THE TREMATASPIDAE.*

PART I.

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ABSTRACT.

The Ostracoderm family Tremataspidae contains but one genus thus far. This genus, *Tremataspis*, has seven species recognized as valid in the present paper. These are: *T. schmidti* Rohon, *T. milleri* Patten, *T. mammillata* Patten, *T. rohoni* n. sp., *T. patteni* n. sp., *T. scalaris* n. sp., and *T. panderi* n. sp. Another variant is listed as a tentative species. *T. simonsoni* Rohon is inadequately known. *T. mickwitzi* Rohon is removed from the family and made the type for a new genus, *Saaremaaspis*. The Lectotypes of the Patten species and the Holotypes of the new species are in the Patten collection at Dartmouth College. The horizon is Middle Ludlow, Upper Silurian, of the Island of Oesel. The present description is based on a study of something in excess of 2000 specimens of the genus in the Patten Collection. Details of brain-case, sense organs, and skeletal structures are described, including both dorsal and ventral lines of the sensory canal system. A new reconstruction of the plates over the oralo-branchial chamber is given.

The earliest vertebrates of which we have fossil record are known from fragments of bony shields found in rocks of Ordovician age. We know little of these Ordovician forms, but the histological structure of the shield seems to place them as Ostracoderms. It is not until Upper Silurian that we find adequately preserved specimens to enable us to study body form and detailed structure, and here we find them existing in diverse forms.

The evolutionary significance of Ostracoderms is a speculative matter. A number of Vertebrate Paleontologists regard some member of this group as ancestral to fishes, but many account for them as specialized side-branches. My inclination is to regard most of them in this latter fashion, but certainly some of the Heterostraci seem close to the ancestral line of fishes.

To me their significance in any theory of vertebrate evolution lies in their geologic antiquity and in their diversity. Even though they are specialized off-shoots which did not endure beyond Devonian times, their diversity is sufficient to enable us, given thorough study of the various types, to strip off specializations and thus to approach more closely to the "archetypal vertebrate" than we could come without that knowledge.

The group of Ostracoderms has been variously delimited by

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different workers, just as it has been assigned to various ranks in vertebrate classification. Most present workers on Paleozoic fishes limit the group to two sub-classes, leaving out the heavily-armored Devonian Placoderms, such as *Bothriolepis* and *Pterichthys.* Still the Ostracoderms, using the term in this limited sense, form a diversified group. If we are justified in inferring habit from form as preserved in fossils, we may conclude that Ostracoderms were adapted to a variety of habitats. None of them had developed the grasping jaws armed with teeth which make vertebrates such effective predators, but their deployment was wide.

The main features which they share and which mark them off from most vertebrates are an encasing armor of bone, though in that they are not unique, lack of true vertebrate jaws, and apparently branchial tubes somewhat like those of modern Cyclostomes.

Among Ostracoderms the mouth is nearly terminal, sometimes located just behind an elongated rostrum, sometimes quite terminal. Some, such as *Drepanaspis*, with wide gape, were probably gulpers. The "jaws," a series of roughly longitudinal plates which served as supporting elements of the lower lip, would hardly have been efficient grasping structures, and teeth appear to have been absent. The Tremataspids, Cephalaspids, and their like, had small mouth openings. The large oralo-branchial chamber which housed mouth and gills was closed ventrally by a membrane strengthened by bony plates, so that it formed a flexible throat. They may have fed by suction. Anaspids seem to have had small terminal mouths and possibly their scale-covered lower "lips" could aid in grasping.

This early deployment of vertebrates included forms like *Drepanaspis*, depressed, probably bottom-living, with broad body, no paired fins, and hypocercal tail; Cephalaspids, also depressed, but with flap-like pectoral appendages and heterocercal tail; Tremataspids, less depressed, with no paired fins and with diphycercal tail; Anaspids, with fusiform body, possibly pectoral fins, represented only by elongated pectoral spines in the fossils, and with hypocercal tail.

One other aspect of their evolutionary rôle concerns their relationship to modern Cyclostomes. As evidence which has been presented by others indicates, and as the descriptive section of the present paper seems to show, the two groups have too many features in common not to have close taxonomic association. Whether we agree with Stensiö in splitting modern Cyclostomes and placing the Myxinoids under the one sub-class, the Petromyzonts under the other, or with White in placing all modern Cyclostomes under one of the sub-classes, there seems to be no escape from placing the Ostracoderms and the Cyclostomes near together. The evidence for this lies in the form of the gill apparatus, the structure of the naso-hypophysial tube and fossa, the lack of true vertebrate jaws, the type of otic structure, the distribution of the sensory canal system, and other lesser features.

The history of Ostracoderm classification has been varied, and at present there are some differences of opinion, although most of these involve problems of inclusiveness of categories rather than more fundamental disagreement. The schema which I use for my own reference undergoes frequent alterations. As it now stands it bears evidence in its structure of diverse influences. Omitting lower categories it is as follows:

- Sub-phylum Vertebrata.
  - Group Agnatha.
    - Class Ostracodermi.
      - Sub-class Pteraspidomorphi.
        - Order Thelodonti.
          - Family Coleolepidae.
        - Order Heterostraci.
          - Family Astraspidae.
          - Family Drepanaspidae.
          - Family Cyathaspidae.
          - Family Pteraspidae.
          - Family Paleaspidae.
          - Family Phyllolepidae.
        - Order Palaeospondyloidea.
        - Order Myxinoidea.
      - Sub-class Cephalaspidomorphi.
        - Order Anaspida.
          - Family Lasaniidae.
          - Family Birkeniidae.
          - Family Pharyngolepidae.
          - Family Pterolepidae.
          - Family Rhyncholepidae.
          - Family Euphaneropidae.
        - Order Osteostraci.
          - Family Cephalaspidae.
          - Family Tremataspidae.
          - Family Dartmuthiidae.
          - Family Oeselaspidae.
        - Order Petromyzontia.

As pointed out above, some workers would place the Cyclostomes entirely under one group and others give them rank equal to the two divisions of Ostracoderms. The Thelodonti are regarded as Elasmobranchs by some and by others are placed as forms of undetermined affinities. The Heterostraci are sometimes given fewer families, sometimes even more. The Anaspida seem by some to be given too many families based on single genera. The classification of Anaspida given here is based on Kiaer's classical work.

It is possible that the Cephalaspidae include forms of more than familial variety. Stensiö splits them into two subfamilies. The Dartmuthiidae and the Oeselaspidae include one genus each. They and the Trematаspidae are known only from the island of Oesel, in the Baltic. The Dartmuthiidae and Oeselaspidae have been founded on the basis of abundant specimens in the Patten collection at Dartmouth College. So far as I am aware the only specimens of either outside that collection are at the Museum of Comparative Zoölogy at Harvard College. My belief is that when the Osteostraci become more thoroughly known the families will be increased not only by new forms but also by the splitting off of certain genera from the Cephalaspidae.

THE TREMATASPIDAE.

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I. HISTORICAL.

The genus *Tremataspis* was founded by F. Schmidt in 1866 (1). In his paper he gave an excellent account of the general anatomy and the microscopic structure of the shield. No trace of the plates covering the dorsal and lateral fields or the oralo-branchial chamber or of the caudal region were found. Schmidt's interpretation of many structural features agrees with that of present workers. Only one species was founded, and since he united it with the inadequately described *Cephalaspis schrenckii* of Pander (2) Schmidt designated the species *Tremataspis schrenckii.* With it he also united two other of Pander's species, *Stigmolepis owenii* and *Odontotodus rootsiküllensis.* In Pander's figures both of these show Trematatspid-like microscopic structure.

In 1891 Smith Woodward (3) raised the new genus to family rank, establishing the Trematatspidae.

In 1892 Rohon (4) gave a comprehensive description of the family, separating Schmidt's material from *T. schrenckii* as *T. schmidti,* and including under it, in addition to the Pander species included by Schmidt, *Melittomalepis elegans* Pander. Rohon described *T. schmidti* in detail, both gross and microscopic anatomy of the shield. He established and described two new species, *T. mickwitzi* and *T. simonsoni,* the first from adequate material, the second from a single fragmentary specimen. He included under *T. mickwitzi* Pander's *Dictyolepis broni* and *Dasylepis keyserlingii.* He also redescribed *T. schrenckii.*

From the view-point of present workers Rohon's interpretation of a number of structures departed from Schmidt's mistakenly. For example the frontal pit, interpreted by Schmidt and by present students as a nasal organ, Rohon believed housed a paraphysis. The anterior pair of lateral fields he held to be the nasal organs, the dorsal field to be the parietal (pineal) organ, the orbital openings together with the pineal, i.e. the "dumb-bell-shaped" aperture, to have housed an unpaired eye. The posterior lateral fields he compared with the pseudo-branchial apertures of certain selachians.

Certain other structures which Schmidt made no attempt to homologize Rohon interpreted in accordance with our present concept. For example he interpreted the apertures posterolateral to the dorsal fields as endolymphatic, the incisions in the anterior margin of the solid portion of the ventral shield as gill apertures.

As regards microscopic structure he distinguished four shield layers instead of three, subdividing the middle layer of Schmidt, an interpretation which has not been upheld by later workers.

In the same year a brief note was published by Schmidt (5) in which he recognized Rohon's separation of *T. schmidti* from *T. schrenckii.* The latter, however, he now restored to its original designation as *Cephalaspis schrenckii.* Moreover he regarded *T. simonsoni* as identical with *C. schrenckii.*

In 1894 Schmidt (6) transferred *Cephalaspis schrenckii* to *Thyestes schrenckii.*

In 1894 Rohon (7) wrote an appendix to his former paper, further describing *T. schmidti,* including some of the plates of the oralo-branchial chamber and plates of the caudal region. A new figure of *T. mickwitzi* was given but no new data. *T. schrenckii* was removed from the genus, *T. simonsoni* somewhat doubtfully retained. In his general discussion he criticized Woodward's diagnosis of the genus. He also placed *Didymaspis grindrodi* in the Trematasaspidae.

In 1895 Rohon (8) appended to a discussion of the segmentation of the primordial cranium of the Upper Silurian Thyestidae a classification in which he included in the Trematasaspidae the genera *Trematasaspis* Schmidt, *Didymaspis* Lankester, and *Oonaspis* Jahn.

In 1899 Rohon (9) discussed the "Parietal organ" and "Paraphysis" in some detail, retaining the same interpretation of Trematasaspid structures as in his earlier work.

In 1902 Patten (10) discussed the structure and classification of the Trematasaspidae. He redescribed *Trematasaspis schmidti* with a reconstruction which has been the basis for most text-book figures of the genus. Patten differed from both Schmidt and Rohon in certain of his interpretations. He regarded the orbits and anterior pit as a "triocular median eye," the dorsal field as a nasal organ, the anterior lateral fields as lateral eyes.

Important additions to knowledge of structures were his further study of the plates over the oralo-branchial chamber; his description of the anterior gill apertures, i.e. those along the lateral margin of the oralo-branchial chamber; and his description of the sensory canal system. Rohon in his 1894 paper had figured the posterior commissure of the sensory canal system, a trace of the post-temporal, and a trace of the main lateral line, but did not recognize them as such. Patten described and figured most of the dorsal lines, i.e. a circum-orbital, including the infra-orbital plus the pineal; a marginal, including the main lateral line plus the median head line; an anterior transverse, i.e. the supra-temporal; and a posterior dorsal, including the posterior commissure and the dorsal lateral line. No trace was found of a canal system on the venter, except that a separate plate which he believed belonged to the oral region had a short groove on its surface.

Two small plates were found separate and these Patten interpreted as segments of a pair of cephalic appendages, presumably homologous with the anterior appendages of *Bothriolepis* and with the large cephalic appendages of *Eurypterus*.

In addition to the descriptive portion of this paper a new classification was proposed. The Ostracoderms, including the Antiarchi, were grouped as the *Peltocephalata*, ranking as a class intermediate between Arthropods and Vertebrates. This group with the Arthropoda and the Vertebrata he proposed to unite as a single phylum, the *Syncephalata*. As we are concerned here only with the Tremataspidae we omit further discussion of the theoretical questions involved and of the literature which concerns Doctor Patten's theory of vertebrate origin.

In 1903 Patten (11) further described the separate plates which he interpreted as parts of cephalic appendages. Later, in 1931 (12), specimens of *Tremataspis* were discovered by Patten with these two plates practically in place, the one proving to be a dorsal "fin" scute, the other a ventrally situated anal plate, according to Patten's interpretation.

If we omit reference to the controversial papers which followed Patten's suggestions as to phylogeny there was little actual work on Tremataspidae published during the subsequent years, until Patten's Evolution of the Vertebrates and their

Kin appeared in 1912 (13). In this publication he added little of detail to the earlier descriptions, but had apparently revised his views as to the identity of certain structures. In Fig. 238 he published a photograph of the orbital region showing the sclerotic plates and the pineal plate, as well as the plates over the dorsal and anterior lateral fields. He also published a semi-diagrammatic cross-section of the sclerotics and pineal plate, recognizing these structures as such. The anterior aperture he now held to be a nasal organ and the lateral and dorsal fields he made no attempt to homologize with organs of other forms aside from Osteostraci.

In 1918 Wiman (14) gave an account of the brain and sense organs of *Tremataspis*. Among the comments and critical analyses of this paper were excellent discussions by Jaekel (15) and by Stensiö (16). Stensiö's monograph (16) includes a discussion of the Tremataspidae, homologizing structures with those of Cephalaspidae. He reinterpreted the homology of the lines of the sensory canal system for which Patten had used non-committal terms. Sections of the shield were also figured for comparison with Cephalaspids. In his classification he was cautious about the placing of *Didymaspis*, and in 1932 (17) he placed this form under the Cephalaspidae.

In 1931 Patten (12) described some new Ostracoderms from Oesel, including two new species of *Tremataspis, T. milleri* and *T. mammillata.*

In a posthumously published paper in 1932 Patten (18) discussed *Tremataspis* very briefly and figured a new reconstruction of the ventral aspect which differs in certain respects from his 1904 reconstruction. The chief differences are in the plates over the oralo-branchial region and in lines of the sensory canal system on the venter. These latter were not discussed in the text.

II. MATERIALS OF PRESENT RESEARCH.

The basis for the present paper is the Patten collection at Dartmouth College. This collection is one objective result of Doctor Patten's zeal in following up his theory of vertebrate origin, in which theory the Ostracoderms played a prominent part. If that theory *never had* further results, the collecting of this beautiful material of Osteostraci and Antiarchi and its preservation for future study have gone far to justify his zeal. Doctor Patten made four trips to the island of Oesel, chiefly after Tremataspids. The first two supplied him with a few specimens but were rather disappointing. The last two trips, in the summers of 1930 and 1932, gave him a collection of Tremataspids which is unequalled in *any* museum. I have not counted the specimens, but 2000 would be a conservative estimate. Doctor Patten returned from his last expedition in September 1932 and died near the end of October. Through the kindness of his son, Dr. B. M. Patten, and of the Administration of Dartmouth College, I have been permitted to work through this collection.

In addition to these specimens, Doctor Barbour kindly arranged to allow me to go over the collection in the Museum of Comparative Zoölogy at Harvard University, a collection made by Doctor Raymond and Mr. Chevrill in the summer of 1934. In this collection there are about 150 specimens of *Trematapis*. Doctor Obrutchev has also kindly furnished me with photographs and with information concerning specimens in the Museum at Moscow, chiefly of *Trematapis mickwitzi.*

Doctor Patten had made many dissections and some years ago a number of thin sections. These have been of great value to me. In my own work I have followed the simple methods which Doctor Patten used, chiefly dissection with fine needles under the binocular.

III. GENERAL DESCRIPTION.

A. *Form and extent of shield.* The general form of a Trematapid is somewhat like that of a tadpole, with a flattened, oval body and a tail which is about one third again as long (Plate I, Fig. 2). The oval contour of the shield is more marked in the smaller forms, such as *T. schmidti* and *T. mammillata,* than in the larger *T. milleri.* This may be due in part to a flattening of the shield during fossilization, with a consequent widening, but is due in large part to the broader truncation of the posterior end of the shield. Both dorsal and ventral surfaces are smoothly arched, giving a more trim appearance than is given by the typical Cephalaspid. The anterior part of the shield is slightly depressed, sloping gently upward from the margin to the nasal eminence and orbital region, then flattening somewhat but still rising slightly to the highest point, generally just posterior to the middle of the shield.

A marked difference between a Trematapid and a Cephalaspid is the firm union of the dorsal and ventral shields in the former into a single box-like encasement rather than upper and lower parts of a box joining at their margins. This same difference is more strikingly seen in contrasting *Tremataspis* with *Dartmuthia,* since in these two forms what Stensiö (16) terms the interzonal part of the shield, i.e. the part posterior to the head proper, is longer than in *Cephalaspis.* The writer has called attention to this in his description of *Dartmuthia* (19). This continuity of the dorsal and ventral shields is responsible for the preservation of a higher percentage of ventral shields among the Tremataspids.

As mentioned above, the interzonal part of the shield is long. The difference between the length of this part and the corresponding part in Cephalaspids, however, is more fundamental than this statement would indicate. The posterior extension of the shield in *Tremataspis* encases at least the greater part of the trunk. In some of the Cephalaspids the shield does extend over a portion of the trunk, but only in one form, so far as the writer is aware, does it extend nearly to the posterior end. This form, *Didymaspis grindrodi,* is placed by Stensiö (17) in the Cephalaspidae, on the basis of the form of the lateral fields. In two other forms the interzonal part is quite long. These are *Thyestes verrucosus* and *Kiaeraspis auchenaspisoides.* When, however, we compare these with *Tremataspis* we find that the extension posterior to the endolymphatic apertures, the length behind the post-temporal commissure of the sensory canal system, and the distance behind the posterior extension of the endocranial component of the shield and the posterior margin are proportionately greater in *Tremataspis. Didymaspis* appears to be more like *Tremataspis* in this respect. *Oeselaspis* and *Dartmuthia* also resemble *Tremataspis* in the extent of the shield over the trunk, although the latter at least does not seem to be quite comparable to *Tremataspis* in this respect.

The general form of the shield is sub-oval, the anterior and lateral margins in general showing a practically smooth contour. In the midline of the anterior margin is a slight concavity (Plate I, Fig. 3). The posterior margin of the shield is truncated, with the dorsal margin concave except for the median part where the crista ends in a backwardly directed angular process; the ventral margin concave, with a small oval concavity further indenting it in the median part.

No trace of cornua or of pectoral sinuses occurs, and it seems reasonable to conclude that no pectoral appendages like those of Cephalaspids were present.

B. *Dorsal shield.* (Text-Figs. 1 and 3.) The surfaces of both dorsal and ventral shields are smooth and polished. Their color varies from very dark brown to light tan. Rohon (7) stated that this difference was due to quantity of pigment alone. Whether the color was present in the living form or was deposited during fossilization I do not know, but am inclined to believe the latter. In some specimens the color varies, and in one a portion of the shield is light tan, another dark brown, with a very sharp contact. The dorsal surface is ornamented with tubercles, over the surface of which the smooth superficial layer of the shield extends unbroken. These tubercles occur along the ridge of the crista, scattered or in uniform arrangement throughout the area posterior to the dorsal field, on the post-orbital prominences, and in some cases on the antorbital prominence and on the ridge surrounding the nasal fossa. The margin of the shield throughout most of its lateral portions is often sculptured with slight, blunt denticulations.

On the dorsal surface are found the naso-hypophysial pit and aperture, the paired orbits, the pineal aperture, the lateral and dorsal fields, and the endolymphatic apertures. The general plan is much like that of a Cephalaspid.

The naso-hypophysial pit is located just anterior to the orbits in the mid-line. Its form differs in different species and even within the same species shows considerable variation. The pit is surrounded by a ridge which may be abrupt or low and rounded. The form of the pit is oval to round. The aperture lies within the pit, sometimes on a median longitudinal elevation. It may pierce the central part of the pit or may lie in part on the front edge. I do not find the double aperture form which is so pronounced in Cephalaspids.

The orbits vary in form from sub-oval, the long axis slightly diagonal, to practically circular. They form cups of bone, narrowed somewhat dorsally. Within them lie the ossified sclerotics, roughly spherical, with narrow oval apertures. Connecting the orbits is a saddle of bone in the center of which is the inner pineal opening. Lying above this is a cylindrical pineal plate, with a small pineal aperture in its center. In most specimens the sclerotics and the pineal plate are missing, leaving a dumb-bell shaped aperture, all the margins of which overhang slightly.

The dorsal field lies behind the pineal region, separated from it by a slight elevation of approximately the same width as that separating the pineal from the nasal field. The dorsal field is roughly elliptical. Its margins may be scalloped or practically smooth. It is shorter than that of Cephalaspids, extending back to a slight distance in front of the endolymphatic apertures. The base of the dorsal field consists of a fenestrated area of bone. Above this, occasionally preserved, are small plates with the same histological structure as the shield.

The lateral fields are divided into anterior and posterior portions, each oval in form. The anterior lies antero-lateral to the orbits, very near the margin of the shield, the posterior postero-lateral to the dorsal field. Their structure is similar to that of the dorsal, with a fenestrated basal portion and similar plates covering each field.

The median crista starts some distance posterior to the dorsal field. Whether it has any anatomical significance I do not know. A median crista is found in many Cephalaspids as well. However, in these it is more properly termed an occipital crista than in Tremataspids, where it is definitely post-cranial. This crista varies in form not only between species but also to some extent within the species. It may be an abrupt ridge or a very gentle one, continuous or, as in *T. milleri*, broken by a low saddle. Its edge is commonly surmounted by a series of tubercles, which in some cases run together to form a denticulated ridge. The crista ends with a backwardly directed angular process, which may be slightly depressed, directly in line with the crista, or slightly upturned. It was probably continued backward onto the tail by the dorsal ridge scales. To what extent these may have formed a sort of unpaired "fin" is not known, but on one specimen (Plate I, Fig. 1) the structure is suggestive of *Hemicyclaspis murchisoni*, figured by Stensiö (17).

A well-developed sensory canal system is indicated, especially on the dorsal surface, by a series of shallow grooves, which in general take the form of short dashes arranged in lines, thus being less continuous than is generally the case in Cephalaspids. In some specimens the grooves form more continuous structures, especially in the infra-orbital line.

C. *Ventral shield.* (Text-Fig. 2.) Ventrally the shield forms a continuous encasement posterior to the oralo-branchial chamber. This surface is unornamented. Traces of sensory canals are found in a few cases. The anterior margin of this continuous portion of the shield, i.e. the posterior margin of the oralo-branchial chamber, has in the mid-part an angular process, the form of which varies somewhat. Flanking this process are the antero-laterally directed rows of gill apertures. There are seven of these indentations or notches on each side along the posterior margin of the chamber, and the series is continued by three more along its lateral margin.

The oralo-branchial chamber is fairly large, with indications that the greater share of the space was taken up by the branchial apparatus, the mouth probably being rather small. The roof of the chamber is formed by the dorsal shield in part and in part by the brain case. Ventrally the chamber was probably closed by a membrane save for the gill apertures and the mouth, this membrane being strengthened by bony plates. These plates are sometimes preserved, although seldom sufficiently to enable one to determine their exact relationships.

D. *Caudal Region.* In no specimen of which the writer has knowledge is the tail completely preserved. In specimen T. 110 (Plate I, Fig. 2) it appears likely that we have its full extent, but the scutes and the caudal fin are not completely preserved. In other specimens scutes are preserved, and it is thus possible to reconstruct the caudal region with some degree of accuracy. In specimen 110 one scute which probably formed part of an unpaired dorsal "fin" is preserved. This lies a short distance behind the posterior end of the shield and closely resembles the posterior scute of such a "fin" in *Hemicyclaspis murchisoni* (17).

The caudal fin is incompletely known. The corresponding fin of Cephalaspids is heterocercal (17) which would lead one to expect a similar form in Tremataspids. The one specimen which shows sufficient of the fin to permit one to hazard an opinion suggests that it was not far from diphycercal, with even a slight tendency to a downward curve. No vertebral axis can be identified, so the judgement as to tail form rests entirely on external appearance. Theoretical considerations would point to the likelihood of either a diphycercal or a hypocercal tail. As Breder (20) pointed out, the effect of a heterocercal tail is to depress the snout, and without pectoral fins to off-set this downward push the animal would be unable to swim up. White (21) calls attention to similar considerations in discussing the Pteraspids. The *Tremataspis* caudal has a decidedly larval cast. While it is difficult to point out the basis for the statement, it gives the writer the impression that, while it is functionally diphycercal, it is morphologically more nearly allied to heterocercal than to hypocercal.

As pointed out above, the anterior scutes of the dorsal ridge formed a distinct elevation, ending with an elongated scute similar to that found in *Hemicyclaspis murchisoni.* Unless this ridge supported some sort of fin it is the nearest approach to an unpaired fin found. There is no trace of paired fins.

IV. HABITAT AND HABITUS.

Chief constituents of the association in which Trematapids are found are Eurypterids, Linguloid Brachiopods, Orthoceratid Cephalopods, Phyllocarid Crustacea, Pterineoid Pelecypods, and other Ostracoderms. The first of these and the last and possibly the Phyllocarids (22) may have been either fresh water or marine. Opinions differ on this point. The other invertebrates are either brackish water or salt water forms, so that there seems little question that the deposits themselves were of marine or lagoonal origin. The matrix is dolomitic limestone with little bedding, in most cases with none.

Aside from the Eurypterids the invertebrate remains are not plentiful. The distribution of the Ostracoderms in this formation is very "spotty." Until Doctor Patten's 1930 expedition the Trematapid finds had been meagre. In his 1930 and 1932 excavations he apparently located rich "pockets" of material. The "spotty" character is well illustrated by the Coelolepids. In 1932 Doctor Patten collected about 100 specimens of this type. In 1934 Doctor Raymond and Mr. Chevrill visited the same outcrops and secured only a few fragments of these forms.

The Ostracoderm specimens commonly lack those structures which were not solidly fused with the shield or intimately sutured. Slabs with numerous specimens jumbled together and with many shield fragments are common. This might have occurred in transport down stream, as I suggested in my account of *Dartmuthia* (19), or it could equally well result from the rolling and sorting action of currents.

A number of workers have stated their belief that Ostracoderms were fresh water forms, but thus far the evidence is not conclusive. Certainly the Oesel material gives little support to this contention. The only conclusion which seems justified is that, whatever their habitat, their deposition was in marine waters. If they were fresh water fish they could have been washed down stream and their spotty distribution, occurrence in pockets, and jumbled condition would fit in with that explanation. But these same conditions could result with marine forms, and the invertebrate fauna with the possible exception of the Eurypterids and Phyllocarids is a marine assemblage.

Cephalaspids were dorso-ventrally depressed and probably bottom-living forms. The eyes, closely approximated and high on the dorsum, would indicate this also. Stensiö (16) suggests passive feeding, probably on small invertebrates, though he made no suggestion as to the mode of feeding. With small mouths, depressed bodies, heterocercal tails, and flap-like pectoral fins, one can visualize them sluggishly swimming close to the bottom, feeding on small invertebrates, or scavenging any available organic matter.

Tremataspids were more tadpole-like, with diphycercal tail, no pectoral fins, and with head and trunk solidly encased. The eyes were high on the dorsum and closely approximated. They were somewhat depressed in form, but less so than Cephalaspids. The mouth was small and ventrally placed. Though possibly more active than Cephalaspids, and with a different mode of swimming, owing to difference in tail form and lack of pectorals, it is difficult to visualize a very different mode of life.

V. ANATOMY.

A. *Sense organs.*

1. *Nasal.* The naso-hypophysial aperture is surrounded by a circum-nasal pit or fossa. It lies on the sloping part of the shield. In *T. mammillata* the fossa is oval and narrow with the long axis longitudinal, and the fossa is surrounded by an abrupt ridge or wall, sloped sharply externally and internally. The ridge is highest in front, lowest in back, bringing the top horizontal. The ridge is frequently ornamented with slight tubercles. The pit is narrow and deep, with the aperture extending practically the entire length, lying in the bottom of the pit rather than on an elevation.

In *T. schmidti* and *T. milleri* the fossa is circular and set into an elevated portion of the shield. Externally there is almost no trace of a definite wall, the nasal eminence rising smoothly to the margin of the pit where it forms a broad rim, descending more abruptly into the fossa. A slight elevation in the floor of the pit gives a contour to that floor of two lateral depressions with a low central ridge. The aperture pierces this ridge, extending from just posterior to the middle of the fossa forward onto its anterior wall.

In *T. rohoni* the form of the fossa is somewhat as in *T. schmidti* and *T. milleri*, except that the pit is relatively deeper, there is no central elevation, and the aperture lies entirely on the anterior face, ending at the deepest point in the pit, approximately in the center.

T. patteni has a nasal fossa somewhat intermediate between the *T. mammillata* type and the *T. schmidti* type, i.e. with a nearly circular wall elevated more than in *T. schmidti* but lower than in *T. mammillata.*

The nasal of *T. scalaris* appears to be of the *T. mammillata* type. That of *T. panderi* is not known.

Below the aperture a cavity is situated which probably housed the hypophysial sac and the nasal organ. Stensiö (16) has worked out the structure of this cavity in Cephalaspids, and in *Trematаspis* the essential features appear to be very similar, although the preservation of deeper structures is less adequate in *Trematаspis.* Below the aperture the cavity widens somewhat. Its anterior blind end is slightly anterior to the aperture. The cavity floor slopes downward and back, the sides curve upward, and just behind the nasal field the entire cavity assumes the form of a tube, slightly oval in section, with the long axis of the oval perpendicular. This tube (Plate I, Fig. 4) in the fossils is continuous with the anterior portion of the brain case, the cavity into which the pineal aperture opens. Beneath the pineal region the sac-like portion expands downward and laterally to form a broad pocket (Plate I, Fig. 5) which probably housed the hypophysial sac (16). The entire structure bears a very striking resemblance to the hypophysial sac of *Petromyzon.*

In minor details the structure differs from that in Cephalaspids. For example in Cephalaspids the nasal fossa is located between the anterior portions of the orbits, extending in front of them, whereas in *Trematаspis* the fossa lies anterior to the front of the orbits, thus making the chamber connecting the nasal organ with the sub-pineal part of the cranium longer than in Cephalaspids.

2. *Pineal.* The pineal organ lies between the orbits, separated from them by a rather heavy bony wall. At the level of this wall the pineal saddle occurs (Plate I, Fig. 3). This is roughly rectangular, but with the corners slightly produced. In its center lies a circular aperture which leads into a pit. The pit expands below the aperture and is continuous with the cranial cavity below, with the chamber into which the nasal aperture opens anteriorly, and posteriorly, via a slightly constricted aperture, with the cavity which probably housed the mesencephalon. Anterior and posterior to this pineal aperture are smaller foramina. The anterior of these lies on the ascending part of the saddle, thus penetrating into the space between the dorsal roof of the olfactory tube and the saddle margin. The posterior foramen is connected by a fine tube with the swelling of the cranial roof which seems to correspond with that which Stensiö (16) indentifies in Cephalaspids as housing the habenular ganglion (Plate I, Fig. 4).

Lying above the pineal saddle, but rarely preserved, is a pineal plate roughly similar to that in *Cephalaspis* (17) and in *Dartmuthia* (19). This pineal plate was figured by Patten (13, Fig. 238). The dorsal surface of the plate is smoothly rounded, as though the plate were cylindrical (Text-Fig. 3). It is coated with the same polished superficial layer as is the general shield surface. In the center of the plate is a circular aperture somewhat smaller than that in the saddle. In one specimen smaller foramina occur at either side of this aperture. In other equally well-preserved specimens no trace of these foramina can be seen. The apparently cylindrical form of the plate is not preserved when one excavates the margins. The posterior margin of the dorsal part overhangs slightly and that of the ventral is somewhat produced, making the posterior aspect of the plate concave. The anterior border does not overhang so definitely as does the posterior, but the contour breaks where the polished surface goes over into the unpolished, the latter forming a short slanting roof over the anterior. The lateral aspects show a sharp overhang. When the plate is excavated ventrally it is found to be a half-cylinder rather than a cylinder, like a curved roofing-tile.

The aperture in the center of the plate opens into a practically spherical chamber, open at the base just above the aperture in the pineal saddle, and open laterally into the lateral portions of the plate. The small foramina in the saddle anterior and posterior to the aperture also lie beneath the plate and probably formed passages for vessels or nerves which served the pineal organ.

As to the nature of the pineal organ itself we cannot be sure. The writer is not inclined to commit himself to any hypothesis unless the evidence seems especially strong. In this case he is forced to admit that the spherical chamber, communicating at its base with the brain case at a point almost exactly above and between the apertures in the walls of that case which open widely into the orbits, and almost certainly gave exit to the optic nerves, and opening at the surface by a circular aperture, strikes him as strong evidence that we have here, as in some other vertebrates, a pineal eye.

In *Petromyzon* the pineal organ consists of a dorsal vescicle and a ventral vescicle, both having a semblance of eye structure, the dorsal perhaps functioning as an eye. The nerve to the dorsal (pineal) organ runs from the large right habenular ganglion and is a fairly long structure. That to the ventral (parapineal) organ comes from the small left habenular ganglion. It occurs to me as possible that in *Tremataspis* we have traces of these two organs, since there is a spherical chamber lying beneath the pineal plate and also one just beneath the aperture in the saddle. The small bone-encased tube leading from the top of the habenular swelling through the posterior aperture in the saddle underneath the posterior part of the pineal plate may have transmitted the nerve to the pineal organ, as in *Petromyzon,* the nerve to the parapineal being within the brain case and therefore not bone-encased.

3. *Lateral eyes.* The lateral walls of the pineal saddle are thick. Medially they form the wall of the brain case in the orbital region, laterally the median walls of the orbits. The orbits are roughly spherical bony chambers slightly narrowed dorsally. Into the median wall just anterior to the center open wide foramina from the brain case, foramina which probably give exit to the optic nerves and also to some vessels. The median part of the posterior wall gives exit to a bone-encased tube (Plate I, Fig. 5) which closely resembles the structure which Stensiö (16) suggested was a myodome. Lateral to this in the posterior wall is another channel into a bone-encased tube which leads backward across the dorsal surface of the vestible, as in Cephalaspids, and in this case also I adopt Stensiö's interpretation that it formed a channel for the *vena capitis lateralis* (Plate I, Fig. 6). As in Cephalaspids this large vessel gives rise to a small branch opposite the posterior

semi-circular canal, and appears to make connection just posterior to the descending portion of this canal with a large channel which probably housed the *occipital venous sinus*. In the upper part of the antero-median wall of the orbit is a small foramen which gives exit to a vessel which turns toward the nasal pouch, then dorsally near the posterior of the nasal fossa (Plate I, Fig. 6). This is farther medial than the anterior branch of the *vena capitis lateralis* of Cephalaspids, but may well be this vessel. At any rate it is the only foramen of sufficient size in the anterior wall of the orbit to take care of the large vessel which opens into the posterior margin.

In most specimens the orbit alone is preserved, but in some cases the ossified sclerotic is also preserved (Text-Fig. 3). This is a nearly spherical, hollow ball, with an oval dorsal aperture. The sclerotic is slightly smaller than the orbit. In the bottom of the cup is a small circular aperture which appears to have been situated close to the optic foramen of the orbit. The exposed dorsal surface of the sclerotic forms a rim around the aperture and is coated with the polished superficial layer. Just below this polished rim is a groove which extends completely around the sclerotic. The remainder of the exterior surface is unpolished, somewhat rugose. Patten (13) believed the eyes to have been stalked, capable of being protruded somewhat.

4. *Otic organs*. The auditory region appears to have been developed much as in Cephalaspids. It was, however, less heavily ossified, so that the structure is less readily followed. The horizontal semi-circular canal was undeveloped, leaving, as in Cephalaspids and Petromyzonts, only the anterior and posterior canals. These were lightly ossified. In a number of specimens they are very prominent in dorsal view, meeting at a rather sharp angle in a commissural division, and diverging, the one antero-laterally, the other postero-laterally, (Plate I, Fig. 6). The commissural portion communicates with a prominent tubular structure with well-ossified walls. This tube also receives a canal which leads posteriorly, giving off a number of branches and connecting with the endolymphatic aperture. This canal Stensiö (16) suggests carried the otical vein and also the *ductus endolymphaticus*. The large tubular structure from the commissural division opens medially into the base of the dorsal field, presumably, as Stensiö suggests, carrying the vascular and nervous supply of that organ (Plate I, Fig. 3).

The anterior semi-circular canal leads antero-laterally to near the border of the orbit, where it turns a little inward and ventrally to the ampulla. This latter is so slightly ossified that the structure is difficult to follow beyond the point where it joins the canal.

The posterior canal leads postero-laterally to the junction between the *occipital venous sinus* and the *vena capitis lateralis,* where it turns ventrally and medially to its ampulla.

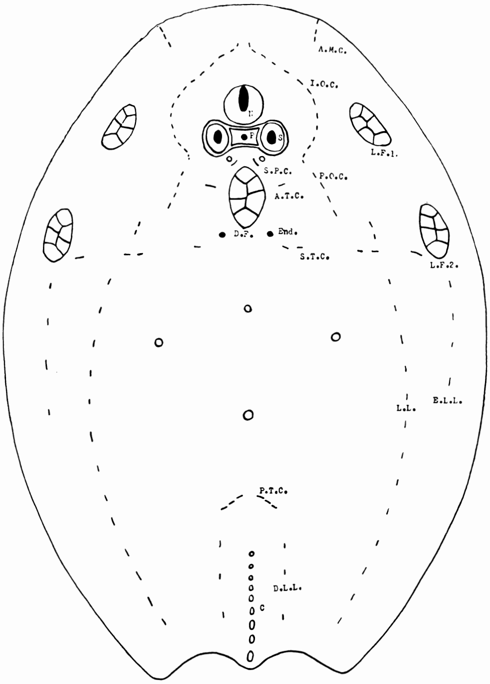

Fig. 1.

Dissecting away the semicircular canals and the vessels one comes to the vestibule. The ossification here is so slight that it appears as a very thin, light brown coating, and without proper lighting might easily be missed. Fortunately two specimens happen to have fractured transversely at the otic region, exposing the vestibules in part from the posterior and supplementing the information gained by dissection. As in Cephalaspids, the vestibule is a rounded vescicle somewhat elongated in the transverse plane. Traces of canals leading from the lateral part of the vestibule have been found, and in one case three of these can be made out. They are insufficiently preserved laterally for identification. The vestibule and semicircular canals so far as I have succeeded in exposing their structure bear a very strong resemblance to the model of these structures figured by Schimkewitsch (23, Fig. 345) for *Petromyzon fluviatilis*.

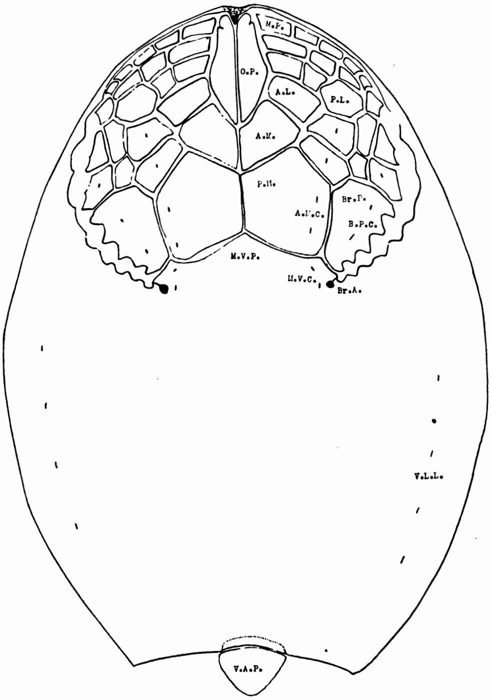

Fig. 2.

In some of the Cephalaspids the ventral aspect of the vestibule is very well preserved. Very frequently the specimen cleaves in such a way as to leave on the counterpart the vestibules and the nerve and vessel canals leading from them. A number of Cephalaspids in the Patten collection exhibit this. I have found no such fortunate cleavage in *Tremataspis* specimens, nor have I been successful in uncovering this ventral aspect.

5. *Sensory canal system.* (Text-Figs. 1 and 2.) The sensory canal system of *Tremataspis* was first described by

Patten (10). The terminology which he adopted differs from that used by Stensiö (16), the different lines being designated in accordance with their positions on the shield, with no attempt to homologize them with those of other vertebrates. In the present paper the terminology of Stensiö will be followed for the most part, since this will facilitate comparison with his work on those structures in Cephalaspids.

Among the Osteostraci the Tremataspids offer advantages over other forms for the study of the sensory canal system. The superficial layer of the shield is smooth and polished, rather than roughened as in *Cephalaspis, Dartmuthia,* and *Oeselaspis.* This makes the detection of the shallow grooves much simpler. The dorsal and ventral shields are more intimately fused, insuring their holding together in a higher percentage of the specimens. This makes possible a study of the ventral surface. The relatively large size of the plates over the oralo-branchial chambers is a decided advantage in the few specimens in which these are preserved. Finally, in the Tremataspids the shield covers not only the head but also a large part of the trunk as well, possibly as far back as the anus, whereas in Cephalaspids it extends only a very short way posterior to the cranium. There is thus in *Tremataspis* the opportunity to follow the course of lines on the trunk.

In the Osteostraci the sensory canal indications are shallow grooves in the superficial part of the shield exoskeleton. In Cephalaspids and *Dartmuthia* they are generally more or less continuous grooves, whereas in *Tremataspis* they are usually series of short dashes. In some specimens certain lines are more continuous.

In fishes generally there are two lines which part company just posterior to the orbit, one, the *infra-orbital,* curving down and forward below the orbit, the other, the *supra-orbital,* forward above the orbit. In the lamprey the *infra-orbital* begins ventro-lateral to the orbit and runs anteriorly to a point antero-lateral to the nasal pit. Just anterior to the nasal pit a series of the *supra-orbital* begins and, according to Johnston (24), extends to the tip of the snout.

In the Cephalaspids no line quite corresponding to the *supra-orbital* series has been found. Stensiö (17) believes that the anterior part of the *infra-orbital* in these forms may correspond to and be innervated by the same nerves as the *supra-orbital.* In general there is no indication that this part is not simply a continuation of the *infra-orbital.* In *Didymaspis,* however, the main *infra-orbital* line meets, just anterior to the lateral field, a line which is directed medially.

The *infra-orbital* of Cephalaspids starts either lateral or postero-lateral to the orbit. Then it swings outward and forward, and in most of the specimens in which the superficial layer of the plates over the lateral field is preserved curves onto these plates near the anterior end of the field and then antero-medially to end near the mid-line not far from the margin of the shield. There are variations in details but the general course is very constant. In *Didymaspis* the *infra-orbital* does not reach the lateral field.

In *Dartmuthia* the *infra-orbital* canal starts postero-lateral to the orbit, swings outward and forward, then inward to end a short distance anterior to the nasal pit. The line never reaches the lateral field.

In *Tremataspis* the *infra-orbital* is much as in *Dartmuthia*. That is, the series starts postero-lateral to the orbit, curves outward to a point medial to the anterior lateral field, then antero-medially to near the mid-line just anterior to the nasal eminence. Here there is some variation in its course, variation which does not seem of taxonomic significance. In some specimens the lines from both sides turn rather abruptly anterior just before they end. In others they turn slightly posterior. In still others they are somewhat wavy. Patten (10) states that the two lines sometimes meet across the mid-line anterior to the nasal, but I have seen no specimen in which I can with certainty detect this. The lines in *Tremataspis* being generally made up of series of short dashes, it is sometimes difficult to be sure. In *Dartmuthia* (19) the canals are difficult to follow and in a few cases it appeared as though they might thus unite.

Another line near the margin in *Tremataspis* appears to me to be similarly situated to either the *supra-orbital* as figured by Johnston (24) or the *oral* line as figured by Stensiö (25) in *Petromyzon*. This line generally consists of one or two short grooves on the margin, but in some specimens extends further onto the shield. In *T. milleri* this line is occasionally a single longer groove. It is situated nearly anterior to the point at which the *infra-orbital* curves inward. As its homology is doubtful I have simply named it the *anterior marginal* canal.

In *Petromyzon* as well as in fishes generally another line extends backward from the junction of the *infra-* and *supra-*

orbital to the main *lateral line* of the trunk. This is variously designated, either as a forward extension of the *lateral line* or as a backward extension of the *infra-orbital.* I am designating it as the *post-orbital,* following Goodrich (26).

In *Tremataspis* this line runs postero-laterally, frequently with a break near the posterior end of the dorsal field. There is always an off-set between the posterior end of this line and the anterior end of the main *lateral line* canal, so that I do not believe they should be designated as a single line. This line is similar in *Dartmuthia.*

In the Cephalaspidae the *post-orbital* is quite variable. In most of those figured by Stensiö (16, 17) it is the only part of the lateral line preserved and he has generally labelled it as the *lateral line.* In some cases it appears to me that he has labelled its anterior part the *"c.m."* groove, i.e. homologous with a transverse line which occurs in some other species and which he regards as probably corresponding to the *jugal* or *pre-opercular* of fishes. This seems to me to be the case in *Cephalaspis lankestri, C. powreii ?, C. salweyi ?, C. pagei,* and *Hemicyclaspis murchisoni.*

The *"c.m."* groove occurs clearly only in *Benneviaspis holtedahli, B. lankestri,* and an unnamed specimen of *Cephalaspis* (17, Fig. 54). In these it is a groove extending laterally and slightly posteriorly (except on the right side of the *B. holtedahli* specimen) from just posterior to the orbits. It does not reach as far laterally as to the lateral field. No clearly corresponding line appears on *Tremataspis.*

In *Petromyzon* a pair of lines, very short, occurs in the pineal region. In *Tremataspis* these are just antero-lateral to the dorsal field and postero-median to the orbits. In most specimens there is a slight eminence on either side of the midline in this region, just behind the juncture of the orbit and the pineal plate. The *supra-pineal* canal occurs on the median side of each eminence. A pair of similarly situated lines occurs in *Hoelaspis angulata* and possibly in *Benneviaspis holtedahli* (16).

In a number of specimens of Cephalaspid and in *Tremataspis* a short line occurs directed laterally from either side of the dorsal field. In *Tremataspis* this is generally a single groove on either side, but occasionally is continued farther laterally. (It may be that this lateral continuation corresponds to the *"c.m."* groove of Stensiö mentioned above.) Stensiö suggests that this transverse line is homologous with the *middle head-*

line of pit-organs in fishes and with the first transverse line behind the pineal in *Petromyzon* (17). I have called it simply the *anterior transverse* line.

Farther back on the shield is a more extensive transverse line. In *Tremataspis* generally it is divided into three short series of grooves, one just postero-lateral to the endolymphatic aperture, the second lateral and slightly posterior to the end of this section, commonly almost directly anterior to the main *lateral line*, the third farther lateral and extending to near the posterior end of the posterior lateral field. Since it is in line, or nearly in line, with the endolymphatic apertures, thus just posterior to the otic region, I believe it to be at least in part homologous with the *supra-temporal* of fishes and of *Petromyzon*. Stensiö (16) states that this line does not occur in all specimens of *Tremataspis* but I have found it very constant.

In Cephalaspids this same series occurs (17). In some, as in *C. spinifer*, *C. pagei*, and *Hemicyclaspis murchisoni*, it starts on the plates over the dorsal field. (In Cephalaspidae the endolymphatic apertures are within this field.) In some, as *Hemicyclaspis murchisoni*, *C. lankestri*, and *Benneviaspis lankestri*, three segments are present. In others two or only one were found.

It is possible that this series of lines may represent more than one of the transverse lines found in other forms. The third of the series in *Tremataspis*, e.g., lies lateral to the main *lateral line* of the trunk, but what the homology would be I am uncertain. The *supra-temporal* of other forms generally does not extend lateral or ventral to the main *lateral line*. Possibly the third of the series may be the *pre-opercular*.

The line interpreted in this paper as homologous with the main *lateral line* starts just at this transverse series, near the lateral end of the second line or possibly just anterior to this. In *Tremataspis* there is usually a lateral off-set just here. From this level the *lateral line* runs roughly parallel to the shield margin as far as the posterior end of the shield. There are indications in *Tremataspis* that this is the posterior end of the trunk. I have found no sufficient indication of this line extending onto the caudal region. On one fragment of this posterior region I found a single short groove, but since it sometimes happens that two adjacent pores of the bone canal system are united by such a groove I hesitate to accept this one groove as sufficient proof of a caudal continuation of the *lateral line*.

I have been unable to detect this main line in either *Dartmuthia* or *Oeselaspis*. So far as I know there are but two species of Cephalaspid in which any trace of the *lateral line* posterior to the *supra-temporal* has been found. These are *Benneviaspis holtedahli* from the Spitzbergen material (16) and *B. lankestri* from the Old Red (17). Since the Cephalaspid shield has very little post-cranial extension this is to be expected.

In *Tremataspis* there is another pair of lines in the posterior region of the shield, lying dorsal to the main *lateral line,* just lateral to the median crista. At their anterior ends there is a curving *transverse commissure.* Probably this pair of lines is homologous with the *dorsal lateral line* of *Petromyzon.*

In a few specimens of *Tremataspis* a line is found lying lateral to the main *lateral line,* beginning just behind the posterior lateral field and running back parallel to the shield margin. I have called it simply the *extra-lateral* line, being uncertain of its homology.

No ventral lines have been found in any of the Osteostraci except *Tremataspis.* In other families, however, the venter is seldom preserved in any degree of completeness. The ventral lines in *Tremataspis* were figured but neither described nor labelled in a posthumus publication by Patten (18).

There are traces of a *ventral lateral line* in the trunk region running parallel to the margin far laterally.

The posterior margin of the oralo-branchial chamber has the form of a roughly triangular process flanked by the rows of gill apertures. On this median process two short grooves can usually be found, the posterior lying just medial to the innermost gill aperture, the anterior medial to this and near the margin of the chamber. These lines I have termed the *median ventral.*

The plates covering the oralo-branchial chamber are seldom preserved, but two "series" of grooves have been found. On the large *median branchial* plates two grooves occur, and on the smaller *second branchial* plate, lateral to this, a single groove. These I have termed the *branchial plate canals.* The second series consists of two grooves near the lateral margin of each of the large *post-medial* plates and one groove on each of the two *lateral plates.* This series is here referred to as the *anterior median ventral canals.*

The homologies of these ventral lines are very doubtful. I would suggest that the lines on the median ventral process plus the *anterior median ventral* lines might represent the *hyomandibular.* In *Petromyzon* a series of pit organs is associated with the gill apertures and possibly the grooves on the branchial plates of *Tremataspis* may be their homologues.

The homologies suggested here are tentative. We know something, thanks to the beautiful work of Stensiö (16), of the cranial nerves in the Cephalaspidae and a little of those in *Tremataspis*, but of their detailed distribution in relation to the sensory canal system we know little. Thus the homologies are based on relation to other anatomical land-marks. It is interesting, in view of the taxonomic relationships which seem to be supported by general anatomical evidence, to summarize in tabular form these lines in *Tremataspis* and *Cephalaspis* and their possible homologues in *Petromyzon.*

OSTEOSTRACI.	PETROMYZON.
	Dorsal.
Anterior marginal (*Tremataspis*).	Supra-orbital or oral.
Infra-orbital.	Infra-orbital (+ supra-orbital?).
Post-orbital.	Post-orbital.
Supra-pineal.	Pineal.
"C. M." (some Cephalaspids).	Jugal?
Anterior transverse.	(Middle head pit-line of fishes?). Second transverse (Stensiö). None (present writer).
Supra-temporal.	Second transverse = supra-temporal, possibly also Pre-opercular.
Lateral line.	Lateral line.
Dorsal line (*Tremataspis*).	Dorsal line.
Posterior commissure (*Tremataspis*).	None.
Extra-lateral (*Tremataspis*).	None.
Ventral.	
Ventral lateral (*Tremataspis* only).	Ventral lateral.
Median ventral + median anterior.	Mandibular.
Branchial.	Branchial.

As pointed out above, the sensory canal system in *Tremataspis* consists of fine, usually discontinuous grooves on the exoskeleton. They do not perforate it. If, following Stensiö (16), we regard the exoskeleton as arising in the corium and mainly confined to this, it may well be that the canals, if such existed, lay in the epidermal tissues superficial to the exoskeleton, only here and there dipping deeply enough to mark the skeletal layer. To this interpretation point certain irregularities in the grooves found. For example, one specimen may show a fairly regularly spaced series of grooves for the main *lateral line*, another with as perfect preservation of the exoskeleton may lack many of these markings. On the other hand we must recall that in *Petromyzon* no grooves are present, the end-organs of the system occurring at the surface, and in groupings rather than as continuous lines (25).

Patten (10) stated, on the basis of his examination of the small number of specimens then available, that the bottoms of the grooves in *Tremataspis* appeared to be smooth and unbroken, and that the organs situated in these grooves cannot have received their innervation through the bony exoskeleton. The large amount of material in Doctor Patten's collection has made possible a more thorough study of this, and shows at least occasional apertures in the bottoms of grooves. These apertures prove, on dissection, to connect with the system of channels which pervades the bony shield in the same way as do the pores so abundant over the general surface. Stensiö (16, 17) states regarding the Cephalaspids that the grooves of the system lie approximately above the course of certain nerve components and must therefore have received their innervation from these nerves, but he does not discuss the pathway by which such nerve fibers would have penetrated the exoskeleton. He does state regarding *Tremataspis* (16,

Fig. 3.

p. 39) that in certain places he has seen "branches from the vascular system opening into the mucous canals on the basal side, a state of things which shows that the mucous canals received vessels and nerves through the vascular canal system." Possibly this is the solution of the innervation difficulty. At least for the present no other appears available.

6. *Dorsal and Lateral fields.* (Text-Fig. 1.) There has been much discussion as to the rôle of these peculiar structures. Some of the older views have been mentioned in an earlier part of this paper. That they had some function fairly well developed, either as effector or as receptor organs, is inferred from the rich innervation, especially of the lateral fields. This has been well studied in the Cephalaspids (16). The type of cleavage referred to above enables one in many cases to follow out the distribution of the nerves to the lateral fields in Cephalaspids. To some extent they are similarly exposed in a few specimens of *Dartmuthia* (19). Stensiö refers to the dorsal and lateral fields as Electric fields and regards them as developed similarly to those in *Malopterurus electricus*, since they lie within the corium. Certainly also, as pointed out by Stensiö, the appearance of the heavy nerve channels as they emerge from the ventral part of the vestibule and spread laterally to the lateral fields is strongly suggestive of the electric nerves of *Torpedo.*

Other views as to their function generally fail to assign similar rôles to lateral and dorsal fields, and while it may be that they were different sorts of organs their structure is so similar that I am inclined to believe they must have had a common function. Smith Woodward (27) speaks of the lateral fields of *Cephalaspis* as probably branchial. Jaekel (28) suggested that the anterior lateral fields of *Tremataspis* formed the base of tentacles of some sort, while the dorsal was a respiratory structure, possible for direct respiration of the brain. In this paper these structures will be referred to by the non-committal term of dorsal and lateral fields.

The plates covering the fields are usually lost, leaving the basal portion only. This presents a fenestrated appearance, which is found on dissection to be due to the branching and ramifying of small channels up through the base. The channels probably housed blood vessels and nerves. If the shield is eroded off, one comes to a plexus of small vessels, ramifying just below the shield, probably identical with what Stensiö (16) terms in Cephalaspids the *subaponeurotic plexus*, believing them to have lain just beneath the *corium aponeurosis.* In *Tremataspis* a number of these run into the lateral and dorsal fields, and laterally they make contact with the large *marginal vein sinus.* Whatever the nature of these fields, then, they were abundantly supplied with blood vessels and nerves.

The lateral fields are paired. The anterior field lies about opposite the orbital region. It is oval in outline, although the form varies somewhat. In some specimens the margins are smooth, in others scalloped. The longer axis of the field is roughly parallel with the shield margin. The plates covering this field are usually five in number, although in some there may be as few as three, in others as many as eight or nine. These plates do not abut directly on the basal part, but a thin layer of matrix is found between them. In the deeper part of the basal layer two or three apertures are found. These run up into the less deep portions, branching to form three or four main channels from which finer twigs branch off, until in the superficial part the surface is almost reticulated.

In the brief account of *Tremataspis* which he gave in his monograph on the Cephalaspids of Spitzbergen (16), Stensiö stated that the nerves to the lateral fields were divided into anterior and posterior groups in accordance with the division of the lateral fields. He placed the number of these nerves at not less than four nor more than six. The nerve channels are less adequately preserved than in Cephalaspids, both peripherally and centrally. In spite of the abundant material I have been unable thus far to expose them completely, although numerous dissections have revealed traces here and there.

As nearly as I can judge from such unsatisfactory data, there are two nerve channels to the anterior fields centrally, the anterior channel forking near the field, somewhat as in the Kiaeraspinae (17) and in *Dartmuthia* (19). I have attempted to check this by dissection of the channels within the basal part of the field, and as nearly as I can judge from this the number of channels entering the field is three. The first two then unite just central to the field and proceed toward the otic region. What their exact course centrally may have been I do not know. One large canal dips downward beneath the *vena capitis lateralis* about opposite the anterior semicircular canal, and from the short portion of its course which is available appears to be directed toward the anterior lateral field (Plate I, Fig. 6).

The posterior lateral field is quite similar to the anterior in form. Its anterior end is opposite the endolymphatic aperture, its median part nearly in line with the *supratemporal* sensory canal. As this is approximately the same relationship which is exhibited by such Cephalaspids as have both lateral field and *supratemporal* canal preserved (17), it would appear that the two lateral fields in *Tremataspis* are morphologically the equivalent of the single lateral field in Cephalaspids. The basal part of this field is similar to that of the anterior. The plates covering the field are very infrequently preserved, four or five being the usual number.

The innervation of the posterior field is even more obscure than is that of the anterior. The number of channels entering the basal portion appears to be three. Centrally there are apparently but two. In one specimen a trace of what I take to be the posterior of these two trunks forks about half way out towards the field, but I cannot trace it because of inadequate preservation.

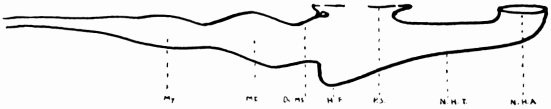

Fig. 4.

The dorsal field is oval to lenticular in form, the long axis being anterior-posterior. It lies just behind the pineal region, separated from it by a slight eminence. It is relatively short, not reaching as far backward as the endolymphatic apertures. The bony plates over this field are variable in number, usually four or five, but as few as two and as many as ten. Between these plates and the basal part lies a layer of matrix, in some cases showing a trace of vessels. The most basal portion of the lower part of the field is in open communication on either side with a large bent tube which leads into the vestibule. It must have been through these two channels that the innervation and some of the vessels reached the field. Coming into the basal portion of the field the apertures on either side open into cup-like spaces, separated by a median wall (Plate I, Fig. 3). As in the case of the lateral fields, these basal channels branch in the more superficial parts to form a reticulated surface.

B. *The brain case.* (Plate I, Figs. 3, 4, 5), (Text-Fig. 4.) In his study of the Cephalaspids of Spitzbergen Stensiö described the brain case in considerable detail, especially in *Cephalaspis hoeli* and in *Kiaeraspis auchenaspisoides.* His description is based on dissection and on serial sections. From these two sources he reconstructed dorsal, lateral, and ventral aspects of the brain case and attempted to reconstruct the form of the brain within. Without this study of Stensiö my analysis of this portion of *Tremataspis* would have been a much more arduous task, if it would have been possible for me at all.

One must remember in studying this portion of the anatomy that it is not the brain but the brain case, or *cavum cerebrale cranii*, which is preserved. This encased the brain and also other structures, such as the brain membranes, blood vessels, etc. So far no trace of internal structure has been found. Thus in attempting to establish the identity of various features of the case one can only do so by comparison with structures of other vertebrates and identifying them in accordance with their spatial relationships. There are exceptions to this, but especially in trying to homologize channels which may have given exit to nerves one cannot be sure whether the channel he follows out carried blood vessels or nerves or both. This gives some uncertainty in the analysis of cranial nerve location.

The olfactory organ has been described. In the fossils the nasal cavity is continuous with the *cavum*, although, as Stensiö points out, in the living state it was probably separated from the brain by a membrane. I think it likely that, as Stensiö suggests, the anterior and ventral portion of the naso-hypophysial cavity housed the hypophysial tube, and that the broad bulging structure seen in ventral exposures of the *cavum* below the pineal region represents the hypophysial sac. (Plate I, Fig. 5.) One fragment in the Patten collection which has puzzled me not a little is a dissection of the ventral aspect of this region made by Doctor Patten and by him labelled "Olfactory lobes." The piece is small, merely the central portion, including the hypophysial sac and short portions anterior and posterior to it, but on either side of the nasal tube lie tubular structures constricted anteriorly. These are what Doctor Patten had identified as Olfactory lobes, but whether they entered the olfactory pit or not I do not know, nor have I been successful thus far in uncovering them in other specimens. It is possible that they are vascular channels instead.

The aperture at the posterior of the nasal organ opens into a tubular structure which leads backward to the pineal region. Here the tube widens and is open above via the foramen in the saddle into the space beneath the pineal plate, where, as suggested previously, there was an organ which may have been an eye. Laterally in this region are the optic foramina, large oval apertures through the walls of the orbits, through which must have passed the optic nerves and some of the blood vessels to the lateral eyes.

Beneath the posterior portion of the pineal saddle the brain case presents a slight median swelling, which specimen 148 shows to be connected by a fine vessel with the posterior foramen in the saddle. This median swelling corresponds to that which Stensiö identified in *Cephalaspis* as the bulge for the Habenular ganglion. From the side of this swelling, slightly anterior to the small vessel spoken of above, and a little above the middle, is a small tube leading into the postero-lateral portion of the orbit. It seems rather far forward and upward for the channel of the third cranial nerve. However, in *Tremataspis* the diencephalon and mesencephalon are very much shortened as compared with Cephalaspids, and a telescoping of these regions would bring this nerve apparently more nearly beneath the 'tween-brain. In fact, unless there is more or less telescoping the mesencephalon must lie almost entirely beneath the downward sloping, slightly constricted portion of the brain case immediately posterior to the habenular swelling.

It was this telescoping of 'tween and mid-brain in *Tremataspis* which led Wiman (14) to identify the entire region of the diencephalon and mesencephalon as diencephalon and the metencephalic swellings as mesencephalon, as pointed out by Stensiö (16).

This same shortening makes it difficult to identify channels for other of the cranial nerves. In specimen 410 there are two nerves or vessels which come from the brain case almost together from the anterior lateral portion of the swelling which follows the constriction which I take to mark the division between mesencephalon and metencephalon. Thus these two channels come from that part of the case which housed the metencephalon. In *Cephalaspis hoeli* Stensiö figures the fourth and a part of the fifth cranial nerves coming off from the posterior of the mid-brain. Unless the channels mentioned above carried these nerves I have failed to locate them. One branch of this pair enters the dorsal part of the posterior wall of the orbit.

The downward slope of the brain case behind the habenular swelling is ended with a slight constriction, and the beginning

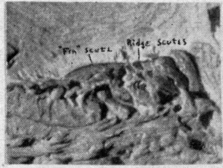

FIG. 1

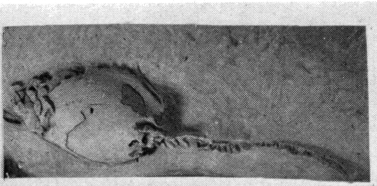

FIG. 2

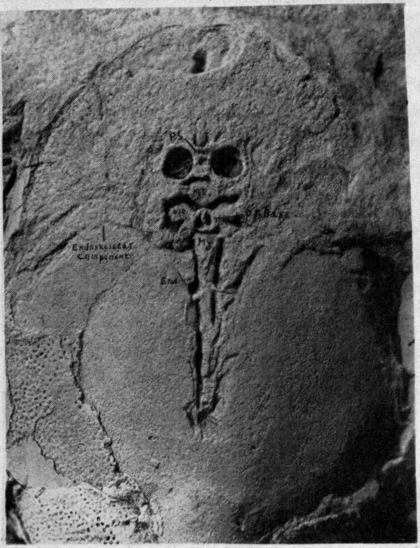

FIG. 3

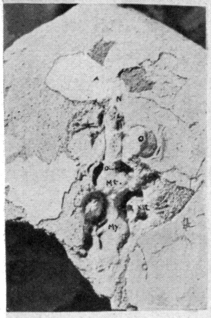

FIG. 4

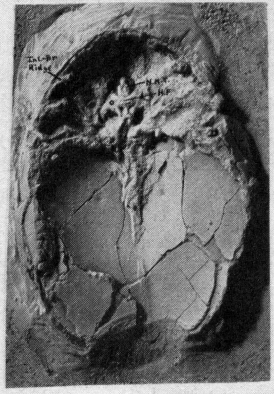

FIG. 5

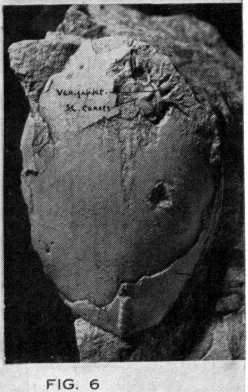

FIG. 6

Plate I.

of the large paired swellings which Stensiö identified as housing the Metencephalon. These swellings bulge upward and laterally, and from their widest part arises on either side a fairly large canal which runs upward and laterally to behind the orbit where it turns laterally and slightly posteriorly, crossing the *vena capitis lateralis.* Since the origin and course of this canal corresponds to that which Stensiö described as the *superficial post-orbital artery* I conclude that this was the same structure. The swellings of the metencephalon end almost at the anterior end of the dorsal field, the brain case dipping downward sharply beneath this structure. There is a slight constriction here, followed by an expansion in width and a dorsal sloping of the *cavum.* This is followed by a narrowing, running into that portion which must have housed the cord.

Just posterior to the large tube which connects the dorsal field and the vestibule a canal leaves the side of the brain case and forks. I regard this as corresponding to the combined seventh and eighth nerves, as figured by Stensiö for *Cephalaspis.* Immediately behind this another canal leads off laterally and posteriorly, probably housing either the ninth or the tenth nerve.

Stensiö found two spinal nerve canals in *Cephalaspis.* So far I have found only one on either side, but as in *Cephalaspis* the one on the right leads off anterior to that on the left.

The ventral aspect of the brain case has been difficult to study. As pointed out in a different connection, the cleavage of the specimens differs from that of Cephalaspids and at least in large part this is due to the less extensive ossification, and thus preservation, of the venter of the cranium. The anterior portion of the *cavum*, the "ethmoidal cavity" as it was called by Stensiö (16), is tubular, sloping slightly downward and then leading into an expanded portion, from the posterior of which arises the broad transverse bulge of the hypophysial sac, which is deepest at its posterior end. This sac forms a slight posterior bulge, and the junction between this and the portion of the brain case underlying the mid-brain is somewhat constricted. This is followed by an expansion and then a dorsal rise and gradual narrowing to the dimensions of the region housing the anterior portion of the cord.

To be continued.

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