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L161—H41
Edited by Lillian A. Ross
INTRODUCTION

The fossil fishes described in this paper were collected many years ago from the Holland Quarry shale, a Devonian formation in northwestern Ohio, by Dr. J. Ernest Carman, Emeritus Professor of Geology at Ohio State University. In 1956 he generously presented the collection to Chicago Natural History Museum, where it is preserved. However, as agreed at the time of his gift, a representative series of specimens has been returned to the Geology Department of Ohio State University. In addition to the fishes, the Holland Quarry shale contains eurypterids and plants. The eurypterids are being described by Dr. Erik Kjellesvig-Waering (in press), but the plants have been returned to Ohio State University for future study.

Previous important discoveries of Lower Devonian vertebrates in North America have been restricted to the Rocky Mountain region and the maritime provinces of eastern Canada. For this reason the Holland Quarry vertebrates are of considerable geographic interest. Since this quarry is no longer operated, and the outcrop of the shale is covered, it is doubtful whether more material will ever be obtained from this site. The geological occurrence has been described by Dr. Carman (1960). The vertebrates indicate a Lower Devonian age, probably lower Siegenian by the European standard. The locality is the Holland Quarry, Monclova Township (south 1/2, sec. 29), Lucas County, Ohio.

HETEROSTRACI
CYATHASPIDAE

Allocryptaspis laticostatus, new species

_Type._—CNHM-PF 1701, a dorsal shield in counterpart (fig. 117, A).

_Referred specimens._—Dorsal shields, mostly incomplete, PF 1702-1736, 1811; ventral shields, incomplete, PF 1737-62, 1826-27; suborbital plates, PF 1777-78, 1831-33; antero-lateral plate, PF 1829; postero-lateral plates, PF 1781-83, 1828; oral-lateral plates, PF 1779-1780; postoral plates, PF 1763-70, 1836-44; possible oral plates,
PF 1775–76, 1830; scales, 1771–74, 1813–22; and undetermined plates, PF 1834–35.

Horizon and locality.—As given above.

Diagnosis.—The dentine ridges are very coarse, 2.3 to 2.8 occupying one millimeter; they are generally flat-topped and very finely tuberculate. The length of the dorsal shield is 81–92 mm.; that of the ventral shield is 81–87 mm. The shields are relatively broader than in other species.

Description and discussion.—Allocryptaspis resembles Poraspis in many respects, but differs from it particularly in two striking features: the presence of distinct lateral laminae on the dorsal shield, and the position of the branchial openings between the dorsal and ventral shields. Since these characters are unique among Cya-thaspidae, Allocryptaspis is a clearly distinct genus. It includes the largest known members of the family.

From the previously described species of the genus, A. laticostatus is distinguished by the characters given in the diagnosis. The type species, A. ellipticus (Bryant, 1934, p. 154; 1935, p. 114), from Beartooth Butte, Wyoming, has much finer dentine ridges (4–5 per mm.) and they are probably smooth-crested. Its dorsal and ventral shields are about the same length as those of A. laticostatus, but they are relatively narrower. A second species from Beartooth Butte, A. flabelliformis (Bryant, 1935, p. 118), is poorly characterized. It was based on a ventral shield that is larger than that of any other species, probably relatively broader, and with dentine ridges that may be slightly coarser than those of A. ellipticus. A. utahensis (Denison, 1953, pp. 294–304), from the Water Canyon formation of Utah, has 3.2–3.6 dentine ridges per millimeter. The ridges generally have a smooth, slightly convex crest, and the dorsal and ventral shields are longer than those of A. laticostatus.

The dorsal shield of Allocryptaspis laticostatus (figs. 117; 119, A; 122, A) has a total length in known specimens of 81–92 mm., the type being one of the smallest. Its shape is similar to that of the other species, except that it is proportionately considerably broader. Nearly all the Holland Quarry specimens are flattened, and so the proportions computed from these shields are very different from those in life. The ratio of width at the orbits to total length is 0.41, and the ratio of width at the branchial openings to total length is 0.77. A similarly computed orbital width ratio in A. utahensis is estimated to be 0.32. Measurements of this type are
Fig. 117. Dorsal shield of Allocryptaspis laticostatus. A, type, PF 1701 (× 1); B, rostral part of PF 1706 (× 2), showing band of transverse dentine ridges; C, postero-lateral part of PF 1722 (× 2), showing branchial notch.
not available for *A. ellipticus*, but this species appears to be intermediate in proportions between *A. laticostatus* and *A. utahensis*.

As a result of crushing, the lateral laminae of the dorsal shield (figs. 119, A; 122, B) are usually closely appressed to the dorsal part of the dorsal shield. In life these laminae were directed ventromesially and separated by a marked lateral edge from the rest of the dorsal shield, as is the case in the type of *A. utahensis* and in the one unflattened dorsal shield of *A. laticostatus*, PF 1726. Each lamina commences anteriorly on the sides of the rostrum, is notched deeply for the orbit, reaches its greatest width opposite the gill pouches, and tapers off and disappears shortly in front of the branchial opening. In my description of *A. utahensis* (Denison, 1953, p. 296), I considered the lateral laminae to be differentiated parts of the dorsal shield. This interpretation was influenced by the presence of two fragments that were believed to be parts of branchial plates. I now think that the latter (PF 743-744) are fragments of the lateral margins of dorsal shields, including parts of lateral laminae. Among the extensive material from the Holland Quarry, Water Canyon, and Beartooth Butte formations there is not a single piece that can be identified as a branchial plate. I have concluded, therefore, that branchial plates did not exist as distinct elements in *Allocryptaspis*, and that the lateral laminae for most of their length represent branchial plates that have fused to the dorsal shield. In *Poraspis* and other Cyathaspidae the branchial plates extend to the posterior end of the shield, and the branchial openings lie between them and the dorsal shield. In *Allocryptaspis* the branchial plate equivalents have been shortened so that they exist only in front of the branchial openings, and the latter come to lie between the dorsal and ventral shields (figs. 117, C; 118, C; 122, B).

On the dorsal shield, short and distinct postbranchial lobes project down behind the branchial openings (fig. 117, C). The postbranchial index (median length behind branchial openings divided by total length) is 0.29-0.31 in *A. laticostatus* compared to 0.35-0.42 in *Poraspis*. In *Allocryptaspis* also the preorbital part of the shield is relatively short; the preorbital index (preorbital length divided by total length) is 0.12-0.14 in *A. laticostatus* compared to 0.14-0.23 in *Poraspis*. The orbits are extremely small in *A. laticostatus*, with a diameter of 2.5 mm. or less.

One fragment of a dorsal shield, PF 1811, has been prepared to show the ventral side of the rostrum. Its anterior margin, called
by Kiaer the "maxillary plate" (1928, p. 123) or more appropriately the "maxillary brim" (1932, p. 8), is formed by a folding under of the dermal rostral shield and is set with dentine ridges and tubercles. In Poraspis the ridges of the brim are nearly parallel to the edge of the rostrum (Kiaer and Heintz, 1935, pl. 26, fig. 1). In Allocryptaspis, on the other hand, the ridges are arranged more or less at right angles to the rostral margin and give way internally to tubercles. Since the first description of pteraspid mouth parts by Kiaer (1928), it has been generally assumed that the maxillary brim formed the upper boundary of the mouth opening and that the antero-internal surfaces of the oral plates actually worked against it. Stensiö (1958, figs. 190; 194, C) has recently published reconstructions of Heterostraci in which he interposed between the oral plates and maxillary brim a hypothetical palato-subnasal cartilaginous lamella. The section of Pteraspis figured by Kiaer (1928, pl. 12, fig. 2) makes it seem most unlikely that such a lamella existed.

The ventral shield of A. laticostatus (figs. 118; 119, B; 122, C) differs from the dorsal shield in lacking differentiated lateral laminae. Its posterior margin has a prominent, rounded, median lobe, and postero-laterally it has deep branchial notches and small post-branchial lobes (figs. 118, C; 119, B). The anterior margin (fig. 118, B) is characterized by a number of paired emarginations for the reception of postoral and lateral plates. A small pair of notches on either side of the median line is bounded laterally by wide concave margins for the large postoral plates (fig. 119, B, npo). Two pairs of small notches at the antero-lateral corners (fig. 119, B, npl) presumably received postero-lateral plates. Though proportional ratios are not obtainable, the ventral shield appears to be relatively much broader than those of A. utahensis and A. ellipticus.

The pattern of the dentine ridges on both the dorsal and ventral shields is essentially longitudinal, as in Poraspis and in other species of Allocryptaspis. Typically there is a fan-like radiation of the ridges at the anterior end of the shields, although in PF 1705, a dorsal shield, the ridges are mainly longitudinal on the rostrum. There are many variations to the simple longitudinal pattern, particularly anteriorly, near the lateral margins and along the lateral line canals. The rostral margin is particularly variable. There the ridges may be continuous or may be broken into short lengths, and they are generally irregular in their course. The rostral region of PF 1706 (fig. 117, B) is anomalous in having a band of transverse ridges with longitudinal or slightly radiating ridges before
Fig. 118. Ventral shield of Allocryptaspis laticostatus (x 1). A, PF 1746; B, anterior part, showing notches for postoral and lateral plates, PF 1744; C, posterior part, showing postero-median lobe and branchial notch, PF 1742.

and behind it. On the lateral laminae of the dorsal shield the ridges are oblique or transverse.

The dentine ridges are separated by narrow grooves marked by very fine pores or foramina. These pores are so small that they do not give a crenulated appearance to the edges of the ridges as in Pteraspis. On the dorsal and ventral shields the tops of the ridges are smooth and convex along the rostral margin, around the orbits, on the lateral laminae anterior to the orbits, and around the branchial openings. Elsewhere the ridges are flat-topped and finely tuberculate (fig. 120). Each ridge generally has a row of tubercles along each margin, and one or two rows in the middle. The narrow ridges around the branchial openings may have only one or two rows of tubercles.

The Holland Quarry collection includes a number of plates from the ventral cover of the oro-pharyngeal area. The most certainly identified are relatively large plates (fig. 121, A, B) that are com-
Fig. 119. Dorsal shield (A) and ventral shield (B) of Allocrepis ophidianus, restored as if completely flattened (×1).

bro, branchial notch; cd - 4, dorsal transverse commissure; cl, lateral ventral canal; ldl, lateral dorsal canal; ltl, lateral transverse commissure; cm, central commissure; mtl, medial transverse commissure; ndt, notches for postero-lateral plates; npo, notch for postoral plate; or, orbit; pol, postoral canal; soc, supraorbital canal; x, unidentified canal.
parable to the paired postoral plates of *Pteraspis rostrata* (White, 1935, p. 409). As oriented in the restoration (fig. 122, C), the posterior margin of each postoral plate fits one of the large emarginations of the anterior edge of the ventral shield. The postero-medial margin must have bounded one or two small, paired, median plates.

![Fig. 120. Ornamentation of Allocryptaspis laticostatus, ventral shield, PF 1744 (× 24).](image)

Presumably the medial margin contacted that of the opposite postoral plate, while the lateral margin adjoined the lateral plates. The anterior margin is remarkable for its series of notches, which are deep medially and shallow laterally, and complicated by a number of irregular projections. The posterior ends of the oral plates must have articulated in these notches. The outer surface of the postoral plate is covered with dentine ridges that are smooth along the anterior edge and elsewhere finely tuberculate. The superficial layer overlaps onto the inner side of the postoral plates along the posterior and postero-medial edges (fig. 121, B), where it forms a very narrow rim, much as in scales. There is no evidence for a deep infolding of the skin in front of and behind the postoral plates, such as was inferred by Stensiö (1958, p. 262) in Pteraspidae.
Lateral plates (orogonial of Stensiö, 1958) have been identified with varying degrees of certainty by their shape, by the direction of their dentine ridges, and, when present, by the course of lateral line canals. Two pairs of small emarginations at the antero-lateral corners of the ventral shield (fig. 119, B, npl) indicate that there were two pairs of postero-lateral plates. PF 1782 (fig. 121, C) and 1783, which lack sensory canals, may represent the lateral pair of postero-laterals. PF 1781 (fig. 121, D) and one of the plates on PF 1828 and 1833 have sensory line pores and have been tentatively identified as the medial postero-laterals. PF 1829 (fig. 121, E) has a curved sensory canal that suggests the infraorbital line on the antero-lateral plate; this plate lay between the suborbital and postoral plates. Suborbital plates (fig. 121, F) are easily identified by the concave border at one corner; this forms about one-quarter of the orbital margin. This plate is crossed by the infraorbital

Fig. 121. Oro-pharyngeal plates of Allocryptaspis laticostatus (× 4). A, right postoral, PF 1768; B, right postoral, inner side, PF 1763; C, lateral postero-lateral, PF 1782; D, medial postero-lateral, PF 1781; E, antero-lateral, PF 1829; F, sub-orbital, PF 1777; G, oral-lateral, PF 1780; H, possible oral plate, PF 1776.
canal and is bounded by all three lateral plates, as well as by the oral-lateral, the orbit, and the lateral lamina of the dorsal shield. In front of the suborbital and antero-lateral plates lies the oral-lateral plate (preorogonial of Stensiö, 1958) (fig. 121, G), which bounded the antero-ventral part of the orbit and transmitted the anterior part of the infraorbital canal. A few small plates (PF 1775–1776, 1830) have been doubtfully determined as oral plates (fig. 121, H). They resemble caudal scales in shape but differ in having their dentine ridges arranged in a diagonal rather than a longitudinal direction.

An attempt has been made in the restoration of *Allocryptaspis laticostatus* (fig. 122, C) to determine the arrangement of these small plates. Articulated oral, lateral, and suborbital plates have been found in only one cyathaspid, an *Anglaspis* from Spitsbergen, but they have not been described. Kiaer and Heintz (1935, p. 46) say that their arrangement is “reminiscent of that which Kiaer has described in *Pteraspis vogti*.” The latter (Kiaer, 1928, fig. 3) has a series of oral plates, and paired oral-lateral and lateral plates, but no postoral plates. *Allocryptaspis*, with its large postoral plates, shows a closer resemblance to *Pteraspis rostrata* as figured by White (1935, figs. 41–47).

The lateral line canals, as determined from the pores by which they open to the surface (figs. 119, 122), agree closely with those of *Allocryptaspis utahensis* and *Poraspis*, except for a few details. The anterior end of the supraorbital canal (fig. 119, A, soc) passes from the dorsal face of the dorsal shield on to the preorbital part of its lateral lamina. The infraorbital line (fig. 119, A, ifc) passes on to the postorbital portion of the lateral lamina and then crosses the posterior half of the suborbital plate; thence it continues over the antero-lateral and oral-lateral plates to meet the supraorbital line. On the ventral shield the lateral ventral line gives off a number of transverse commissures; six of these (fig. 119, B, evl) have been identified, though not all on any one specimen. Near the mid-line of the ventral shield there are five pairs of short transverse commissures (fig. 119, B, evm), which are so identified (rather than as parts of medial ventral lines) because the more posterior three are in line with the anterior three lateral transverse commissures. Posteriorly on the ventral shield there is a pair of medial longitudinal

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Fig. 122. Restoration of *Allocryptaspis laticostatus*, approximately natural size. A, dorsal view; B, lateral view; C, ventral view.
canals (fig. 119, B, *mel*) broken into short lengths, which are in line with the fourth lateral transverse commissures. Anterior to the medial transverse commissures is a pair of lines of similar arrangement (fig. 119, B, *pol*) that has been distinguished as the

![Figure 123](image)

**Fig. 123.** Scales of *Allocryptaspis laticostatus*. A, lateral scale, PF 1817 (*×* 3); B, anterior median scale, PF 1814; C, median scale from mid-length, PF 1816; D, posterior median scale, PF 1815; E, caudal scale, PF 1820; F, ventro-lateral scale, PF 1821. B–F (*×* 9/2).

postoral lines by Stensiö (1958, fig. 216); they pass off the ventral shield presumably on to the postero-lateral plates. There is a short lateral branch (fig. 119, B, *x*), not known in other cyathaspids, from the lateral ventral line anterior to the first transverse commissure. Usually it has only two pores, but there may be as many
as seven. Its continuation onto the dorsal shield, if such exists, has not been found.

The scales covering the posterior part of the body and tail are similar to those of *Poraspis*, as described in detail by Kiaer and Heintz (1935, pp. 108-118). Median dorsal and median ventral scales are not distinguishable at present. Anterior median scales (fig. 123, B) are relatively broad and short and only slightly convex. Their dentine ridges are nearly flat and are generally smooth. On the anterior part of these scales the ridges usually are divergent and finely tuberculate. Farther back, the median scales (fig. 123, C) become relatively longer and narrower, and are strongly convex. Their ridges are sharply crested, and usually converge and become tuberculate anteriorly. The posterior median scales (fig. 123, D) are long and narrow, and are sharply folded in the median line; crested dentine ridges also characterize these scales. A single anterior transverse ridge may or may not be present on median scales.

Lateral scales (fig. 123, A) differ from those of *Poraspis* in that their dentine ridges turn down strongly toward the anterior edge. Their ridges are flat and may be either tuberculate or smooth, although fine tuberculation is usual on the anterior part. An anterior transverse ridge may be absent but is sometimes present along all or part of the margin. Anteriorly the lateral scales are very deep dorso-ventrally; more posteriorly they become much shorter in this dimension.

Ventre-lateral scales (fig. 123, F) also have flat dentine ridges that are often smooth, although the larger, more anterior scales of this type are commonly finely tuberculate. A single anterior transverse ridge is occasionally present, and pores of the lateral line are sometimes seen. Small scales of the tail (fig. 123, E) are irregular in shape and are of undeterminable position except for the long, narrow, crested median or fulcral scales.

The smooth, anterior, overlapped margins of the scales are quite variable in development, in some cases being very broad, in others quite narrow. As in *Poraspis*, the superficial layer of the scale extends around its border to form an internal rim of dentine along the posterior margin.
Pteraspis carmani, ¹ new species

Type.—CNHM-PF 2018, a partially articulated shield, incomplete posteriorly, with dorsal and ventral discs, rostral, orbital, branchial, lateral, oral-lateral, oral, and postoral plates (fig. 124).


Horizon and locality.—As given on page 555.

Diagnosis.—Pteraspis carmani has a relatively wide shield and a broadly rounded rostrum (fig. 125). The dorsal disc attains a median length of 71 mm., the largest ventral disc has a length of about 100 mm., and the rostral plate is as much as 22 mm. long. In the rostral plate, the ratio of width to length is 1.7 to 2.1. The orbital plates have long medial processes that meet the subrectangular to nearly semicircular pineal plate. The branchial openings are placed posteriorly but still well in advance of the postero-lateral corners of the dorsal disc. The branchial plates are long. The dorsal spine is short, broad, and scale-like. Dentine ridges vary from 3.6 to 10 per mm. but average 5.6 per mm. in the mid-line of the dorsal disc, 4.0 per mm. in the mid-line of the ventral disc, and 6.5 per mm. in the mid-line of the rostrum; their crests are flatly rounded or locally sharply ridged, and are smooth or faintly tuberculate.

Description and discussion.—Pteraspis carmani is intermediate between Pteraspis and Protaspis and for this reason its generic reference is difficult. The most important diagnostic character of Protaspis is the posterior position of the branchial openings, accompanied, at least in those specimens that have this region well preserved, by peculiar modifications of the surrounding branchial and cornual plates and dorsal disc. In Pteraspis carmani the branchial openings (fig. 125, bro) are more posterior than in typical Pteraspis such as P. rostrata, but they are still well in advance of the postero-

¹ In honor of Dr. J. Ernest Carman, Emeritus Professor of Geology at Ohio State University.
Fig. 124. Type of Petrospis cormani, FF 2018 (X 1). A, dorsal view; B, ventral view.
lateral corners of the dorsal disc, where they lie in specialized \textit{Protaspis} such as \textit{P. bucheri} (Denison, 1953, fig. 79) and \textit{P. arnelli} (Brotzen, 1936, fig. 6). \textit{Pteraspis carmani} lacks any of the specializations that characterize the branchial opening in \textit{Protaspis}: the dorsal disc is notched only slightly, the branchial plates bound the opening only anteriorly and ventrally, and, though cornual plates have not been definitely identified, it is probable that they retain the usual \textit{Pteraspis} relationships. Therefore this species is placed in \textit{Pteraspis}, although it is clearly near to \textit{Protaspis}.

\textit{Pteraspis carmani} is distinguished as follows from other species of \textit{Pteraspis} and \textit{Protaspis} with short rostra, broad shields, and scale-like dorsal spines: Those species of \textit{Pteraspis} that have been assigned to the subgenus \textit{Protopteraspis} differ in their small size, in the absence of medial processes on the orbital plates, and in the more anterior position of their branchial openings. Those species of \textit{Pteraspis} that were referred to \textit{Brachipteraspis} by Brotzen (1936) differ as follows: \textit{P. heintzi} has a long, slender dorsal spine; \textit{P. latissima} has a relatively longer rostrum; \textit{P. bryanti} appears to have a relatively longer rostrum and a broader shield; \textit{P. grossi} has much more anterior branchial openings. Other broad-shielded European \textit{Pteraspis} include: \textit{P. rotunda}, whose dorsal disc is relatively much broader; \textit{P. traquairi}, which is smaller and has deeper notches in the dorsal disc for the pineal plate and dorsal spine; and \textit{P. brevirostra}, which has a relatively longer, narrower rostrum. In the genus \textit{Protaspis}, the subgenus \textit{Cyrtaspidichthys} is distinguished by its subdivided dentine ridges, \textit{Protaspis dorfi} by its fine ridges, the \textit{P. amplus-perlatus-perryi} group by its longer rostra, and \textit{P. arnelli} by its more posterior branchial openings. \textit{Protaspis wiheriesiensis} has been referred by Fahrbusch (1957, p. 51) to \textit{Pteraspis rotunda}; however, the type (Leriche, 1926, pl. 2, fig. 1, "\textit{Pteraspis dunensis}") appears to belong to \textit{Protaspis}; its branchial openings are certainly more posterior than in \textit{Pteraspis carmani}, and the rostrum is relatively longer. This leaves only \textit{Protaspis bucheri} (including \textit{P. brevirostris}), which of all pteraspids is the most similar to \textit{Pteraspis carmani}. \textit{Protaspis bucheri} differs in having the branchial openings placed nearly or quite at the postero-lateral corners of the shield, in having a longer and more slender dorsal spine, and in having on the anterior edges of the orbital plates prominences that fit corresponding notches on the rostral plate. Even though these two species are arbitrarily placed in different genera, it is probable that they are closely related.
Dorsal disc.—The compression of the Holland Quarry shale has flattened most plates to such an extent that their proportions have been altered significantly. For this reason it is not easy to make proportional comparisons with other species. However, some of the flattened dorsal discs of *Pteraspis carmani* are well suited for analysis of proportional changes during growth, although of course the proportions studied are not those of the living animal. It has been assumed that the dentine ridges represent stages in the growth of the disc. At arbitrary 5 mm. intervals, measured anterior to the center of growth in the mid-line, the dentine ridges have been

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**FIG. 125.** Restoration of dorsal shield of *Pteraspis carmani* (× 1). No corrections for flattening have been introduced.

BR, branchial plate; CO, cornual plate; DD, dorsal disc; OR, orbital plate; PI, pineal plate; RO, rostral plate; SP, dorsal spine; bro, branchial opening; orb, orbit.
traced on enlarged photographs of five specimens selected for their completeness, flatness, and large size. The traced dentine ridges give the shape of the dorsal disc at each arbitrary interval, and at each of these stages the following measurements and counts were taken:

La, length in mid-line anterior to center of growth
Lp, maximum length posterior to center of growth
TL, total length or La + Lp
W, maximum width
Ra, number of dentine ridges anterior to center of growth in mid-line
Rl, number of dentine ridges lateral to mid-line
Rp, number of dentine ridges posterior to center of growth

Figure 126 shows the arbitrary 5 mm. stages as traced on one specimen. Figure 127 shows a "growth line" in which total length is plotted against maximum width; this is based on averages of five measured specimens and is compared with actual maximum dimensions of comparably preserved specimens. The average measurements (in millimeters) and proportional changes of the five specimens (PF 1868–70, 1872, 1875) are given below:

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<th>Stage</th>
<th>La</th>
<th>Increment</th>
<th>Increment</th>
<th>W</th>
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<td></td>
<td></td>
<td>Lp</td>
<td>W/2</td>
<td>TL</td>
<td>Ra</td>
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<td>0</td>
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</table>

The earliest growth is similar to that described in detail for *Pteraspis dunensis* by Fahrbusch (1957, pp. 23–24), except that the initial antero-posterior ridge is single and not subdivided into three segments as in *P. dunensis*. Addition of ridges on each side of the initial one soon forms the narrow-oval disc of stage 1; at this stage the dorsal disc is usually less than half as wide as long. In stages 2 and 3 growth on each side is slightly greater than anteriorly; this is simply the result of the addition of more ridges laterally, for the ridges in the mid-line anteriorly are coarser. Beyond stage 3 lateral growth is always less than anterior growth, largely because at the sides the ridges are finer, but also in later stages because they are fewer. Anterior to the growth center there
Fig. 126. Dorsal disc of *Pteraspis carmani*, PF 1869 (× 3/2). The numbered stages are tracings of dentine ridges at arbitrary intervals of 5 mm., measured in the mid-line anterior to the center of growth.

are, on the average, 5.6 ridges per mm., while laterally there are 7.5. Of course the dentine ridges vary considerably in width; anteriorly they range from 4.6 to 6.8 per mm., while laterally the range is from 5.3 to 10.1 per mm. Posterior to the center there is usually an appreciable growth in the earliest stages, but in later stages there may be small or no additions at the posterior edge of the disc. This slight posterior growth, which is found in many pteraspids, is a result not only of the addition of relatively few ridges, but also of very narrow ridges; they average 9.0 per mm. in this region.
Fig. 127. Graph showing the changes in proportions during the growth of the dorsal and ventral discs of *Pteraspis carmani*. The lines are plotted from averages of measurements of arbitrary stages of several specimens, as explained in the text. They are compared to maximum dimensions of specimens whose catalogue numbers are shown, except that the plots of PF 1921 are based on growth lines of early stages.

The net result of the differential growth is a change in proportions illustrated by the growth curve (fig. 127) and the relative width 

\[ \frac{W}{TL} \]

The relative width increases rapidly at first, then more gradually until stage 6, when there appears to be a slow decrease in the ratio.

A number of small dorsal discs in the collection support the belief that the arbitrary measured stages might represent actual juvenile stages. The smallest dorsal disc that is accurately measurable is PF 1891 whose total median length is 28.5 mm.; when its length is plotted against its width on the graph (fig. 127) the point falls almost exactly on the growth line constructed from the averages.
of arbitrary stages. Still smaller dorsal discs are: PF 1898, with \( TL = 22 \) mm.; PF 1904, with \( TL = 19.1 \) mm.; and PF 1902, with \( TL = 15.5 \) mm. Since these very small discs are thin and always poorly preserved, they may not be complete.

At intervals on the dorsal disc there are clearly marked grooves that are more or less parallel to the dentine ridges. These have been called growth lines or "Randlage" (Fahlbusch, 1957, pp. 17-19) and are believed to mark periods of rest between times of periodic growth. In a general way they are comparable to annuli in modern fish scales, though of course there is no evidence in *Pteraspis* that
the periodic growth was annual. The earliest growth lines are often obscure, but in *P. carmani* they commonly occur in stage 3, even quite early in the stage (in PF 1869 at *La*=10.3 mm.), and possibly even in the later part of stage 2. From this it is probable that there were actual juvenile discs as small as 18 or 19 mm. in total length. By contrast, the largest measurable dorsal disc of *P. carmani* has a total median length of 71 mm. (PF 1876).

Of interest are certain morphological stages in the growth of the dorsal disc. No notch for the pineal plate is ever apparent in stage 1 or 2. Beyond that it is quite variable in its appearance: in PF 1869 it is seen at *La*=10.5 mm.; in PF 1873 there is no pineal notch until *La*=25 mm. A first appearance in stage 3 (*La*=10–15 mm.) is common. The presence of a pineal notch indicates that the dorsal disc and pineal plate are adjacent and suggests a nearly complete coverage of the anterior part of the body by the shield. The inclusion of the main lateral line canals in the dorsal disc is another important growth landmark. On the average these canals (or rather the pores by which they open to the surface) are included in stage 5 (*La*=24 mm.), when the maximum width is 39 mm. They are, of course, not included in the smallest discs such as PF 1891 and 1898, and at such a juvenile stage the canals must have existed in soft tissue between the dorsal disc and the branchial plates. Notches for the branchial openings first appear in stage 6 or 7 and become more marked in later stages. The notch for the dorsal spine first appears in the middle or later part of stage 2; it will be discussed further below.

A few features of the dentine ridge pattern are worthy of mention. A dentine ridge may, after the initial growth (early stage 1), be continuous around the dorsal disc. Commonly after stage 3 ridges terminate when they reach the posterior edge. Short ridges may occur in regions of maximum growth. Thus, in stages 2 and 3, when lateral growth is rapid, there may be ridges laterally that do not extend to the anterior or posterior parts of the disc. Likewise, when the notch for the pineal plate is forming, there are often short ridges restricted to the rapidly growing lobes on each side of the notch. There are common irregularities of the dentine ridge pattern. Ridges depart slightly from a regular course at lateral line pores. In stage 9 of PF 1870 (fig. 128) there is an anomalous ridge pattern anteriorly which includes medially a unit resembling a pineal plate that has been incorporated into the disc.

*Dorsal spine.*—This relatively insignificant part of the exoskeleton is of particular interest in *Pteraspis carmani*. It is small, rises only
slightly above the dorsal disc, and is very scale-like (fig. 125, SP). It occupies a deep notch or socket in the mid-line of the posterior border of the dorsal disc. In 19 measured specimens the socket begins at an average of 8.2 mm. (range 7.2–9.9 mm.) behind the center of growth of the dorsal disc, or in stage 2 of the growth of the latter. As the posterior edge of the dorsal disc is lengthened slowly and intermittently during growth, the depth of the socket increases, but, because of the irregularity of this growth after stage 3, there is no close correlation between the depth of the socket and the size of the dorsal disc. In 16 measured specimens the depth of the socket ranged between 3.1 and 7.9 mm., and the ratio of this depth to the median length of the dorsal disc ranged between 0.06 and 0.13. In general, larger dorsal discs have deeper sockets, though PF 1869 (fig. 126), a large specimen, has a socket only 4.3 mm. deep. The relative depth of the socket in *Pteraspis carmani* is much less than in small species such as those that have been assigned to *Protopteraspis*, where it may occupy as much as one-third of the length of the dorsal disc. This is simply the result of the relatively slight posterior growth and the relatively great anterior growth of the dorsal disc of *P. carmani* after stage 3. The spine is rarely found attached to dorsal discs having a median length of less than 50 mm. Occasionally it has come free in larger specimens, in one case in a disc with a length of 70 mm. (PF 1872). In the one specimen that has been prepared from the inner side (PF 2073), the suture between the spine and the dorsal disc is not visible, presumably because of an overgrowth by the basal layer of the exoskeleton similar to that reported in *P. dunensis* by Fahlbusch (1957, p. 43).

The size of the dorsal spine is variable in *P. carmani*. Its length, which ranges between 8.0 and 18.5 mm., shows no correlation with the size of the dorsal disc. The ratio of the length of the spine to the median length of the dorsal disc ranges in ten specimens between 0.12 and 0.30. Its proportions are extremely variable. The ratio of width to length is as low as 0.19 in one long, slender spine (PF 1871, fig. 129, C), as high as 0.58 in one short, broad spine (PF 2082, fig. 129, F), and averages 0.41 in 17 specimens. In larger individuals approximately half of the spine is inserted in the socket in the dorsal disc.

The ornamentation of dorsal spines shows great variation. At one extreme the dentine ridge pattern resembles that of ridge scales: in this type (PF 1887, fig. 129, E) the short longitudinal ridges are grouped in rows that parallel the anterior and antero-lateral edges
of the spine. This pattern differs from that usual in ridge scales only in that the dentine ridges lengthen at either side, where they run parallel to the edges of the spine. Commonly the scale-like pattern is varied in the anterior or younger part of the dorsal spine by the replacement of row arrangement by long, continuous ridges parallel to the socket edge (PF 2077, fig. 129, A). The row arrangement may be obscured by a tendency of the dentine ridges to flare postero-laterally, or in one specimen (PF 2082, fig. 129, F) by a very irregular ridge arrangement. At the other extreme the ridge pattern may differ completely from that of scales. In PF 2070 (fig. 129, B) the ridges are long and form a series of concentric loops parallel to the socket edge. In PF 1871 (fig. 129, C) the ridges are predominantly longitudinal, though there are a few loops anteriorly. PF 2075 (fig. 129, D) is notable for the tendency of the ridges to subdivide into small denticles in the central part of the spine.

As far as I know, comparable scale-like dorsal spines occur in Protaspis (Denison, 1953, fig. 75) but not in other species of Pteraspis. The similarity to a ridge scale in Pteraspis carmani suggests that the dorsal spine originated by attachment of such a scale to the dorsal disc, as has been suggested by others. A difficulty in this theory is that Protaspis and Pteraspis carmani are not primitive pteraspids in many respects, while primitive species such as Pteraspis primaeva have a dorsal spine that is really spine-like, more or less elevated, round in cross section, and with parallel, longitudinal ridges. This difficulty may be explained on functional grounds. Large, elevated dorsal spines are usually associated with enlarged and flaring cornual plates, all of which presumably served as keels to promote stability in swimming. The relatively flat-bodied Protaspis and Pteraspis carmani may have been essentially bottom dwellers, and as such they may not have required strongly functional keels and so retained the primitive scale-like spines.

Rostral plate.—Pteraspis carmani retains the relatively short, broad rostrum of primitive species belonging to the subgenus Protopteraspis. The ratio of maximum width to median length ranges from 1.72 to 2.14, with an average of 2.00 in 22 measured specimens. No correlation was found between size and proportions, although such exists in some Protaspis (Denison, 1953, p. 331). The variation in proportions in P. carmani may be attributed in part to crushing. The rostral plate (fig. 130, B) is broadly rounded in front. The posterior edge is concavo-convex laterally where it meets the orbital plates, and straight or slightly concave in the medial part that joins the pineal plate. The dentine ridges on the rostral plate are some-
Fig. 129. Dorsal spines of *Pteraspis carmani* (× 3). A, PF 2077; B, PF 2070; C, PF 1871; D, PF 2075; E, PF 1887; F, PF 2082.

what finer than those on the mid-line of the dorsal disc, as is true also in *Protaspis*. In the mid-line there are 5.5 to 7.6 per mm., with an average of 6.5.

The growth of the rostral plate as determined from the dentine ridges commences at an antero-median center whose ridge arrangement is extremely variable. Commonly there are one or two short, longitudinal ridges (fig. 130, A) or a short transverse ridge. In PF 1935 the center is marked by a small group of denticles. In PF 1939, 1945, and 1947 the primary ridges are asymmetrically arranged. Whatever the shape of the primordium, the ridges, and presumably the posterior edge of the juvenile plate, soon become strongly convex posteriorly. PF 1941 (fig. 130, A) is a juvenile rostral plate at this early stage, with a length of 5.1 mm. occupied by 28 dentine ridges. Other specimens preserve the form of early stages by growth lines, which may appear within 2.8 mm. of the
anterior end of the rostrum. After this juvenile stage the rostrum soon acquires the typical adult shape. The largest rostral plate in the collection is PF 1931, with a medium length of 22.3 mm. and a maximum width of 45.3 mm.

Antero-medially the rostrum curves down and under to form a ventral rim that is covered with segmented dentine ridges arranged parallel to the margin. Medially on this rim is a slight ventral projection. In the type (figs. 124, B; 140, srl) a small subrostral lamina is present behind the rim, from which it is separated by a well-marked groove. The shape and development of this lamina are similar to those of the "maxillary tooth plate" described by Kiaer (1928, pp. 123–124) in *Pteraspis vogti*. Kiaer’s section (op. cit., pl. 12, fig. 2) shows that the "maxillary tooth plate" forms the anterior border of the mouth, though in a recent reconstruction Stensiö (1958, fig. 190) has interposed a hypothetical prenasal sinus and a palato-subnasal lamina between it and the mouth. The presence of these hypothetical structures is not confirmed by any fossils of which I am aware. In ventral view the postero-lateral parts of the rostral plate are developed much as in *Pteraspis vogti* (Kiaer, 1928, pl. 12, fig. 1) and are presumed to contact the oral-lateral, lateral, and orbital plates in a similar fashion.

Fig. 130. Rostral plates of *Pteraspis carmani*. A, juvenile, PF 1941 (× 4); B, PF 1932 (× 2).
Pineal plate.—The shape and proportions of the pineal plate are variable. PF 2017 (fig. 131, A) is subrectangular, with a straight or slightly convex anterior edge, relatively long and nearly straight lateral edges, and a moderately convex posterior edge. PF 2010 (fig. 131, B) is nearly semicircular because the lateral and posterior edges are more or less continuous. In plates of these types the length is 3.7–4.5 mm., the width is 6.1–8.1 mm., and the ratio of width to length is 0.51–0.65. PF 2012 (fig. 131, C) is a relatively wide plate with strongly developed lateral wings. Its measurements are: length=3.4 mm.; width=9.0 mm.; and width/length=0.38.

The primary dentine ridge is short, thick, and antero-posteriorly directed except in PF 2016 where it is subtriangular. It is surrounded by a few concentric ridges that result in an oval shape. Later ridges generally do not continue onto the posterior edge, and the latest ridges are mostly restricted to the lateral wings.

Orbital plates.—Each orbital plate (figs. 132, 133) has a long, concave, postero-medial edge that abuts against the dorsal disc, a long, tapering posterior or branchial process that overlaps the anterior edge of the branchial plate, and, in adults, a moderately long medial or pineal process that meets the pineal plate in a square or bluntly rounded contact. Dentine ridges extend downward around the lateral edge to meet the well-marked sutural area (fig. 132, B, SBR) where the orbital plate was attached to the dorsal edge of the anterior end of the branchial plate. This sutural area extends about as far forward as the posterior edge of the orbit. The anterior edge of the orbital plate abuts against the rostral plate. The latter
Fig. 132. Orbital plates of *Pteraspis carmani* (× 4). A, outer face, PF 1960; B, inner face, PF 1973; C, outer face of juvenile plate, PF 1977.

*SBR*, suture for branchial plate; *SRO*, suture for rostral plate.
extends its contact around the antero-lateral convexity of the orbital plate into a ventral groove antero-lateral to the orbit (fig. 132, B, SRO). As this groove does not meet the sutural area for the branchial plate, there can be no contact between the rostral and branchial plates such as occurs in some Protaspis. Between the rostral and branchial plates it is assumed that the orbital plate had a short contact with the lateral plate. The orbital plate had no anterior process such as is developed commonly in Pteraspis and Protaspis.

The orbit is extremely small, having a maximum diameter of 1.6–2.1 mm.; it is oval with the shorter diameter laterally. It forms a short, dorso-laterally directed tunnel through the plate. The lateral line canals (fig. 133), as shown by their pores, are typically developed, with the main dorsal lateral line passing into the infraorbital canal behind the orbit and into the transverse commissure in the pineal process. No trace of the so-called pineal canal has been seen antero-medial to the orbit.

The center of growth is along the anterior part of the lateral edge with the long primary ridge lying parallel to this edge (fig. 133, pr). The earliest growth involves the addition of ridges parallel and medial to the primary ridge. Newer ridges wrap around the ends of the next older ridge, resulting anteriorly in the formation of a lobe-like growth of ridges that defines the antero-lateral corner of the plate. All of these early ridges are broad, about 5 per mm., suggesting rapid growth. After 15 or 16 ridges have formed, the
orbit is reached and is soon enclosed by the growth of the anterior lobe and by corresponding additions at its posterior edge. Soon after the inclusion of the orbit, growth becomes increasingly differential. The pineal and branchial processes are lengthened by the addition of relatively broad ridges, while between them posterior-medial growth is slower because of the addition of fewer and finer ridges. In the latest stage there is little growth toward the dorsal disc and on the branchial process, but the pineal process is lengthened considerably.

A juvenile orbital plate, PF 1977 (fig. 132, C), resembles that of the subgenus *Protopteraspis* in lacking a distinct pineal process. Its dimensions, compared to the largest orbital plate, PF 1962, are:

<table>
<thead>
<tr>
<th></th>
<th>PF 1977</th>
<th>PF 1962</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum length</td>
<td>(est.) 15 mm.</td>
<td>28.4 mm.</td>
</tr>
<tr>
<td>Center of orbit to end of pineal process</td>
<td>3.5</td>
<td>16.3</td>
</tr>
<tr>
<td>Center of orbit to end of branchial process</td>
<td>(est.) 11.5</td>
<td>20.8</td>
</tr>
</tbody>
</table>

**Branchial plates.**—The branchial plates (figs. 125, 134) are long and slender, and are curved to fit the lateral margins of the dorsal and ventral shields. Each tapers anteriorly and is divided externally by a longitudinal angulation into dorsal and ventral laminae. Anteriorly the dorsal lamina usually has a clearly marked edge that abuts against the sutural surface of the branchial process of the orbital plate. Behind this, and separated by a slight angle, is the long edge that joins the dorsal disc. The edge of the ventral lamina is believed to bound the ventral disc posteriorly and the postero-lateral and lateral plates anteriorly. The maximum length of the branchial plates ranges between 41 and 60 mm.

The posterior end of the branchial plate forms the anterior edge of the branchial opening. The great length of this plate and the position of the branchial notch on the dorsal disc indicate that this opening had a more posterior position than in typical *Pteraspis*. In fact it approaches the position in certain *Protaspis* where the branchial opening is at or near the posterior end of the shield. However, *Pteraspis carmani* lacks in this region any of the peculiar specializations of *Protaspis* (Denison, 1953, pp. 320–322). The dorsal lamina terminates in an oblique edge that bounds the branchial opening anteriorly. The wider ventral lamina usually has a blunt, transverse termination, but in PF 1991 (fig. 134, B) it is pointed and has what appears to be a sutural edge for a cornual plate.

In the rare Holland Quarry specimens that are uncrushed the form of the inner face is well preserved. The space between the dor-
sal and ventral laminae is so filled with spongiosa that the inner face is convex, rather than concave as in crushed specimens. A groove for the common branchial duct does not appear until near the posterior end, where it lies against the dorsal lamina and is bounded ventromedially by a ridge along the medial side of the ventral lamina.

![Fig. 134. Branchial plates of Pteraspis carmani (× 2). A, outer face, PF 1980; B, inner face, PF 1991.](image)

The dentine ridge pattern indicates that growth of the branchial plate started in the posterior half along the lateral angulation. Here the ridges are parallel to the angulation, terminate against the posterior edge, and meet the corresponding ridge of the opposite lamina in a loop anteriorly. Growth takes place by the addition of similar ridges but is most rapid anteriorly, where the ridges are coarser and more numerous. These coarse ridges are often subdivided into short lengths or even small denticles along the angulation. Elsewhere the ridges that run parallel to the edges of the dorsal and ventral laminae are fine, about 7 per mm., indicating relatively slow growth of the plate in breadth. There is probably no growth of the plate posteriorly.

**Cornual plates.**—Definite identification of any plates as cornual has not been possible in *Pteraspis carmani*, but this species probably possessed them, since the branchial openings, though somewhat posterior in position, have the same relations to the branchial plates as in typical *Pteraspis*. The openings are bounded anteriorly and ventrally by the branchial plates, and it is probable that there were cornual plates to form their dorsal and posterior borders. In *Pteraspis dunensis*, which lacks cornual plates, their place is taken in part by cornual processes of the dorsal disc (Fahlbusch, 1957, p. 21);
no such processes occur in *Pteraspis carmani*. Confirmation of the presence of cornual plates in the latter is furnished by one well-preserved branchial plate, PF 1991 (fig. 134, B); on the posterior end of its ventral lamina there is a clearly marked sutural area that presumably overlapped a cornual plate.

Fig. 135. Possible cornual plates of *Pteraspis carmani* (× 5). A, PF 1995; B, PF 2067; C, PF 2046.

In the Carman collection there are two types of plates, otherwise undetermined, that may represent cornual plates. The first type, represented by PF 1995 (fig. 135, A), resembles a small branchial plate in that it is elongate and gently curved and tapers to a point at one end. Its length is 19.2 mm., and its breadth at the wider end is 3.0 mm. A relatively wide overlapped area on the concave edge may have contacted the dorsal disc above and behind the branchial opening. The exposed face is broad and rounded at one end and tapers to a point at the other end. The dentine ridges run parallel to the edge opposite the overlapped area. Toward the pointed end of the plate they loop back to the edge of the overlapped area. On the wide end of the plate some of them follow the rounded contour, rather than terminating against that end as they always do in
branchial plates. One difficulty in interpreting this specimen as a cornual plate is that one cannot see how it could have met the posterior end of the ventral lamina of the branchial plate, as is usual in *Pteraspis* (Brotzen, 1936, fig. 1).

The second type of possible cornual plate is represented by eleven specimens (PF 2067–68, 2046) with a dentine ridge arrangement similar to that of scales. The anterior and posterior orientation as used below is based upon comparisons with the ridge pattern of scales and dorsal spines. These small plates (fig. 135, B) are asymmetrical, bluntly pointed posteriorly, and truncate anteriorly; generally the two sides are gently curved in the same direction. As commonly preserved, the central area is rather flat, and from this the sides slope off steeply. The length ranges between 10 and 20 mm. and the width is from 4 to 5 mm. The usual ornamentation consists of several rows of short, longitudinal ridges, but in contrast to scales the rows disappear at the sides where the ridges are elongate parallel to the long edges of the plate. PF 2046 (fig. 135, C) at first sight appears to be a quite different type of plate, but it is connected with those described above by intermediates. A prominent crest divides it into two laminae, a condition possibly obscured in other plates by crushing. There is a pronounced broadening of the plate near the posterior end. The ornament shows only traces of scale-like pattern and consists predominantly of curved, parallel ridges, convex anteriorly. If this represents a cornual plate, the blunt anterior end must have contacted the ventral lamina of the branchial plate, and the crest must have been a continuation of the angulation of the branchial plate.

**Ventral disc.**—The growth of the ventral disc resembles that of the dorsal disc in most respects, and it has been studied in a similar fashion. Dentine ridges have been traced on enlarged photographs at arbitrary 5 mm. intervals (fig. 136). A growth line has been plotted from averages of measurements of four specimens (PF 1909–12) and has been compared to maximum dimensions of a number of specimens (fig. 127). The average measurements (in millimeters), proportions, and ridge counts of these four specimens are given in the table (p. 588). The abbreviations are the same as those used for the dorsal disc (p. 572).

Starting from a single median ridge, the ventral disc passes through a long, narrow, elliptical phase, and then rapidly broadens. In contrast to the dorsal disc, there is usually no growth at the posterior edge; instead, the dentine ridges end abruptly at this edge.
In PF 1910 (fig. 137) four ridges (approximately 1 mm.) are added at the posterior edge in stage 7. There are slight additions to the posterior edge also in PF 1913. As in the dorsal disc, the proportions change during growth, and this is well shown by the ratio of width to length (W/TL). From very slender beginnings, maximum relative breadth is attained at stage 6, after which the relative breadth decreases slightly. The ventral disc never becomes as broad as the dorsal disc. Growth at each side is less than it is anteriorly, as the ridges are broader and more numerous anteriorly. In the mid-line there are, on the average, 4.0 ridges per mm., while laterally there are 6.7 per mm. In some specimens at certain growth stages ridges are added anteriorly and antero-laterally only, and no growth at all takes place at the sides.

<table>
<thead>
<tr>
<th>Stage</th>
<th>La</th>
<th>Increment</th>
<th>W/TL</th>
<th>Number of Ridges</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>W/2</td>
<td></td>
<td>Ra</td>
</tr>
<tr>
<td>2</td>
<td>10</td>
<td>2.7</td>
<td>0.34</td>
<td>11 (11)</td>
</tr>
<tr>
<td>3</td>
<td>15</td>
<td>4.0</td>
<td>0.63</td>
<td>18</td>
</tr>
<tr>
<td>4</td>
<td>20</td>
<td>3.4</td>
<td>0.77</td>
<td>20</td>
</tr>
<tr>
<td>5</td>
<td>25</td>
<td>2.8</td>
<td>0.83</td>
<td>19</td>
</tr>
<tr>
<td>6</td>
<td>30</td>
<td>2.6</td>
<td>0.86</td>
<td>19</td>
</tr>
<tr>
<td>7</td>
<td>35</td>
<td>1.7</td>
<td>0.84</td>
<td>18</td>
</tr>
<tr>
<td>8</td>
<td>40</td>
<td>1.7</td>
<td>0.82</td>
<td>18</td>
</tr>
<tr>
<td>9</td>
<td>45</td>
<td>1.4</td>
<td>0.79</td>
<td>19</td>
</tr>
<tr>
<td>10</td>
<td>50</td>
<td>1.8</td>
<td>0.79</td>
<td>21</td>
</tr>
<tr>
<td>11</td>
<td>55</td>
<td>1.8</td>
<td>0.78</td>
<td>20</td>
</tr>
<tr>
<td>12</td>
<td>60</td>
<td>1.2</td>
<td>0.77</td>
<td>23</td>
</tr>
</tbody>
</table>

There are a number of juvenile ventral discs, but none of them is complete enough to furnish measurements of both width and length. Two early growth stages of PF 1921 are well indicated by growth lines, and these have been measured and plotted on the graph (fig. 127); they correspond well with the plotted line. The smallest measurable ventral disc, PF 1928, has a total median length of 29 mm. The largest complete disc, PF 1920, has a total length of 81 mm., but PF 1908 is considerably larger; estimating the amount missing at the anterior end, its total length may have been 100 mm.

An interesting growth anomaly is shown in PF 1922 (fig. 138). On either side near the antero-lateral corner of the disc is a small subtriangular or oval area in which the dentine ridges are concentric around a small central ridge. On one side this area is completely surrounded by the normal ridges of the ventral disc, while on the other side it terminates anteriorly in a notch in the ventral disc that presumably was occupied by a small plate. These small areas were probably separate ossifications that have been partly or entirely incorporated into the ventral disc. They are not lateral plates since
they lack lateral line pores, but are small, anamestic plates of irregular occurrence.

_Lateral plates._—These plates, recently renamed "orogonial" by Stensiö (1958, p. 260), are variable in their development in pteraspid. They were first described in _Pteraspis vogti_ (Kiaer, 1928, p. 123, fig. 2), which possesses only a single pair, each of which is surrounded by the ventral disc, and the branchial, orbital, rostral, and oral-lateral plates. In _Pteraspis rostrata_ there are two pairs (White, 1935, p. 408, figs. 41-47), and in certain pteraspid from Podolia figured by Stensiö (1958, figs. 140, B; 143, A) there are three or perhaps four pairs. _Pteraspis carmani_ has at least four pairs, and

![Fig. 136. Ventral disc of _Pteraspis carmani_, based on PF 1911 (× 3/2). The numbered stages are tracings of dentine ridges at arbitrary intervals of 5 mm., measured in the mid-line anterior to the center of growth.](image-url)
Fig. 137. Ventral disc of *Pteraspis carmani*, PF 1910 ($\times$ 2).
their arrangement is different from that known in other species of the genus. The largest and most characteristic, here referred to simply as the lateral plate, lies not far from its correct position on the right side of the type (fig. 124, B). It has a pointed anterior end, relatively long medial and lateral edges, and a long, slender projection on its posterior end (fig. 139, A). Its probable relations to neighboring plates are shown in figure 140 (la). The posterior projection lies between two small postero-lateral plates. The medial side of the anterior point presumably contacts the antero-lateral plate. The position of the lateral side of the anterior point is difficult to determine; it may abut against the rostral plate as shown, or it may lie farther posterior against the orbital and branchial plates. The ventral lateral sensory line traverses the lateral plate and presumably meets the infraorbital line in its anterior part, though the course of the latter is difficult to determine in available specimens.

The medial postero-lateral plate is preserved in the type (figs. 124, B; 140, mpl). It occupies the notch between the posterior process of the lateral plate and the ventral disc, and carries the ventral lateral line from one to the other. A number of isolated small plates (fig. 139, C) showing lateral line pores have been provisionally identified as this plate. No lateral postero-lateral plate is seen in the type, but the presence of a notch laterad to the posterior process of the lateral plate indicates that there must have been one. A small elongate plate, PF 2030 (fig. 139, B), may be this plate, and in PF 2025 a similar one is associated with a probable medial postero-lateral plate.

Fig. 138. Anterior part of ventral disc of Pteraspis carmani, PF 1922 (× 2), showing growth anomaly.
In the type a small pyritic nodule has obscured the right anterolateral plate, but what is probably the left one is present, though incompletely exposed and displaced somewhat forward. A number of isolated antero-laterals (fig. 139, E) show this to be a subrhombic plate with the infraorbital lateral line traversing one corner. Its correct position (fig. 140, al) is difficult to determine precisely, largely because the continuation of the infraorbital canal on the oral-lateral or rostral plates cannot be traced.

Postoral plates.—In *Pteraspis vogti* (Kiaer, 1928, fig. 2) there are no postoral plates, and the oral plates articulate directly with the anterior edge of the ventral disc. In *Pteraspis rostrata*, White (1935,
figs. 41–47) found one pair of postoral plates lying between the ventral disc and oral plates. Stensiö (1958, p. 261, fig. 140, B) has indicated that there is a complicated development of these plates in a Podolian pteraspid. In the type of *Pteraspis carmani* (fig. 124, B) there are numerous small plates lying between the ventral disc and oral plates, suggesting a complicated development of the postoral plates in this species also. Unfortunately they are disarranged and it is impossible to reconstruct this region with any confidence.

**Oral-lateral plates.**—These plates, first named by Kiaer (1928, p. 123), and renamed “preorogonial” by Stensiö (1958, p. 258), lie between the antero-lateral and rostral plates, and form the sides of the mouth region. In *Pteraspis vogti* (Kiaer, 1928, fig. 2) there is a single pair lying medial to the infraorbital lines, which appear to pass directly from the lateral plates to the rostral plates. In *Pteraspis rostrata*, White (1935, p. 409) found two pairs of oral-lateral plates, a very small anterior pair and a large posterior pair, the latter traversed by the infraorbital canal. On the left side of the type of *Pteraspis carmani* (fig. 124, B) there are two plates of which the posterior is identified as the antero-lateral, and the anterior as the oral-lateral, both displaced somewhat antero-laterally. The oral-lateral is a small, subtriangular plate that probably lay laterally against the

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**Fig. 140.** Partial restoration of the oro-pharyngeal region of *Pteraspis carmani*, ventral view (× 3/2).

*al*, antero-lateral plate; *br*, branchial plate; *la*, lateral plate; *mpl*, medial postero-lateral plate; *srl*, subrostral lamina; *vd*, ventral disc; *or*, oral plate; *orb*, orbital plate; *po*, postoral plates; *ro*, rostral plate; *sd*, ventral disc.
ventral lamina of the rostral plate, as shown in figure 140 (ol). Whether or not it was crossed by the infraorbital sensory canal cannot be determined with certainty.

**Oral plates.**—At least eleven of the oral plates are preserved in the type (fig. 124, B), and a number of isolated ones have been found in the collection. They agree in general with those described in *Pteraspis vogti* and *P. rostrata*. They are long and narrow, slightly curved, broader posteriorly, and tapering anteriorly. On their ventral or outer surface they are ornamented with more or less transverse dentine ridges that curve forward at the sides into longitudinal ridges. On the inner or dorsal side the oral plates have a strongly developed ridge that may extend the full length of the plate or may be restricted to its anterior end. The longitudinal dentine ridges on one side of the plate extend anteriorly onto this ridge (fig. 139, D), where they fan out to form what was called the "tooth plate" by Kiaer (1928, p. 123).

**Scales.**—The most complete account of pteraspid scales has been given by White (1935, pp. 412–418), who has based his description on the articulated specimens from the Wayne Herbert Quarry in Herefordshire, England. Since there are no specimens with articulated scales in the Carman collection, I have relied on White's description for location and orientation of the numerous isolated scales.

All ridge scales were originally symmetrical and strongly arched, but in the Holland Quarry shale they have often been flattened and distorted. A number of different types may be distinguished, but all intergradations between them occur. One type includes large ridge scales (PF 2061–62, fig. 141, A) with an exposed surface as much as 16.5 mm. long. These are of moderate width and taper to a point posteriorly; they have a deeply rounded notch in the middle of an otherwise convex anterior edge, and a narrow overlap area along this edge. These are possibly ventral ridge scales, since in *Protaspis dorfii* the largest scales occur here (Denison, 1953, fig. 74). Another type (PF 2059–60) differs only in its smaller size (length 8–9 mm.) and relatively broader proportions. These scales grade into two types. The first of these (PF 2055–56, fig. 141, B) is small, about 6 mm. long, relatively very broad, and bluntly pointed posteriorly; the anterior edge is always convex. The second type includes more slender ridge scales (PF 2063–64, fig. 141, C) that are sharply pointed posteriorly and may have the anterior edge either notched or convex. This type, in turn, grades into the long, very slender, fulcral scales of the caudal region (PF 2065–66, fig. 141, D).
Fig. 141. Scales of *Pteraspis carmani* (× 5). A–D, ridge scales; E–H, flank scales; I, aberrant ridge scale; J, inner side of ridge scale. A, PF 2061; B, PF 2055; C, PF 2063; D, PF 2065; E, PF 2047; F, PF 2051; G, PF 2048; H, PF 2053; I, PF 2069; J, PF 2057.
Flank scales have typically a rounded anterior border, a pointed posterior end, and a nearly symmetrical, subrhombic shape (PF 2047-49, fig. 141, E). Rarely both the anterior and posterior ends are pointed, in which case the scales are approximately diamond-shaped (PF 2051-52, fig. 141, F). Not uncommonly the anterior border is notched, and in this case there is a slight to marked asymmetry of development on either side of the notch (PF 2053-54, fig. 141, H). Some of these asymmetrical scales correspond to the so-called double scales described by White (1935, p. 414; 1950, p. 79) in *Pteraspis rostrata* and *P. leathensis*. The anterior overlapped area of flank scales may be slightly or strongly developed.

The ornamentation of both ridge and flank scales consists basically of a number of narrow rows of short, longitudinal ridges. Each row is parallel to the anterior edge of the scale and is thus either convex anteriorly or, when the scale has an anterior notch, has this convexity modified by a median concavity. Within each row the short dentine ridges are arranged mainly antero-posteriorly though in some scales the ridges tend to flare towards the sides. The ridges have round to sharp crests and are usually faintly denticulate. In the posterior and ontogenetically original row the ridges are two or more times as long as in the more anterior rows. Variations in this pattern are not uncommon and include such things as occasional ridges that extend across two rows, rows that do not extend across the whole width of the scale, and denticulate areas where the ridges are subdivided and the row pattern is not apparent. Transverse ridges parallel to the anterior edge, such as are characteristic of *Pteraspis leathensis* and *P. rostrata toombi*, have been noted only in a few scales of *P. carmani* (PF 2048, fig. 141, G), and in these they are usually incomplete mesially. Along the posterior edges where they overlap the scales behind, the dentine ridges extend onto the inner surface, and may cover a relatively large area at the posterior tip (fig. 141, J).

One aberrant scale, PF 2069 (fig. 141, I), is worthy of mention. It is relatively short (length=7.9 mm.) and broad (width=5.0 mm.), considerably arched, and apparently symmetrical. Its most striking feature is that most of the surface is covered with dentine ridges radiating from a point near the center of the scale. A few transverse ridges lie in the mid-line at one end of the radiating ridges, while the opposite end of the scale is covered by six narrow rows of short, antero-posteriorly directed ridges.

*Lateral line canals.*—As far as it has been determined, the arrangement of the lateral line canals of the shield is similar to that of *Pter-
aspis rostrata as described by White (1935, pp. 421-426). The course of the infraorbital canal on the ventro-lateral rim of the rostral plate has not been found, and only an occasional pore of the ventral transverse commissures has been seen. I have been unable to identify any pores of the postoral canal on the anterior part of the ventral disc, though some of the irregularities of the dentine ridge pattern here may indicate the presence of such pores.

Form of the dentine ridges.—There is a correlation in Pteraspis carmani between the width of the dentine ridges and the shape of their crests. The extremely broad ridges that usually occur on the antero-median part of the ventral disc have nearly flat crests without any tuberculation; their edges are finely scalloped by the basilar foramina that open into the very narrow grooves between the ridges. The broad ridges of other plates, and on the antero-lateral parts of the ventral disc, have gently rounded crests that are usually faintly tuberculate; their margins are also crenate. Very fine ridges such as occur on the postero-lateral parts of the dorsal and ventral discs, on the branchial process of the orbital plate, and on both laminae of the branchial plate, are sharply crested and separated by widely open grooves; they are commonly crenate. Occasionally and locally the ridges are divided into discrete denticles or partially divided so that they present a beaded appearance. In scales the ridges are subdivided into short lengths. In the posterior part of each scale the ridges are sharply crested, while in the anterior part they are generally broader and less sharply or rarely round crested. The indentations on the sides usually do not extend to the top of the crests. The dorsal spines with a scale-like ridge pattern have the ridges shaped like those of scales.

EUARTHRODIRA

PHLYCATAENASPIDAE

Aethaspis ohioensis, new species

Type.—CNHM = PF 1661, a nearly complete cranial roof with associated intero-lateral, spinal, and incomplete anterior ventro-lateral and antero-ventral plates (fig. 142).

Referred specimens.—Incomplete impression of a cranial roof, PF 1662; incomplete cranial roof, inner side, PF 1850; left paranuchal, inner side, PF 1852; median dorsals, PF 1663-64; posterior dorsals, PF 1855–57; anterior laterals, PF 1666, 1846; anterior ventro-
latterals, PF 1848–49; anterior ventro-laterals and spinals, PF 1667–1668; spinals, PF 1665, 1853; posterior ventro-lateral, PF 1847; undetermined plates, PF 1851, 1854.

**Horizon and locality.**—As given on page 555.

**Diagnosis.**—A small species whose cranial roof has a median length, excluding the rostral and pineal, of 25 mm. in the type, and whose median dorsal plate is 16 to 23 mm. in median length. The rostral and pineal plates are not fused to the rest of the cranial roof. The postorbital plates contact the nuchal plate, separating the centrals and preorbitals. The central sensory canal is restricted to the postorbital plate and does not extend unto the central plate. The nuchal plate has little development of an antero-median projection and of lateral notches for the paranuchals. The anterior lateral plate has a relatively long ventral edge and the inner wing is little developed. The spinal plate is relatively long compared to the anterior ventro-lateral; it projects behind the posterior edge of the anterior ventro-lateral and is provided with several relatively strong spinelets on its medial edge. The surface of the dermal bones is ornamented with small, widely spaced tubercles, rather uniform in size, and lacking any pronounced linear orientation.

**Description and discussion.**—*Aethaspis ohioensis* is a very small arthrodire, particularly when compared to the other two species of the genus, *A. major* and *A. utahensis*, from the Water Canyon formation of Utah (Denison, 1958). I believe, however, that most of the known specimens are not juvenile. The known cranial roofs have most of their plates fused, the only exceptions being the rostral, pineal, postnasals, and postmarginals; these are not attached in the Ohio species though they are firmly fused in known specimens of *A. major* and *A. utahensis*. There is some reason for believing that the unfused condition of the most anterior plates is primitive, and that fusion took place in larger individuals and in more advanced species and genera.

The ornamentation of *Aethaspis ohioensis* is not particularly distinctive. It has been shown elsewhere (Denison, 1958, p. 470) that the character of arthrodire ornamentation may change considerably in old individuals as larger tubercles are developed near the plate margins and overgrow the smaller primary tubercles near the center of the plates. Secondary as well as primary tubercles occur in *A. ohioensis*; this is shown best on the nuchal plate of PF 1662 (fig. 144), where minute primary tubercles are scattered between moderate-sized secondary tubercles near the center of the plate.
Fig. 142. *Aethaspis ohioensis*, type, PF 1661 (× 5/2). A, cranial roof; B, anterior ventro-lateral, intero-lateral, and spinal plates.
The cranial roof (figs. 142–144) shows clearly that this species belongs to *Aethaspis*. An elongate nuchal that meets the preorbitals and separates the centrals is not known in any other euarthrodire. The contact of the preorbitals with the nuchal is a character of *A.*

Fig. 143. Restoration of the cranial roof of *Aethaspis ohioensis* (X 3).

CE, central; MG, marginal; NU, nuchal; PAN, paranuchal; PRO, preorbital; PTO, postorbital; RC, endoskeletal rhino-capsular ossification; cc, central canal; ifc, infraorbital canal; lc, main lateral line; mp, middle pit line; poc, preopercular canal; pp, posterior pit line; soc, supraorbital canal.

*ohioensis* that distinguishes it from *A. major* and *A. utahensis*. Likewise, the restriction of the central sensory canals to the postorbitals, and the absence of any extensions onto the central plates is distinctive of the Ohio species. The preorbitals are not as greatly elongate posteriorly as in the other species of the genus. The pattern of the cranial roofing bones has been determined from PF 1662 (fig. 144), where the sutures are discernible. Neither the sutures nor the bone radiation can be seen in the type.

The dermal bones of the snout (rostral, pineal, and postnasals) are not known in *A. ohioensis*, but the type (fig. 142, A) shows at its anterior end the imperfectly preserved endoskeletal, rhino-cap-
sular ossification, as well as the subnasal shelf of the posterior endocranial ossification. Though the preservation is so poor that it does not permit a reconstruction, the extent and shape of the anterior part of the cranium are indicated (fig. 143). The snout is relatively short and wide, being intermediate between the broad-snouted *Kujdanowiaspis* and the narrow-snouted *Aethaspis major* and *A. utahensis*.

The inner side of the cranial roof is shown incompletely in PF 1850, and it agrees in most respects with that of *Kujdanowiaspis* (Stensiö, 1945, fig. 8, B). The endocranium is absent and may not have been ossified in this specimen, but the median depressed area that it occupied is clearly marked by the surrounding ridges on the inner side of the dermal bones. On the right side a prominent ridge on the medial part of the paranuchal plate presumably enclosed the endolymphatic duct. It occupies the position of the depression on the dorsal face of the endocranium of *Kujdanowiaspis* in which this duct passed into the paranuchal plate (Stensiö, 1945, fig. 1).
Fig. 145. Plates of the trunk shield of *Aethaspis ohiensis* (X 3). A, median dorsal, PF 1664; B, spinal, PF 1853; C, posterior dorsal, PF 1855; D, posterior dorsal, PF 1856; E, anterior ventro-lateral, PF 1849; F, posterior ventro-lateral, PF 1847.

The median dorsal plate (figs. 145, A; 146, C) is similar to that of other *Aethaspis* and is of the short, broad type that typifies the Actinolepinae. Its highest point is near the center, and from here a low external ridge extends about half the distance to the posterior edge. The small, anterior, external, unornamented areas (fig. 146, C, x) that occur in other *Aethaspis* are indicated in PF 1664. The inner surface has no median keel, and even the small median ridge that occurs in *A. major* is lacking. In the central part of the inner surface
**Fig. 146.** Restorations of plates of the trunk shield of *Aethaspis ohioensis*. A, right anterior lateral, based on PF 1666 (× 5); B, right posterior ventro-lateral, based on PF 1847 (× 5); C, median dorsal, based on PF 1663–64 (× 5/2); D, right anterior ventro-lateral (AVL), antero-ventral (AV), intero-lateral (IL), and spinal (SP), based on PF 1661, 1667–68 (× 5/2).

*end*, limits of endoskeleton of trunk shield; *s.ADl, s.AVL, s.PDL, s.PVL, and s.SP*, overlap areas for, respectively, the anterior dorso-lateral, anterior ventro-lateral, posterior dorso-lateral, posterior ventro-lateral, and spinal plates; *x*, external unornamented area.
there is a deep depression which is abruptly terminated posteriorly but which opens into the general concavity of the antero-medial part of the plate.

Three small, bilaterally symmetrical plates, PF 1855–57, are identified as posterior dorsal plates and presumably lay in the mid-line behind the median dorsal plate (Denison, 1958, pp. 482, 518). PF 1855 (fig. 145, C) resembles a plate from Utah that was believed to be a posterior dorsal of a juvenile *Aethaspis* (op. cit., p. 482, fig. 93, C). It is remarkable for having a posterior median slot immediately behind a high median ridge. This is of the type referred to as posterior dorsal, type 2 (op. cit., p. 482). PF 1856–57 (fig. 145, D) are relatively narrower posterior dorsals that lack the posterior slot. As in PF 1855, there is a median ridge that is high posteriorly and disappears at the gently arched anterior end. This type does not agree well in shape with the posterior dorsal, type 1, of *Aethaspis major* (op. cit., fig. 93, A), and may have occupied a more posterior position.

The anterior lateral plate (fig. 146, A) differs considerably from that of *Aethaspis major*. The ventral or spinal edge is relatively longer, the center of ossification is more posterior, and the external surface is relatively flat, with the inner wing only slightly differentiated. In all these features it is more primitive than *A. major* and approaches the condition of *Kujdanowiaspis*.

The anterior ventro-lateral plates (figs. 142, B; 145, E; 146, D) are similar to those of *A. major* and *A. utahensis*. One specimen, PF 1848, is much smaller and relatively much narrower than the others. If this belongs to a juvenile *A. ohioensis* it would indicate that there was considerable proportional change during growth. The intero-lateral and antero-ventral plates are present in the type (fig. 142, B), but the preservation is such that their shape and structure cannot be determined. The spinal plate (figs. 142, B; 145, B; 146, D) is relatively longer than in *A. major* and *A. utahensis*. As has been mentioned previously (Denison, 1958, p. 487), a long spinal appears to occur in small *Aethaspis* and a relatively short one in larger forms, and *A. ohioensis* agrees with this correlation. The relative proportions of spinal and anterior ventro-lateral plates in *Aethaspis* are as follows:

<table>
<thead>
<tr>
<th></th>
<th>Length AVL</th>
<th>Length SP</th>
<th>Length SP AVL</th>
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<tbody>
<tr>
<td><em>Aethaspis major</em>, PF 939</td>
<td>69 mm.</td>
<td>55 mm.</td>
<td>0.80</td>
</tr>
<tr>
<td><em>Aethaspis utahensis</em>, PF 321</td>
<td>36</td>
<td>32</td>
<td>0.89</td>
</tr>
<tr>
<td><em>Aethaspis sp.</em>, PF 547</td>
<td>35</td>
<td>39</td>
<td>1.11</td>
</tr>
<tr>
<td><em>Aethaspis ohioensis</em>, PF 1667</td>
<td>17</td>
<td>21</td>
<td>1.23</td>
</tr>
</tbody>
</table>
The posterior ventro-lateral plate of *Aethaspis ohioensis* (figs. 145, F; 146, B) has a relatively long ventral lamina. In *A. major* and *A. utahensis* this lamina was restored as being quite short (Denison, 1958, figs. 99, A, 114, C), but since the known plates are incomplete posteriorly, this may be incorrect. The lateral lamina in *A. ohioensis* is short antero-posteriorly as in other *Aethaspis*, but it is relatively higher than in the other species.

*Aethaspis ohioensis* is believed to be more primitive than *A. major* and *A. utahensis* in the following characters: the small size; the broad, unreduced snout with its dermal bones not fused to the cranial roof; the moderate elongation of the preorbital plates; the long spinal edge and little-developed inner wing of the anterior lateral plate; and the relatively long spinal plate. In most of these features it approaches *Kujdanowiaspis*, which is perhaps the most primitive of known Arcotolepida.

**Euarthrodire indet.**

A minute dermal jaw element, PF 2086 (fig. 147), resembles one (PF 526) from the Water Canyon formation of Utah that was considered (Denison, 1958, p. 496, fig. 102, D–E) to be a supragnathal of an undetermined arctolepid. Its size is about what would be expected for a gnathal of *Aethaspis ohioensis*. Its reference to the latter could be defended on the grounds that it is the only arthrodire known from the Holland Quarry shale. However, because very little is known of the jaws of Lower Devonian arthrodires, and because PF 2086 shows possible specializations, I consider it more prudent to leave this specimen unnamed.

This small gnathal has lost one tip, and where it is broken it is seen to be deeply excavated on the unexposed side. It is believed that this side attached to the palato-quadrates or Meckel's cartilage. The opposite surface (fig. 147) is nearly flat except for four faint
longitudinal ridges. One of the sides adjacent to the ridged surface is slightly convex and is covered with low, blunt, and apparently worn denticles. The ridged and denticulate surfaces are of a dark color and together are probably the biting surface. The side opposite the denticulate surface is slightly concave and smooth. The unbroken end is depressed below the ridged biting surface and forms a sort of neck.

This gnathal is quite different from the shearing type, as exemplified by Coccosteus and Dinichthys, and is comparable only with crushing dentitions such as occur in ptyctodonts. A crushing dentition is presumably a specialization in arthrodires, and it is surprising to find it in such an early form. With the exception of the Water Canyon formation specimen, no gnathals of this type have yet been described from the Lower Devonian.

**ACANTHODII**

**Onchus cf. peracutus** Bryant

The acanthodian fin spines from the Holland Quarry shale (PF 2087–96) are long, straight, slender, and gradually tapering to a point (fig. 148). The surface of the exserted portion is smooth, lacking the ridges or ribs usually present in Onchus spines, except that faint ridges may be present proximally on the postero-lateral edges. The inserted base is longitudinally striated. The pulp or main canal is widely open at the base (fig. 149, C, mc) and continues to be open for about the proximal third of the total length of the spine. In the distal two-thirds, the pulp canal is partly, then completely enclosed by processes of the walls of the spine. Near the middle of the spine these processes do not quite meet, with the result that the pulp canal retains an external connection through a narrow slit (fig. 149, B). The processes that enclose the pulp canal are set in front of the postero-lateral edges of the spine so that there is a channel on the posterior surface of the spine all the way to the tip (fig. 148, B).

The histological structure of these acanthodian spines (fig. 149) shows a general correspondence to that of elasmobranchs (Peyer, 1946, pp. 83–98). An elasmobranch spine is a complex structure, really a "spine within a spine," with the inner spine or "Stammtel" (op. cit., p. 97) arising ontogenetically quite separately from the outer spine or "Mantelteil" which surrounds it. In Onchus cf. peracutus the pulp canal or main canal, as the terms are commonly used,
Fig. 148. *Onchus* cf. *peracutus*, fin spines (× 2). A, PF 2090, anterior face; B, PF 2087, posterior face.

Fig. 149. Transverse sections of fin spines of *Onchus* cf. *peracutus* (× 30). A, PF 2096, distal part of spine; B, PF 2096, near middle of spine; C, PF 2095, proximal part of spine.

*dt*, dentine tubules; *mc*, main canal; *pc*, pulp canal of inner spine; *po*, pulp canals of outer spine; *spi*, inner spine or "Stammteil"; *spo*, outer spine or "Mantelleil."
is the pulp cavity of the inner spine, and from it the dentine tubules radiate outward to the boundary of the outer spine. The pulp cavity of the outer spine is variously developed. *Devononchus* was characterized by Gross (1940, p. 15) in part by the presence of an upper canal, which is the main pulp canal of the outer spine. On the other hand, *Onchus* has a diffuse outer pulp, consisting of many irregular but mainly longitudinal canals from which the dentine tubules extend outward. This is the situation in *Onchus cf. peracutus*, except that there may be a small upper canal centered in the diffuse pulp of the proximal half of the spine.

Reference of the Holland Quarry shale specimens to *Onchus peracutus* is uncertain because of the poor preservation of the type specimen from Beartooth Butte, Wyoming (Bryant, 1934, p. 149, pl. 18, fig. 3). According to Bryant, the sides are ornamented with a median series of several sharp, longitudinal ridges, but the only ridges visible on the type are two or three fine ones on the postero-lateral edges. The surface of most of the spine is smooth, as in the Ohio specimens. The type is obliquely crushed and incompletely preserved, but it can be interpreted as having a shape and structure similar to that of the Ohio specimens. A second Beartooth Butte species, *Onchus penetrans* (Bryant, 1932, p. 252, pl. 10, fig. 4), differs in its curvature and fine longitudinal ridges. The spine described as *Machaeracanthus minor* (Bryant, 1934, p. 148, pl. 18, fig. 1) may be *Onchus penetrans*. The type is a poorly preserved natural cast, and so what Bryant believed to be a longitudinal ridge on the side could be one of the postero-lateral edges of an obliquely crushed spine.

**AGE OF THE HOLLAND QUARRY SHALE**

The vertebrate fauna of the Holland Quarry shale is comparable to that of the Beartooth Butte formation of Wyoming (Bryant, 1932; 1934; 1935) and the Water Canyon formation of Utah (Denison, 1953; 1958). *Allocryptaspis* occurs in all three formations, but not elsewhere. This is the largest of known Cyathaspidae and its size is suggestive of a late or post-Dittonian age (Denison, 1953, p. 296). *Protaspis* is the pteraspid of the Wyoming and Utah formations, but the reference of the Holland Quarry species to *Pteraspis* is purely arbitrary. *Pteraspis carmani* is closely related to *Protaspis*, approaches it in most respects, and could well be nearly and directly ancestral to it. This species suggests, therefore, that the Holland Quarry shale is slightly older than the Beartooth Butte and Water Canyon formations. The importance of pteraspids in Lower Devonian correlations
has been emphasized by White (1956) and Schmidt (1959). The earliest members of the family, small species with short, blunt rostra, are characteristic of the lower Dittonian. They are succeeded in the middle Dittonian and equivalent upper Gedinnian by larger species, typified by *Pteraspis rostrata* and *P. crouchi*, which show various specializations. In the upper Dittonian and equivalent lower Siegenian comes the first appearance of species with long rostra, exemplified by *Pteraspis leachi*. It is in this zone that *Protaspis* makes its first appearance. Finally there is the zone of the very long snouted *Pteraspis dunensis*, beginning with the lower Breconian and middle Siegenian, and continuing into the Emsian. If *Protaspis* indicates an upper Dittonian or lower Siegenian age, the slightly more primitive condition of *Pteraspis carmani* suggests that the Holland Quarry shale was a bit older.

The arthrodiré of the Holland Quarry shale, *Aethaspis*, is known elsewhere only from the Water Canyon formation. The Ohio species, *A. ohioensis*, is more primitive than those from the Water Canyon formation, which suggests that it is somewhat older. But *Aethaspis* is a specialized arctolepid, at least in comparison to *Kujdanowiaspis* (Denison, 1958, p. 545), and one would expect it to be younger than the latter. *Kujdanowiaspis* occurs in upper Gedinnian and lower Siegenian equivalents in Podolia and Spitsbergen. *Aethaspis* thus suggests an age no older than lower Siegenian.

The acanthodian of the Holland Quarry shale, *Onchus cf. peracutus*, indicates little more than a general correspondence with the Beartooth Butte and Water Canyon formations.

In summary, the vertebrates of the Holland Quarry shale favor a correlation with the upper Dittonian of England and the lower Siegenian of continental Europe. Correlation with the North American standard section can be accomplished only indirectly. According to Cooper *et al.* (1942), the Siegenian (or lower part of the Coblenzian) is to be correlated with the Deerpark stage. This correlation, based on the vertebrate fossils, agrees with the stratigraphical evidence that Dr. Carman has summarized (1960, p. 4). The Holland Quarry shale was formed in the interval between the deposition of the Raisin River dolomite and the Sylvania sandstone. This interval covered the Helderberg, Deerpark, and part of the Onesquethaw stages. It should be noted that by American usage the Onesquethaw stage is referred to the Middle Devonian, and the Holland Quarry shale would occupy some of the upper part of the Lower Devonian. In Europe presumed Onesquethaw equivalents are referred to the Lower De-
vonian (Emsian), and the Holland Quarry shale would fall into the middle part of the Lower Devonian.

**ECOLOGY OF THE HOLLAND QUARRY SHALE**

Since the Holland Quarry shale is known from a single small outcrop that has never been well exposed and is now completely covered, there is little geologic information available for the determination of the manner of its deposition. Carman (1960, p. 2) has shown that the Holland Quarry outcrop could be interpreted as a filling of (1) a roughly circular pit, or (2) a valley. The presence of aquatic vertebrates favors the second interpretation, since they must have had access to stream or sea.

The individual groups of vertebrates found in the shale are of little help in determining the depositional environment. *Allocryptaspis* belongs to the subfamily Poraspinae, which occurs in marginal marine and fluvial deposits, but not in typical marine sediments (Denison, 1956, pp. 416-417). *Pteraspis* belongs to a family that occurs in freshwater, marginal marine, and marine formations. Some pteraspids may have been adapted to particular habitats within this range; others may have been euryhaline (op. cit., pp. 417-418). *Aethaspis* belongs to the Euarthrodira, a group that may have been originally restricted to fresh waters but at the time of the deposition of the Holland Quarry shale was also found in marine and marginal marine deposits (op. cit., pp. 426-427). *Onchus* belongs to the Acanthodii, which in Lower Devonian times lived in marine, marginal, and freshwater habitats (op. cit., p. 425).

Though the individual vertebrates have little ecological significance, the whole assemblage, including the eurypterids and plants, shows such striking resemblance to that of the Beartooth Butte formation of Wyoming that it is safe to assume some similarity in environment. The Beartooth Butte formation has the appearance of a channel fill and has been interpreted as a stream or estuarine deposit. But a similar vertebrate assemblage occurs in the Water Canyon formation of Utah, and this is a widespread deposit, with gastropods, brachiopods, and ostracods, some of which are definitely marine. I believe that it is a marginal marine sediment deposited in a large bay whose waters were salt or brackish (Denison, 1956, pp. 413-415). If the Water Canyon formation is a marginal marine deposit, the same is probably true of the Beartooth Butte and Holland Quarry formations. The Holland Quarry shale may have been deposited in a channel or estuary opening into the transgressing sea to the north.
Its waters may have been brackish or salt, and the absence of any definitely marine invertebrates may be due to a foul, muddy bottom.\(^1\)

**SUMMARY**

The Holland Quarry shale, a Lower Devonian formation known from a single small exposure in Lucas County, northwestern Ohio, has yielded plants, eurypterids, and vertebrates. The vertebrates are described in this paper. The Cyathaspidae are represented by *Allocryptaspis laticostatus*, new species. The most abundant form belongs to the Pteraspidae and has been named *Pteraspis carmani*, new species. Its generic reference is arbitrary, and it is closely related and may be ancestral to *Protaspis*. Some aspects of its growth and individual variation have been considered. The arthrodire, a relatively rare element in the fauna, is *Aethaspis ohioensis*, new species, a small and primitive member of the genus. Spines of acanthodians have been referred to *Onchus cf. peracutus* Bryant.

The vertebrates indicate that the Holland Quarry shale should be correlated with the upper Dittonian or equivalent lower Siegenian of the European Lower Devonian. This is probably of the same age as the Deerpark stage of the North American standard section. The vertebrate assemblage is similar to those of the Beartooth Butte formation of Wyoming and the Water Canyon formation of Utah. I believe that the Holland Quarry shale was deposited in salt or brackish water, possibly in a channel or estuary opening into the transgressing sea to the north.

\(^1\) As this was in press, Dr. E. Kjellesvig-Waering found a piece of Holland Quarry shale containing ostracods, and Dr. E. S. Richardson, Jr., found another with not only ostracods, but also gastropods, articulate and inarticulate brachiopods, tubicolous annelids, and a crinoid.
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