites.



TEXT-FIG. 1. Locality map for Late Devonian fish sites in Victoria. Generalized geology from the 1:1 000 000 Victorian Geology mapsheet (Department of Minerals and Energy, Melbourne). 1. Blue Hills, near Taggerty. 2. Tatong. 3. Amphitheatre ridge, South Blue Range. 4. SEC transmission line cutting, South Blue Range. 5. Delatite River. 6. Jamieson Road cutting. 7. Bindaree Road cutting. 8. Mt. Howitt Spur. 9. Snowy Bluff. 10. Freestone Creek localities. Sites 4–6 and 9 were recently discovered and their faunas have not yet been studied in detail. These sites are not discussed in the text.

Stratigraphical and faunal relationships of the Late Devonian fish bearing successions in Victoria are shown in text-fig. 2. The geological settings of these localities are outlined in Marsden (1976) with a discussion of taphonomy in Long (1982). Faunal lists for these sites given by Marsden (1976, p. 122) have been extended by recent collecting (Long, in press).

Hills (1931) records *Bothriolepis gippslandiensis* Hills from Freestone Creek, and Talent (1975) based correlations upon this identification. Hills, however, studied a limited collection of quite small fish plates from this region, being much smaller than the average sized plates from Taggerty. Large headshields and trunkplates from several sites in the Freestone Creek region indicate that *B. gippslandiensis* is not present in the faunas from the Wellington Rhyolite sediments or the basal section of the Mt. Kent Conglomerate. Instead, the new species *B. cullodenensis* and *B. warreni* are present. New material from Taggerty has clarified the cranial morphology of *B. gippslandiensis* enabling identification of the species at Mt. Howitt. A large number of specimens from Mt. Howitt show *B. gippslandiensis* in all stages of growth. This clarifies the misconceptions concerning the



TEXT-FIG. 2. Biostratigraphic correlation of Late Devonian sequences in Victoria. Radiometric dates from Williams *et. al.* (1983). Geology from Marsden 1976. Bc. *Bothriolepis cullodenensis* n. sp. Bg. *B. gippslandiensis* Hills. G. *Groenlandaspis*. P. *Phyllolepis*.

Freestone Creek fossils and permits the species to be determined even from juvenile material. The suggested presence of *Remigolepis* (by Stensiö, in Hills 1932, p. 855) at Taggerty is based on a single mixilateral plate. Young (1974, p. 254) has questioned this identification and there is no doubt that the specimen (MUGD 1886) is attributable to *B. gippslandiensis* by means of its ornamentation and proportions.

FAUNAL LISTS

Mt. Howitt Spur

- Placoderms *Bothriolepis gippslandiensis*, *B. cullodenensis* n. sp., *B. fergusonii* n. sp., *Phyllolepis* sp., *Groenlandaspis*, sp.

Mt. Howitt Spur (*cont.*)

- Acanthodians at least three forms have been recognized, all probably belonging to the family Acanthodiiformes (Marsden 1976, p. 122).
 Dipnoans two forms occur, both short snouted (*ibid.*).
 Crossopterygians an osteolepid crossopterygian is present.
 Palaeoniscids at least one type of palaeoniscid is present which has both cheirolepid and stegotrachelid affinities.

Bindaree Road

- Placoderms *Bothriolepis culloidenensis* n. sp., *B. bindareei* n. sp., *B. warreni* n. sp., *Groenlandaspis* sp., *Phyllolepis* sp.
 Others isolated dipnoan scales, an acanthodian fin spine, isolated palaeoniscid bones.

Freestone Creek

- Placoderms *Bothriolepis culloidenensis* n. sp., *B. warreni* n. sp., *Bothriolepis* sp. indet., *Groenlandaspis* sp., *Phyllolepis* sp.
 Others *Striacanthus sicaeformis* (Hills 1931). Dipnoan and crossopterygian (osteolepid?) scales. Isolated palaeoniscid dermal bones.

Blue Hills, Taggerty

- Placoderms *Bothriolepis gippslandiensis*, *Phyllolepis*, sp.
 Others The dipnoan *Dipterus* (*Eoctenodus* Hills 1929).

South Blue Range, Mansfield

- Placoderms *Bothriolepis* sp., *Phyllolepis* sp. (Hills 1936), *Groenlandaspis* sp.

Tatong

- Indeterminable placoderm fragments, including a bothriolepidoid pectoral appendage bone.

Genoa River

- Bothriolepis* sp. (Professor J. Warren, pers. comm.); crossopterygians, amphibian footprints (Warren and Wakefield 1972).

Mt. Tambo

- A small tuberculated fish plate (Marsden, 1976, p. 122).

BIOSTRATIGRAPHY AND THE AGE OF FAUNAS

The Late Devonian freshwater fish faunas of Victoria can be subdivided into three relative age categories using the entry and disappearance of key placoderm taxa, as shown in text-fig. 2.

The Taggerty Fauna contains *Bothriolepis gippslandiensis* and *Phyllolepis* sp., both of which occur at Mt. Howitt. Radiometric dates above and below the fish bearing strata at Taggerty indicate an early Frasnian age (Richards and Singleton 1981; Williams *et al.* 1983). The absence of characteristic Famennian forms such as *Groenlandaspis* and *Remigolepis* supports the older age assessment. Young (1974) reviewed the age ranges of biostratigraphically useful placoderms and places the Australian entry of *Groenlandaspis* and *Remigolepis* close to the Frasnian Famennian boundary. *Phyllolepis*, a Famennian zone fossil in European successions (Bendix-Almgreen 1976; Denison 1978, p. 42), occurs in the Frasnian Boyd Volcanic Complex (Fergusson *et al.* 1979, p. 103) and at Braidwood, where the fish fossils underlie a marine intercalation of at least Frasnian age (Dr A. Ritchie, pers. comm.).

The Mt. Howitt Fauna is regarded as Frasnian by Marsden (1976) on comparison with the dipnoans from Escuminac Bay, Canada. The presence of *B. gippslandiensis* and a similar form of *Phyllolepis* from this locality and Taggerty indicates the close age affinity of these faunas. The presence of *Groenlandaspis* at Mt Howitt suggests that this fauna is slightly younger than the Taggerty Fauna, possibly still within the Frasnian if the exclusion of *Remigolepis* is considered. The

entry of *B. cullogenensis* with *B. gippslandiensis* at Mt. Howitt is an important event which permits correlation with the Freestone Creek Fauna over 80 km to the south-east. Talant (1975, in Boucot) gives a Frasnian age to the Freestone Creek Fauna on palynological data.

The Bindaree Road Fauna is found within the Upper Conglomerate unit (Marsden, 1976) stratigraphically superpositioned on the Mt. Howitt Fauna. The disappearance of *B. gippslandiensis* with the abundance of high crested *B. cullogenensis* makes this fauna identical to that of Freestone Creek. *Phyllolepis* and *Groenlandaspis* occur in both these faunas although specific identifications have not yet been clarified.

The absence of *Remigolepis* from the Victorian faunas indicates that either they are all Frasnian in age or that the genus did not extend its range far enough to reach the state. The appearance of *Groenlandaspis* may be earlier in this state than indicated by Young (1974), preceding *Remigolepis*, and if the age proximity of the Taggerty and Mt. Howitt Faunas is correct, a Frasnian appearance of *Groenlandaspis* is most probable. *Groenlandaspis* have been recorded from the Middle Devonian of Mt. Grenfell, western New South Wales (Dr. A. Ritchie, pers. comm.), suggesting an even earlier entry for the genus.

The South Blue Range Fauna is believed to be contemporary with the Mt. Howitt and Freestone Creek Faunas on the common presence of *Bothriolepis* sp., *Phyllolepis* sp., and *Groenlandaspis* sp. Further collecting from this site is necessary for more accurate age assessment to be made. Comparisons with the volcanics from this succession with the Toombullup Rhyodacite in the Tolmie Igneous Complex indicates that the fish bearing horizon would be younger than the Givetian age obtained on the Tolmie volcanics (Richards and Singleton 1981; Dr. John Clemens,¹ pers. comm. concerning the petrographical and geochemical similarities between the igneous rocks). This reinforces the Frasnian age assessment for the Victorian faunas discussed above.

Fragmentary placoderm remains collected from the basal conglomerates in the Tolmie Igneous Complex (Brown 1961) are inferred to be Givetian age from the radiometric dates on the volcanics higher in the sequence (Richards and Singleton 1981). Re-examination of this material has turned up a bothriolepidoid pectoral appendage bone. Absence of the characteristic ornament of *Phyllolepis* supports the early age assigned to this site, yet on the paucity of the present collection it would be unethical to make statements concerning faunal correlations.

The Genoa River and Mt. Tambo fish sites do not have large enough faunas at this stage to make age assessments. Warren and Wakefield (1972) have compared the red mudstone succession of the Genoa River Beds to the similar lithologies occurring around Eden, although only Late Devonian age status was assigned.

Correlations with the Middle and Late Devonian fish faunas of New South Wales are shown in text-fig. 3, incorporating all relevant radiometric dates and marine invertebrate faunas. The present age ranges of the placoderms discussed above are shown in text-fig. 4, modified from Young (1974).

SYSTEMATIC PALAEOLOGY

The following species will be described in detail in a separate paper as this work is primarily of local interest for its use in biostratigraphy. Synoptic descriptions are presented here in the species definition. Plate measurements are taken from points designated in Stensiö (1948, pp. 11-16). External measurements refer to the dimensions of a plate as seen in the articulated armour hence excluding overlap areas.

Genus *BOTHRIOLEPIS* Eichwald 1840, designated by Woodward 1891

Type species. Bothriolepis ornata Eichwald.

Diagnosis. See Young and Gorter 1981, p. 93.

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		VICTORIA	N.S.W.	VIC.	N.S.W.
CARB.	Tour.?	★Mansfield NO PLACODERMS			
LATE DEVONIAN	Fam.		★Woranga Point ¹ □▲		?
	Fras.	★Freestone Ck. ○□□ ★Bindaree Road ○□□ ★Mt Howitt ●○□□ 367 ★Taggerty ●● _{max 373}	★Canowindra ³ △□▲ ★Jemalong ³ △□□▲ ② -363 ¹ ★Braidwood △■ ★Eden, Pambula ¹ △■	?? B. gipps ● B. cull ○ Phyll ■ Groen □	?? Groen □ Remig ▲ ?
MID. DEV.	Giv.	★Tatong △? 384 Mt Stirling Granodiorite 381	★Bunga Beach -381 ¹	B. gipps ● Phyll ■	Phyll ■
	Eif.		★Hatchery Ck. ² ②		Both. spp. ▲

TEXT-FIG. 3. Correlation between Devonian fish faunas from Victoria and New South Wales. 1. Fergusson *et al.* 1979. 2. Young and Gorter, 1981. 3. Campbell and Bell 1977. Marine invertebrate horizons are discussed in the above references.

Bothriolepis gippslandiensis Hills 1929

Plate 42, fig. 10; text-figs. 5, 6, 8, 9, 12, 13

- 1929 *Bothriolepis gippslandiensis* Hills, pp. 195-197, text-fig. 2, p. 118, fig. 8.
 1931 *Bothriolepis gippslandiensis* Hills, pp. 214-222, text figs. 5, 7, plate 11, figs. 1-6.
 1932 *Remigolepis* sp. Hills, p. 855.
 1948 *Bothriolepis gippslandiensis* Stensiö, pp. 74, 77, 516-521, text-figs. 264, 265.
 1968 *Bothriolepis gippslandiensis* Gilbert-Tomlinson, pp. 191, 193, 199, 206, 209.
 1969b *Hillsaspis gippslandiensis* Stensiö, pp. 515, 516, 669, text-fig. 210D.
 1978 *Hillsaspis gippslandiensis* Denison, pp. 109, 111, 112, text-fig. 86D, G.
 1981 *Bothriolepis gippslandiensis* Young and Gorter, p. 93.

Diagnosis. A *Bothriolepis* with a maximum mid-dorsal armour length of about 170 mm. Anterior median dorsal and posterior median dorsal plates bear a well-developed, smooth median dorsal crest which is higher on the posterior median dorsal plate. Trunkshield broad and moderately high vaulted, the dorsal walls enclosing an angle of at least 90° and meeting the lateral walls at 120-130°. Headshield weakly vaulted with a breadth/length index around 135 or 145-160 for flattened specimens. Postpineal plate is symmetrical about a transverse plane through the lateral corners in maturity. Orbital fenestra broad and short, the length being under half the breadth. Lateral pits on the ventral surface of the headshield are large but shallow. Anterior median dorsal plate having an anterior breadth around 1.2 times the extent of the posterior margin. Anterior dorsolateral plate square with a dorsal lamina having an external height/length index around 60. Pectoral appendages

		Greenland ¹	Scotland ²	USSR ³	China ⁴	Australia ⁵
CARB	Tour					
LATE DEV	Fam	B P R G	B P ?R G	P		R
	Fras		B	B	A R	P G
MID DEV	Giv	A	A	A	B	B ?A
	Eif					
Early DEV	Ems					

TEXT-FIG. 4. Age ranges of biostratigraphically useful placoderms. 1. Bendix-Almgreen 1976. 2. Miles 1968. 3. Young 1974. 4. P'an Kiang 1981. 5. Young 1974; Campbell and Bell 1977.

broad, the proximal segment having a breadth/length index up to 30 and being about 1.5 times the length of the distal segment. Central ventral plate 2 has short contact with the mesial marginal plate 2. Tail has two rows of large ventrolateral scales with minute dermal denticles covering the flanks. A single dorsal fin is preceded by an anterior fin spine. Ornament of coarse, short blunt ridges with tubercles developed prominently on the headshield and lateral laminae.

Holotype. This is a small juvenile headshield collected from the Blue Hills, near Taggerty by Hills (Hills 1929, pp. 195-197, plate xviii, fig. 8). MUGD 776. Figured in Young and Gorter 1981, plate 2, fig. 3.

Material studied. The original material collected by Hills from Taggerty (Hills 1929, 1931); new material from the Mt. Howitt site collected by Professor J. Warren and Dr. M. Marsden; new material collected from Taggerty by the writer and friends. A complete listing of specimens will be published in another paper dealing with the detailed systematics.

Remarks. This species was first recorded from Taggerty in 1929 and later recognized from the Freestone Creek area (Hills 1931). The material studied by Hills from the latter site consisted entirely of small trunkshield and rare headshield plates belonging to a population of juveniles. This is ascertained by the reticulate ornament and juvenile state of the sensory canal system (Stensiö 1948, pp. 211-212). Recent additions to the Freestone Creek collection have shown that the mature plates from this site are all referable to at least two new species *B. cullodenensis* and *B. warreni*. The presence of *B. gippslandiensis* has not been confirmed from this region.

Stensiö (1969b, p. 515) erected the new genus *Hillsaspis* for *B. gippslandiensis* because of the nuchal plate not participating in the orbital fenestra. Recently Young and Gorter (1981, p. 93) re-examined the holotype and found orbital facets to be present on the nuchal plate, demonstrating the condition

which is usual for *Bothriolepis*. The well-preserved Mt. Howitt specimens confirm this observation for the species in all stages of growth. Although this species and other new species described below differ from *B. canadensis* in the structure of the tail, it would be confusing to alter the generic status of those species on this character alone, as this feature is very rarely preserved on other species. In the relative shapes and sizes of the dermal plates, *B. gippslandiensis* resembled other species and is here retained within the genus.

B. gippslandiensis is distinguished from all other species of *Bothriolepis* by having a broad headshield with large, shallow lateral pits and a broad, short orbital fenestra; a broad, laterally symmetric postpineal plate; and bearing a smooth median dorsal crest on the relatively high trunkshield.

Bothriolepis cullodenensis sp. nov.

Plate 42, figs. 4, 6, 8, 9, 11; text-figs. 5, 6, 9, 13

1931 *Bothriolepis gippslandiensis* Hills, p. 220, fig. 7, no. 3.

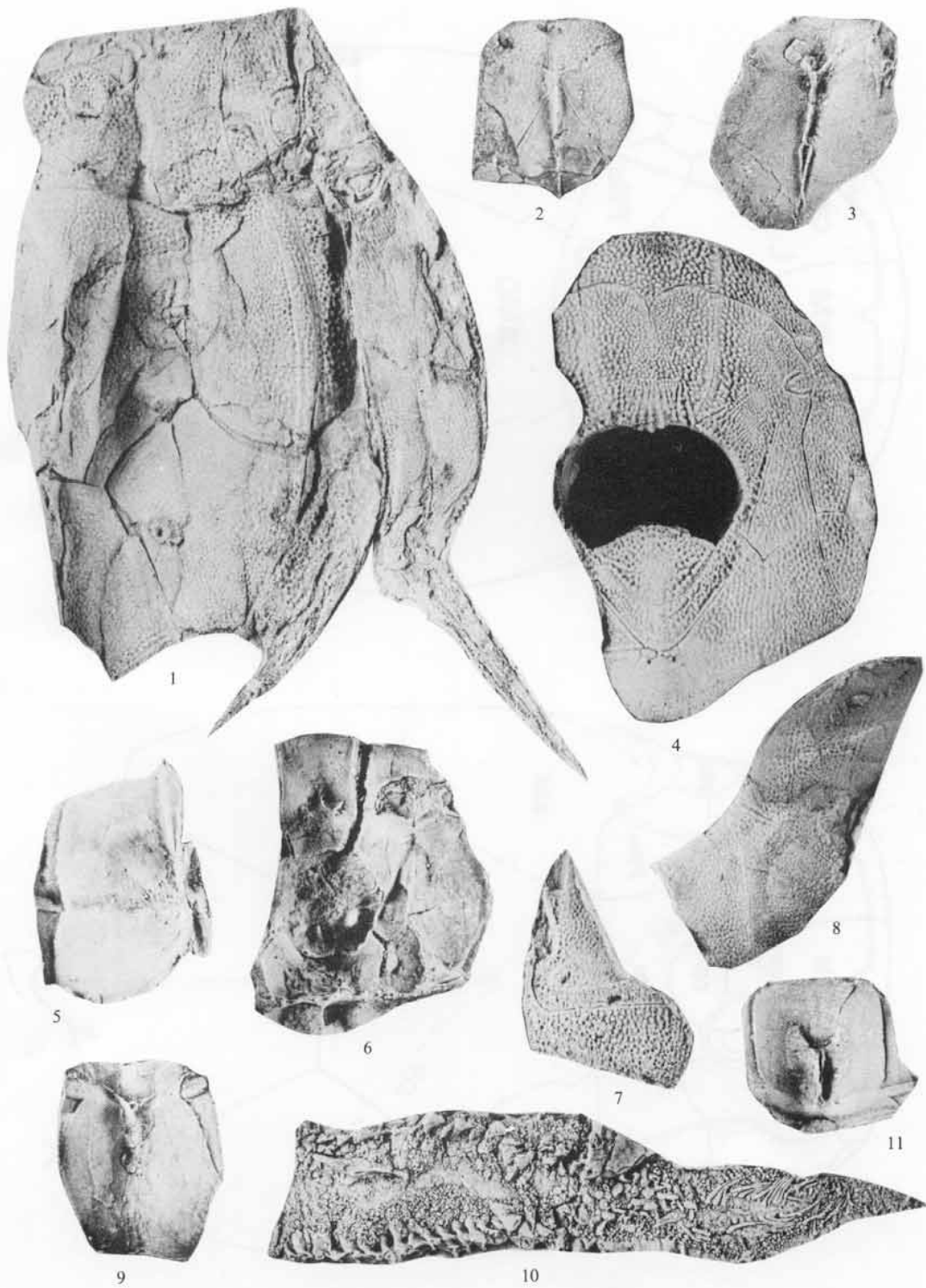
Derivation of Name. From the town of Culloden, 7 km north of Briagolong where the fossils are found. The name was coined by Mr. P. Kenley of the Victorian Mines Department, who collected and informally described material from the region.

Diagnosis. A cristate *Bothriolepis* reaching an estimated dorsal armour length of at least 200 mm. Trunkshield moderately high vaulted with the dorsal walls enclosing an angle of 90° and meeting the lateral walls at 125°. The headshield is elongate, having an external breadth/length index of 100–118 or 120–138 when flattened in a plane. Orbital fenestra large. Ventral surface of the headshield characterized by possessing large, deep lateral pits and paired premedian pits separated by a prominent vertical ridge. Premedian plate narrow, rectangular in shape. Anterior median dorsal and posterior median dorsal plates bear a well-developed median dorsal crest which may extend as high as the anterior median dorsal plate is long and may be serrated along the posterior edge. The anterior median dorsal plate bears a prominent ventral lamina formed by the merging postlevator cristae. The posterior median dorsal plate bears a semicircular ridge anterior to the narrow posterior ventral pit, and has well-developed lateral processes. Mixilateral plate with a strongly convex external ventral margin. Anterior ventrolateral and posterior ventrolateral plates with high lateral laminae, up to 0.6 times the plate length in height. Posterior ventrolateral plate with a well-marked posteromesial angle. Pectoral fin having the central ventral plate 2 contacting the mesial marginal plate 2, as in *B. gippslandiensis*. Tail of similar structure to *B. gippslandiensis*. Ornamentation of short linear ridges and tubercles, often forming a concentric grid-like pattern.

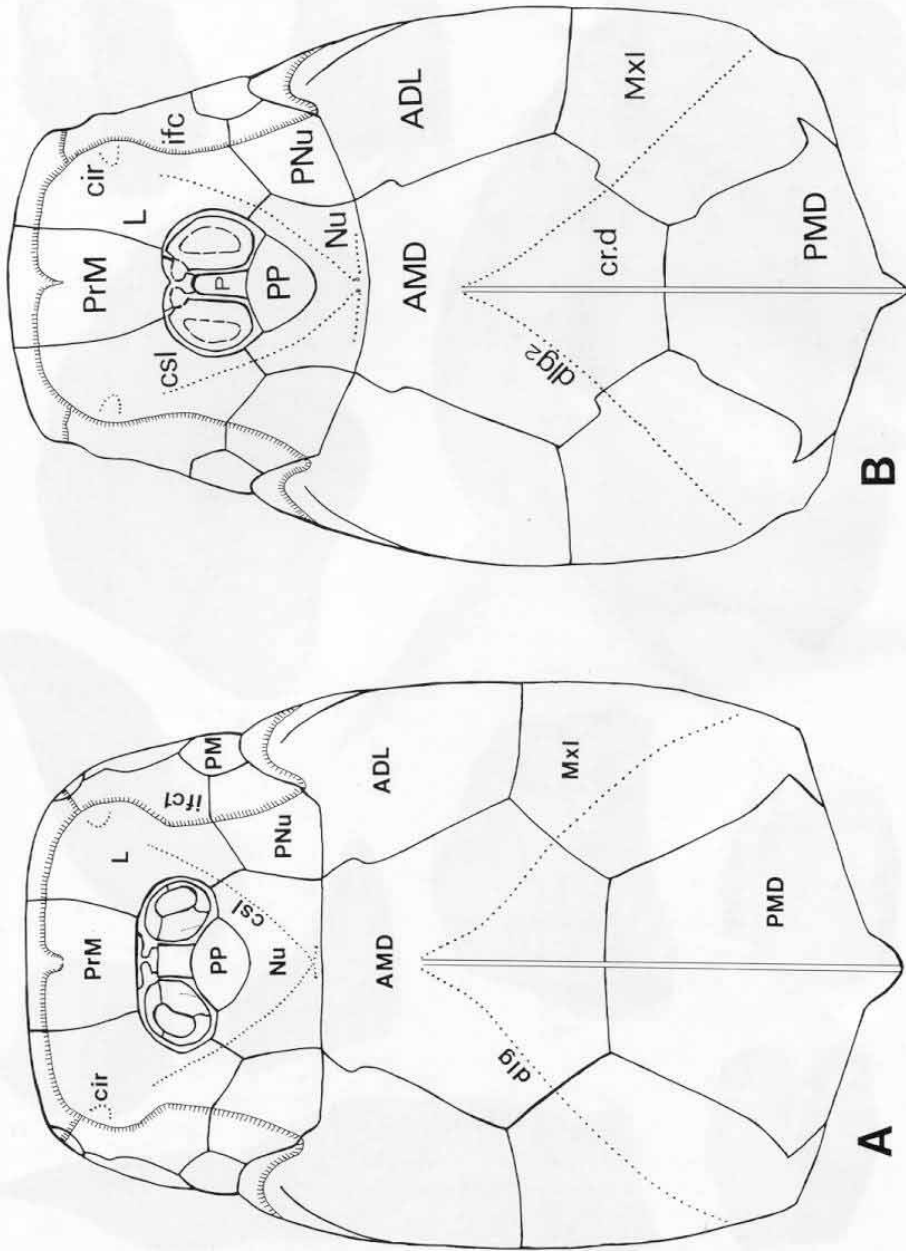
Holotype. A large near complete headshield from the upper Freestone Creek locality. NMV P31296.

EXPLANATION OF PLATE 42

- Fig. 1. *Bothriolepis fergusonii* sp. nov. Holotype, almost complete armour in dorsal view, × 1. NMV P157152.
 Figs. 2, 3. *B. warreni* sp. nov. 2. Holotype, anterior median dorsal plate in dorsal view. NMV P158767. × 2.
 3. Anterior median dorsal plate in ventral view. NMV P158770. × 2.
 Figs. 4, 6, 8, 9, 11. *B. cullodenensis* sp. nov. 4. Holotype, headshield in dorsal view. NMV P31296. × 1.
 6. Headshield in ventral view. NMV P157226. × 1. 8. Anterior median dorsal plate in dorsolateral view. NMV P158764. × 2. 9. Anterior median dorsal plate in ventral view. NMV P158765. × 1. 11. Posterior median dorsal plate in ventral view. NMV P157207. × 1.
 Figs. 5, 7. *B. bindareei* sp. nov. Holotype, anterior dorsolateral plate, internal (5) and external (7) aspects. NMV P157195. × 2.
 Fig. 10. *B. gippslandiensis* Hills tail. NMV P157149. × 1. P157152, P157149 from Mt. Howitt. P158767 from the lower site at Freestone Creek. P31296, P157226, P158764, P158765, P157207 from the upper site at Freestone Creek. P158770, P157195 from the Bindaree Road locality. All latex casts whitened with ammonium chloride sublimate.



LONG, Victorian bothriolepids



TEXT-FIG. 5. Restoration of armours in dorsal view. A. *Bothriolepis gippstandiensis* Hills. B. *B. culodenensis* sp. nov. Natural size.

Material studied. Entire articulated specimens and incomplete specimens from Mt. Howitt; isolated plates and semi-articulated specimens from Bindaree Road; isolated plates and articulated headshields from Freestone Creek.

Remarks. Two varieties are found within this species, distinguished only by the relative height and shape of the median dorsal crest, and their stratigraphic positions. From the lower Mt. Howitt Spur site all specimens bear a low, smooth crest and in the topmost horizons the crest is high and posteriorly serrated. Specimens from the Bindaree Road and Freestone Creek localities all bear a high crest in maturity. Aside from this difference the two varieties are morphologically identical and hence regarded as conspecific. It is highly probable that a continuum of crest heights is exhibited by the species with the younger forms being selective for a higher crest. Alternatively crest height could reflect sexual dimorphism, though more material is necessary before any quantitative analysis of this hypothesis could be attempted.

Bothriolepis cullodenensis is distinguished from all other species of *Bothriolepis* by the long, narrow headshield with the large orbital fenestra; possessing large, deep lateral pits and paired premedian pits on the visceral surface; by the well-developed high median dorsal crest; and by possessing a crescentic transverse ridge on the visceral surface of the posterior median dorsal plate.

Bothriolepis fergusonii sp. nov.

Plate 42, fig. 1; text-figs. 7, 13

Derivation of name. After the geologist W. M. Ferguson who not only found fish remains in the Grampians (Ferguson 1917) but also collected material from Freestone Creek (Ferguson 1937).

Diagnosis. A *Bothriolepis* with a mid-dorsal armour length of at least 120 mm, probably much larger. Trunk armour low and narrow with a slight median dorsal crest developed, dorsal and lateral walls meeting at about 100°. Headshield broad, arched both rostrocaudally and transversely, with a short preorbital division. Preorbital recess semilunar with the floor extending well beneath the broad orbital fenestra. Premedian plate broad with a breadth/length index close to 100. Nuchal plate having an external length/breadth index around 80. Anterior median dorsal plate with a flat breadth/length index around 96, the anterior margin being 1.8 times the extent of the posterior margin. Posterior median dorsal plate slightly smaller than the anterior median dorsal plate, lacking lateral processes. Anterior dorsolateral plate having a dorsal lamina under half as high as long, forming a strongly curved external suture with the mixilateral plate. Pectoral appendage slender with noticeable incurvature; the distal segment is striated. Ornament of variable coarseness, changing from a finely reticulate pattern to coarser ridges on a single plate.

Holotype. An almost complete individual, lacking the preorbital division of the headshield. NMV P157152.

Material studied. All from Mt. Howitt, five specimens.

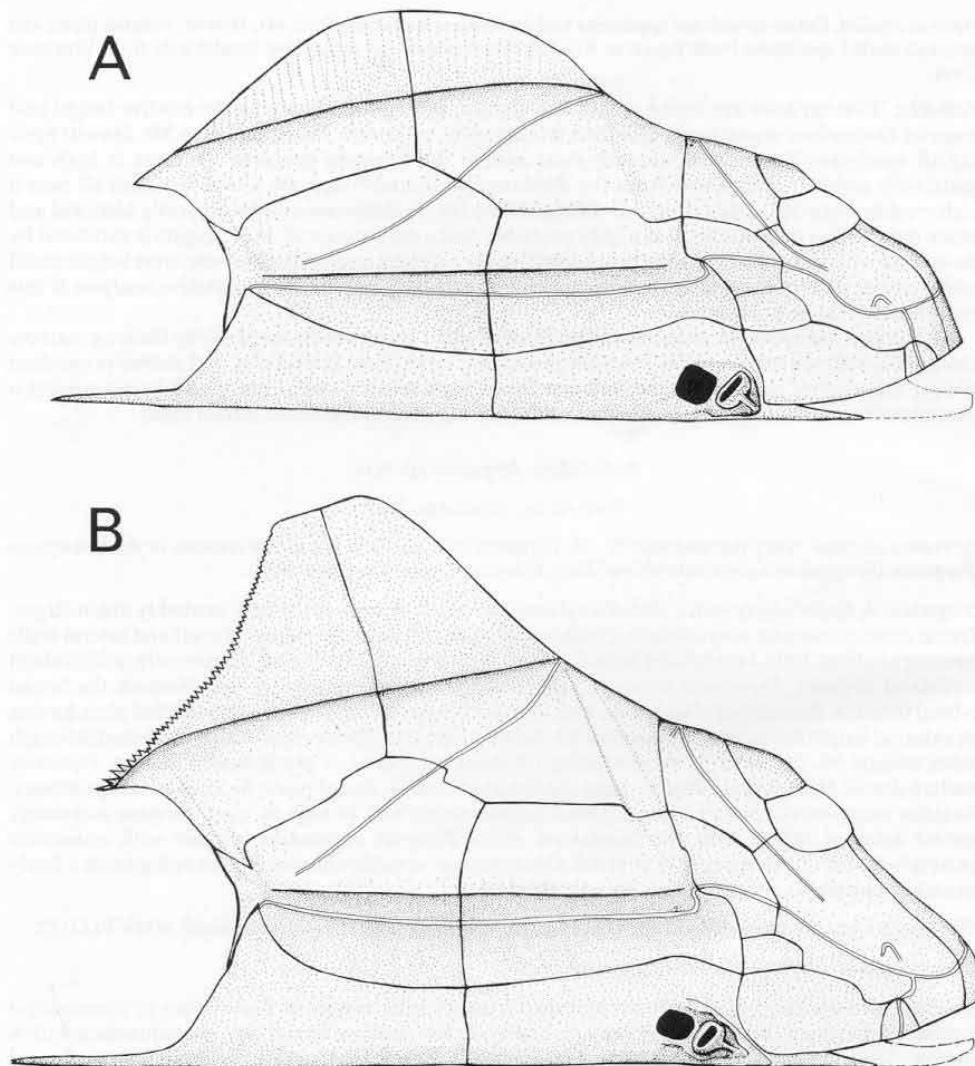
Remarks. *Bothriolepis fergusonii* is distinguished from all other species of *Bothriolepis* by possessing a headshield having a broad orbital fenestra, and large but shallow lateral pits in conjunction with a narrow, long trunkshield having an anterior median dorsal plate which is broad anteriorly and narrow posteriorly.

Bothriolepis bindareei sp. nov.

Plate 42, figs. 5, 7.

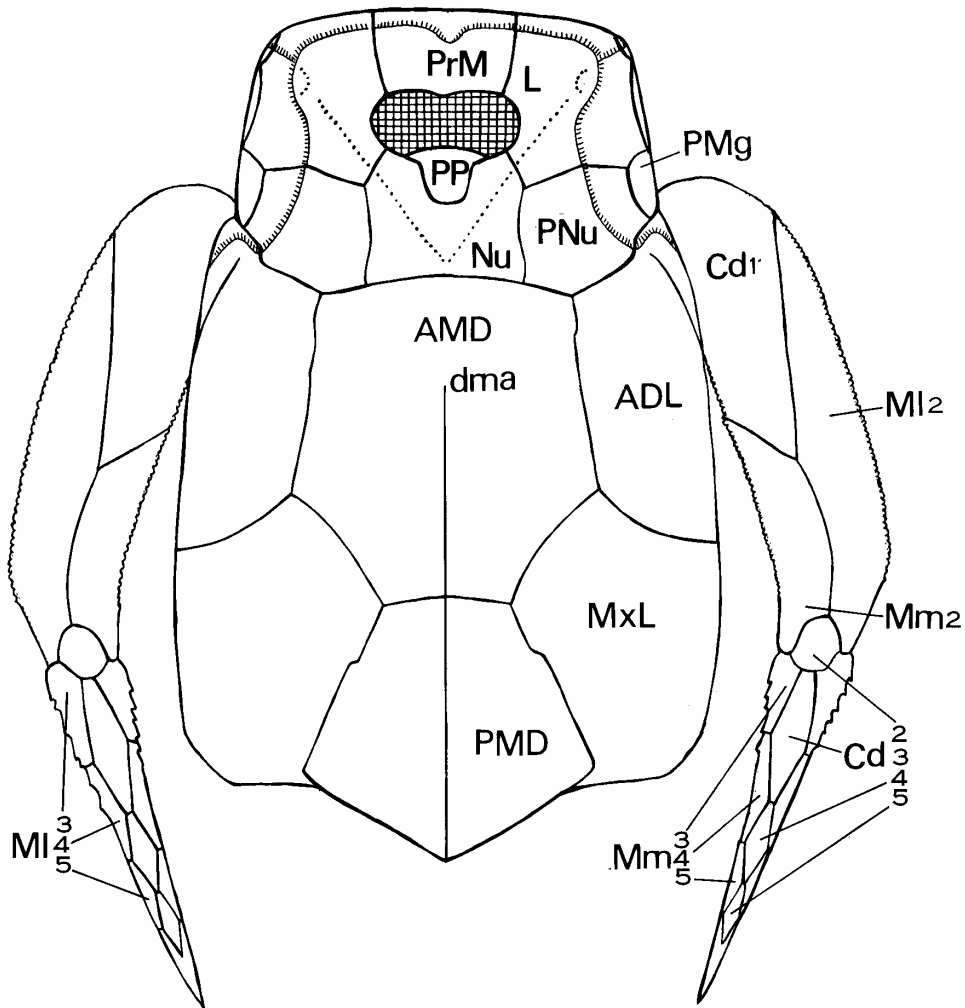
Derivation of name. From the Bindaree Road cutting, second bend up from the junction of the Howqua River track, where the specimens were found. 'Bindaree' is Aboriginal for river which also coincides with the shallow stream environment the species inhabited.

Diagnosis. A *Bothriolepis* with an estimated maximum dorsal armour length of 60 mm. Nuchal plate has an external length/breadth index of 65 and is broadest across the anterolateral corners.



TEXT-FIG. 6. Restoration of armours in lateral view. A. *Bothriolepis gippslandiensis* Hills. B. *B. cullodenensis* sp. nov. Natural size.

Trunkshield short and high. The anterior dorsolateral plate is broader than long, having a breadth/length index of 135. The mixilateral plate is of similar proportions to the anterior dorsolateral plate, the dorsal lamina being equally as high as long. Dorsal and lateral laminae meet at 135° . Posterior ventrolateral plate with a lateral lamina having a height/length index around 75. Ornamentation tubercular on the lateral lamina, being reticulate with tubercular swellings at nodes on the dorsal surface.



TEXT-FIG. 7. *Bothriolepis fergusoni* sp. nov. Restoration of armour in dorsal view. About half natural size.

Holotype. An almost complete anterior dorsolateral plate from the Bindaree Road cutting. NMV P157195.

Material studied. Five isolated plates from Bindaree Road.

Remarks. A new species, *B. bindareei*, is proposed for a few plates displaying proportions quite different from any other known species of the genus. It is retained within the genus *Bothriolepis* because of the anterior dorsolateral, mixilateral, and posterior ventrolateral plates being of proportionate size relative to each other for the genus, and because the nuchal plate bears orbital facets.

Bothriolepis warreni sp. nov.

Plate 42, figs. 2, 3

Derivation of name. After Professor J. W. Warren (Zoology, Monash).

Diagnosis. A *Bothriolepis* with an estimated mid-dorsal length of the trunkshield reaching at least 35 mm. Lateral plate having a breadth/length index close to 80, lacking lateral pits. Trunkshield fairly flat with the dorsal walls enclosing an angle of about 140° at the tergal angle and meeting the lateral walls at 90°. Median dorsal ridge developed as a raised keel. Anterior median dorsal plate having a breadth/length index close to 85 with a short posterior margin. Posterior median dorsal plate having a breadth/length index around 140, with well-developed lateral processes. Mixilateral plate narrow, the dorsal lamina having an estimated breadth/length index of 36, the lateral lamina having a height/length index around 30. Ornament of radiating isolated tubercles on the dorsal surfaces, being sparser or absent on the lateral walls.

Holotype. The almost complete dorsal impression of an anterior median dorsal plate, from the lower site at Freestone Creek. NMV P158767.

Material studied. Ten isolated plates.

Remarks. This species resembles *B. verrucosa* (Young and Gorter 1981) in possessing ornamentation of isolated tubercles, but is distinguished from that species by the absence of the transverse crescentic ridge and stronger development of the median ventral ridge and groove on the anterior median dorsal plate, and by the proportions of the posterior medial dorsal plate. The tubercles of *B. verrucosa* are seen to be coarser and more densely packed around the centres of ossification than for *B. warreni*.

UNUSUAL MORPHOLOGICAL FEATURES OF THE VICTORIAN BOTHRIOLEPIDS

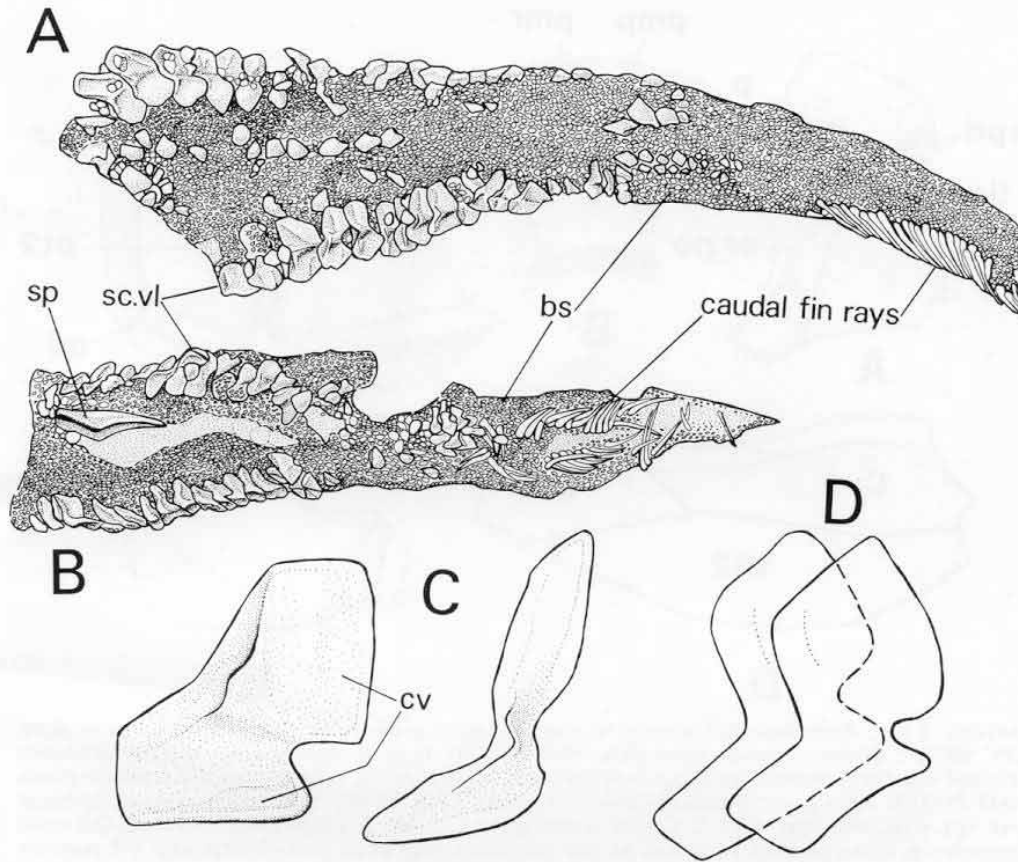
Although the morphology of bothriolepids has been thoroughly treated by Stensiö (1931, 1948) and Miles (1968), a few noteworthy points of interest are seen on the Victorian specimens, such as the structure of the tail, and on the ventral surfaces of the headshield and trunkshield.

The tail of *B. canadensis* is presently the only well-known example of this feature on bothriolepids (Stensiö 1948). In *B. gippslandiensis* and *B. cullodenensis* the tail is characterized by the two large ventrolateral scale rows with minute body scales covering the flanks (plate 42, text-fig. 8). A single dorsal fin is indicated by the prominent fin spine which is probably a composite scale structure as in *Pterichthyodes* (Hemmings 1978, p. 37). As the material is studied from latex casts the internal construction of the scales is unknown. No evidence of pelvic fins could be observed in the material, including radiographs of unprepared specimens. This implies that either the pelvic fins were naked or not present. A final point concerning the tail is that in juveniles the ratio of tail length to armour length is proportionately greater. A restoration of *B. gippslandiensis* is shown in text-fig. 12.

The ventral surface of the headshields of *B. gippslandiensis*, *B. cullodenensis*, and *B. fergusonii* show the development of large lateral pits (prespiracular pit of Stensiö). In *B. cullodenensis* this feature is of greater area and depth than for the other species (plate 42, fig. 6). Stensiö (1948, p. 61) notes that in *B. canadensis* these pits may invariably be absent, and in all other species they are weakly developed if present.

The premedian plate of *B. cullodenensis* has a pair of oval depressions separated by a median vertical ridge (plate 42, fig. 6) on the ventral surface. Similar structures are encountered in other antiarchs, for example *Microbrachius* (Hemmings 1978, p. 45) although it is not clear if they are strictly homologous.

The ventral surface of the anterior median dorsal plate of *B. gippslandiensis* has been described by Hills (1931) and Stensiö (1948, p. 519) as bearing a prominent horizontal lamina which floored the levator fossa. This feature is even better developed in *B. cullodenensis* where a strong but short median vertical ridge supports the crescentic lamina formed by the merged postlevator cristae. The posterior median dorsal plate of this species (plate 42, text-fig. 9) has a peculiar crescentic ridge in the



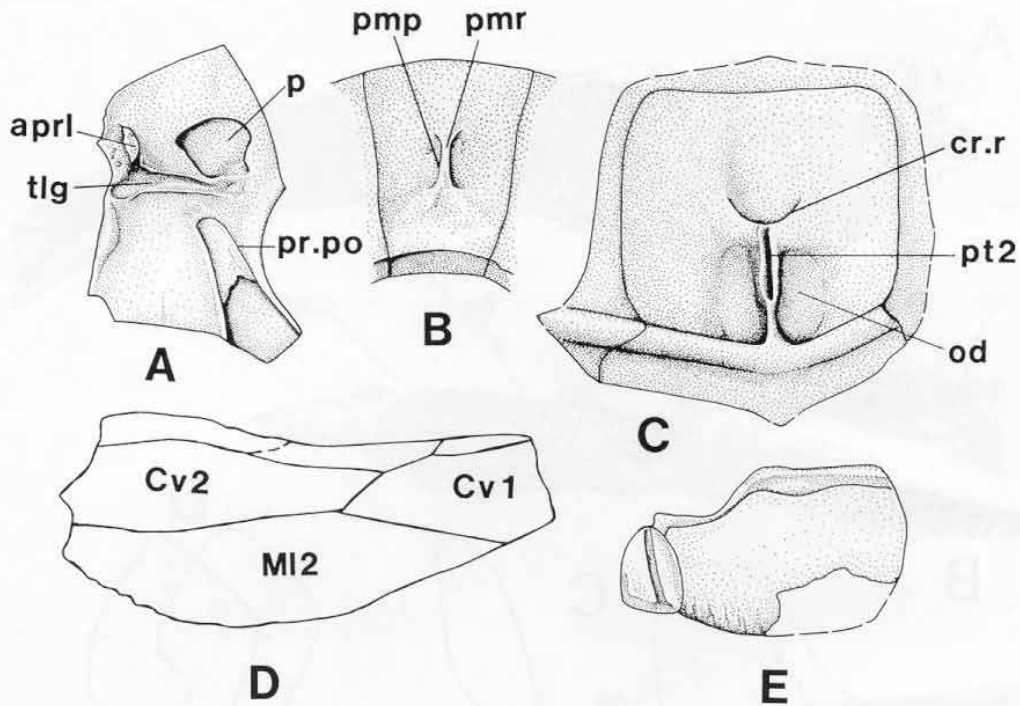
TEXT-FIG. 8. *Bothriolepis gippslandiensis* Hills. Tail and squamation. A. NMV P157170. B. NMV P157149. Natural size. C. internal lateral view and anterior view of a ventrolateral scale from NMV P157170. D. Overlap relations of scales. C, D. $\times 6$. From Mt. Howitt. bs. body scales. cv. overlap areas. scvl. ventrolateral scales. sp. dorsal fin spine.

centre of the ventral surface, immediately anterior to the narrow posterior ventral process which contains the posterior ventral pit.

Without going into more detailed descriptions of the new species, the following morphological features are worthy of note: the extralateral plates of *B. gippslandiensis* and *B. cullodenensis* are broader and shorter than for other species whose extralateral plates are essentially similar to that of *B. canadensis* (Stensiö 1948, p. 89); the central ventral plate 1 and mesial marginal plate 2 of the pectoral appendages of *B. gippslandiensis* and *B. cullodenensis* have extensive contact, similar to *B. verrucosa* (Young and Gorter 1981, p. 101); the preorbital region of the headshield of *B. fergusonii* is very short by comparison with other species.

INTERRELATIONSHIPS OF ANTIARCHS

In order to evaluate the taxonomic position of the Victorian bothriolepids it is first necessary to consider the relationship of *Bothriolepis* to other antiarchs. Young (1981, p. 238) has put forward

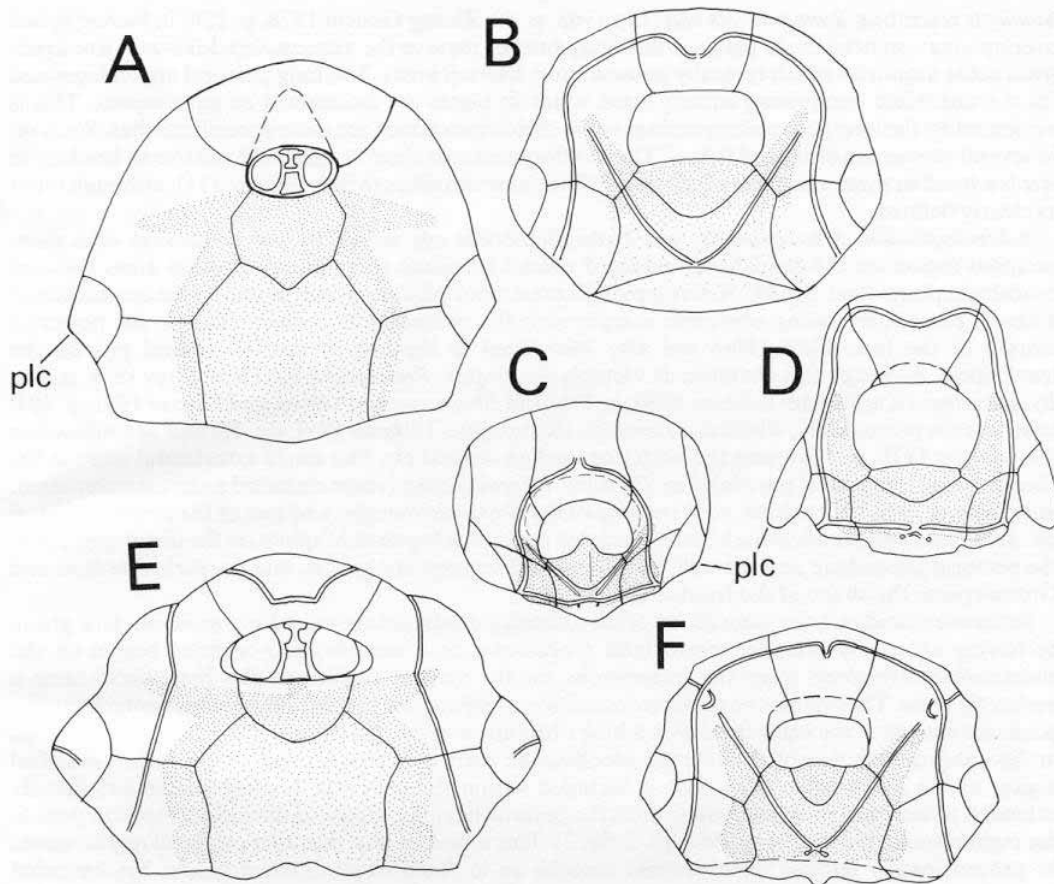


TEXT-FIG. 9. A-C. *Bothriolepis cullodenensis* sp. nov. A. Lateral plate, NMV P158762. B. Premedian plate, CPC 54651. C. Posterior median dorsal plate, NMV P157207. D, E. *B. gippslandiensis* Hills. D. Incomplete proximal segment of pectoral appendage in ventral view, NMV P160702. E. Extralateral and prelateral plates, NMV P157168. All $\times 2$. A-C. Freestone Creek. D. Taggerty. E. Mt. Howitt. Aprl. prelateral plate attachment area. cr.r. Crescentic ridge. Cv1, 2. Central ventral plates 1, 2. MI. 2. lateral marginal plate 2. Od. ovoid depression. p. lateral pit. pmp. premedian pit. pmr. premedian ridge. pr.po. postorbital process. pt2. posterior median ventral pit. tlg. transverse groove.

a cladogram of antiarchan interrelationships using biogeographic data. I intend to outline the morphological evidence for this hypothesis before discussing the interrelationships of bothriolepids.

I accept the hypothesis of Miles and Young (1977, p. 133) that antiarchs are the sister group of euarthrodires (*sensu* Young 1979, p. 344), and that antiarchs and euarthrodires are the sister group of *Phyllolepis*. Antiarchs are specialized in possessing a posterior median dorsal plate, mid-dorsal orbital fenestra and a cranio-thoracic articulation having the trochlea on the paranuchal plate. The premedian plate is believed to be acquired independently in antiarchs and some rhenanids (Miles and Young, 1977, p. 135).

Yunnanolepidoids (Zhang Guorui 1978, p. 184) are the most primitive of the antiarchs (*ibid.* p. 186, Young 1981, p. 236) and may be separated from all other genera by the absence of a true brachial process. They are specialized amongst antiarchs in possessing an external rhombic depression (Zhang Guorui 1978, p. 184) and a subpremedian ridge (Zhang Mi-man 1980, p. 180). A specialization of yunnanolepidoids which is retained in bothriolepidoids (see 'Classification') but lost in asterolepidoids (*sensu* Hemmings 1978, p. 3) is the well-formed median ventral pits of the trunkshield. Euarthrodires primitively possess a ventral ridge on the median dorsal plate (Miles and Dennis 1979, p. 43) which is developed into a carinal process in higher forms (*ibid.* p. 48), but lack the pits seen in antiarchs.



TEXT-FIG. 10. Headshields of various antiarchs. A. *Sinolepis* restored with long obstantic margins, modified from Liu and P'an 1958. B. *Dianolepis*, from pl. 2 in Chang 1965. C. *Microbrachius*, from Hemmings 1978. D. *Pterichthyodes*, from Hemmings 1978. E. *Yunnanolepis* from Zhang Mi-man 1980. F. *Bothriolepis canadensis*, from Stensiö 1948. Inferred endocranial outlines stippled. Not to scale. plc. posterolateral corner.

Sinolepids are similar to *yunnanolepidoids* in retaining a long occipital (preorbital) division of the headshield, small, anteriorly situated orbital fenestra and short, flaired premedian plate. They are more specialized than *yunnanolepidoids* in possessing a brachial process. The brachial process of *Sinolepis* has not been described by Liu and P'an (1958), but is assumed to be present because of the well-developed pectoral appendages. An antiarch from Grenfell, New South Wales, which may be a *sinolepid* (Young 1981, p. 237) lacks the brachial process on all specimens of the anterior ventrolateral plate. However, the proximal bones of the pectoral fin show an articular region for the brachial process, suggesting that this feature was originally present. A thin *pars pedalis* is present on the anterior ventrolateral plate which indicates that the brachial process may have had weak connection to the trunkshield, consequently breaking off easily after death.

Although *Sinolepis* is restored with the preobstantic corners situated on the posterior margin of the headshield, closer examination of the plates in Liu and P'an (1958, pls. 3, 5, figs. 1a, b; 6, figs. 1a, b) indicates that the postmarginal plate has a more anterior position on the headshield (text-fig. 29). The obstantic margin is developed essentially as in *Yunnanolepis* but is relatively shorter in *Sinolepis*.

Sinolepis resembles *Yunnanolepis chii* (Liu 1963, p. 40; Zhang Guorui 1978, p. 156) in having broad overlap areas on headshield plates, which may further remove the yunnanolepidoids and sinolepids from other antiarchs which typically possess short overlap areas. The long pectoral appendages and short trunkshield comprising equally sized squarish plates are interpreted as parallelisms. This is evidenced by the long pectoral appendages of bothriolepids which are more specialized than *Sinolepis* in several characters discussed below. The development of a short trunkshield relative to headshield size is a trend in some antiarchs which parallels the euarthrodires (Miles 1969, p. 131), although is not as clearly defined.

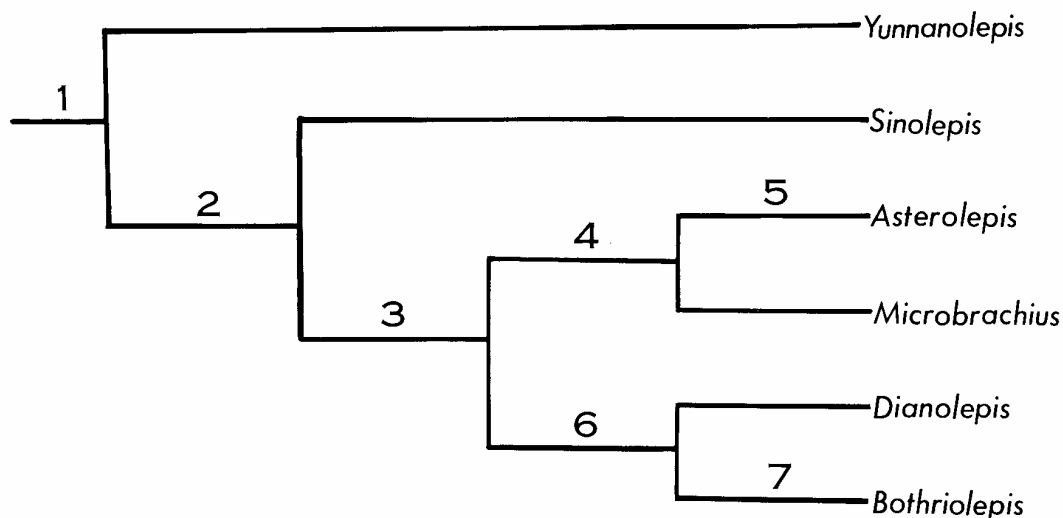
Asterolepidoids, *Microbrachius* and bothriolepidoids are united by the possession of a short occipital region on the headshield, enlarged orbital fenestrae and reduced overlap areas between headshield plates (text-fig. 29). Asterolepidoids are a monophyletic group united by the acquisition of a short, posteriorly facing obstantic margin with the preobstantic corners close to the posterior margin of the headshield. They are also specialized in the loss of median ventral pits on the trunkshield, although this character is variably developed. *Pterichthyodes* (Hemmings 1978, p. 24), *Byssacanthus* (Karatajute-Talimaa 1960, p. 296) and *Sherbonaspis* (Young and Gorter 1981, p. 105) have lost the pits entirely, whereas *Asterolepis* (Karatajute-Talimaa 1963, fig. 45) and *Microbrachius* (Hemmings 1978, p. 51) retain the posterior median ventral pit. The single extralateral plate in the cheek of asterolepidoids is paralleled in *Sinolepis*. *Microbrachius* is here classified as an asterolepidoid, in agreement with Miles (1968, p. 3) because of the obstantic margins and loss of the anterior ventral pit. *Microbrachius* parallels the bothriolepidoids in the development of spines on the distal segment of the pectoral appendage and the well-formed central sensory line canals, and parallels *Sinolepis* and *Grossilepis* in the shape of the trunkshield plates.

Bothriolepidoids are the sister group of the asterolepidoids and are united as a monophyletic group by having anteriorly extended postorbital processes with a narrow otico-occipital region on the endocranium (restored from the impressions on the ventral surface of the headshield), and a prelateral plate. They retain the primitive condition of having the preobstantic corners anterior to the posterior margin of the headshield with a long obstantic margin. *Wudinlepis* is provisionally included in this suborder because of the anterior preobstantic corners in conjunction with the short occipital region of the headshield. *Dianolepis* is included within the suborder because of the anteriorly extended postorbital processes which meet the paranuchal plate closer to the orbital fenestra than to the postmarginal plate (Chang 1965, pl. 2, fig. 2). This indicates that the otico-occipital region would be proportionally narrow to headshield breadth as in *Bothriolepis*. *Pterichthyodes* has extended postorbital processes yet retains a proportionally broad otico-occipital region as in other asterolepidoids (Hemmings 1978, p. 13). Chang does not state that a prelateral plate is present on *Dianolepis*. However, close examination of fig. 2, pl. 2 (Chang 1965) shows a broad attachment area anterior to the transverse lateral groove, similar to the prelateral attachment area on *Bothriolepis*. The attachment area for the anterior division of the extralateral plate in asterolepidoids is typically rostrocaudally elongate, as in *Pterichthyodes*, *Microbrachius*, *Asterolepis*, and *Sherbonaspis*. The bothriolepidoid affinity of *Dianolepis* is further suggested by the postpineal plate which is more convex posteriorly than anteriorly, well-developed central sensory canals and relatively broad lateral plate. *Bothriolepis* and *Grossilepis* are united by having the postpineal plate not contacting the lateral plates, and possibly by the presence of a well-developed median occipital crista on the posterior ventral face of the headshield.

INTERRELATIONSHIPS OF BOTHRIOLEPIDS

Of over sixty described species of *Bothriolepis* and further specimens awaiting description, only twenty-five or so are known by headshields and trunkshields, and only in *B. canadensis*, *B. gippslandiensis*, and *B. cullogenensis* is the squamation and structure of the tail known. In the following discussion only these species or particularly relevant species such as *B. verrucosa* are considered.

B. verrucosa is the most primitive species in possessing a small axillary foramen, weakly developed



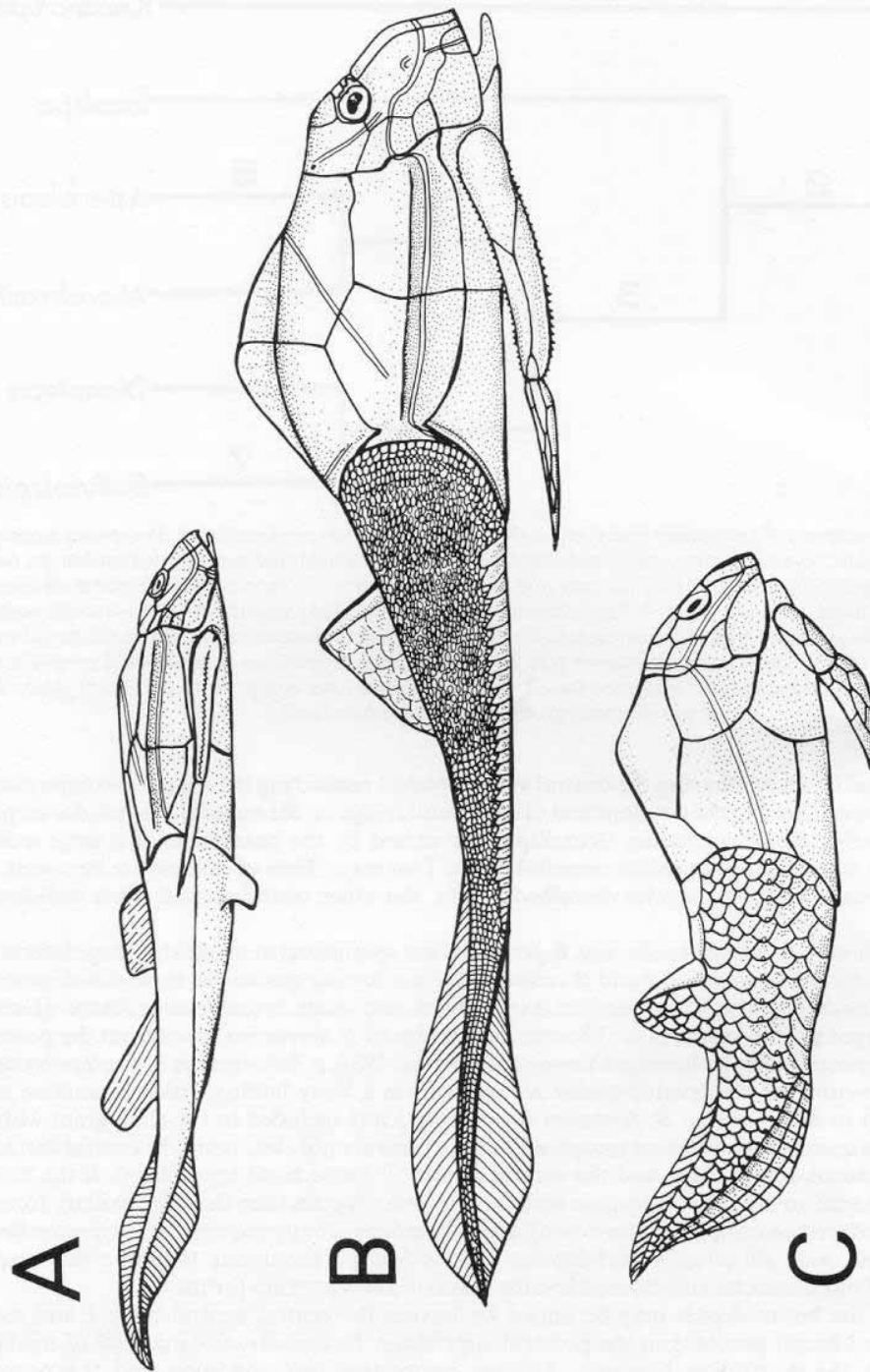
TEXT-FIG. 11. Hypothesis of antiarchan interrelationships. Numbered synapomorphies: 1. Possessing a posterior median dorsal plate, eyes and nares meet mid-dorsally on the headshield and are situated within an orbital fenestra. 2. Acquisition of a brachial process and axillary foramen. 3. Shortened postorbital division of exocranium, enlarged orbital fenestra. 4. Preobstantic corners of headshield situated on or close to the posterior margin, loss of the anterior cheek element (prelateral). 5. Loss of anterior median ventral pit on the dorsal wall of the trunkshield, or both anterior and posterior pits. 6. Otico-occipital depression of headshield proportionally narrow with well-developed postorbital processes. 7. Postpineal plate loses contact with the lateral plates. Each genus is representative of the respective family.

median occipital crista and having the central ventral plate 1 contacting the mesial marginal plate 2. This species is specialized in the development of a crescentic ridge on the anterior median dorsal plate.

All other bothriolepids, including *Grossilepis*, are united by the possession of a large axillary foramen and a well-developed median occipital crista. Two major lines of descent are apparent: one comprising certain Victorian species described herein, the other containing all other well-known species.

B. gippslandiensis, *B. cullodenensis*, and *B. fergusonii* are specialized in possessing large lateral pits on the headshield. *B. gippslandiensis* and *B. cullodenensis* are further specialized in the development of short, high trunkshields which bear median dorsal crests, and short, broad levator fossae which are floored by merged postlevator cristae. The crescentic ridge of *B. verrucosa* arises from the posterior margins of the postlevator thickenings (Young and Gorter, 1981, p. 95) whereas in *B. gippslandiensis* and *B. cullodenensis* the postlevator cristae merge to form a bony lamina which is situated more anteriorly than in *B. verrucosa*. *B. fergusonii* is parenthetically included in the cladogram with the other Victorian species because some morphological features are not clear (as in the central surface of the anterior median dorsal plate, and the ventral aspect of the pectoral appendage). If the floored levator fossa is used to unite *B. verrucosa* with the Victorian species then the large axillary foramen and well-formed median occipital crista would have to be independently acquired in *B. gippslandiensis*, *B. cullodenensis*, and all other bothriolepids. This is less parsimonious than the independent acquisitions of one character (the floored levator fossa) in the Victorian forms.

The rest of the bothriolepids may be united by having the central ventral plate 1 and mesial marginal plate 2 barely touching in the pectoral appendage. Examination of material of the Gogo *Bothriolepis* in the Australian Museum, Sydney, shows that this condition and the primitive condition seen in *B. verrucosa* and the relevant Victorian species can occur within a single species (personal observation). However, as this is the only species displaying this kind of variation, and this



TEXT-FIG. 12. Comparison of the tail of *Bothriolepis canadensis* (A) with *B. gippslandiensis* (B) and *Pterichthyodes* (C). A, after Stensjö 1948. Hemmings 1978. Not to scale.

is observed in one specimen only, it is assumed that the contact relationship of the central ventral plate 2 and the mesial marginal plate 1 is not typically variable for other species of *Bothriolepis*.

The tail of *B. canadensis* has little scale covering (Stensiö 1948, p. 167) whereas large ventrolateral scales and minute body scales cover the tails of *B. gippslandiensis*, *B. cullodenensis*, and presumably *B. fergusonii*. The tail of antiarchs is primitively covered by large scales, as in *Yunnanolepis*, *Sinolepis*, *Pterichthyodes*, *Asterolepis* (Stensiö 1969, p. 656), and *Remigolepis* (Dr. A. Ritchie, pers. comm.). The reduced squamation of *B. canadensis* is therefore apomorphic relative to the Victorian species (text-fig. 12). *Bothriolepis* sp. from Canowindra, New South Wales, also possesses the reduced squamation of *B. canadensis* (personal observation), and it is possible that many of the typical Euramerican species may have had little scale cover on the tail. This character may further separate the Victorian species when more is known of the tail of other *Bothriolepis* species. The use of this character in the cladogram implies that *B. verrucosa* had some degree of scale cover on the tail. However, as material of this species occurs as isolated plates it would be difficult to test this hypothesis.

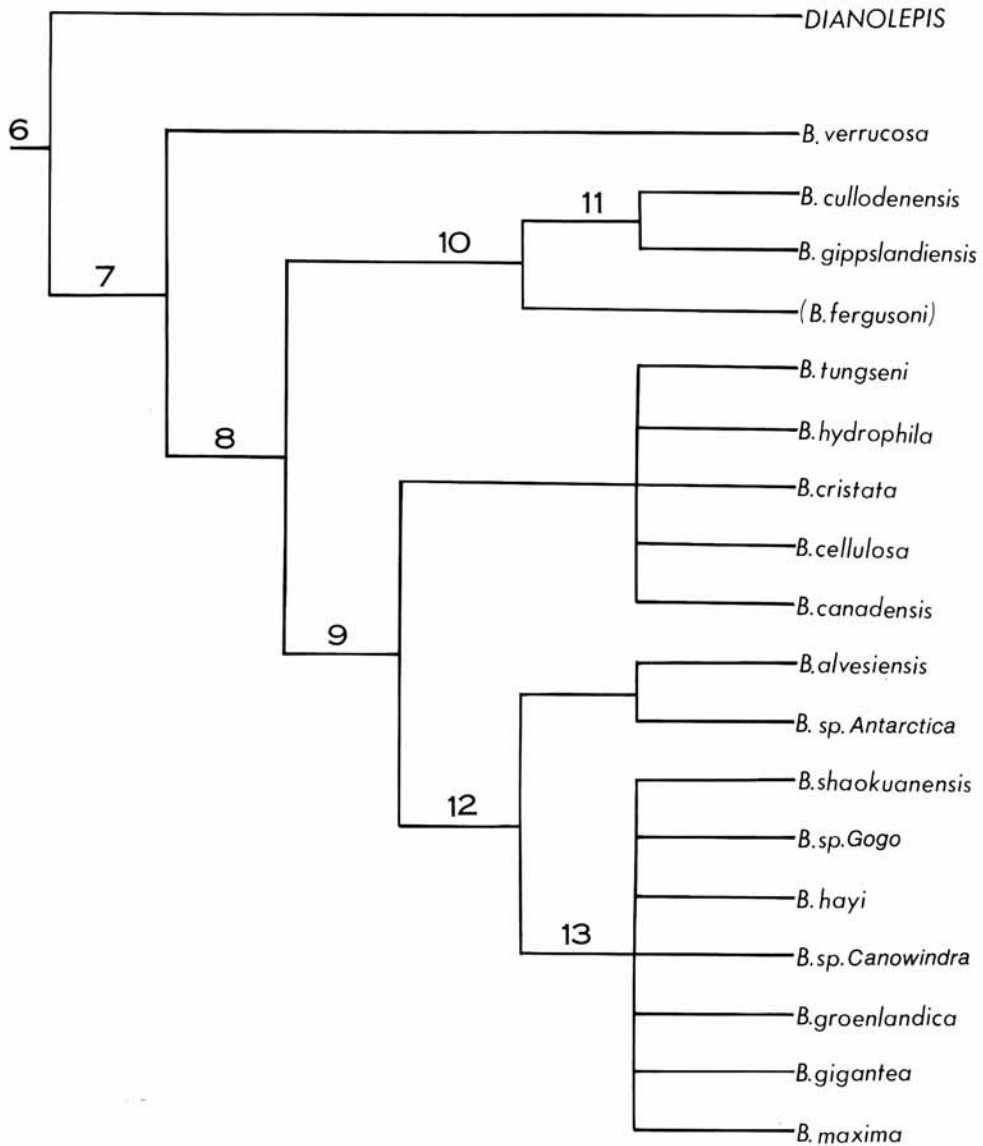
The preorbital recess is primitively developed in antiarchs in a semicircular shape, as in *Pterichthyodes* (Hemmings 1978, p. 14) and *Asterolepis* (Stensiö 1948, p. 52). The trifold preorbital recess is unique to certain species of *Bothriolepis* and is more complex than the semicircular type in having extended medial and lateral divisions. *B. alvesiensis* and a species from Antarctica (Dr. G. Young, pers. comm.) possess a preorbital recess which has an extended medial division with simple lateral divisions, intermediate between the two prevalent types. *B. tungseni* from the Eifelian of China is the oldest known species and has a semicircular preorbital recess (Chang 1965, p. 9). However, *B. shaokuanensis* from the Givetian of China (Liu 1963) possesses a trifold preorbital recess, indicating that the two varieties appeared close together in time.

The bothriolepid diversity gave rise to much parallelism. *B. gippslandiensis* and *B. tungseni* possess postpineal plates with strongly convex anterior margins and broad orbital fenestrae. *B. tungseni*, *B. fergusonii*, *B. hayi*, *B. nitida*, and *Bothriolepis* sp., Antarctica (Dr. G. Young, pers. comm.), possess striae on the distal segment of the pectoral appendage. *B. verrucosa* and *B. paradoxa* possess a shallow depression in the centre of the supraotic thickening of the nuchal plate. *B. cristata* and *B. groenlandica* possess a median vertical ridge on the premedian plate (Miles 1968, p. 57), but the ridge developed on the premedian of *B. hayi* is more like that of *B. cullodenensis* in being outside of the preorbital recess. The development of median dorsal crests on *B. gippslandiensis* and *B. cristata* is another example of parallelism. The shape of the headshield in bothriolepids varies from being narrow with a strongly convex rostral margin (*B. cullodenensis*, *B. tungseni*, *B. alvesiensis*, *B. shaokuanensis*) to being broader with a fairly straight rostral margin (*B. gippslandiensis*, *B. canadensis*, *B. gigantea*, *B. hicklingi*, *B. leptochaira*, *B. maxima*). The early appearance of *B. tungseni* and *B. shaokuanensis* suggests that the straight rostral margin was independently developed in bothriolepids possessing semicircular and trifold preorbital recesses. The straight rostral margin is seen on the most specialized of the bothriolepids, those possessing trifold preorbital recesses and attaining large size (*B. gigantea*, *B. maxima*). *B. maxima* is specialized in possessing a relatively narrow, long orbital fenestra and a large posterior ventral pit situated centrally on the posterior median dorsal plate (Gross 1948, p. 446).

Extremes on bothriolepid diversity are exemplified by such forms as *B. kwangtungensis* which had unusually narrow, flat armour (P'an Kiang 1964) and *B. bindareei* which had very high, short armour. Size ranges of *Bothriolepis* armours vary from 60 mm (*B. verrucosa*) to 500 mm (*B. maxima*), being the largest of the antiarchs.

CLASSIFICATION

The classification of antiarchs by Miles (1968, p. 3) agrees with that of Gross (1965, p. 13) in using the exoskeletal characteristics of the armour as a whole, rather than the structure of the pectoral fin (Stensiö 1931, 1948, 1969). However, unlike Gross, Miles erected a new suborder for the Lower Devonian yunnanolepids. Zhang Guorui (1978) and Zhang Mi-man (1980) have recently shown that the primitive organization of the group deserves subordinal rank. Hemmings (1978, p. 3) placed the enigmatic families Sinolepididae (Liu and P'an 1958) and Microbrachiidae (Miles 1968) within the



TEXT-FIG. 13. Hypothesis of bothriolepid interrelationships. Numbered synapomorphies: 6, 7 see text fig. 11. 8. Median occipital crista well developed, axillary foramen enlarged. 9. Mesial marginal plate 2 barely touches central ventral plate 1, squamation on tail reduced. 10. Large lateral pits on ventral surface of headshield. 11. Armour short, high, cristate. Cristae (forming horizontal laminae). 12. Preorbital recess with an enlarged median division. 13. Preorbital recess with extended lateral divisions. These species represent the well-known types of the genus. Material of *Bothriolepis* sp. from Gogo, Western Australia, Canowindra, New South Wales, and Antarctica kept in the Australian Museum, Sydney and the Bureau of Mineral Resources, Canberra.

suborder Bothriolepidoidei (Miles 1968), though this is refuted by Young and Gorter (1981, p. 93) who retain the single family Bothriolepididae within the suborder. Young and Gorter have given new definitions of the suborder Bothriolepidoidei which incorporates the postpineal plate not contacting the lateral plates as a diagnostic feature. In defining the Asterolepidoidei Young and Gorter (*ibid.*, p. 100) use the characters 'antiarchs with the posterolateral angle of the headshield situated at or just in front of the posterior margin . . . prelateral plate absent'. These statements exclude *Dianolepis* from either suborders (see above for comments concerning the possible presence of a prelateral plate in *Dianolepis*), yet it is suggested that the genus does not belong in the Bothriolepidoidei so is more closely allied to the asterolepidoids. I have proposed a closer affinity between *Dianolepis* and *Bothriolepis* and include these genera with *Grossilepis* in the Bothriolepidoidei. *Dianolepis* is here referred to its own family, Dianolepididae, on the basis of the postpineal plate contacting the lateral plates. The following classification of antiarchs recognizes *Sinolepis* as the sister group to both asterolepidoids and bothriolepidoids and places the genus in its own suborder, the Sinolepidoidei. *Xichonolepis* (Zhang Guorui, 1980) is classified as an asterolepidoid but in possessing well-developed median ventral pits on the trunkshield and a single mixilateral plate this genus is more closely allied to *Sinolepis*. In view of the fragmentary nature of *Xichonolepis*, the genus is provisionally included within the new suborder. Sinolepid remains may also be present from Australia. An antiarch having rectangular median dorsal plates with well-developed median ventral pits and an unusually long nuchal plate has been found from the Mt. Grenfell area in New South Wales (Dr. A. Ritchie, pers. comm.).

The classification of antiarchs presented here is fundamentally similar to that of Miles (1968) with modifications concerning the systematic status of sinolepids and the genus *Dianolepis*. It has not been reorganized as a cladistic classification for the following reasons: (1) inadequate knowledge of asterolepidoid interrelationships; (2) the possibility of decreasing the number of current species of *Bothriolepis* by recognition of morphotypic groups; and finally (3) the need of further data on many of the poorly known Chinese forms. When these problems have been dealt with then perhaps a revised classification of the Antiarcha can be confidently attempted.

Order ANTIARCHA Cope 1885

Suborder YUNNANOLEPIDOIDEI Miles 1968

Diagnosis. As in Zhang Guorui 1978 (in Chinese).

Family YUNNANOLEPIDAE Zhang Guorui 1978

Diagnosis. As in above.

Genera *Yunnanolepis*, *Phymolepis*, ?*Zhanjilepis*

Family QUIJINOLEPIDAE

Diagnosis. As in above.

Genus *Quijinolepis*

Suborder SINOLEPIDOIDEI

Diagnosis. Antiarchs having a headshield with a relatively long postorbital region. Trunkshield with well-developed median ventral pits on the dorsal wall; brachial process present.

Family SINOLEPIDAE Liu and P'an 1958

Diagnosis. As above.

Genera *Sinolepis*, ?*Xichonolepis*

Suborder BOTHRIOLEPIDOIDEI Miles 1968

Diagnosis. Antiarchs having a short postorbital region on the headshield; postpineal plate separated or almost separated from the lateral plates; otico-occipital depression narrow relative to headshield breadth; prelateral plate present. Anterior median dorsal plate with a broad anterior margin; single mixilateral plate replacing posterior dorsal and posterior dorsolateral plates. Semilunar plate unpaired.

Family DIANOLEPIDIDAE

Diagnosis. Bothriolepidoids with the postpineal plate contacting the lateral plates.

Genera *Dianolepis*, ?*Wudinolepis*

Family BOTHRIOLEPIDIDAE Cope 1886

Diagnosis. Bothriolepidoids having the postpineal plate excluded from the lateral plates. Preorbital recess well developed. Pectoral appendages extending beyond trunkshield when adducted; dorsal central plate 2 small, not contacting dorsal central plate 1.

Genera *Bothriolepis*, *Grossilepis*

Suborder ASTEROLEPIDOIDEI Miles 1968

Diagnosis. Antiarchs having a short postorbital region on the headshield; preobstantic corners situated on or close to the posterior margin of the headshield. Prelateral plate absent. Otico-occipital depression broad. Postpineal plate contacting lateral plates, usually broad in proportion to its length. Median ventral pits poorly developed or absent.

Family ASTEROLEPIDIDAE Miles 1968; Traquair 1888

Diagnosis. Asterolepidoids having a low trunkshield; preorbital division of headshield very short. Orbital fenestra large.

Genera *Asterolepis*, *Remigolepis*

Family PTERICHTHYODIDAE Stensiö 1948

Diagnosis. As in Young and Gorter 1981, p. 100.

Genera *Pterichyodes*, *Sherbonaspis*, *Stegolepis*, *Gerdalepis*, *Lepadolepis*, *Grossaspis*, *Byssacanthus*

Family MICROBRACHIIDAE Miles 1968

Diagnosis. As in Hemmings 1978, p. 42.

Genus *Microbrachius*

All other general *Incertae sedis*.

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