

THE OSTRACODERM GENUS DARTMUTHIA PATTEN.

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The ostracoderm order Osteostraci has been variously divided into families. The Cephalaspidae and the Tremataspidae are recognized as distinct. *Ateleaspis* and *Astraspis* are variously disposed of. Traquair (1) gave the former family rank, although later (2) he reduced it to a genus of the family Cephalaspidae, a position which Stensiö (3) also takes. Woodward (4) unites *Astraspis* with *Ateleaspis* as Ateleaspidae. Romer (5) gives *Ateleaspis* family rank and ranks *Astraspis* as constituting a family of uncertain position. Stensiö (6) assigns *Astraspis* to the Heterostraci under the Drepanaspidae, while Eastman (7) and Schlosser (8) give it family rank in that same order.

The principal distinctions between the Cephalaspidae and the Tremataspidae are the possession of cornua on the posterolateral corners of the head and trunk shield in cephalaspids and their absence in tremataspids; and the subdivision of the lateral sensory or electric fields in tremataspids into two short lenticular areas on either side, their persistence as single elongated organs on either side in cephalaspids. Stensiö (6) regards the absence of cornua as implying absence of pectoral appendages such as those of cephalaspids, since these lie in indentations, the pectoral sinuses, produced in the posterior margin of the shield just within the cornua. There are also some differences in the minute structure of the exoskeleton, but with increased knowledge of the variety of forms, especially among Cephalaspidae, these differences become less significant. It will probably happen that in time some new genera of the Tremataspidae will be found which may still further bridge the gap between these families. A family represented by a single genus can hardly be regarded as sufficient basis for broad generalization.

In 1931 Dr. William Patten (9) described a new form, *Dartmuthia gemmifera*, n.g., n.sp., which in some ways is intermediate between the cephalaspids and the tremataspids. Like the Cephalaspidae it has the lateral fields continuous rather than broken, and has a rugose rather than a smooth dorsal shield surface. Like the Tremataspidae it lacks cornua to the shield, and thus presumably had no pectoral appendages. The median, unpaired section of the shield which lies behind the

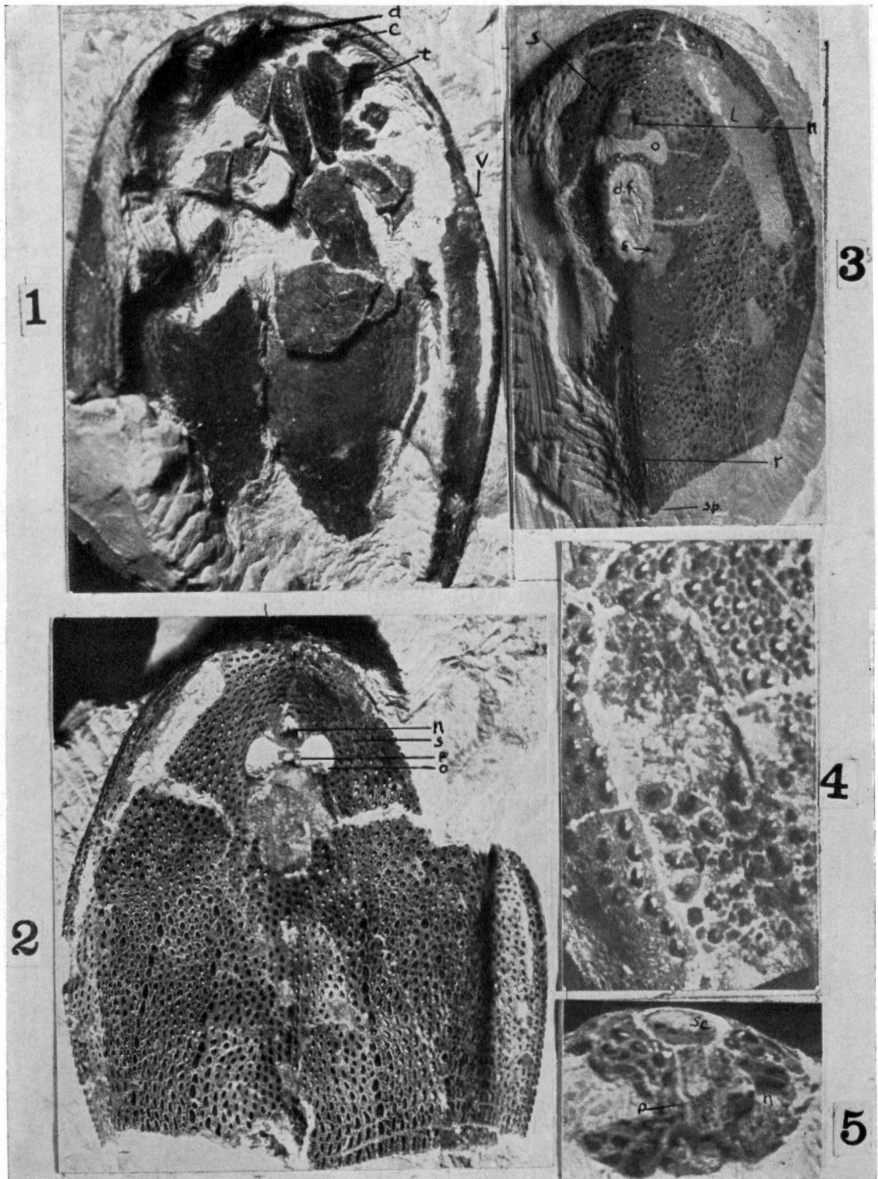


Fig. 1. Specimen No. 71. Ventral aspect. \times ca. 2. (d) depressed area; (c) centrally-directed process; (t) triangular plates; (v) ventral shelf.

Fig. 2. Specimen No. 70. Dorsal aspect showing ornamentation. \times ca. 2. (n) nasal organ; (o) orbit; (p) pineal; (s) circumorbital sensory canal.

Fig. 3. Specimen No. 85. Dorsal aspect. \times ca. $1\frac{1}{4}$. (n) nasal; (o) orbit; (d, f) dorsal field; (l) lateral field; (e) endolymphatic aperture; (s) circumorbital sensory canal; (r) mid-dorsal ridge; (sp) dorsal spine.

Fig. 4. Specimen No. 106. Part of left lateral sensory or electric field showing separate plates over part of the field. Also shows superficial scales surrounding tubercles. \times ca. 4.5.

Fig. 5. Specimen No. 94. Dorsal aspect of left sclerotic (sc) and pineal plate (p). \times ca. 3. (n) nasal.

branchial region and so belongs to the trunk, that section which Stensiö (6) designates as the interzonal part, is long in *Dartmuthia* as in *Tremataspis*. The exoskeleton of the dorsal shield differs from that in Cephalaspidae as well as from that in Tremataspidae. In cephalaspids the superficial layer is generally smooth and continuous save for grooves or for tubercles, whereas in *Dartmuthia* the superficial layer is broken into minute polygonal areas, almost scale-like, surrounding tubercles which arise from the middle layer (Fig. 4).

The fossils of this genus, as of the Osteostraci in general, usually consist of the anterior portion of the body only. This was encased in bony dorsal and ventral shields. In *Tremataspis* the dorsal and ventral armor was continuous, which accounts for the more frequent occurrence of specimens with both dorsal and ventral surfaces available. In *Dartmuthia* dorsal shields have been much more abundantly preserved, the ventral shield being sutured to a narrow ventral shelf or rim which is continuous with the dorsal shield (Fig. 1). There are no individuals in the collection of something over 300 specimens with this ventral surface completely preserved, even in the post-branchial region. Fig. 1 is a photograph of the most complete ventrum in the collection. In cephalaspids as well, though (3, 6) in many forms the ventral interzonal part was continuous, good ventral aspects are rare. Among the fossils brought back by Doctor Patten on his last expedition to Oesel are about 100 cephalaspids or cephalaspid fragments. Of these only a few show any trace of ventrum and in none thus far worked out has the region just central to the ventral rim been preserved. The shortness of this portion of the ventral shield in cephalaspids may have made preservation more rare.

It appears probable that the Osteostraci were fresh-water forms, the deposits consisting of remains which were carried down stream, suffering considerable damage en route. In some cephalaspids, notably from the Old Red Sandstone formations, the tail region has been preserved (3). In the tremataspid such preservation is rare. In *Dartmuthia* few specimens so far examined have shown this region, and in none has it been at all complete. Since the scales of this posterior region were not interlocked in such fashion as to hold the form together after the soft parts had macerated, and since, if our supposition as to the taxonomic position of the ostracoderms is correct, the notochord was persistent, there

would be little chance of this portion of a carcass remaining together and associated with the head and trunk shield during its peregrinations prior to deposit.

The same conditions have brought about the loss of other loosely connected parts, such as the plates which acted as armor over the oralo-branchial chamber on the ventral side of the head, termed by Stensiö (3) the ventral visceral exoskeleton. This lack of preservation has led to uncertainty as to the make-up of this region. In the specimens of *Dartmuthia* in the Patten collection none has this region complete, but a few have some of the plates apparently nearly in place (Fig. 1), permitting comparison with *Tremataspis*. Some specimens of this latter genus have the plates more completely preserved. One in particular in the Patten collection has the anterior median plates together with most of the plates of the left side of this region practically in place. This specimen, as nearly as can be ascertained, formed the basis for Doctor Patten's last reconstruction of *Tremataspis* (10).

The collection of *Dartmuthia* comes from the Island of Oesel (Saaremaa), in Estonia. The horizon is middle Ludlow, upper Silurian. The stratigraphy of this region has been discussed by Luha (11). Some of the specimens were collected by Doctor Patten in the summer of 1930, the rest in the summer of 1932. Thus far I do not distinguish more than one species, *Dartmuthia gemmifera* Patten. There are variations in some features, such as ornamentation, but if two or more of the variable features are studied it will be found that all combinations occur, indicating, in my opinion, simply variations within the species. Other differences such as size seem to grade together as though indicative of age and of those obscure factors which condition size variation among the individuals of a species.

Dartmuthia is a small form, the length of the shield being seldom over 50 millimeters, the width usually under 40. The dorsal shield is ornamented with tubercles (Figs. 2, 4), averaging a trifle over two to the square millimeter on the general surface, each surrounded by small, polygonal, scale-like plates. The tubercles vary from round to elongate, blunt to pointed. The arrangement of the tubercles is variable, possibly sufficiently to be of taxonomic significance. In the anterior portion especially there is some alignment of tubercles (Figs. 2, 3), the lines following the curve of the shield. This is especially marked just anterior and lateral to the nasal eminence. The

mid-dorsal line also shows alignment, and in some cases the regions flanking this show the same feature, usually less marked. In some specimens this alignment can be detected over the general dorsal surface. In others the tubercles show little evidence of any arrangement over this general region. The mid-dorsal ridge, usually elevated somewhat, is capped by a line of more prominent tubercles, which commonly become more pronounced posteriorly, while the ridge itself becomes more marked. In some specimens (Fig. 2) short lines of more pronounced tubercles occur here and there on the lateral regions of the dorsum, usually two or three lines on either side. The capping tubercles of the mid-dorsal ridge are sometimes in a single line, sometimes irregular, sometimes double. At the posterior end of the shield is a backwardly and slightly upwardly directed process, the dorsal spine (Fig. 3). The tubercles on this portion may run together to form more massive structures or may be only slightly elongated. The running together of tubercles, either end to end or side by side, is not uncommon, especially in regions where the tubercles are most pronounced or numerous. The dorsal spine varies somewhat in form, being in most cases decidedly triangular, somewhat as in *Kiaeraspis auchenaspidoides* figured by Stensiö (6); in other cases being more spine-like, with a more abrupt origin from the posterior line of the shield, and less triangular, somewhat similar to *Cephalaspis lankestri* (3).

In those cephalaspids in which this portion is well preserved along with the posterior trunk region it has been found that the dorsal crest forms a direct continuation of the median dorsal ridge of the shield, and is thus continuous with the spine. In one specimen of *Tremataspis* (*T. mickwitzii* ?) in the Patten collection a similar situation occurs, the whole structure, in fact, being strongly like that figured by Stensiö (3, p. 53) for *Hemicyclaspis murchisoni*. This portion of the trunk region is insufficiently preserved to be reconstructed in any of the *Dartmuthia* material, although some fragments which may well have been dorsal crest scales or scutes have been found.

Laterally the posterior portion of the dorsal shield shows indications of segmentation (Fig. 2), each segment being separated from the rest of the shield and from its neighbors by shallow grooves. In some cases the tubercles of each segment are elongated and are arranged as a single row, a condition which carries over to the anterior lateral plates or

"scales" of the posterior trunk region. A similar segmentation has been noted in a number of cephalaspids, notably *Thyestes* and *Kiaeraspis*.

The tuberculation occurs on the plates which cover the dorsal and lateral sensory or electric fields. These plates are in fact so similar to the general dorsal surface that in some cases it is not possible to find any trace of the lateral fields, especially if there has been lateral compression which has forced this region up to the general surface level. One specimen (Fig. 4) shows the plates over a part of the left lateral field especially well. The structure is like that of the general dorsal surface save that each tubercle forms the center of a separate plate. Were the plates to fuse together the structure would be identical with that seen in the exoskeleton lateral to the field. The pineal plate and the sclerotics (Fig. 5) are also tuberculated on their upper surfaces.

Where the superficial layer of the shield is missing the tubercles show somewhat crenulated margins, actually fine ridges ornamenting their borders and flowing into the general surface of the middle layer. This appearance is most marked on the lateral margins of more elongated tubercles, such as those ornamenting the segmented portions of the shield, the posterior portion of the mid-dorsal ridge, and on the inner edge of the ventral rim, where the ornamentation gives a feather-like appearance to the tubercles. Doctor Patten (9) called attention to this feather-like ornamentation, especially in the region of the ventral surface near the gill openings.

Toward the lateral and anterior margins of the shield the tubercles become more definitely aligned and the lines closer together. Here too the tubercles become elongated and nearly confluent, forming a marginal armor (Fig. 2). The tuberculation continues over the ventral rim, where its character is somewhat altered, the tubercles becoming blunt. In some specimens the tubercles of the ventral rim are aligned, the lines running diagonally outward and posteriorly. In others the lines are not observable.

The ventral rim (Fig. 1) forms a narrow shelf in the trunk region, narrowing abruptly at the posterior end of the branchial area. Anterior to this the branchial pouches modify the contour of the rim, the marginal region becomes more rounded, and the ornamentation becomes throughout similar to that of the dorsal rim. Central to the shelf in the post-branchial region the ventral surface is ornamented with polygonal areas

or plates with crenulated borders. These polygonal scales or plates (Fig. 1) are largest toward the mid-ventral line, where they may measure up to two millimeters across. Toward the lateral margins they become smaller, eventually giving place to the flattened tubercles of the central portion of the shelf. There the minute polygonal scales of the superficial layer come in between the tubercles.

It is of interest that the polygonal scales of the ventrum appear to grade into the flattened tubercles of the ventral shelf. Fig. 1 shows this slightly. In some specimens this transition is very apparent. The plates are flattened and thinner, so thin that in many cases the reticulated structure of the skeletal layer immediately beneath them is quite visible. In both scales and flattened tubercles the polished layer strips or chips off very readily and discloses very similar structure underneath. The dorsal tubercles differ from both in more massive structure. They do not scale off readily, but break with an irregular fracture. However, if one follows the ornamentation the tubercles of the general surface grade into those of the dorsal rim, which in turn are carried over onto the ventral rim.

Such a transition suggests either that the continuous dorsal armor studded with tubercles may have arisen by fusion of scales or plates such as those of the ventrum, the middle layer becoming more dense and the polished portion becoming reduced to tubercles, accompanied by development of the minute scales which surround the tubercles, or that the reverse procedure has been followed. The separate plates over the lateral fields might be regarded as a transition stage, in which the denser middle layer has encroached on the polished portion and in turn been coated with the minute scales of the superficial layer, the separate plates or scales not yet having fused.

A somewhat similar situation exists in *Hemicyclaspis* (3) in which the post-branchial ventrum is not continuous but is made up of scales. *Ateleaspis* might represent another stage, near the beginning or the end of such a series, since in it the dorsal shield also consists of separate plates or scales (1, 2).

The ventral surface of the oralo-branchial region (Fig. 1) was as in Tremataspidae and Cephalaspidae, probably having been closed by a flexible membrane in which were embedded the plates which served as armor over the oralo-branchial chamber. In most fossils the plates are lost. In a few specimens some of them are preserved, and they appear to resemble closely

those of *Tremataspis* figured by Doctor Patten in his last paper (10). The inner edge of the anterior rim bears in the mid-line a small triangular process, ornamented with tubercles of relatively small size. This is directed backward, and in the fossils is slightly depressed. A similar depressed area occurs in both cephalaspids and tremataspids. On either side of this, separated from the triangular process by about its own width, is a centrally directed process. Lying in the mid-line in this region are two triangular plates, about ten millimeters in length, about three millimeters in basal width. They are directed posteriorly and the basal width of the two together fills the gap between the central ends of the inwardly directed processes. These triangular plates are ornamented with polygonal scales similar to those of the general ventral surface. These are largest toward the center of each plate, growing smaller and more tubercle-like toward their margins. The other plates of the oralo-branchial region were similarly ornamented, as can be seen in Fig. 1. They apparently were quite similar to the corresponding plates of *Tremataspis*, although they are not sufficiently closely in place to allow complete reconstruction of the region.

The external gill apertures are similar to those of *Tremataspis* and *Cephalaspis*, a number of small openings (at least five), in a series running diagonally inward and backward at the border of the post-branchial region, and indications of probably four more along the lateral margin of the oralo-branchial chamber. The endoskeleton of the oralo-branchial region of the dorsal shield shows, as it does in cephalaspids, what lend themselves readily to interpretation as gill pouches.

On the dorsal surface (Fig. 3) three sensory or electric fields are situated somewhat as in *Cephalaspis*, i.e. a single elongated lenticular field, 8 to 10 millimeters in length, about 4 millimeters at its greatest width, directly behind the pineal region, and a pair of lateral fields about 20 millimeters long by 3 to 4 millimeters wide. The dorsal field does not include the openings of the paired canals interpreted as housing the endolymphatic ducts. These apertures lie just lateral to the posterior end of the dorsal field (Figs. 2, 3). The field is thus somewhat longer than that of *Tremataspis*, in which the canal openings lie posterior to the field. In most cephalaspids (3) the canals open within the dorsal field.

The lateral fields are less extensive than in cephalaspids. They commence lateral to the anterior part of the infra-orbital

sensory canal groove and extend about half way back on the shield. The innervation of these fields is, so far as can be determined at present, practically identical with that in the cephalaspids. None of the specimens thus far uncovered shows the degree of completeness of these structures shown by some of the cephalaspids figured by Stensiö (6, Pl. 49), but sufficient is preserved to demonstrate that in essentials the *Dartmuthia* lateral fields were innervated by the same nerve elements as were those of the cephalaspids. In cephalaspids there are six branches, of which the two anterior remain together until they near the inner border of the field. The anterior branches in *Dartmuthia* are similarly associated, separating practically at the border of the lateral field, as in the *Kiaeraspinae* (3). The other branches show a distribution similar to those of *Cephalaspis*, but in no case thus far worked out has it been possible to ascertain the exact number of branches. There are at least five altogether, and in a few cases indications that a sixth may have been present.

The lateral fields are, as indicated previously (Fig. 4), covered by small plates of typical exoskeletal structure. They are in turn underlain by the endoskeleton. Since the skeletal relationships of *Dartmuthia* are the same as in *Cephalaspis*, including a subaponeurotic vascular plexus between the exo- and endoskeleton (6), it seems probable that the exoskeleton belongs to the corium and that the lateral fields are of similar origin.

The orbits (Figs. 2, 3) lie close together as in the other families of this order. They are oval in form, the long axis longitudinal. As in *Cephalaspidae* and *Tremataspidae*, ossified sclerotics are present (Fig. 5). The upper surface of the sclerotics is tuberculated.

Between the orbits lies the pineal plate. This plate is rarely preserved in any of the ostracoderms. It has been found complete in but one specimen of *Dartmuthia* (Fig. 5), out of approximately 400 examined, a good share of which have the orbital region fairly well preserved. The pineal plate is cylindrical, with upper and lower foramina. In general form it is like that in cephalaspids (3) and tremataspid. It is tuberculated on its upper surface.

The naso-hypophysial aperture is located just anterior to the pineal plate, separated from it by about the same distance as is the dorsal field (Figs. 2, 3, 5). The aperture is located in the bottom of a depression which occupies the top of a

slight eminence. The state of preservation of the material makes it uncertain what amount of variation occurs in the form and ornamentation of this region. The general condition found in specimens is that the aperture is on a slight elevation in the center of a cup-shaped depression whose margins are in turn slightly elevated. On either side of the center elevation the floor of the pit is especially depressed. In some specimens the cup-shaped depression is somewhat triangular, with one point forward. In a number of specimens the middle of the posterior rim of the pit is occupied by a large, horseshoe-shaped tubercle, with the points of the shoe downward and forward, the aperture, which is slit-like, piercing the open part of the shoe and extending from that along the floor in the mid-line. It seems probable that this type of structure may have been present in the specimens in general, but in many cases the posterior rim of the depression is eroded or broken. The specimen photographed for Fig. 2 shows such a tubercle, although the illustration does not bring it out. In Fig. 5 the depression can be seen, and at its posterior edge the broken front of the horseshoe.

In 1903 Doctor Patten (12, 13) described the lateral line system of *Tremataspis*. The lines which are found on the dorsal surface of the *Tremataspis* shield consist of broken grooves, a series of dashes. One set of these encircles the orbital region, the two halves meeting or nearly meeting anterior to the nasal opening. This canal Doctor Patten termed the circumorbital. In the cephalaspids the grooves appear to be more nearly continuous where they are found, but the whole system is either less fully developed than that of *Tremataspis* or may have been more superficially situated (3, 6).

In *Dartmuthia* little of the system is preserved. The only part which can be certainly demonstrated is the circumorbital, or in the terminology of Stensiö (6), the infraorbital (Figs. 2, 3). This is very similar to that shown in *Hemicyclaspis* (3, Fig. 23), running very close to the orbits, then forward and curving inward some distance anterior to the nasal opening. It does not flare outward anterior to the orbits as in the specimen figured by Stensiö. In some specimens of *Tremataspis* the two sides of this groove may be united across the anterior end; in some others they stop short of this; while in others the system on one side may be continued to the mid-

line and its mate stop short of this point. In the *Dartmuthia* material showing this portion of the system a similar situation exists, although it is more difficult to be sure of the termination of the lines than in *Tremataspis*. In some cases it has been possible to follow a connection between the lines. As in cephalaspids, the lateral line system is usually exhibited only in those specimens in which the superficial layer of the exoskeleton is preserved or in the counterpart which has stripped off from such specimens.

The exoskeleton of the dorsal shield consists of three layers as it does in the other families of the order. The superficial layer consists of glossy scales (Figs. 2, 4), darker in the center. The tubercles protrude through this layer, so that each tubercle is surrounded by a series of the scales. Both scales and tubercles are stippled with minute indentations. Whether the superficial layer is of enamel has not been ascertained.

The middle layer is heavy. It consists of bone, as usual. The tubercles grow out from this layer. The separation between this and the basal layer is not always demonstrable, but where it shows it indicates a basal layer somewhat thinner than the middle layer, divided into polygonal areas with raised borders.

The thickness of the exoskeleton varies as it does in *Cephalaspis*, being thickest around the margin, especially the anterior rim, thinnest anterior to the nasal eminence and lateral to the orbits, between them and the lateral fields. The basal layer appears to be made up of fibrous laminae as in cephalaspids.

Beneath the exoskeleton lies an endoskeleton. As in cephalaspids (6), perichondrial bone of this endoskeleton lines the labyrinth cavity, the orbits, the canals for nerves and vessels which traverse the endoskeleton, the oralo-branchial chamber, and the brain case. Thus it is possible to make out many details of structure such as the form of the gill pouches, the distribution of nerves and vessels, the form of the labyrinth cavity, and in a few instances, some features of the brain case. In one fossil, for example, a good part of the cerebellum is exposed, and it is hoped that this specimen will show further portions of the posterior region on further dissection.

The posterior portion of the trunk and the tail are not preserved in any degree of completeness. Nevertheless frag-

ments of that region are available, and from information derived from these fragments enough can be determined to show that this region is essentially like that in *Tremataspis* and *Cephalaspis*. The anterior portion of this post-shield region continues the ornamentation of the segmented portion of the shield, i.e., each of the "scales" or plates was ornamented with a row of low, elongated tubercles. No positively identifiable plates of the dorsal ridge just posterior to the dorsal spine have been found, although some fragments may be such plates.

On one specimen a single posteriorly situated dorsal fin and a heterocercal caudal are incompletely preserved. The specimens showing traces of this region are distorted, making orientation difficult. It appears safe to state that there is on either side a lateral row of scales or plates, with a dorsal row of shorter plates or scutes, fairly marked ventro-lateral ridges, and on the ventrum diagonally arranged rows of smaller scales, each row directed inward and forward to meet its mate from the opposite side in the mid-ventral line.

I wish to express my gratitude to Dr. B. M. Patten for placing the material of his father's collection in my hands for description, also to Mr. H. H. Barrett, Dartmouth College photographer, for producing the figures accompanying this paper. Finally, I wish to acknowledge my debt to the late Dr. William Patten. His devotion to the task which he set himself as a young man was responsible for the assembling of one of the outstanding collections of these primitive armored fishes in the world. An artist of no mean ability, an ingenious technician, a tireless worker, his was the skill and patience which is largely responsible for the preparation of the fossils on which this description is based. As he left practically no notes on the material as he prepared it, full responsibility for interpretation of structures rests on me, and errors which that involves are of my own making.

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