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Source: Proceedings of the Academy of Natural Sciences of Philadelphia, 161(1):191-203.

Published By: The Academy of Natural Sciences of Philadelphia

<https://doi.org/10.1635/053.161.0111>

URL: <http://www.bioone.org/doi/full/10.1635/053.161.0111>

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Mass mortality of juvenile antiarchs (*Bothriolepis* sp.) from the Catskill Formation (Upper Devonian, Famennian Stage), Tioga County, Pennsylvania

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ABSTRACT.—We analyze a new sample of very small *Bothriolepis* from the Catskill Formation (Upper Devonian, Famennian Stage) in Tioga County, Pennsylvania, USA. The material was collected in a series of rock slabs, each of which carries as many as thirty-one individuals in densely-packed groups with little to no overlap and with a preferred orientation. Although the taxonomy of Catskill *Bothriolepis* does not allow for a species diagnosis, morphometric comparison between the new sample and a growth series of *Bothriolepis canadensis* supports the juvenile status of the individuals in the new Catskill sample. By comparing the new material with other worldwide occurrences of small antiarchs, we recognize anatomical features that indicate juvenile status in antiarchs, including a large median ventral fenestra lacking a median ventral skeletal element, especially large medial serrations on the pectoral appendages, and a strongly convex rostral margin of the postpineal element. The geological and taphonomic context of the new material suggests death events of *Bothriolepis* hatchlings due to anoxia and desiccation in marginal aquatic environments. We highlight the implications for reproductive strategy in antiarchs.

Key words: *Bothriolepis*, antiarch, Catskill Formation, ontogeny

INTRODUCTION

We report here on the discovery of a large sample of very small individuals of *Bothriolepis* from the Catskill Formation (Upper Devonian, Famennian Stage) in Tioga County, Pennsylvania. *Bothriolepis* comprises a cosmopolitan collection of antiarch species restricted in time to the Middle-Late Devonian and found in a variety of paleoenvironments from nearshore marine into estuarine and freshwater depositional settings (Wang, 1993; Young, 1993; Vézina, 1996). The new Catskill Formation sample consists of more than two hundred individuals on rock slabs that carry as many as thirty-one individuals on a single bedding plane. The specimens are partial to complete, articulated, external skeletons that average 28 mm in length (head + trunk shield) and were deposited in densely packed groups with little to no overlap. These conditions of preservation and the morphological consistency among associated individuals indicate a collection of similar age

members of a single species. Here we hypothesize that the sample represents multiple death assemblages of young juveniles. Their occurrence is explained as cohorts of hatchlings in an ephemeral aquatic environment whose shrinking volume promoted crowding of the individuals prior to anoxia, desiccation, and death. The sample suggests a reproductive strategy of antiarchs that includes deposition of large numbers of eggs in shallow floodplain settings. We test our age class hypothesis using the developmental profile of *Bothriolepis canadensis*; we test our paleoenvironment hypotheses using sedimentological and taphonomic data.

Taxonomy.—All individuals in the Catskill sample are diagnosed as *Bothriolepis* sp. based on the combination of a nuchal element that contributes to the orbital margin and an anterior median dorsal element that is broader at its lateral corners than at the cranial or caudal ends (Stensiö, 1948; Young and Gorter, 1981). More precise taxonomic determination depends on the current status of previously

described species of Catskill Formation *Bothriolepis*. Of primary interest is whether the individuals of the new sample represent a new species with small adult body size, or whether they are juveniles of a previously described or undescribed species. Recent discussion of the status of Catskill Formation *Bothriolepis* plays out in a series of papers (Weems *et al.*, 1981; Thomson and Thomas, 2001; Weems, 2004) that do not come to any agreement on the problem.

A brief history of *Bothriolepis* taxonomy for the Catskill/"Chemung" Formations provides context for the current disagreements. Joseph Leidy (1856a, 1856b, 1856c) described *Stenacanthus nitidus* from a portion of the distal pectoral appendage recovered from the Catskill Formation near Mansfield, Tioga County, Pennsylvania. Leidy (1856b) also described, mistakenly, a partial antiarch mixilateral as a "branchiostegal plate" of *Holoptychius americanus* (Leidy, 1856b:164). Newberry (1889) described a new species, *Bothriolepis leidy*, from the Catskill Formation of Mansfield. He established this new species name despite acknowledging a synonymy with *Stenacanthus nitidus*. Newberry (1889) additionally described a second species, *Bothriolepis minor*, from the Late Devonian of Bradford County, Pennsylvania. This taxon, diagnosed by a smaller size and finer ornament than *Bothriolepis leidy*, is questioned or rejected outright by most authors (*e.g.*, Stensiö, 1948; Dension, 1951; Weems *et al.*, 1981; Thomson and Thomas, 2001). Cope (1891) described a distal pectoral appendage of *Bothriolepis* as *Holonema rugosa*, an error that was corrected by Eastman (1907). Cope (1892), recognizing the priority of Leidy's species name, changed the name of *Bothriolepis leidy* to *Bothriolepis nitidus*. In order to correct the gender disagreement between the two names of the binomial, Eastman (1907) changed the species name one more time to *Bothriolepis nitida*. Recently, *Bothriolepis nitida* has been used to refer to all (Thomson and Thomas, 2001) or nearly all (Weems, 2004) *Bothriolepis* material from the United States.

Weems *et al.* (1981) described *Bothriolepis virginienensis* from the "Chemung" Formation near Winchester, Virginia. The original diagnosis of *Bothriolepis virginienensis* included many characters that were within the range of variation observed in *Bothriolepis nitida*, a fact that prompted Thomson and Thomas (2001) to include all *Bothriolepis virginienensis* material in their emended diagnosis of *Bothriolepis nitida*. Weems (2004) resurrected the name *Bothriolepis virginienensis* with an emended diagnosis, wherein much emphasis is placed on a purported fusion among the elements of the head shield and the relative length dimensions therein. The species remains controversial, however, a result of small sample

size, a lack of detailed diagnosis, and perhaps ontogenetic factors. For example, the cluster analysis of Weems (2004:Fig. 2) includes only eight specimens and therefore does little to demonstrate the presence of two non-overlapping head shield morphs in the Catskill/"Chemung" Formations. Revision of *Bothriolepis* alpha taxonomy for the Catskill/"Chemung" Formations is beyond the scope of the present analysis, and the pervasive issues with species-level taxonomy of *Bothriolepis* require that we leave the individuals of the new sample undiagnosed, especially in light of ontogenetic issues that are developed below.

The current situation as regards the alpha taxonomy of Catskill Formation *Bothriolepis* is a microcosm of issues that plague the taxonomy of the group globally. The cosmopolitan distribution of *Bothriolepis* during the Late Devonian has always held the promise of biostratigraphic and paleobiogeographic utility. While *Bothriolepis* species have been used for Middle-Late Devonian biostratigraphic zonations in East Gondwana (Wang, 1993; Young, 1993), the group's potential has not been fully realized, in North America especially. This is almost certainly due to chaotic alpha taxonomy, the result of new species names being assigned for many new occurrences of the taxon. Despite its distribution, relatively few species of *Bothriolepis* are represented by complete individuals and fewer still are represented by large samples. As a result, type specimens can be single elements of the external skeleton (*e.g.*, *Bothriolepis obesa*, GSE 1239) or even a fragment of a single element (*e.g.*, *Bothriolepis stevensoni*, RSM 1859.33.644). Many species diagnoses for *Bothriolepis* are accordingly scant and lack discreet diagnostic characters. These problems are compounded by the conservative morphology of the dermal skeleton; difficulty in identifying autapomorphies translates to difficulty in diagnosing new material or re-diagnosing old specimens.

Geological and taphonomic setting.—During improvements to Route 15 (Interstate 99) in 2003 and 2004, engineers created a by-pass of the town of Covington, Tioga County, Pennsylvania, by relocating the road bed from the valley floor to the east side of the Tioga River along the western-facing slope of Pine Hill (Fig. 1). As the new roadway traversed the steep slope, a bench was cut into the hillside and side cast material from the excavations was used to create an apron upon which part of the road was built. This section of new road runs north-south through the northern limb of the east-west trending Blossburg Syncline so that the stratigraphic section along the Covington bypass includes the Lock Haven, Catskill, and Huntley Mountain Formations. This stratigraphic section is almost completely exposed in the cuts on the east side of the road and the geological units grade into one another conformably, documenting a transition (moving

up section, north to south) from marine to non-marine conditions, with a wide range of non-marine depositional settings during the Upper Devonian into the Lower Carboniferous.

The side cast material forming the apron of the new roadbed is the source of the specimens that are the subject of this study. The road building methods and a thorough exploration of the material along much of the Covington by-pass suggest that the side cast material was dumped near the location where it was excavated from the hillside. Thus, the current location of the material along the roadbed reliably reveals the original stratigraphic position. In the case of the small *Bothriolepis* material, all of the specimens were derived from an area of about 100 square meters on the debris slope adjacent to one part of the roadbed. Direct examination of the bedrock along the road cut from which the material was presumably derived has not revealed a mass mortality horizon with small *Bothriolepis in situ*. We have, however, documented and collected a mass mortality horizon of articulated, more typically “adult-sized” *Bothriolepis* (head + trunk length of large

individuals approximately 15 cm) from slightly lower in the same section. The location of the small-bodied fossils, as well as the lithologic character of their surrounding rock matrix, indicates that the study sample is derived from the upper half of the Catskill Formation. The formation, at this location, is approximately 300 meters thick and is undifferentiated with regard to member designation (Daeschler and Cressler, 2011).

The Catskill Formation of north-central Pennsylvania is a sequence of clastics that eroded westward and northwestward from the rising Acadian Mountains into a foreland basin on the North American craton (Faill, 1985) during the Late Devonian. The sediments of the Catskill Formation form a northwestwardly-thinning clastic wedge that is often referred to as the Catskill Delta, although it represents a variety of depositional environments from proximal terrestrial alluvial plains to distal basinal shales (Woodrow, *et al.*, 1995; Sevon, 1985). The external skeletons of the small *Bothriolepis* specimens are contained within slabs of red siltstone to fine sandstone with no clear sedimentary structures. These specimens are sometimes draped or enclosed by a thin layer of clay-sized sediment, suggestive of a mud drape deposited penecontemporaneously with the specimens.

Variation in lithology among the sandstone slabs suggests that the groups of individuals in the sample were not derived from a single mortality horizon, but rather represent multiple death assemblages from multiple stratigraphic and/or geographical positions. Interestingly, occurrences of articulated, small *Bothriolepis* have not been found elsewhere in the same section, or the region, although we found occurrences of abundant disarticulated remains of small *Bothriolepis* in the Catskill Formation during the construction of the Tioga Welcome Center 40 km to the north. Such occurrences presumably also represent mass mortality events, but in these assemblages, the remains were disarticulated and possibly hydrodynamically sorted subsequent to death.

The specimens of the study sample consist of articulated head and trunk shields including the pectoral appendages. They are closely-packed, non-overlapping, and demonstrate a preferred orientation (Fig. 2). The majority (57%) of specimens expose the ventral shield; this is likely due to the flatness of their ventral surfaces that, collectively, create a plane of weakness along which the rock slabs preferentially split. That the ventral surfaces of associated specimens rest in a single, shared plane is consistent with ventral/stable-side-down deposition. Dorsal-side-down deposition is unlikely to have yielded the same observation due to the domed nature of the trunk shield. This, combined with the non-overlapping, preferred orientation, indicates ventral/stable-side-down,

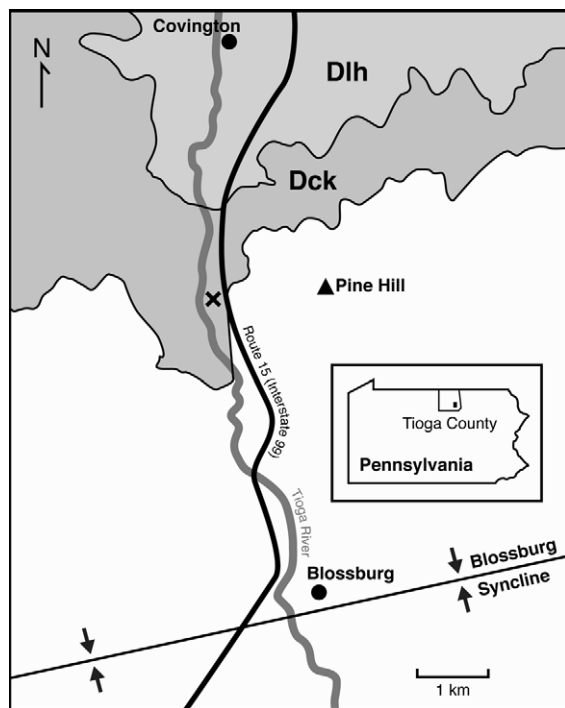


Fig. 1. Map of southeastern Tioga County, Pennsylvania, showing the location of the site (marked “x”) from which we recovered the sample of small *Bothriolepis*. The stratigraphic units in the north limb of the Blossburg Syncline include Dlh (Lock Haven Formation), Dck (Catskill Formation) and a series of younger units in the core of the syncline.

autochthonous, contemporaneous deposition of individuals on a single slab.

Institutional abbreviations.—ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum of Natural History, London; GSE, Institute of Geological Sciences, Scotland; RSM, Royal Scottish Museum, Edinburgh

Anatomical abbreviations.—ADL, anterior dorsal lateral; AMD, anterior median dorsal; AVL, anterior ventral lateral; DC1, dorsal central 1; La, lateral; MV, median ventral; MVf, median ventral fenestra; Mx1, mixilateral; Of, orbital fenestra; PMD, posterior median dorsal; Pn-M, paranuchal-marginal; Pp, postpineal; PrM, premedian; PVL, posterior ventral lateral; Sl, semilunar; VC1, ventral central 1.

Morphometric abbreviations.—LAMd, maximum length of the anterior median dorsal; LPrM, maximum length of the premedian; WAMd, maximum width of the anterior median dorsal; WaPMD, cranial width of the posterior median dorsal; WHs, maximum width of the head shield; WOf, maximum width of the orbital fenestra;

WoPrM, width of the orbital edge of the premedian; WPMd, maximum width of the posterior median dorsal; WrPrM, width of the rostral edge of the premedian; WTs, maximum width of the trunk shield.

MATERIAL AND METHODS

Specimens examined.—Catalogue numbers generally refer to rock slabs that may carry more than a single individual. ANSP 22129, ANSP 22336-22337, ANSP 22344, ANSP 23136-23140, ANSP 23142-23143, ANSP 23147, ANSP 23149-23150, ANSP 23152, ANSP 23154-23155, ANSP 23157, ANSP 23160-23162, ANSP 23165, ANSP 23167, ANSP 23172, ANSP 23174-23175.

Morphometric analysis.—Twenty-nine individuals of the Catskill sample were exposed dorsally and complete enough for us to collect relevant linear measurements (Fig. 3), although not all measurements were possible on all twenty-nine individuals. We used digital calipers for all measurements and recorded data to the nearest tenth of a millimeter. The narrow body size range of the Catskill sample prevented comparison of allometric growth trends between Catskill and Miguasha samples. Instead, for each of the seven significant allometric variable pairs listed below, each relevant individual from the Catskill sample was plotted against the regression line established by *Bothriolepis canadensis* based on data used by Werdelin and Long (1986). To fall on the regression line is to fit the allometric growth trend of *B. canadensis* and thus enable assessment of the relative growth stage of the Catskill individual. The variable pair of the Catskill individual was said to fall on the regression line if within the 95% prediction interval about the regression ($p < 0.05$). Prediction intervals are confidence intervals about the Y value predicted from a given X value. These were calculated using the 'Regression with Prediction Intervals' macro for Microsoft Excel (McClain, 2007). All measurements were converted to \log_{10} scale prior to manipulation in order to linearize the relationship between variable pairs.

Test for preferred orientation.—In order to test for a preferred orientation of associated individuals, we photographed each slab with more than six individuals and measured the orientation of each individual's midline relative to an arbitrary standard unique to the slab. The slabs were collected as float, and so the recorded angles of orientation pertain only to each slab individually and have no meaning among slabs. The total number of specimens on each slab studied for orientation ranges from six to thirty-one. Using the graphing software, Oriana, we generated rose diagrams comprised of eighteen sections, each representing a 20° range.



Fig 2. ANSP 23162, sandstone slab with multiple, associated, articulated external skeletons of *Bothriolepis* sp., in ventral view, from the Catskill Formation, Tioga County, Pennsylvania. scale bar = 1 cm.

RESULTS

Morphometric analysis.—Growth in antiarch placoderms has long attracted interest due to questions regarding their growth from within an enclosed space. In antiarchs, that enclosure is the result of cranial, trunk, and pectoral “armors,” each of which is a continuous shell of articulated dermal skeletal plates. If these external skeletal elements remain in articulation throughout growth, it follows that shape changes in a single plate must translate to shape changes within surrounding plates. Werdelin and Long (1986) quantified these ontogenetic shape changes for *Bothriolepis canadensis*, a taxon that often serves as the model antiarch due to the enormous sample (5000+ individuals) of articulated, complete skeletal specimens from the Escuminac Formation (Givetian/early Frasnian Stage; Miguasha, Quebec, Canada) that represent nearly all stages of ontogeny (Werdelin and Long, 1986). *Bothriolepis canadensis* therefore serves as the best source of growth data against which we may compare the new

sample of small specimens from the Catskill Formation. By comparing the size-shape characteristics of the small *Bothriolepis* from the Catskill sample with allometric growth data for *B. canadensis*, we address whether our sample demonstrates shape characteristics that are indicative of a juvenile growth stage in *Bothriolepis*.

Our analysis utilized morphometric data for *B. canadensis* that was collected by Werdelin and Long (1986) from 104 specimens at the Swedish Museum of Natural History (NRM) in Stockholm. From eighteen measurements of the cranial and trunk external skeletons, the authors tested for allometry in sixteen variable pairs and discovered significant allometric growth patterns (regression coefficient (slope) of \log_{10} transformed data significantly higher/lower than unity; $p < 0.05$) in seven of the sixteen. Certainly, this does not capture the full extent of skeletal allometry in *Bothriolepis*; nor is seven of sixteen a representative ratio of allometric to isometric growth trends within the skeleton. These seven allometric variable pairs, however, do contribute to our study the best means of identifying juvenile shape characteristics in *Bothriolepis*. In cases of isometric growth, shape does not change through ontogeny and, therefore, juvenile morphology is indistinguishable from adult morphology.

Of the seven allometric variable pairs identified in *B. canadensis*, two were found to be most significant ($p < 0.001$). The first, WOf/WHs, demonstrates that the relative size of the orbital fenestra decreased during ontogeny. The second, WHs/WTs, shows that the relative width of the head shield decreased with growth. The next most significant allometric variable pairs ($p < 0.01$) are WrPrM/WoPrM and TMs/WAMD. These communicate that the orbital edge of the premedian became relatively narrower and the anterior median dorsal became relatively wider during ontogeny. The remaining three significant allometric variable pairs show the least degree of allometry ($p < 0.05$). The first of these, LPrM/WrPrM, shows that the length of the premedian increases at a higher rate than does the rostral width of the element. The second, LAMD/WAMD, demonstrates that the width of the anterior median dorsal increases at a faster rate than does length of the element. The final allometric variable pair, WaPMD/WPMD, shows that, during growth, the greatest width of the posterior median dorsal increases at a higher rate than cranial width of the element.

For five of the seven allometric variable pairs (WOf/WHs, TMs/WAMD, LPrM/WrPrM, LAMD/WAMD, WaPMD/WPMD), the Catskill sample demonstrates juvenile morphology as predicted by *B. canadensis* (Fig. 4A–E). In these five cases, with the exception of a single shape characteristic in a single individual, the morphology of the Catskill individuals either fit the *B. canadensis* regression

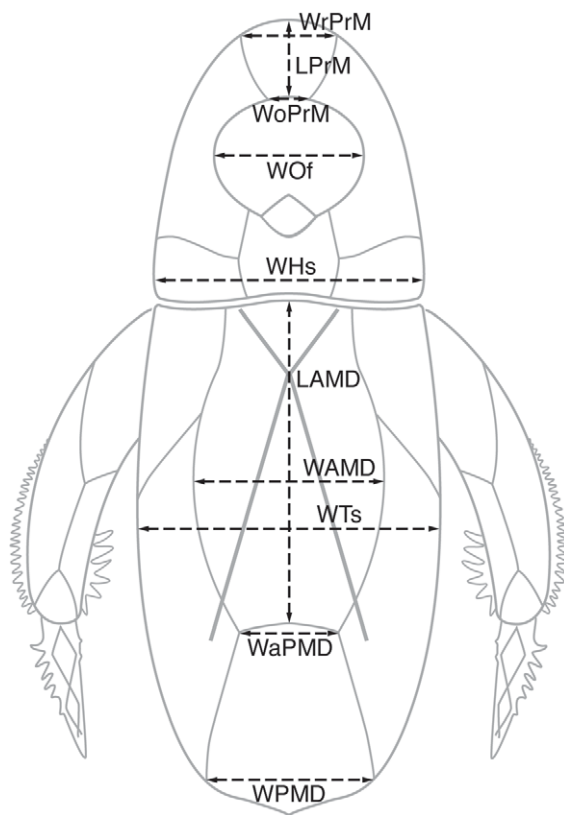
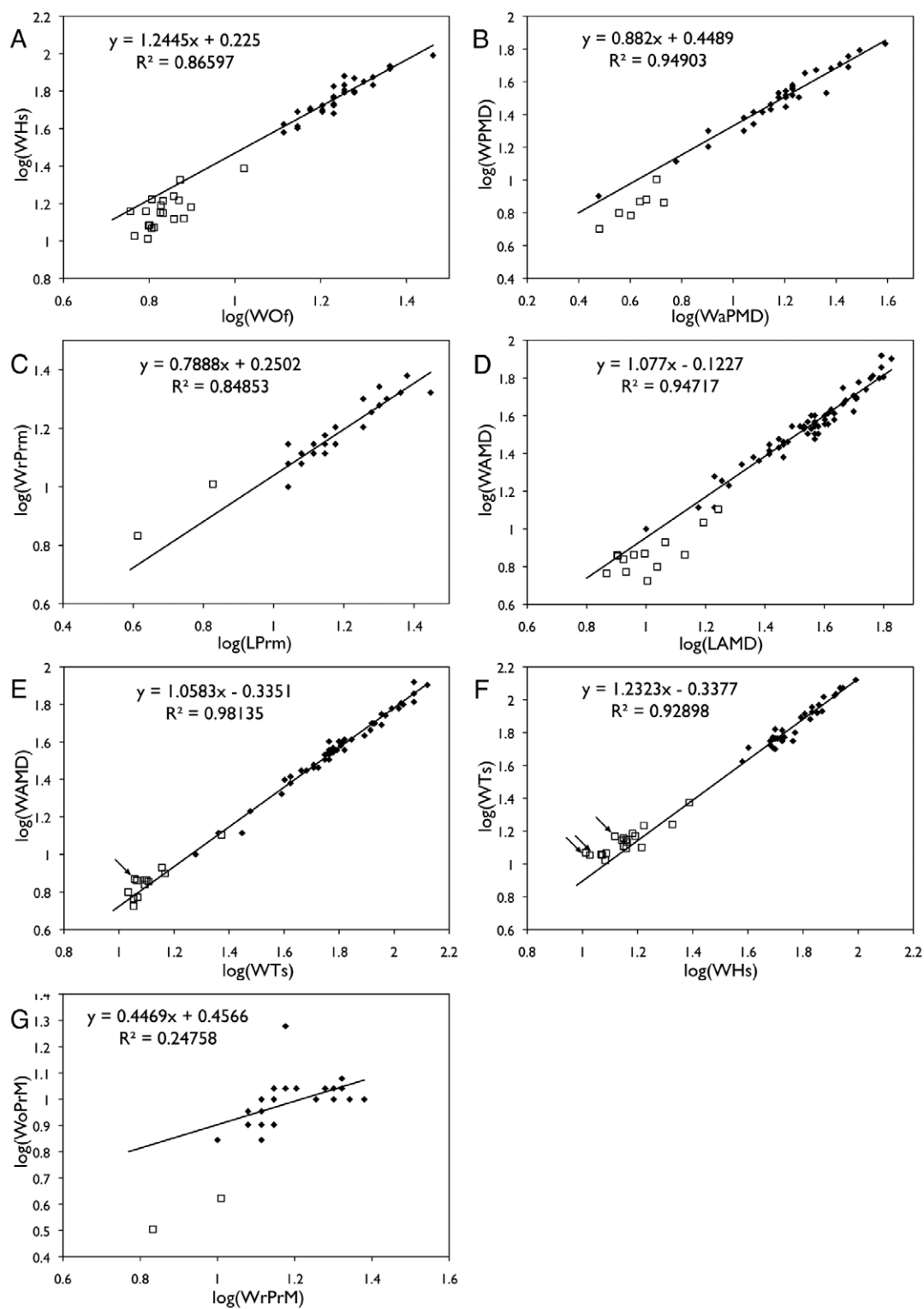


Fig. 3. External skeletal reconstruction, in dorsal view, of a juvenile individual in the Catskill sample. Arrows indicate the measurements used in the morphometric analysis.



line or demonstrated more extreme juvenile morphology than was predicted by *B. canadensis* (ie., a relative orbital width even greater than predicted for hypothetical same-sized individuals of *B. canadensis*). For these five variable pairs, the one exception (ANSP 23143) falls outside the expectations of juvenile morphology by exhibiting an anterior median dorsal element that is significantly wider than predicted by the trunk shield width (Fig. 4E). For the WHs/WTs variable pair, sixteen of the nineteen individuals measured fall on the regression line and therefore meet the expectations of juvenile *Bothriolepis* morphology. The remaining three exhibit morphology that is more adult-like (a relatively wide trunk shield, Fig. 4F). Post-mortem deformation may explain the several outliers. For the WrPrM/WoPrM variable pair, the measurements were only available on two specimens and both displayed more adult-like morphology than predicted (a relatively narrow orbital width of the premedian element, Fig. 4G). This particular result may be explained by the highly variable morphology of the premedian element in antiarchs (Young, 1984) and the correspondingly ill-defined relationship between WoPrM and WrPrM in *B. canadensis* ($R^2=0.25$). Throughout, disagreement between the Miguasha and Catskill samples is expected due to taxonomic distinctions and the fact that the *B. canadensis* regression did not include the

smaller body sizes represented in the Catskill sample.

Orientation study.—The cranial-caudal axes of at least 50% of the individuals on each of the six measured slabs were oriented within 60° one another (e.g., Fig. 5). Random orientation would find 16.67% of individuals within any 60° range. As a result, the Catskill sample visually demonstrates a preferred orientation. Two specimens, ANSP 23152 and 22336, show the strongest preferred orientation (67% of individuals within 60° of one another). See Table 1.

DISCUSSION

Characteristics of juvenile Bothriolepis.—Using a comparative context established by *Bothriolepis canadensis*, the morphometric study above highlights certain shape characteristics that are indicative of juvenile status in *Bothriolepis*, including a relatively large orbital fenestra and a relatively large head (Fig. 6). Stensiö (1948) recognized these morphometric characteristics in the smallest (dorsal length of trunk shield less than 40 mm) *B. canadensis* individuals. The Catskill sample exhibits several other features that Stensiö (1948) attributed to very young individuals: delicate dermal bones with ornament consisting of continuous anastomosing ridges rather than

Table 1. Orientation data for juvenile Catskill *Bothriolepis* individuals on six measured slabs.

Specimen number	Total number of individuals on slab	Greatest number of individuals within a single 60° range	Highest percentage of individuals within a single 60° range
ANSP 23136A	7	4	57%
ANSP 23138	10	5	50%
ANSP 23152	9	6	67%
ANSP 23162	31	16	52%
ANSP 23167	19	11	58%
ANSP 22336	6	4	67%

Fig. 4. (Page 196) Biplots of log-transformed morphometric data for *Bothriolepis canadensis* (filled diamonds) and the small Catskill *Bothriolepis* sp. (open squares). Because we are testing the juvenile status of the Catskill *Bothriolepis*, the linear regression lines describe the *B. canadensis* data alone. Regression equation and R^2 value appear above each plot. R^2 is the proportion of total variability in x that is explained by the variability in y, and is therefore used as an indication of the strength of the x-y relationship. A.-E. With the exception of one shape characteristic in one individual (WTs/WAMD in ANSP 23143, marked by arrow in E.), all Catskill individuals fit the *B. canadensis* regression line or demonstrate more extreme juvenile morphology than is predicted by *B. canadensis* (A., $n_1=32$, $n_2=20$; B., $n_1=34$, $n_2=7$; C., $n_1=25$, $n_2=2$; D., $n_1=61$, $n_2=13$; E., $n_1=50$, $n_2=13$). F. three of nineteen measured individuals (ANSP 22336.4, 23138.4, 23138.6; each marked by an arrow) exhibit more adult-like morphology than predicted ($n_1=30$, $n_2=19$). G. both measured Catskill individuals (ANSP 22336.1, 23154) exhibit more adult-like morphology than is predicted by *B. canadensis*; however, a low R^2 value (0.25) demonstrates that the relationship between these two variables, WoPrM and WrPrM, is ill-defined for *B. canadensis* ($n_1=23$, $n_2=2$). n_1 , sample size of measured *B. canadensis* individuals; n_2 , sample size of measured Catskill *Bothriolepis* individuals.

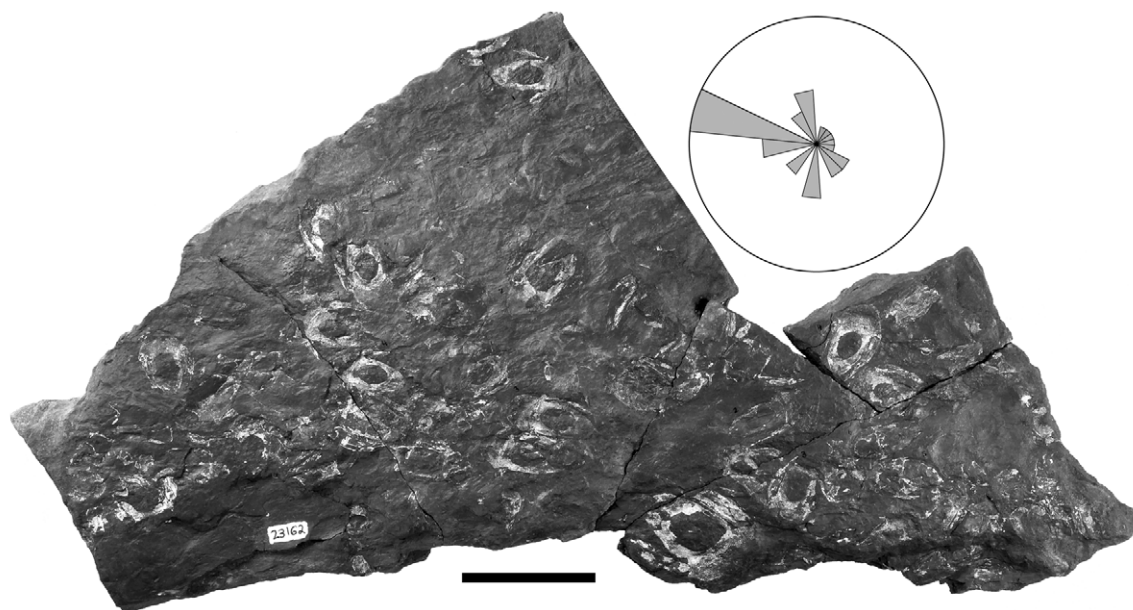


Fig. 5. ANSP 23162, sandstone slab with thirty-one associated, articulated external skeletons of *Bothriolepis* sp., in ventral view, from the Catskill Formation, Tioga County, Pennsylvania. This specimen served as one of six used in the orientation analysis. Rose diagram depicts relative body orientations of the thirty-one individuals on the slab. Visual evidence suggests a preferred orientation. Note the single individual of larger size and presumed later growth stage that retains the large, open median ventral fenestra of the smaller individuals. Scale bar = 5 cm.

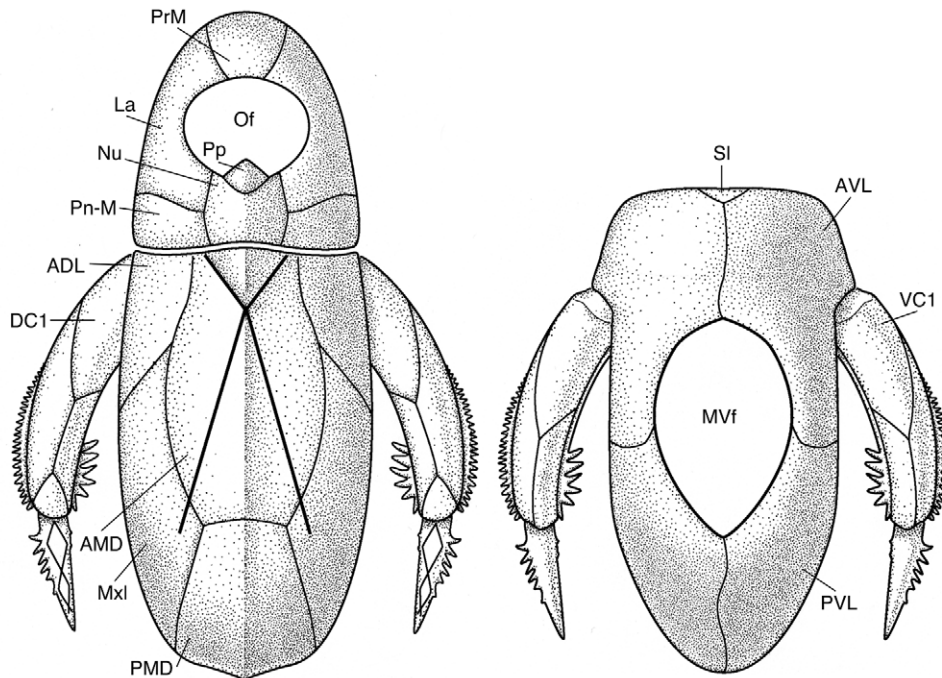


Fig. 6. External skeletal reconstruction of a juvenile individual in the Catskill sample in dorsal (left) and ventral (right) views. Illustration is a generalized depiction of a young juvenile based on the entirety of the sample.

tubercles, a dorsal trunk shield narrower than long and with a continuous and pronounced dorsal median ridge, and a premedian plate that is wider than it is long. When comparing the new sample of juvenile *Bothriolepis* from the Catskill Formation to other occurrences of small antiarchs worldwide, additional features are recognized that may be used to indicate juvenile status in antiarchs.

The juveniles of the Catskill sample exhibit a postpineal plate with a strongly convex rostral margin that protrudes well into the orbital fenestra and also exhibit especially strong development of spines (serrations) on the medial margin of the pectoral appendage (Fig. 7, 8B). Both of these are features observed in *Bothriolepis hydrophila*. Miles (1968) reviewed *B. hydrophila* from Upper Old Red Sandstone deposits and supported the assertion of Stensiö (1948) that the taxon is composed of juveniles of one or more species with larger adult sizes. In addition to the two mentioned above, Miles (1968) provides a list of juvenile features seen in *B. hydrophila* that are consistent with Stensiö's aforementioned observations of juvenile *B. canadensis*.

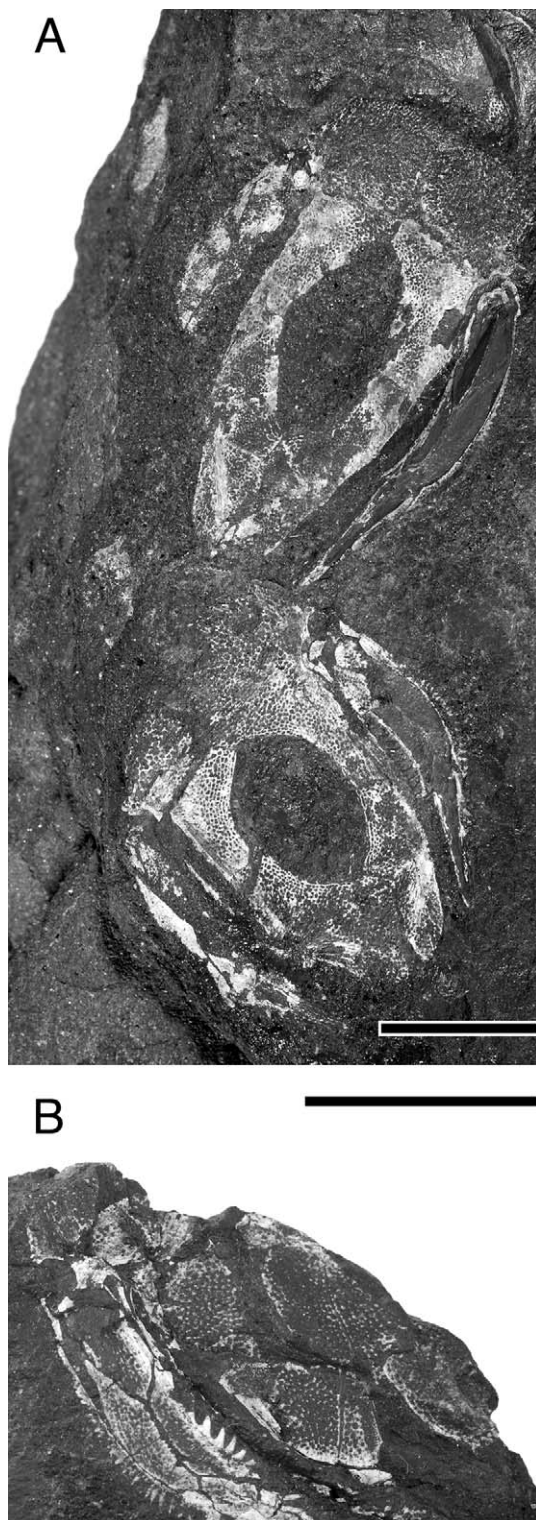
One of the most striking aspects of the trunk shield of the Catskill juveniles is an especially large median ventral fenestra that, in all specimens, is lacking the MV plate (Fig. 8A). The ratio of fenestra length to total trunk length is 0.48 (mean value for thirty-one individuals); the same ratio in a large "adult" Catskill *Bothriolepis* is 0.26 (ANSP 20923). The lack of an MV overlap zone on the visceral surface of the ventral trunk shield supports the lack of an MV element at this early life stage rather than the alternate possibility that the element is simply missing from all observed specimens. However, it remains possible that the MV began ossifying later than the remainder of the external skeleton and had yet to fill in the fenestra and articulate with the surrounding AVL and PVL elements. Prior to such articulation, the element would have been more susceptible to mobility and loss following death. A large, open median ventral fenestra appears in small, reportedly juvenile, individuals of the Antarctic bothriolepid, *Bothriolepis askinae* (Young, 1988). Young (1988) interpreted the presence of a very large MV plate through observation of especially long caudomedial and craniomedial margins of the AVL and PVL plates, respectively, rather than direct observation of the MV plate itself. As in the Catskill sample, no MV plates are reported for juvenile *B. askinae*. One of us (EBD) observed this same condition, a large median ventral fenestra and lack of an MV, in a single, juvenile specimen of *B. canadensis* (BMNH P6784: length of head + trunk shield = 32 mm). The large, open, median ventral fenestra in *Bothriolepis* juveniles may have accommodated an external yolk sac that was connected to the viscera via this ventral opening

in the trunk shield (J. Lundberg, pers. comm.).

Juvenile remains of the antiarch *Asterolepis ornata* from the Lode quarry in Latvia (Upeniece and Upenieks, 1992) demonstrate that aspects of the juvenile morphology indentified for *Bothriolepis* may be more broadly applicable to antiarchs in general. Adult-sized *A. ornata* (length of head + trunk shield \approx 300 mm) are found widely in the Lode quarry deposit, but one grey clay lens also produced many complete specimens of very young individuals, most with total head and trunk length between 11 and 18 mm. Upeniece and Upenieks (1992) recognize significant morphological differences between the juvenile and adult *Asterolepis* specimens at Lode. As in the Catskill juveniles and juvenile *B. canadensis*, the orbit



Fig. 7. ANSP 23143, external skeleton of juvenile *Bothriolepis* sp., in dorsal view, from the Catskill Formation, Tioga County, Pennsylvania. Note the large orbital fenestra, convex rostral margin of the postpineal, and narrow AMD. Scale bar = 1 cm.



and the head shield are proportionally larger in juvenile *A. ornata*, the “central part of the ventral wall of the youngest individuals” (Upeniec and Upenieks, 1992:171) lacks an MV plate; and the dermal elements, often deformed, suggest thin bone.

Reproductive biology of Bothriolepis.—The presence of multiple individuals on a single bedding plane suggests a group of individuals that died in a single event and were buried in place. Allochthony and time averaging may be dismissed on the basis of several observations. First, much of the material is in articulation, indicating a lack of transport and even most post-mortem disturbances like scavenging or the reworking of sediment. Second, there is no obvious variation in the preservation of the fossils, a quality that is used to identify a time-averaged sample (Fürsich and Aberhan, 1990). Finally, associated individuals are arranged on single bedding planes and the orientation of many individuals is influenced by surrounding individuals. These are indications of coeval burial. Time averaged samples tend to yield thicker zones of fossil-bearing strata (Johanson, 1998) and the orientation of more recently deposited specimens would show no relation to that of those previously buried.

Individuals of a single slab demonstrate a slight tendency toward a shared orientation in the plane upon which they rest (Table 1). On certain blocks, the individuals are densely distributed with groups lying side by side and with parallel body axes. Above, we use a shared orientation to indicate mass mortality events; this orientation also provides evidence regarding the circumstances of death. That these individuals died and were buried at the substrate surface and not within the water column is supported by their orientation. It is certainly true that environmental factors, a low-velocity current for example, could explain aspects of the preferred orientation. The flat ventral surface of *Bothriolepis* likely means that the stable resting orientation of an individual is dorsal surface up, and so this alone does not suggest death upon the substrate. Perhaps, the fact that many individuals do not comply with the preferred orientation is the best evidence against reworking of dead individuals by a current. Finally, contemporaneous deposition of all individuals from a single slab is inconsistent with individuals dying in the water column and accumulating on the substrate. The single plane of burial, the side-by-side crowding of individuals and resulting alignment of

Fig. 8. (left) External skeletons of juvenile *Bothriolepis* sp. from the Catskill Formation, Tioga County, Pennsylvania, **A**. ANSP 22129A, ventral shield in visceral view, note the open median ventral fenestra, **B**. ANSP 22129B, dorsal shield in visceral view, note the strong medial serrations on the pectoral appendage. Scale bars = 1 cm.

body axes point to an aggregation of individuals prior to death (Weigelt, 1989).

Because their orientation suggests that the individuals were lying upon the substrate at the moment of death, a likely explanation for the circumstances of death is that these animals were in a shrinking pool of water that ultimately dried or became too anoxic to support life. That the pool did not completely dry before death is supported by a thin layer of fine-grained sediment that is deposited directly upon the fossils. This sediment may have been settling out of the relatively still pool of water as it shrunk, serving as the immediate source of burial. Quick burial is supported by the articulation of the skeletons and the quality of preservation.

The preceding discussion establishes the sample as groups of juveniles that died in mass mortality events, thus prompting an interpretation of the reproductive strategy of *Bothriolepis*. Stream currents present a particular challenge to freshwater fish and anadromous fish when spawning. Without a strategy to escape strong currents, the flow of water will carry eggs downstream. One such strategy that is employed by some aquatic vertebrates involves the selection of a spawning/nursery site within the river system where the flow velocity is minimized (Groot and Margolis, 1991). The shallows of the channel, close to the banks, and small tributaries of the river offer the appropriate conditions. Such sites may have the added benefit of placing the eggs and eventual hatchlings beyond

the reach of potential predators. A decrease in river level can isolate these marginal settings from the channel and the resulting pools of water can trap the eggs or the hatchlings.

Recent evidence suggests that some “placoderms” were viviparous (ptyctodontids: Long, *et al.*, 2008; *Incisoscutum ritchiei*: Ahlberg, *et al.*, 2009), and others laid egg cases that contained several large eggs (Carr, 2010) or hundreds of tiny eggs (phyllolepid: Ritchie, 2005). The Catskill sample shows crowding of many same-sized juveniles in what were likely to have been spawning/nursery sites. The taphonomic context supports the hypothesis that these juveniles hatched from large numbers of eggs that were laid and fertilized within areas of reduced flow along the shallow margins of a fluvial system. Large numbers of same-sized individuals on single slabs suggest a relatively large brood size for this species of *Bothriolepis*. Some slabs preserve juvenile individuals at more than one growth stage (Fig. 5), further promoting the interpretation of *Bothriolepis* as a taxon that utilized common nursery grounds. The mass mortality events represented by the new sample could easily have been triggered by anoxia and desiccation in these marginal settings.

ACKNOWLEDGEMENTS

We gratefully acknowledge Lars Werdelin and John Long for providing their raw morphometric data for *Bothriolepis canadensis*. We thank C Frederick Mullison,

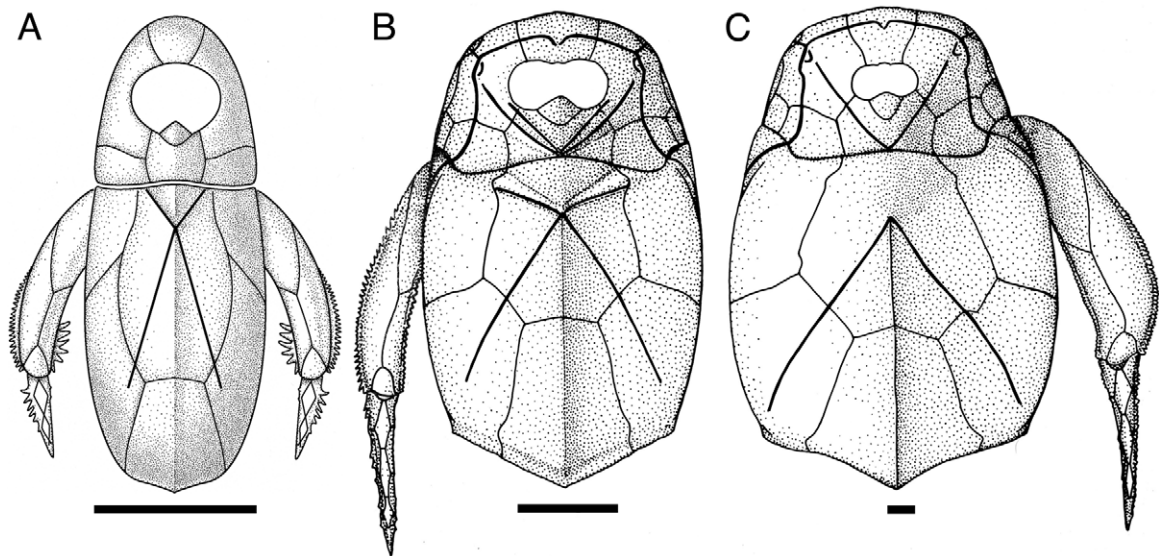


Fig. 9. External skeletal reconstructions, in dorsal view, of **A.**, juvenile *Bothriolepis* sp. from the Catskill Formation, **B.**, juvenile *B. canadensis*, and **C.**, adult *B. canadensis*. The individuals in the Catskill sample are not likely to be *B. canadensis* though may be indicative of generalized early juvenile morphology for *Bothriolepis*. Reconstructions of *B. canadensis* were redrawn by Werdelin and Long (1986) after Stensiö (1948). Scale bars = 1 cm.

Albert Visco, and Ariel Dombrowski for their preparation of the Catskill fossils; Scott Rawlins for his reconstruction of juvenile Catskill *Bothriolepis*; Kyle Luckenbill for his line art; Seth Koren for his photography and figures; and Melinda Yang for her improvement of the morphometric analysis. John Lundberg kindly shared his knowledge of reproductive biology of fishes. The comments of John Long and Ieva Upeniece improved the quality of this manuscript. This project was funded by a National Science Foundation Research Experience for Undergraduates (REU) fellowship awarded to K. Criswell. The NSF REU Site program at the Academy of Natural Sciences of Philadelphia, "Collections-Based Undergraduate Research at The Academy of the Natural Sciences" was funded by grant #0353930.

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