

A NEW SPECIES OF *BOTHRIOLEPIS* (PLACODERMI: BOTHRIOLEPIDAE) FROM THE UPPER DEVONIAN OF VIRGINIA (USA)

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Abstract.—A new species of placoderm fish, *Bothriolepis virginiensis*, is described from specimens found in Upper Devonian rocks near Winchester, Virginia. This species is characterized by the combined occurrence of at least seven traits not found together in any other species of *Bothriolepis*. These traits are: 1, a largely fused head shield; 2, an exceptionally long premedian plate; 3, orbital fenestra that is longest at the midline of the head shield; 4, posterior oblique cephalic pit lines that meet near the center of the unobtected portion of the nuchal plate; 5, a strongly V-shaped border between the anterior median dorsal plate and the posterior median dorsal plate; 6, lack of a prominent medial crest on the anterior median dorsal plate; 7, fused elements in the distal pectoral fin segment. This is the oldest validly determined vertebrate animal so far described from Virginia. Traits of all described species of bothriolepids are summarized for comparison with our new species, but the intrafamilial relationships are still obscure because the family has undergone extensive parallel evolution. A detailed section of the type locality is given to aid future studies on the paleoecology and taphonomy of bothriolepids.

Geologic Setting

While studying Upper Devonian Chemung Formation outcrops in Maryland and Virginia, Beem discovered two beds about a meter apart that were rich in bony plates of *Bothriolepis* and scales of crossopterygians (beds 50 and 52, Appendix 1). The beds dip 40°–50° SE along U.S. Route 522 northwest of Winchester, Virginia (Fig. 1). Fragmentary acanthodian spines are possibly represented as well (Donald Kirkpatrick, personal communication). Although the lower bone-bearing bed (50) is a greenish-gray to medium-gray shale and the upper (52) is a grayish-brown, fine-grained sandstone, no obvious differences in vertebrate faunal content were noted. Most of the bony plates are of approximately equal size, are stacked imbricately along each bedding surface and appear to have been current sorted. The lack of extensive wear or breakage indicates that transport was not prolonged or distant. In addition to the vertebrate remains, rare linguloid brachiopods were found in the greenish-gray *Bothriolepis*-bearing bed, bed 50, which suggests that it accumulated in brackish water. Bed 52 may have accumulated in fresh water. Elsewhere in the outcrop, beds contain fragments of plants (32, 38,

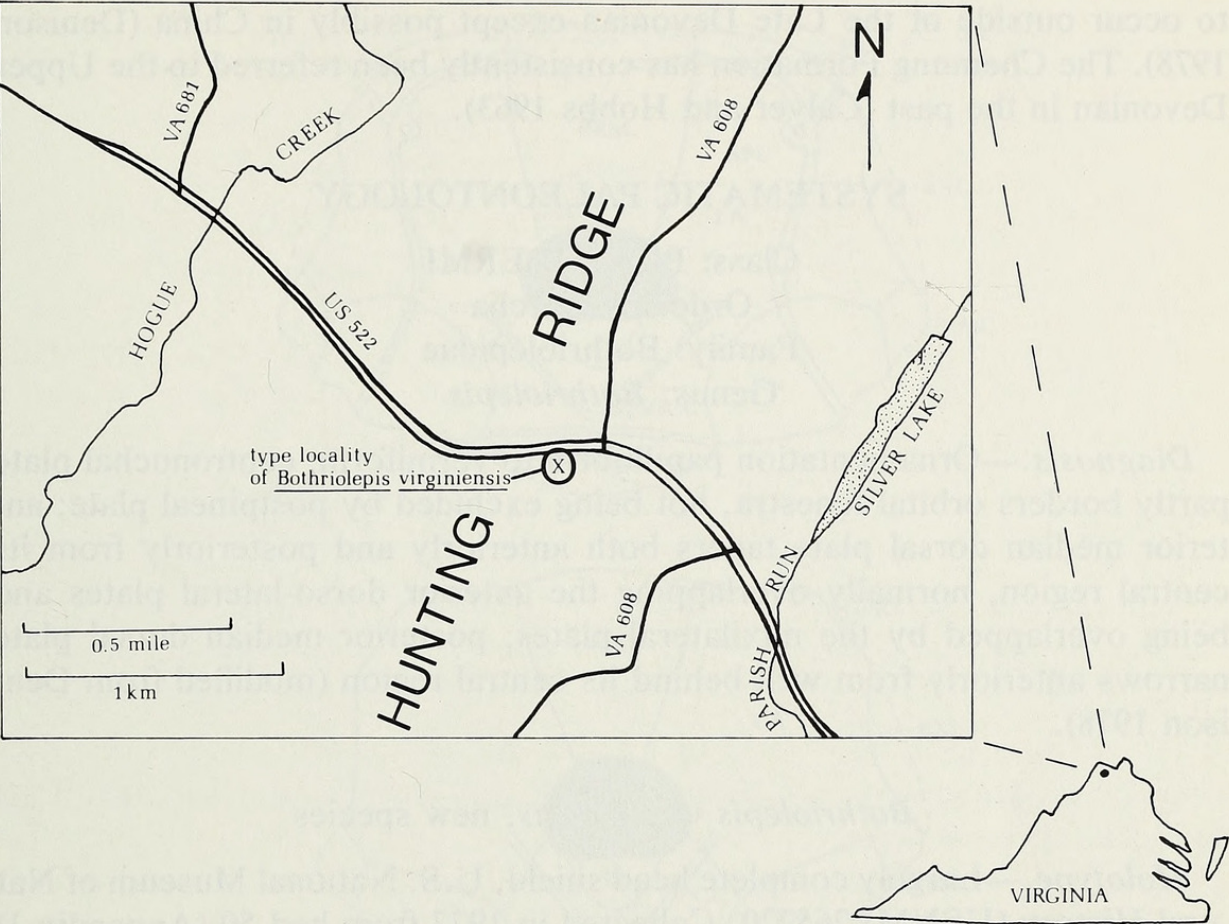


Fig. 1. Type locality of *Bothriolepis virginiensis* in the Chemung Formation (Upper Devonian).

40, and 62) or poorly preserved brachiopod and echinoderm molds (beds 17, 26, 41, and 68). Whereas much of the outcrop consists of monotonously interbedded medium-gray to grayish-orange siltstones and sandstones, two intervals (beds 16–25 and 46–63) are dominated by grayish-brown beds. From the suite of rock types and the fossils present, it seems likely that the rocks are marine, brackish, and freshwater in origin and formed in a marginal marine setting along the southeast edge of the Late Devonian Appalachian seaway. Because the *Bothriolepis*-bearing beds are in a dominantly grayish-brown part of the section and the remains of linguloid brachiopods are present in bed 50, the environment of postmortem vertebrate accumulation probably was a tidally influenced, brackish to freshwater lagoon.

Samples of greenish-gray shale from the lower *Bothriolepis*-bearing bed were analyzed for palynomorphs, but almost no plant matter of any kind was found in the samples (Robert Kosanke, United States Geological Survey, written communication, 1978). Therefore, in the absence of other diagnostic macrofossil or microfossil remains, the Late Devonian age assigned to these beds must rest on the presence of *Bothriolepis*, which is not known

to occur outside of the Late Devonian except possibly in China (Denison 1978). The Chemung Formation has consistently been referred to the Upper Devonian in the past (Calver and Hobbs 1963).

SYSTEMATIC PALEONTOLOGY

Class: PLACODERMI

Order: Antiarcha

Family: Bothriolepidae

Genus: *Bothriolepis*

Diagnosis.—Ornamentation papilliform to vermiform; centronuchal plate partly borders orbital fenestra, not being excluded by postpineal plate; anterior median dorsal plate tapers both anteriorly and posteriorly from its central region, normally overlapping the anterior dorso-lateral plates and being overlapped by the mixilateral plates; posterior median dorsal plate narrows anteriorly from well behind its central region (modified from Denison 1978).

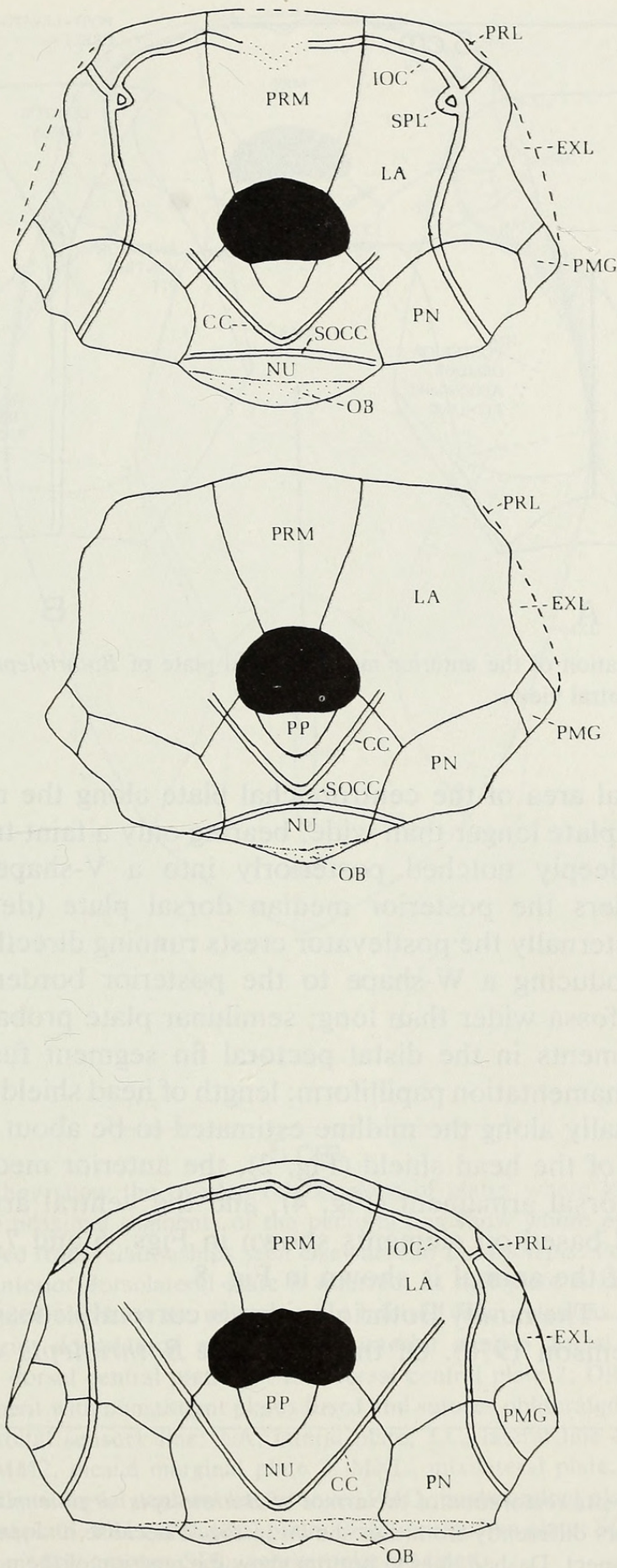
Bothriolepis virginiensis, new species

Holotype.—Largely complete head shield, U.S. National Museum of Natural History (USNM) 265220. Collected in 1977 from bed 50 (Appendix 1), south side roadcut on U.S. 522 through Hunting Ridge near Winchester, Virginia. Chemung Formation (Upper Devonian).

Referred specimens.—USNM 265221, USNM 265222, USNM 265223, USNM 265224, USNM 265225, USNM 265226, USNM 265227. Collected in 1977 and 1978 from beds 50 and 52. Other data as for holotype.

Diagnosis.—As for genus and in addition: dorsal head shield elements fully fused in adult individuals except for the extralateral and prelateral plates; pre-orbital rostrum elongate, forming $47\% \pm 4\%$ of the total head shield length as measured along the midline and excluding the obtected nuchal area; orbital fenestra elliptically shaped, not constricted anteroposteriorly along the midline; premedian plate longer than wide; posterior cephalic pit lines meet nearly midway between the postpineal plate and the

Fig. 2. Comparison of configurations of head shield elements in two specimens of *Bothriolepis virginiensis* and one specimen of *B. canadensis*. (Top) *B. virginiensis*, USNM 265220; (Middle) *B. virginiensis*, USNM 265221; (Bottom) *B. canadensis*, after Stensio (1948). CC, central sensory line; EXL, extralateral plate; IOC, infraorbital sensory line; LA, lateral plate; NU, nuchal plate; OB, obtected nuchal area; PMG, postmarginal plate; PN, paranuchal plate; PP, postpineal plate; PRL, prelateral plate; PRM, premedian plate; SOCC, supraoccipital cross-commissural pit-line groove; SPL, semicircular pit line.



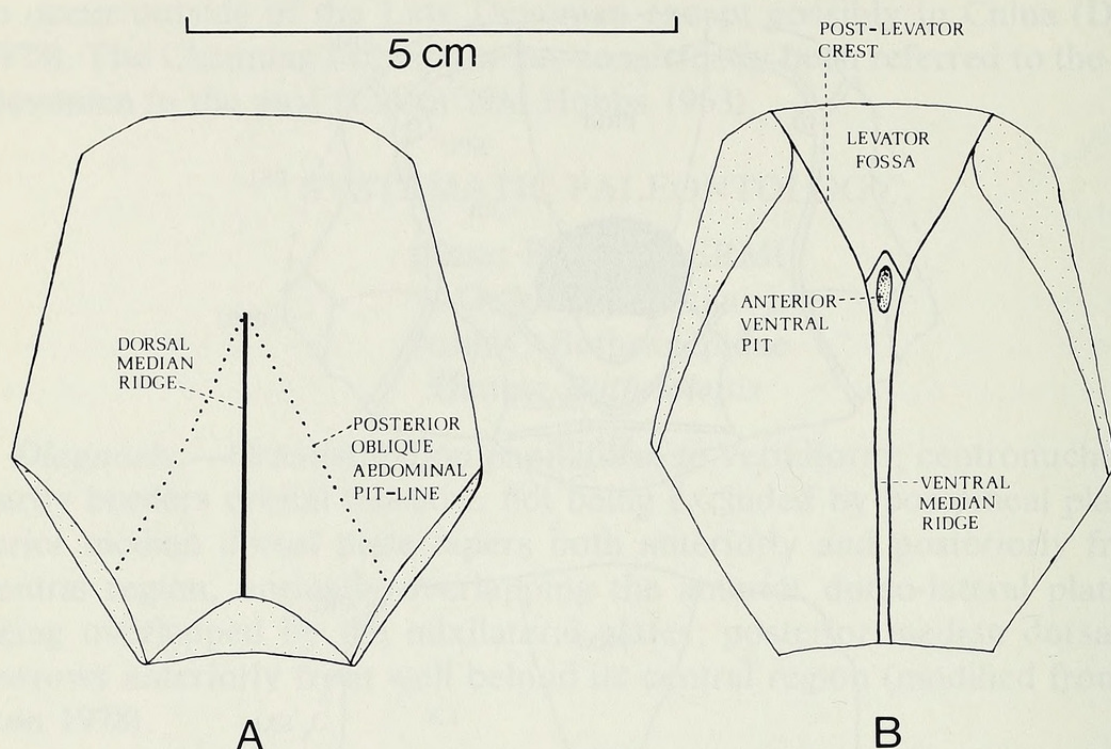


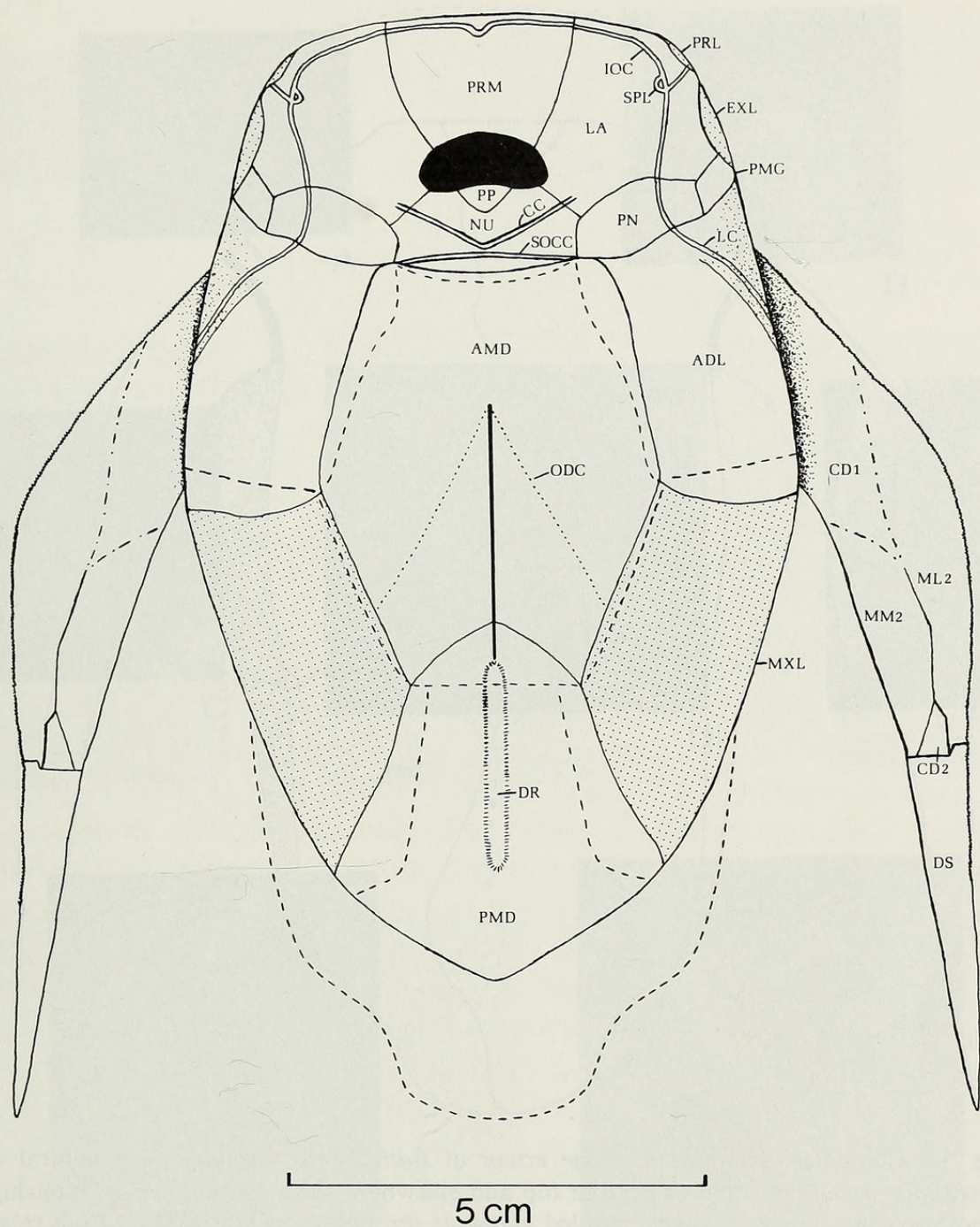
Fig. 3. Restoration of the anterior median dorsal plate of *Bothriolepis virginiensis* in (A) dorsal and (B) ventral view.

obtected nuchal area of the centronuchal plate along the midline; anterior median dorsal plate longer than wide, bearing only a faint trace of a median dorsal keel, deeply notched posteriorly into a V-shaped configuration where it borders the posterior median dorsal plate (depth/width ratio: $32\% \pm 7\%$); internally the postlevator crests running directly to the anterior ventral pit producing a W-shape to the posterior border of the levator fossa, levator fossa wider than long; semilunar plate probably much wider than long; elements in the distal pectoral fin segment fused and sutures obliterated; ornamentation papilliform; length of head shield and trunk armor measured dorsally along the midline estimated to be about 13 cm.

Restoration of the head shield (Fig. 2), the anterior median dorsal plate (Fig. 3), the dorsal armament (Fig. 4), and the ventral armament (Fig. 5) was attempted based on elements shown in Figs. 6 and 7. A tentative reconstruction of the animal is shown in Fig. 8.

Discussion.—The family Bothriolepidae is currently considered to include six genera (Denison 1978). Of these, all but *Bothriolepis* can be excluded

Fig. 4. Composite restoration of the armor of *Bothriolepis virginiensis* in dorsal view. The head shield appears differently from that shown in Fig. 2 because it slopes down and away in a strictly dorsal aspect. Dashed lines at bottom show the position of the posterior ventrolateral



plates, elsewhere they show the overlap relationships of plates where known. Dashed and dotted lines on the proximal segments of the pectoral fins show where plate boundaries are unknown but inferred from relationships seen elsewhere in *Bothriolepis*. Position of the lateral line canal on the anterior dorsolateral plate is inferred, as that plate is known only from an internal mold. Stippled elements are unknown but inferred from relations of surrounding elements. ADL, anterior dorsolateral plate; AMD, anterior median dorsal plate; CC, central sensory line; CD1, dorsal central plate 1; CD2, dorsal central plate 2; DR, dorsal ridge; DS, distal pectoral segment with constituent plates fused and sutures obliterated; EXL, extralateral plate; IOC, infraorbital sensory line; LA, lateral plate; LC, lateral line canal; ML2, lateral marginal plate 2; MM2, mesial marginal plate 2; MXL, mixilateral plate; NU, nuchal plate; ODC, posterior oblique dorsal sensory line groove; PMG, postmarginal plate; PN, paranuchal plate; PP, postpineal plate; PRL, prelateral plate; PRM, premedian plate; SOCC, supraoccipital cross-commissural pit-line groove; SPL, semicircular pit line.

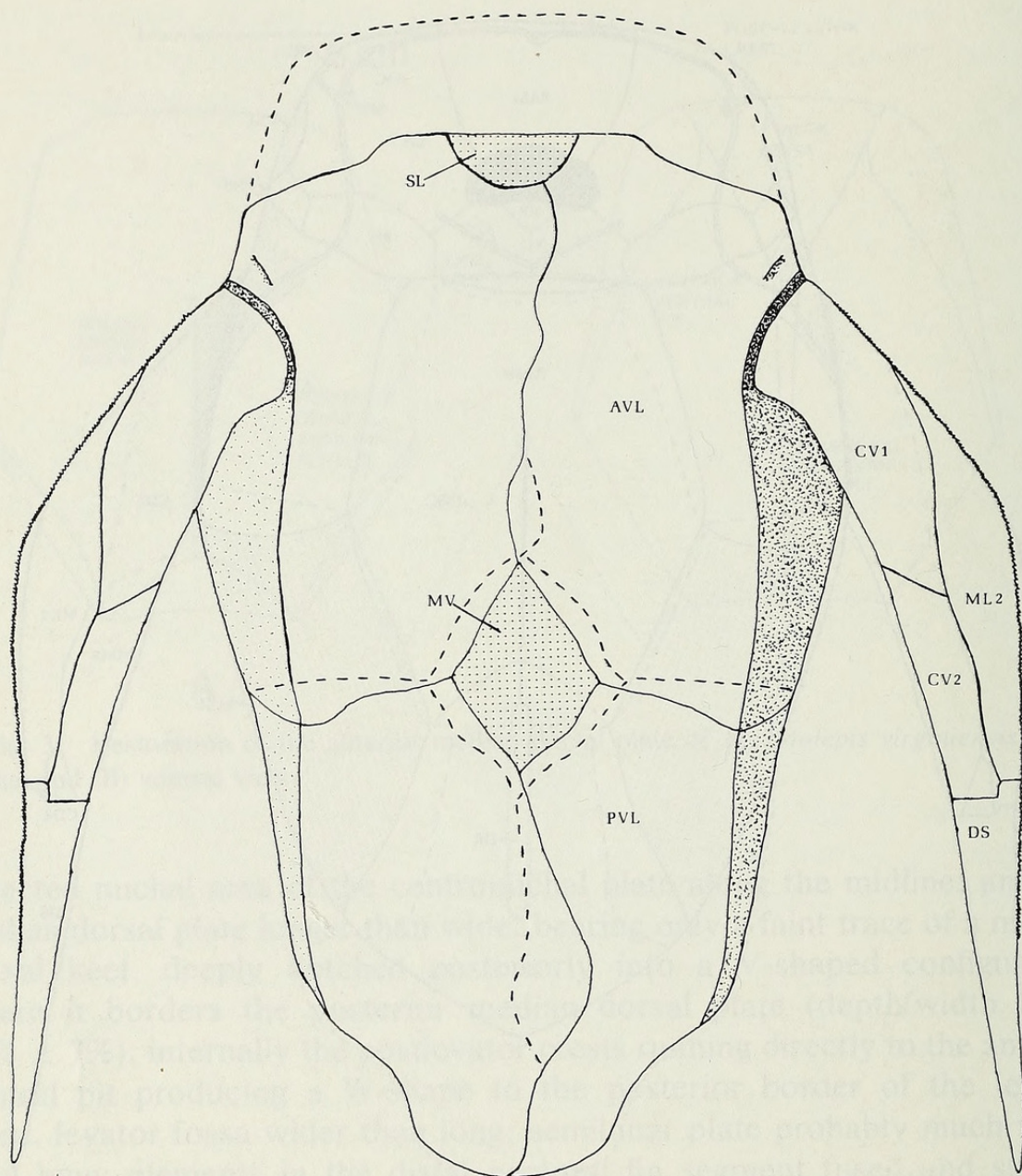
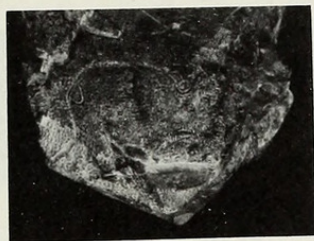
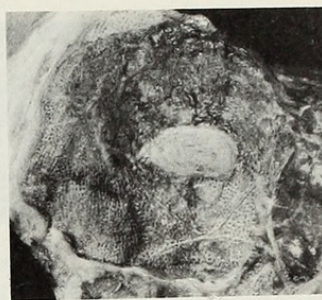


Fig. 5. Composite restoration of the armor of *Bothriolepis virginiensis* in ventral view. Dashed lines outline position of head at top and elsewhere show the overlap relationships of the various plates where known. Stippled elements are unknown but inferred from relations of surrounding elements. AVL, anterior ventrolateral plate; CV1, ventral central plate 1; CV2, ventral central plate 2; DS, distal pectoral segment with constituent plates fused and sutures obliterated; ML2, lateral marginal plate 2; MV, median ventral plate; PVL, posterior ventrolateral plate; SL, semilunar plate.

from further consideration with our material for the following reasons. In *Dianolepis* the postpineal plate excludes the nuchal from the orbit and the trunk shield has a prominent dorsal crest (Chang 1965). *Hillsaspis* (Stensio, 1969) has a very prominent medial dorsal crest. *Grossilepis* has both a posterior median dorsal plate that comes to a very shallow angle posteriorly and an anterior median dorsal plate of nearly uniform breadth along its



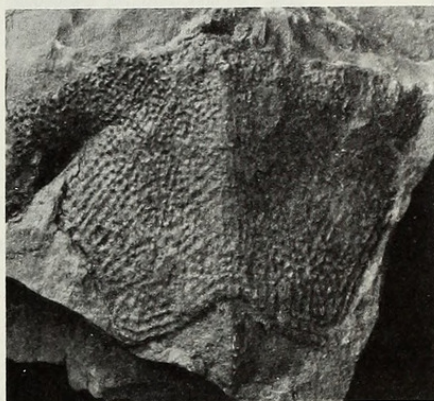
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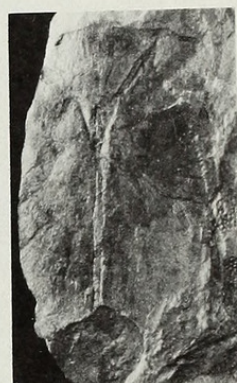
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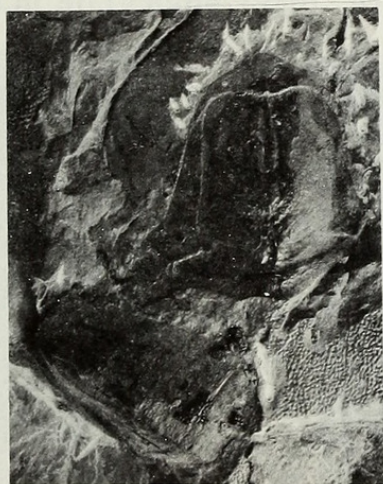
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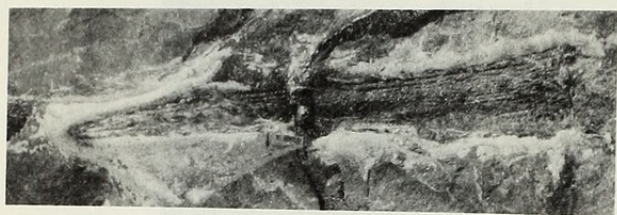


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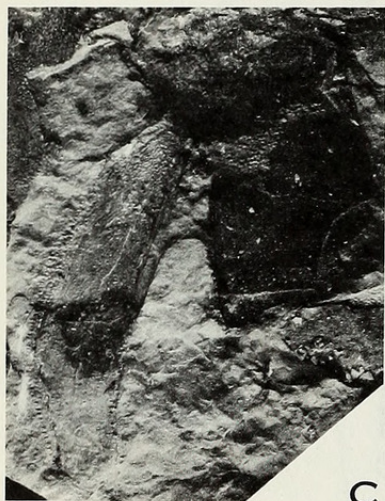
Fig. 6. A. Anterior part of distorted head shield, showing lateral line groove along anterior part of head shield. Length of rostrum 2.0 cm. USNM 265227. B. Dorsal view of head shield, holotype of *Bothriolepis virginiensis*. Length of head shield 4.1 cm. USNM 265220. C. Internal view of anteromedial dorsal plate, anterior half. Length as preserved, 4.8 cm. D. External view of anteromedial dorsal plate, posterior half. Length as preserved, 2.6 cm. USNM 265224. E. Internal view of natural mold of an anteromedial dorsal plate, anterior half. Length as preserved, 4.7 cm. F. (Upper right) Mold of internal surface of posteromedial dorsal plate, note pointed anterior (top) end, length, 3.8 cm; (lower left) natural mold of left anterodorsolateral plate; length, 3.4 cm. G. (Center right) Internal view of posteromedial dorsal plate, note pointed anterior (top) end; length, 4.3 cm; (left) natural mold of proximal segment of pectoral appendage, (top center) crossopterygian scale.



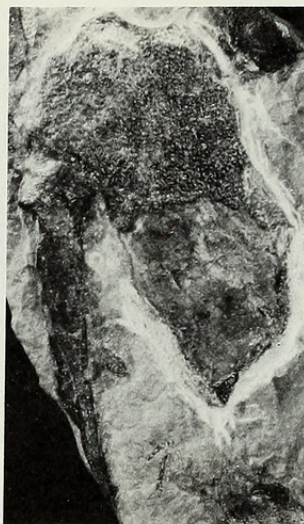
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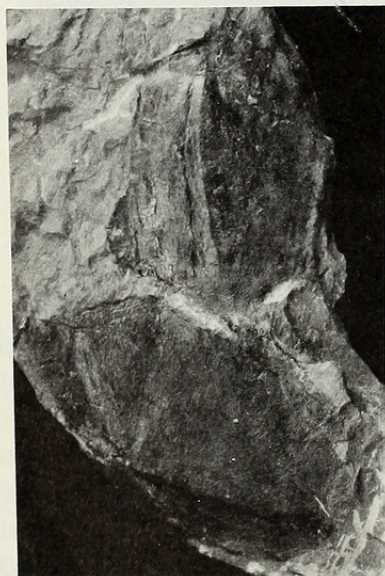
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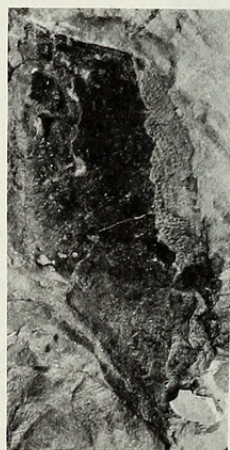
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H

Fig. 7. A. Distal segment of a pectoral appendage. Length, 4.1 cm. B. Proximal segment of a pectoral appendage, ventral view. Length, 5.4 cm. C. Proximal left segment of a pectoral appendage articulated with its anteroventral element (latter seen in internal view). Proximal pectoral segment is 5.5 cm long as preserved. D. Proximal right segment of a pectoral appendage articulated with its anteroventral element (latter seen in external view). Length of anteroventral plate, 6.2 cm. E. Proximal left segment of a pectoral appendage articulated with its anteroventral element (latter seen in external view). Length of anteroventral plate, 6.3 cm. F. Internal molds of left anterodorsolateral plate (upper) and left posteroventral plate (lower).

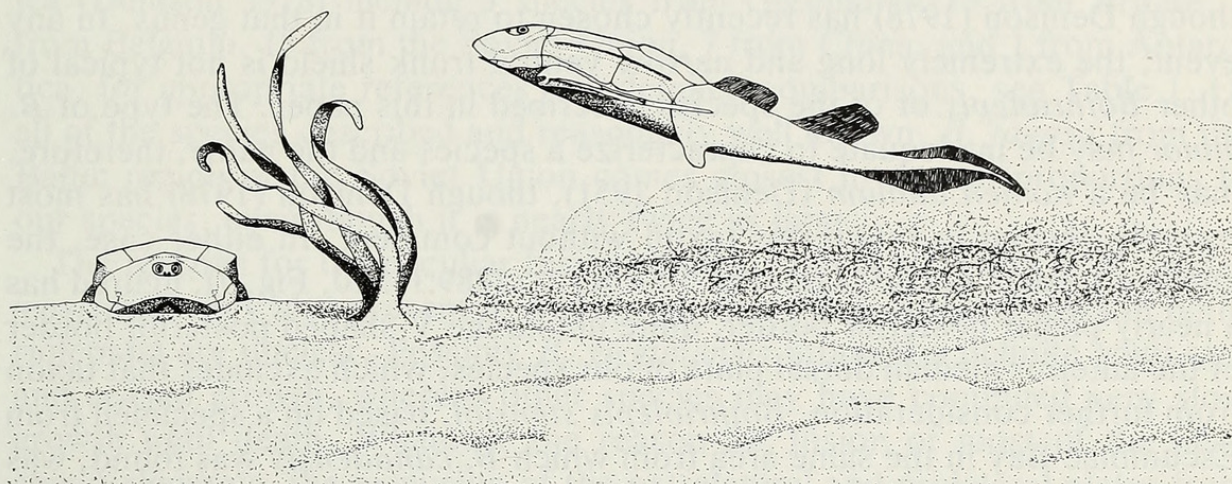


Fig. 8. Attempt at restoration of *Bothriolepis virginiensis* based on Figs. 4 and 5. Jaws and tail are based on the restorations given in Stensio (1948); plant hypothetical. Note the lack of a prominent ridge on the anterior median dorsal plate in both lateral and anterior views and the relatively close-set eyes. Length of the species estimated to be about 25 cm.

length, which overlaps the mixilateral plates (Stensio 1948). *Wudinolepis* is distinctive for its possession of a rostral circumorbital ridge and possibly for its small size (total shield length less than 2 cm) (Chang 1965). *Yunnanolepis* is distinctive with its very short premedian plate and correspondingly quite long postpineal and nuchal plates (Liu 1963); this genus may not be a bothriolepid at all (Zhang 1980). All of these character states are quite different from those present in our species, which agrees entirely with the definition of the genus *Bothriolepis* (Denison, 1978) as currently recognized.

The first species of *Bothriolepis* described from North America was *B. nitida* (Leidy, 1856a, 1856b), from the Chemung Formation of the Appalachian Mountains of Pennsylvania. Subsequently, six other species have been described: *B. canadensis* from the Escuminac Formation, Escuminac Bay, Quebec (Whiteaves 1880; Stensio 1948); *B. minor* from the Oneonta, Chemung, and Catskill formations of New York and Pennsylvania (Newberry 1889); *B. coloradensis* from the Elbert Formation of Colorado (Eastman 1904; Denison 1951); *B. traquairi* from the Escuminac Formation, Quebec (Bryant 1924); *B. stensioi* (Sohn, 1938) from the Escuminac Formation, Escuminac Bay, Quebec; and *B. darbiensis* from the Darby Formation, Wyoming (Denison 1951). Of these seven taxa, *B. traquairi* is so different from the others that it has generally not been considered to be a valid member of the genus *Bothriolepis* (Stensio, 1948; Denison, 1951),

←

Length of anterodorsolateral plate, 4.8 cm. G. Internal view of left posteroventral plate. Length 6.8 cm. H. Internal view of left posteroventral plate; length, 5.8 cm. Crossopterygian scale at base.

though Denison (1978) has recently chosen to retain it in that genus. In any event, the extremely long and narrow ventral trunk shield is not typical of other *Bothriolepis* or of the species described in this paper. The type of *B. minor* may be inadequate to characterize a species and the name, therefore, may be a *nomen dubium* (Denison 1951), though Denison (1978) has most recently chosen to retain this taxon without comment. In either case, the anterior median dorsal plate that Newberry (1889:Pl. 20, Fig. 7), figured has a nearly planar posterior border, quite unlike the V-shaped posterior border of the anterior median dorsal plate of our species, which excludes that taxon from further consideration. *Bothriolepis stensioi*, based on a specimen from Escuminac Bay in the same area from which *B. canadensis* was found, was considered by Robertson (1938) to be only a variant of *B. canadensis*. This conclusion seems quite probable in view of the range of variability later documented in the osteology of *B. canadensis* by Stensio (1948) and in the sensory line system by Graham-Smith (1978). Neither Stensio (1948) nor Denison (1951, 1978) recognized *B. stensioi* and it is here considered to be a synonym of *B. canadensis*. *Bothriolepis canadensis* differs from our new species in the following traits: 1, the head shield elements are unfused, even in large specimens; 2, the premedian plate is not as elongated anteroposteriorly; 3, the orbital fenestra is constricted along the midline, giving it a peanut shape; 4, the posterior oblique cephalic pit lines meet much farther posteriorly on the centronuchal plate, nearly at the obteched nuchal area; 5, the border between the anterior and posterior median dorsal plates is only gently arched into a C-shaped configuration; 6, a median dorsal crest is well developed on the anterior median dorsal plate; 7, the semilunar plate appears to be much narrower than the corresponding element in our species; and 8, the maximum size attained is almost 50% greater than that indicated for our species, which is assumed to be adult since the head shield elements are fused. *Bothriolepis coloradensis* and *B. darbiensis* differ from our species in the presence of a Y-shaped configuration of the postlevator crests on the ventral surface of the anterior median dorsal plate, resulting from these crests meeting anterior to the anterior ventral pit and then extending posteriorly along a common ridge toward that pit. In our species the ridges extend independently to the anterior ventral pit and merge with it from both sides, resulting in a W-shaped configuration (Fig. 3). Additionally, both species attain a size about 50% larger than our species. *Bothriolepis nitida* is poorly known, although additional material from the type area has been uncertainly referred to that species. The type-specimen, consisting of a distal pectoral segment, differs from the corresponding element of our species by having prominent spines along its lateral border and by its size, which suggests it came from an animal at least 50% larger than our species.

Accepted species of *Bothriolepis* described from outside of North Amer-

ica (Denison 1978) include 3 species from Greenland, 15 from Britain, 1 from Belgium, 15 from the Soviet Union, 7 from China, and 1 from Antarctica; for appropriate references and detailed comparisons, see Table 1. Of all of the species described and reasonably well known, *B. favosa* from the Baltic region of the Soviet Union comes closest in overall proportions to our species, even though it is nearly twice as large.

The reasons for the peculiar fusion of most cranial elements in *B. virginiensis* (possibly also present in *Dianolepis*, but otherwise unknown in bothriolepids) are unclear. Possibly *B. virginiensis* attained a definite adult size and ceased growth, whereas other species may have continued very slow growth until death. Whatever the reason for fusion of most of the head shield elements, the exclusion of the extralateral and prelateral plates from this pattern seems clear; these plates border the mouth and obviously needed to be mobile during feeding (and respiration?). Intracranial mobility of the remaining elements of the head shield was apparently not necessary for the survival of this species.

The greatest diversity of bothriolepids is in China, and the only occurrences which may be as old as Middle Devonian come from there as well. China may be the center of bothriolepid evolution, with only the most vigorous forms gaining worldwide distribution late in the Devonian. Since North America, even allowing a pangean distribution of the Paleozoic land masses, would have been quite distant from China, the lack of any genus of bothriolepid in North America except *Bothriolepis* may reflect paleogeographic effects rather than an uneven pattern of collection and identification by paleoichthyologists.

Table 1 shows that the family Bothriolepidae has a mosaic distribution of character states, indicating that extensive parallel evolution has occurred in this group. Because the age distribution of these species in the Devonian is poorly known, we consider it to be premature to try to sort out which characters are of phylogenetic importance and which are not. Therefore, no attempt is made here to sort out the detailed evolutionary history of the family.

Paleoecology of *Bothriolepis virginiensis*

Species of the genus *Bothriolepis*, with their catfish-like shape and proportions, have been generally interpreted to have been mudgrubbing animals (Denison 1941). Because remains of this genus are largely, though not entirely, found in freshwater to brackish deposits, its preferred habitats have been assumed to be freshwater rivers and perhaps lakes (Denison 1978). These interpretations could be reasonably applied to *B. virginiensis* as well.

The presence of occasional scattered scales of at least one species of crossopterygian (Fig. 7H) makes it plausible to suggest that these animals may have been the chief predators upon *Bothriolepis*. Generally, Paleozoic

Table 1.—Comparison of selected characters in the species of the family Bothriolepidae. Location of the posterior cephalic pit line is determined by measuring the distance from the front of the obstructed nuchal area to where the pit lines meet and dividing that by the distance from the obstructed nuchal area to the rear of the postpineal plate along the midline, and multiplying the resulting ratio by 100. Other ratios multiplied by 100 as well. Configuration of the

	Location of posterior cephalic pit line	Rostrum/ head shield length	Orbit shape (width/length)	Premedian plate (width/ length)	Head shield elements
British Species					
1) <i>Bothriolepis alvesiensis</i>	28	35	180–190	~115	unfused
2) <i>B. cristata</i>	38	38	275	~100	unfused
3) <i>B. gigantea</i>	36	36	215	100–105	unfused
4) <i>B. hayi</i>	33	40	185	110	unfused
5) <i>B. hicklingi</i>	22	44	200	110	unfused
6) <i>B. hydrophila</i>	21–32	34	205–235	>100	unfused
7) <i>B. laverocklochensis</i>	31	~38	265	?	unfused
8) <i>B. leptocheira</i>	28	37	200	114–128	unfused
9) <i>B. macrocephala</i>	?	?	?	?	?
10) <i>B. major</i>	?	?	?	?	?
11) <i>B. obesa</i>	?	?	?	?	?
12) <i>B. paradoxa</i>	29	?	?	?	unfused
13) <i>B. stevensoni</i>	?	?	?	?	unfused
14) <i>B. taylori</i>	33	?	?	95–100	unfused
15) <i>B. wilsoni</i>	31	42	205	95	unfused
16) <i>Grossilepis brandi</i>	?	?	?	?	unfused
Greenland Species					
17) <i>B. groenlandica</i>	26–47	40	165	100–125	unfused
18) <i>B. jarviki</i>	17–26	?	?	~110	unfused
19) <i>B. nielsenii</i>	?	?	?	?	?
Soviet Species					
20) <i>B. cellulosa</i>	18	43	205	85	unfused
21) <i>B. ciecere</i>	0	38	?	115	unfused
22) <i>B. curonica</i>	35?	~37	~145	~115	unfused
23) <i>B. extensa</i>	?	?	?	?	?
24) <i>B. favosa</i>	43	40	200	105	unfused
25) <i>B. jeremijevi</i>	?	?	?	?	?
26) <i>B. maendrina</i>	?	?	?	?	?
27) <i>B. maxima</i>	30	44	180	110	unfused
28) <i>B. obrutschewi</i>	?	?	?	?	unfused
29) <i>B. ornata</i>	?	?	?	?	?
30) <i>B. pavariensis</i>	38	~33	200	~175	unfused
31) <i>B. prima</i>	?	?	?	?	?
32) <i>B. sibirica</i>	?	?	?	?	?
33) <i>B. turanica</i>	?	?	?	?	?
34) <i>Grossilepis spinosa</i>	45	?	?	?	unfused
35) <i>G. tuberculata</i>	22	40	180	95	unfused

levator fossa is discussed in the text, as is the configuration of the posterior border of the anterior median dorsal plate. Lengths of fragmentary species were roughly computed by comparing the size of elements of each species (usually the anterior median dorsal plate) with the same element of *B. virginensis* and making appropriate scaling corrections. Sources of data for each species are indicated at the end of the table.

Distal fin segment		Anterior median dorsal plate					Total length of armor (cm)
		Levator fossa			Median keel	Posterior border shape	
External lateral margin	Width/Length	Width/Length	Width/Length	Shape			
?	?	70	?	?	low	^	18-19
nearly smooth	23	~110	?	?	very high	^	10
smooth	~15	~95	?	?	low	^	≥40
sparsely spiny	21	80	195	W	low	^	15
nearly smooth	?	~90	155	W	low	^	~20
smooth	24	87-95	235	W	high	^	≥10
?	?	~95	?	?	high	^	≥11
sparsely spiny	17	~75	95	W	low	^	14
?	?	~135?	?	?	?	?	2.5
?	?	?	?	?	?	?	~12
?	?	~100	125	Y	high	—	~25
nearly smooth	?	~90	160	W	low	^	20
?	?	~80	65	W	low	?	~25
spiny	15	~95	?	?	low	^	25
?	?	~95	?	?	high	—	30
?	?	?	?	?	?	?	~7
sparsely spiny	24	75-100	100-140	W	high	^	36
spiny	21	68-80	80	W	low	^	27
smooth	20	~90?	?	?	low?	?	12
spiny	22	80-93	130	W	low	^	19
?	?	~80	140	Y	low	^	~8
?	?	82-94	?	?	none	^	24
?	?	?	?	?	?	^	~12
?	?	82-93	130	W	low	^	23
?	?	?	?	?	?	^	~11
spiny	25	?	?	?	?	?	?
sparsely spiny	16	~95	130	W	low	^	50
?	?	?	?	?	?	?	~10
?	?	80	?	?	low	^	~25
?	?	~95	140	Y	low	^	~13
?	?	~100	90	W	?	?	~7
?	?	?	?	?	low?	^	~14
?	?	?	?	?	very high	?	~6
?	?	?	105	W	?	?	~15
spiny	?	~70-80	100	W	low	^	~11

Table 1.—Continued.

	Location of posterior cephalic pit line	Rostrum/ head shield length	Orbit shape (width/length)	Premedian plate (width/ length)	Head shield elements
Chinese Species					
36) <i>B. kwangtungensis</i>	?	?	?	?	?
37) <i>B. lochangensis</i>	?	?	?	?	unfused
38) <i>B. niushoushanensis</i>	20	45	215	135	unfused?
39) <i>B. shaokuanensis</i>	25	36	175	~100	unfused
40) <i>B. sinensis</i>	?	?	?	?	?
41) <i>B. tungseni</i>	?	~38	~175	?	?
42) <i>B. yunnanensis</i>	?	?	~	?	?
43) <i>Dianolepis liui</i>	15	29	190	140	fused?
44) <i>Wudinolepis weni</i>	?	~40	~140	?	unfused?
45) <i>Yunnanolepis chii</i>	?	22	200	230	unfused
Australian Species					
46) <i>Hillsaspis gippslandiensis</i>	20	?	?	?	unfused
Antarctic Species					
47) <i>B. antarctica</i>	?	?	?	?	?
Belgian Species					
48) <i>B. lohesti</i>	?	?	?	?	?
American Species					
49) <i>B. canadensis</i>	5	34	230	118	unfused
50) <i>B. coloradensis</i>	?	?	?	?	unfused
51) <i>B. darbiensis</i>	45	?	?	?	unfused
52) <i>B. minor</i>	?	?	?	?	?
53) <i>B. nitida</i>	?	?	?	?	?
54) <i>B. traquairi</i>	?	?	?	?	?
55) <i>B. virginensis</i>	40	47	170	93	fused

References. 1) Miles 1968, Stensio 1948; 2–8) Miles 1968; 9) Miles 1968, Egerton 1862, Stensio 1948; 10–16) Miles 1968; 17) Stensio 1948, Heintz 1930; 18–19) Stensio 1948; 20) Stensio 1948; 21) Lyarskaia and Savvaitova 1974; 22) Stensio 1948, Gross 1942; 23) Sergienko 1961; 24) Stensio 1948; 25) Rohon 1900; 26) Hoffman 1911; 27) Stensio 1948; 28) Stensio 1948, Gross 1942; 29) Stensio 1948; 30) Lyarskaia and Savvaitova 1974; 31) Stensio 1948, Gross 1942; 32) Obruchev and Sergienko 1961; 33) Obruchev 1939, Stensio 1948; 34) Stensio 1948, Gross 1942;

crossopterygians have impressive dental batteries, and they were probably quite capable of attacking a *Bothriolepis* of the relatively modest size of *B. virginensis*.

Another, probably spurious report of a Paleozoic fish from Virginia.—At present, *B. virginensis* is the oldest vertebrate animal from Virginia well enough known to be even tentatively reconstructed. Putative fish remains

Table 1.—Continued.

Distal fin segment		Anterior median dorsal plate					Total length of armor (cm)
		Levator fossa			Median keel	Posterior border shape	
External lateral margin	Width/Length	Width/Length	Width/Length	Shape			
?	?	50–52	45	W	high	^	~16
?	?	105–115	130	W	low	—	~7
spiny	22	45	?	?	high	—	~15
?	?	?	?	?	?	?	~8
?	?	~70–80	100	W	?	?	~11
smooth	~15	80–90	?	?	low?	?	~12
?	?	80–85	100	W	high	—	~12
?	?	?	?	?	very high	?	~18
?	?	<100	?	?	high	?	<2
?	?	?	?	?	?	?	~12
spiny	~20	~105	325	W	very high	—	~10
spiny	~20	?	?	?	high	^	~9
?	?	~100–105	155	W	low	—	~10
spiny	24	mostly 90–95	185	W	high	—	19
?	?	~95	170	Y	?	?	~20
smooth	21	?	150	Y	?	?	~20
?	?	±90?	?	?	low	—	~8
spiny	19	±90–100?	?	?	low?	?	~20
?	?	?	?	?	?	?	~8?
distally smooth	19	~85	140	W	low	^	13

35) Stensio 1948; 36–37) P'an 1964; 38) Pan 1980; 39) Chang 1963; 40) Stensio 1948, Chi 1940; 41) Chang 1965; 42) Liu 1962; 43–44) Chang 1965; 45) Liu 1963; 46) Hills 1931, Stensio 1948; 47) Woodward 1921, Stensio 1948, White 1968; 48) Leriche 1931, Stensio 1948; 49) Stensio 1948, Denison 1951; 50–51) Denison 1951; 52) Newberry 1889, Denison 1951, Stensio 1948; 53) Leidy 1856a, 1856b, Denison 1951, Stensio 1948; 54) Bryant 1924; 55) this report.

from the Middle and Upper Ordovician Martinsburg Shale ("Formation No. III") near Lexington, Virginia, cited by Rogers (1882) are much older but are of very questionable validity. Rogers' specimens could not be found, but the remains were quite fragmentary, judged by their description. An attempt was made by Weems to relocate one of Rogers' localities, but the only fossils found in the indicated interval were fragments of graptolites.

Because cleavage in the rock was subparallel to bedding, most of the graptolite specimens broke out of the rock as carbonized rhomboidal fragments rather than as whole specimens. These rhomboids look rather like fish scales and may be what Rogers collected, because he did not report graptolite remains from these beds. Because other definitely known Ordovician fish localities seem to be in shallow marine environments (e.g., Eliuk 1973), fish in the deep-water Martinsburg flysch deposits are anomalous. Therefore, although Rogers' report cannot be refuted unless his specimens are relocated, it seems best for now to consider his a spurious report of Ordovician fish remains.

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Appendix 1

Measured section in Chemung Formation (Upper Devonian) along U.S. 522 (southwest side) at Hunting Ridge, Frederick County, Virginia; southeast end of outcrop. Color designations (in parentheses) based on the Rock Color Chart of the National Research Council (Goddard and others 1948).

Bed	Lithology	Thickness		
		ft.	in.	m
73	Shale and siltstone, medium-gray (N5) to grayish-orange (10YR7/4), partly covered by talus and complexly faulted	153	0	46.65
72	Shale, medium-gray (N5), fissile	4	8	1.42
71	Sandstone, coarse-grained, medium-gray (N5)	0	2	0.05
70	Siltstone and shale interbedded, medium-gray (N5)	10	4	3.20
69	Shale, medium-gray (N5), partly covered by talus	56	4	17.17
68	Sandstone, medium- to coarse-grained, light-gray (N7), containing layers of brachiopod molds	11	10	3.61
67	Shale, medium-gray (N5) silty, containing cobbly layer 10 in. (0.25 m) below top	8	11	2.72
66	Siltstone, medium-gray (N5), sandy	3	11	1.19
65	Siltstone, variegated grayish-brown (5YR3/2)	4	6	1.37
64	Siltstone, medium-gray (N5), sandy to shaly and with a few fine-grained sandstone and shale interbeds	9	3	2.82
63	Siltstone, grayish-brown (5YR3/2), sandy to shaly and with a few fine-grained sandstone and shale interbeds	13	1	4.00
62	Sandstone, medium-grained, medium-gray (N5), 4 in. (0.10 m) conglomerate at base, plant fragments just above the conglomerate	17	9	5.41
61	Siltstone, medium-gray (N5) to greenish-gray (5GY6/1), shaly, fissile	1	2	0.36
60	Siltstone, grayish-brown (5YR3/2), shaly, fissile	9	4	2.84

Appendix 1.—Continued.

Bed	Lithology	Thickness		
		ft.	in.	m
59	Sandstone, fine-grained, grayish-brown (5YR3/2)	0	5	0.13
58	Siltstone, grayish-brown (5YR3/2), shaly to sandy	23	0	7.02
57	Siltstone, grayish-brown (5YR3/2)	3	0	0.91
56	Sandstone, fine-grained, medium-gray (N5)	0	6	0.15
55	Shale, greenish-gray (5GY6/1) to grayish-brown (5YR3/2), silty, fissile	0	10	0.25
54	Sandstone, fine-grained, medium-gray (N5), massive	1	6	0.46
53	Shale, silty, and sandstone, fine-grained, interbedded, grayish- brown (5YR3/2)	17	9	5.42
52	Sandstone, fine-grained, grayish-brown (5YR3/2), silty, containing placoderm plates	1	11	0.58
51	Siltstone, grayish-brown (5YR3/2)	4	4	1.32
50	Shale, medium-gray (N5) to greenish-gray (5GY6/1) containing scattered placoderm plates and occasional linguloid brachiopod shells	2	0	0.61
49	Sandstone, fine-grained, light-gray (N7), massive, varying in thickness from 3 to 24 inches because upper surface has a rolling, sinusoidal geometry (ripples?); average thickness is	0	9	0.23
48	Shale, silty, fissile, siltstone, sandy, and sandstone, fine-grained, silty, thinly interbedded, grayish-brown (5YR3/2)	4	7	1.40
47	Sandstone, fine- to medium-grained, silty, and shale, silty, medium-gray (N5)	7	1	2.15
46	Shale, silty, and sandstone, fine-grained, silty, grayish-brown (5YR3/2)	7	10	2.40
45	Shale, greenish-gray (5GY6/1)	2	11	0.89
44	Sandstone, fine-grained, medium-gray (N5)	0	1	0.03
43	Siltstone, medium-gray (N5)	3	9	1.14
42	Siltstone, grayish-orange (10YR7/4)	0	3	0.08
41	Shale, medium-gray (N5) to grayish-orange (10YR7/4), silty, containing molds of crinoid columnals	2	2	0.66
40	Sandstone, medium-grained, medium-gray (N5) to grayish-orange (10YR7/4), crossbedded in upper part, containing plant fragments in lower part	6	11	2.11
39	Shale, silty, fissile, sandstone, fine-grained, and siltstone, shaly, fissile, thinly interbedded, ranges in color from light-gray (N7) to dark gray (N3)	20	6	6.26
38	Sandstone, fine-grained, light-gray (N7), massive, containing plant debris in upper part, crinoid columnal molds at base	0	10	0.25
37	Shale, dark-gray (N3), fissile, containing light-gray (N7) fine- grained sandstone partings	0	6	0.15
36	Sandstone, medium-grained, medium-gray (N5), massive, containing crinoid columnal molds	3	6	1.07
35	Shale, dusky-blue (5PB3/2), fissile	0	2	0.05
34	Sandstone, fine-grained, light-gray (N7)	0	4	0.10
33	Shale, medium-gray (N5), silty	0	3	0.08

Appendix 1.—Continued.

Bed	Lithology	Thickness		
		ft.	in.	m
32	Sandstone, medium-grained, greenish-gray (5GY6/1), massive, containing abundant plant fragments in lower half	6	2	1.88
31	Sandstone, fine-grained, siltstone, sandy, and shale, silty, fissile, thinly interbedded, medium-gray to light-gray	7	3	2.21
30	Sandstone, fine-grained, light-gray (N7), cobbly	0	8	0.20
29	Shale, medium-gray (N5)	1	3	0.38
28	Siltstone, dusky-blue (5YR3/2), massive	4	1	1.24
27	Sandstone, fine-grained, silty, and shale, fissile, thinly interbedded, medium-gray (N5)	18	9	5.70
26	Sandstone, fine-grained, medium-gray (N5) to grayish-orange (10YR7/4), massive, containing molds of brachiopods and crinoid columnals just below top	1	2	0.36
25	Shale, grayish-brown (5YR3/2) to greenish-gray (5GY6/1), silty . .	0	2	0.05
24	Sandstone, fine-grained, grayish-brown (5YR3/2) to greenish-gray (5GY6/1), massive	1	4	0.41
23	Shale, grayish-brown (5YR3/2)	0	7	0.18
22	Sandstone, fine-grained, medium-gray (N5)	0	3	0.08
21	Shale, grayish-brown (5YR3/2)	0	6	0.15
20	Sandstone, fine-grained, medium-gray (N5), massive	2	8	0.81
19	Siltstone, medium-gray (N5), alternating with bands of fine-grained, medium-gray (N5) sandstone	4	3	1.30
18	Shale, variegated grayish-brown (5YR3/2), light-brown (5YR6/4) and medium-gray (N5), crumbly	14	2	4.32
17	Sandstone, fine-grained, grayish-orange (10YR7/4), containing brachiopod molds	0	10	0.25
16	Shale and siltstone, grayish-brown (5YR3/2), fissile	7	4	2.23
15	Shale, light-gray (N7)	0	11	0.28
14	Shale, medium-gray (N5) to grayish-orange (10YR7/4), fissile	1	9	0.53
13	Sandstone, fine-grained, medium-gray (N5), silty	0	6	0.15
12	Siltstone, light-gray (N7), crumbly	0	2	0.05
11	Sandstone, fine-grained, medium-gray (N5), silty, massive	5	5	1.65
10	Siltstone and shale, fissile, medium-gray (N5)	20	10	6.35
9	Sandstone, fine-grained, medium-gray (N5), shaly	1	3	0.38
8	Shale, medium-gray (N5), fissile	1	9	0.53
7	Siltstone, grayish-orange (10YR7/4)	0	5	0.13
6	Shale, medium-gray (N5), fissile, containing fine-grained sandstone partings	8	1	2.46
5	Sandstone, fine-grained, grayish-orange (10YR7/4), silty	4	7	1.40
4	Shale, grayish-orange (10YR7/4), fissile	1	6	0.46
3	Sandstone, fine-grained, grayish-orange (10YR7/4), shaly	0	10	0.25
2	Shale, greenish-gray (5GY6/1) to light-brown (5YR6/4), crumbly ..	61	10	18.85
1	Covered to end of culvert, northwest end of outcrop	74	0	22.56
Total thickness		677	4	206.49



Weems, R. E., Beem, Kenneth A., and Miller, T A. 1981. "A new species of *Bothriolepis* (Placodermi: Bothriolepidae) from the Upper Devonian of Virginia (USA)." *Proceedings of the Biological Society of Washington* 94, 984–1004.

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