THE STRUCTURE OF THE MOUTH OF THE OLDEST KNOWN VERTEBRATES, PTERASPIDS AND CEPHALASPIDS

By

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The structure of the mouth of the oldest known vertebrates — the Silurian-Devonian Pteraspids and Cephalaspids — has been hitherto unknown, notwithstanding the fact that many of these forms are not very uncommon in some regions; partly also in a fairly good state of preservation. This fact has led the greater number of authors to presume that the afore-mentioned forms had a soft mouth, capable of protruding and devoid of ossified parts, whereon some have based further conclusions.

I shall describe in the following some new finds, which show that these conclusions have been too hasty, as these forms have in reality possessed an ossified mouth-skeleton of an extremely peculiar development.

One of these finds, that of a new Pteraspis-form, was made on TH. VOGT'S Spitsbergen-Expedition in 1925. This finding will be described in detail in the monographical description which I am now preparing out of the considerable Norwegian material of Pteraspid fishes from the Downtonian and Devonian series of Spitsbergen. This work I hope will be finished next year.

I consider this find to be one of the most interesting that has been made in recent years, and I shall therefore give a preliminary report of it.

The other find is of a Cephalaspid, from the rich Downtonian fauna which I discovered some years ago in Ringerike in the Oslo region. Of this fauna I have hitherto described the Anaspida.

In connection with these finds not before described I shall shortly give the details of the mouth structure of some earlier known forms.

Earlier opinions regarding the structure of the mouth of Pteraspids and Cephalaspids.

A complete summary of the views which have been earlier advanced regarding the structure of the mouth of the Pteraspids and Cephalaspids will not be given here. I shall only cite the opinions of those authorities who have made a special study of these forms.

In his well-known monograph LANKASTER does not express himself definitely regarding this question. In connection with his reconstruction of Pteraspis he thinks it very improbable that the mouth of this form was

provided with hard teeth. He thinks, consequently, that it had a suctorial mouth evidently assuming the same to be the case in the Cephalaspids.

This conclusion was obviously founded on the fact that no trace of solid skeleton parts indicative of jaws or other parts of the mouth could be found.

SMITH-WOODWARD speaks with more caution in the second volume of his Catalogue. He finds the non-existence of a bony structure around the mouth adequately proved; but nevertheless his opinion is not that jaws were missing. A similar presumption is also maintained by TRAQUAIR in his summary of the Ostracoderms in 1898.

Meanwhile there have already been found in Estland some remains of the peculiar Cephalaspid Trematapis in such a good state of preservation that a surer assumption regarding the structure of the mouth was made possible. ROHON was in 1893 able to describe a specimen with an intact ventral side and could prove that an area of small plates was developed underneath the snout. Posteriorly these plates bordered the gill openings, in front they constituted the lower side of the mouth opening. The latter was thus, according to ROHON, bordered by the lower edge of the dorsal shield and underneath by a number of mouth-plates the construction of which, however, could not be ascertained. ROHON speaks with great caution and uncertainty regarding this mouth structure. He writes that we here evidently have to do with *„einem geschlossenen Mund"* Herewith he obviously implies that the mouth consisted of ossified skeleton parts.

Not many years after follows TRAQUAIR'S well-known description of „The lower Devonian Fishes of Gemünden" Therein he describes some greatly compressed, but otherwise completely preserved specimens of the genus Drepanaspis, which is a later pteraspidian offshoot. TRAQUAIR discovered that the mouth in this genus formed a transversal opening, which was directly bordered by skeleton plates; he could not, however, prove the existence of a tooth construction of any sort whatever.

According to this it was possible to define the function of the mouth in different ways and the greater number of authors deemed it still probable that these earliest fish-like forms had a soft suctorial mouth.

The last opinion has especially been emphasized by JAEKEL in a number of his interesting works on the earliest fishes and their structure. In *„Die Wirbeltiere"* (1911) he has placed the forms here dealt with together with the Cyclostomata in a special class which he calls Malacostomata; these are fish types of the lowest order; their main characteristic is a soft, evidently toothless and suctorial development of the mouth.

In the Palaeostraci to which belong Pteraspids, Cephalaspids and Anaspids, he assumes that the parts of the mouth were unossified, and that the mouth in the earliest forms was a protractile, suctorial mouth as in the amphibian-larvae of the present day. He maintains the same opinions in his later treatise called *„Die Mundbildung der Placodermen"* (1919).

Quite a different explanation is maintained by PATTEN, who, as is known, believes the Vertebrates to be derived directly from the Arachnids and Merostomes, and assumes the Ostracoderms to be a transitional group, the Peltocephalata, possessing distinct transitional characters.

Of importance to this study is his work „On the structure and classification of the Trematastpidae" (1903), in which he gives an excellent reconstruction of this peculiar form. PATTEN was able to point out a great number of interesting details which I shall mention later. He reached the result that the mouth was not bordered above by the lower edge of the dorsal shield, as ROHON maintained, but was situated centrally in the oral area of small plates; further that the whole construction of the mouth was in accordance with that of the Arachnids and not with that of the Vertebrates. He also mentions that he has discovered in the Cephalaspis „indications of the presence of a pair of heavy crushing mandibles, so situated that they must have acted against each other, at right angles to the sagittal plane, instead of parallel with it, as in true Vertebrates." I have, however, been unable to find a closer description of the material to which PATTEN here alludes.

The same assumption regarding the mouth structure of Trematastpis we may find again in his large work „The Evolution of the Vertebrates and their Kin" (1912).

By this short summary we may see the uncertainty apparent in the interpretation of the structure of the mouth in these earliest known vertebrates.

The structure of the mouth in Pteraspis Vogti nov. sp. (manuscr.).

Norwegian expeditions to Spitsbergen have collected a huge material of Palaeaspids and Pteraspids in a large number of new forms which will greatly enlarge our knowledge of these primitive vertebrates. The greater number of these forms have been hitherto only found in the usual state of preservation with isolated plates and scales. On the expedition made by TH. VOGT in 1925, several forms were at last found almost completely preserved. One of the most important of these finds is that of a new Pteraspis, which was found by the Paleontologist of the expedition, A. HEINTZ, in the Red Bay Series (Downtonian). In honour of the leader of the expedition I have called this form *Pteraspis Vogti*.

This find is highly peculiar, as, in the small piece of reddish-brown limestone, not bigger than a hand, the remains of 6 completely preserved specimens were found. Most of these specimens are highly eroded, but together afford, after being prepared by Conservator HEINTZ, a nearly complete reconstruction of the animal. In two specimens the mouth-apparatus was prepared out, in the one from the outside, and in the other from the inside. The preparation was carried out with the help of fine needles under a strong binocular instrument and took a very long time. One of these specimens after preparation (on the outside) may be seen in Pl. XII, fig. 1, about 4 times enlarged. A third specimen was used to a section series affording an excellent material for the study and reconstruction of the different plates and scales.

I shall not here give any general description of this new species. I only mention that it represents a comparatively small form, the length of the dorsal shield being not longer than about 50 mm. This shield is rather broad and flat with quite short cornual plates and an uncommonly short, flat, and broad rostral-area (Fig. 1).

Underneath the rostral-area there appeared a hitherto quite unknown system of small plates, which serve to fill out the space between the front edge of the ventral shield and the lower edge of the rostral plate.

It was at once made clear that this system of plates constituted a highly peculiar mouth apparatus in these ancient forms.

In order to understand how these plates join with the remaining plates I

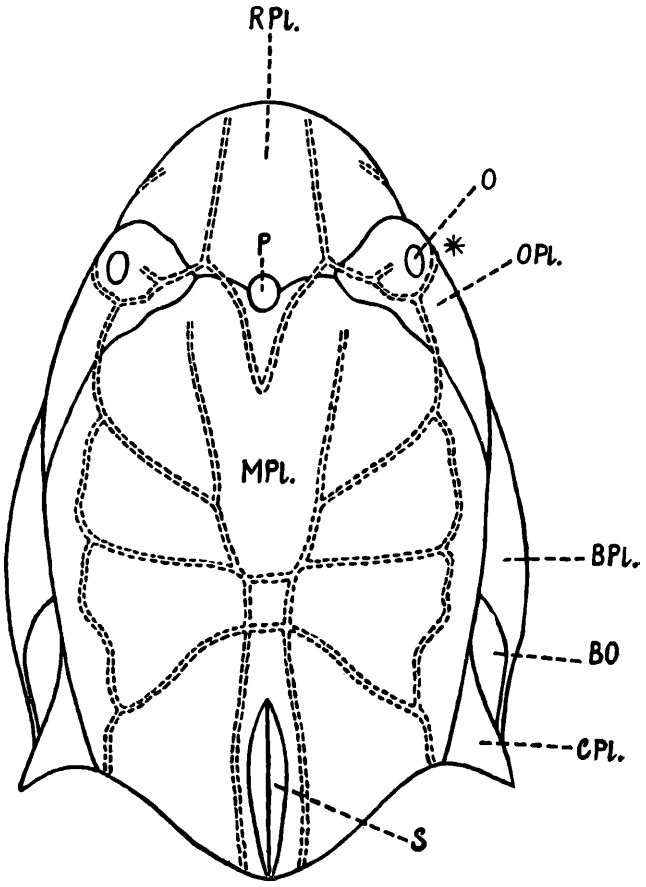

Fig. 1. Dorsal shield of *Pteraspis primaevus* nov. sp. (Manuscr.), seen from above, × 3, Diagrammatical sketch after specimens in Pal. Mus. Univers. Oslo from Red Bay series (Downtonian), Spitsbergen. Lateral line system (stippled lines) after grinding preparations of the author. — BO. Branchial opening. BPl. Branchial plate. CPl. Cornual plate. MPl. Median dorsal plate. O. Orbita. OPl. Orbital plate. RPl Rostral plate. P. Pineal covering. S. Dorsal spine. The asterisk shows where the lateral line system from the dorsal side goes over to the ventral side.

must mention with a few words the construction of the dermal armour in the Pteraspids.

The hitherto known dermal plates of this armour are the large d o r s a l s h i e l d on the upper side and the somewhat smaller v e n t r a l s h i e l d on the under side of the animal. While the latter forms a single plate, the dorsal shield appears to consist of a number of smaller plates which I shall

denominate in the same manner as Professor STENSJÖ has done in his last great work[1]). In front lies the r o s t r a l p l a t e which is very differently developed in different specimens. Behind this plate comes the large dorso-median plate which at the back embraces the dorsal spine or the dorsal spinal plate. At the sides are the paired ocular plates lying around the orbits; behind these come the branchial plates, which at the back of their upper side border the front of the branchial openings, and lastly come the cornual

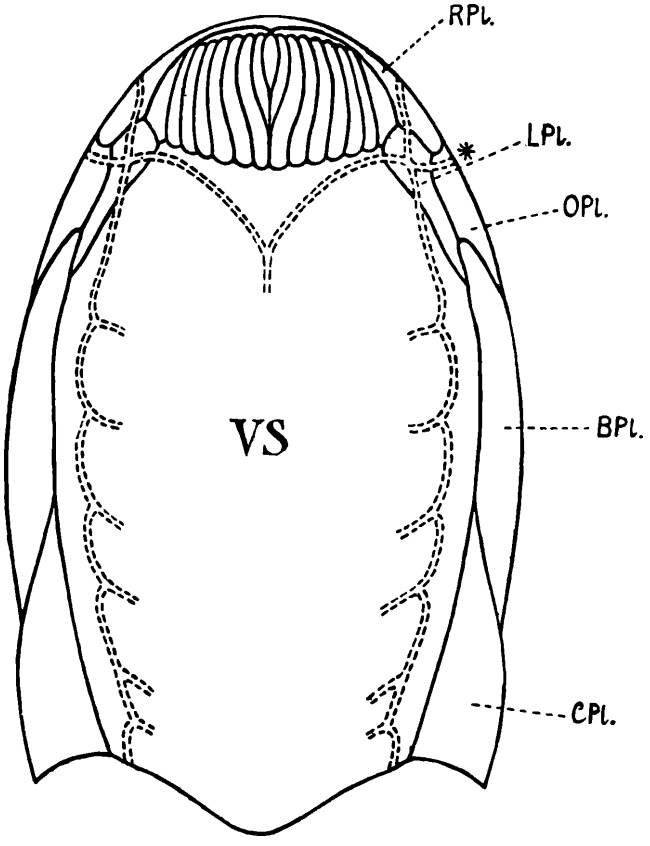

Fig. 2. The ventral side of *Pteraspis Vogti* nov sp. (Manuscr.) × 2. Diagrammatical sketch after specimens in Pal. Mus. Univers. Oslo from Red Bay series (Downtonian), Spitsbergen. Lateral line system (stippled lines) after grinding preparations of the author. — BPl. Branchial plate. CPl. Cornual plate. LPl. Lateral plate. OPl. Orbital plate. RPl. Rostral plate. VS. Ventral shield. For explanation of the mouth and the oral plates see fig. 3 in the text. The asterisk shows where the lateral line system from the ventral side goes over to the dorsal side.

plates which make up the back corners of the dorsal shield. The latter vary greatly in development in the different species. All these plates are generally strongly joined together. Their boundaries are marked by a break in the dentine ridges of the surface, and cannot be seen in the middle and basal skeleton layers. As these parts of the dorsal shield are bordered more faintly

[1]) The author has had occasion to see the manuscript of Professor S t e n s j ö's monography of the Cephalaspids from Spitsbergen, in which he also mentions the construction of the Pteraspids.

or not all in the more primitive Palaeaspidae JAEKEL holds that there has originally existed a completely connected, unbroken dorsal shield. I believe JAEKEL is right in this instance. The development of the dorsal shield which has taken place in this group has therefore not been a melting together of originally isolated plates but a gradual breaking up in minor elements.

As the branchial plate in the more primitive Palaeaspids is quite free and isolated[1]), it appears as if these two families constitute two diverging lines proceeding from still more primitive forms. As I shall show in my monography, such forms actually exist in the Downtonian of Spitsbergen.

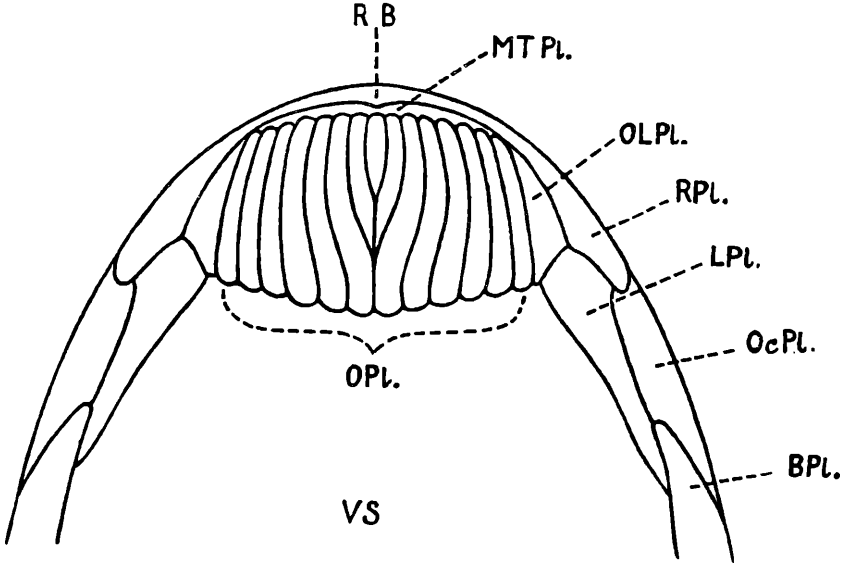

Fig. 3. The ventral side of *Pteraspis Vogti* nov. sp. (Manuscr.) with the mouth-apparatus after a specimen in Pal. Mus. Univers. Oslo from Red Bay Series (Downtonian), Spitsbergen, × 4. This diagrammatical sketch explains fig. 1, Pl. XII. BPl. Branchial plate. LPl. Lateral plate. MTPl. Maxillary tooth plate. RB. Rostral ventral beach. RPl. Rostral plate. OPl. Oral plates. OcPl. Ocular plate. OLPl. Oral lateral plate. VS Ventral shield.

Both the dorsal shield and the ventral one are — as is known — traversed by a highly developed system of lateral lines which during recent times have especially been described by LERICHE and STENSJÖ. In my large material I have been well able to study this system of sense organs. The lines have been prepared out in several forms and I can prove that they vary in quite a large degree both in the Palaeaspids and the Pteraspids. The newly-discovered plates beneath the head are also important in this respect, as they show how the dorsal and ventral system join together (Fig. 2).

In Pteraspis Vogti I discovered on each side in front of the ventral shield a long plate which is pointed at the back, the outer side of which joins up with the back part of the rostral plate, the ocular plate and the

[1]) This plate was described by Lindström as belonging to an appendage, an idea which Patten eagerly adopted. It is, however, as I shall show, correctly perceived by Jaekel who has figured it in a number of his reconstructions.

front part of the branchial plate. The inside overlaps the front part of the ventral shield which is quite rounded off, while the shorter side in front borders the actual mouth-area (oral-area). This plate I have named the lateral plate (Fig. 2). It is very important as the two branches of the lateral lines of the dorsal shield, which run in front of and behind the eye, continue across this plate into the characteristic lateral line-system of the ventral shield, as may be seen in Fig. 1—2. In this way the lateral plate shows a large number of lateral-line pores.

In front of the lateral plates comes the oral area. On each side is situated a triangular plate which joins closely up to the undermost edge of the rostral plate and the slanting anterior edge of the lateral plate. The inner side of this plate is the longest. Between the two side plates, which I have named the oral-lateral plates, lie the actual mouth or oral plates. They constitute a whole row (16) of long, small plates which are broader at the back and narrow off in front, and which at the back overlap the front edge of the ventral shield.

In the figured specimen which, as usual, is compressed in a dorso-ventral direction, the ventral shield has been pressed rather strongly in and also a little forwards. Both the oral and lateral plates have therefore been pushed more over the ventral shield than has originally been the case. At the same time the oral plates have been pressed a little over each other. Originally they must have lain quite regularly side by side and made up a completely symmetrical system of nearly straight and slightly bent plates. In the middle they have included a few shorter plates that have not reached back to the ventral plate (Fig. 3).

The oral plates show, as is also the case in the remaining plates, the typical Pteraspis sculpturing with fine dentine ridges, the arrangement of which I shall not describe in this preliminary report. They are situated close together and overlap each other with slanting edges without ridges. Their front points make up together the underneath border of the mouth opening itself, which is completely transversely placed.

The specimen which has been prepared out from the inside together with the series of sections has given an exellent idea of the construction of these different plates. They all consist of the same skeleton layers as do the remaining plates of the dermal skeleton. Their front point is provided on the inside with a strongly projecting tooth-plate which shows a highly peculiar construction. The tooth plates on all these oral plates are completely alike; they are all connected to the oral plates themselves and appear in the shape of short rostral-caudally placed ridges which show almost vertical outer sides and more slantingly placed inner ones. The latter ones are closely set with fine, tooth-like dentine processes which probably represent dentine ridges which have been divided into separate points.

The upper edges of the tooth plates are somewhat horizontal and have obviously worked together with the correspondingly constructed maxillary plate which is developed behind the front edge of the rostral plate. The longitudinal section (Pl. XII, fig. 2) demonstrates this in an excellent manner.

This maxillary plate came out well in both the prepared specimens and in the section series. I have also been able to make it out in other

forms by longitudinal sections through the rostral area. As may be seen in the figures (Pl. XII and fig. 3 in the text) the front edge of the rostral area bends down a trifle in the shape of a beak. Inside there lies, divided by a marked groove, a projecting edge which is sligthly convex, and in a light curve stretches out to the sides as far as the oral plates reach. The outer surface of this maxillary-plate has extremely fine dentine points arranged in rows, very much like the tooth plates of the oral plates. Here also we have evidently to deal with the dentine ridges of the dermal skeleton which has been divided up into fine tooth-like points.

The idea that this ossified mouth skeleton with its tooth plates (the oral plate and the maxillary plate) has worked together and formed a type of jaws I believe will plainly be conveyed even by this short, preliminary description.

As I shall show in my monography this mouth skeleton undergoes a peculiar transformation in certain types of lower Devonian Pteraspids. The material in my possession shows further that a corresponding mouth apparatus, although in a somewhat varying form, existed also in the Palaeaspids. The whole group of these pteraspidomorphian fishes did not have therefore a soft mouth, but a peculiar biting mouth made up of skeleton plates. The connections with the mouth structure in other primitive vertebrates and the function of this mouth I shall endeavour to illustrate in a few concluding remarks.

The structure of the mouth in the Norwegian Downtonian Cephalaspids.

In the Downtonian fauna of Ringerike wherefrom I have hitherto only described monographically the Anaspids, there appear two new genera of Cephalaspids. One of these forms. *Aceraspis robustus Kiaer*, is especially common, and is often very well preserved. By carefully etching with fluoric acid, many details have appeared which up to day have been unknown. These I shall describe more detailed in a future monography; here a few specimens may only be mentioned that show something of the mouth structure of these forms.

The head shield of Aceraspis figured in Pl. XIII, fig. 2—3 is exposed from the underside. The skin beneath the head and the front of the body is in this form covered by extremely fine Thelodus-like scales. This ventral skin has been here eroded away, and the dorsal shield may be seen from the inside. One of the orbital openings may be seen and to the left of this an apparently faintly developed neurocranium, which in this case is very indistinct. Along the edge may be seen the underside of the highly developed marginal border; in front of the latter may be seen some broad dentine ridges which, going back towards the pectoral fins, dissolve into coarse tubercles. In the front of the back edge of the marginal border may be seen a slight incurvation in which there appears a somewhat slantingly placed plate with some quite fine, blunt, toothlike dentine processes. They may plainly be seen in Pl. XIII, fig. 2, which is photographed four times enlarged. I take this for a tooth plate on the upper side of the mouth opening. It reminds one strongly of the maxillary tooth-plate in the Pteraspids, and I believe its function has been the same.

In another specimen, which I have not figured here, may be seen clusters of similar dentine structures lying in a curve behind this front part of the maxillary tooth-plate. They may be seen lying pressed up against the inner side of the dorsal shield, but have evidently originally composed the sides of a broad maxillary tooth-plate which has been united in a curve to the hind edge of the lower side of the marginal border.

I suppose, therefore, that the Cephalaspids have possessed a transversely placed slit-like mouth lying directly behind the marginal border, and that on the upper side of the former there has been developed a maxillary tooth-plate as in the Pteraspids. The development of the teeth on this plate is, however, in close accordance with the development of the dermal skeleton, different in the two groups. In the Pteraspids the typical dentine ridges have thus dissolved into quite fine dentine points; in the Cephalaspids we find, however, the maxillary plate set with fine, rather blunt dentine processes, which resemble the similar sculpturing found in some places on the dorsal shield.

From this I further draw the conclusion that the mouth opening was also on the under side provided with one or more tooth plates as in the Pteraspids. I cannot yet, however, prove this with full certainty, but otherwise I could not understand the existence of the maxillary tooth plate.

In the genus Aceraspis this structure is extremely difficult to be proved because the ventral side of the dorsal shield has in this genus a very fine dermal skeleton consisting of extremely fine Thelodus-like scales. This ventral skin-covering, therefore, has generally been bent and disarranged.

The other Norwegian Downtonian genus, Micraspis, is in this respect more advantageous, as the dermal skeleton on the ventral side of the dorsal shield is more strongly developed.

I shall not give here a complete description of the ventral dermal skeleton of this form. I only figure one of the best of my specimens (Pl. XIII, fig. 1). A somewhat irregular, though symmetrical system of larger and smaller thin dermal plates may be seen, which at the back pass into the ventral scale of the body.

On the inside of the edge faint traces of the branchial openings may be seen, arranged in two curved rows. In front the dermal plates become gradually smaller and are here partly torn to pieces. Right in front one side of the mouth opening appears; it forms a transverse slit, which is bordered in front by the somewhat incompletely preserved marginal border, and at the back by a row of fairly long-stretched oral plates. The state of preservation is here not so good, so that no traces of inner tooth plates may be expected to be found.

The structure of the mouth in some other earlier described forms.

The new finds of which I have given here a preliminary report, serve to enlighten us regarding the structure of the mouth in a number of the earlier known forms. Two of these forms I shall mention especially.

One of these is Drepanaspis Gemündenensis, which has been made very well known by TRAQUAIR'S reconstructions (fig. 4). As has been

pointed out by DEAN and the present author, TRAQUAIR has mistaken the dorsal for the ventral side. By a correct orientation, the construction of the armour coincides very well with that of Pteraspis. Accordingly, also the mouth and its development are in good agreement. Especially convincing in this respect is the beautiful figure in TRAQUAIR'S Pl. III, a part of which is reproduced in fig. 5. The transversely placed mouth opening appears to be situated remarkably enough, on the upper side of the snout. It seems

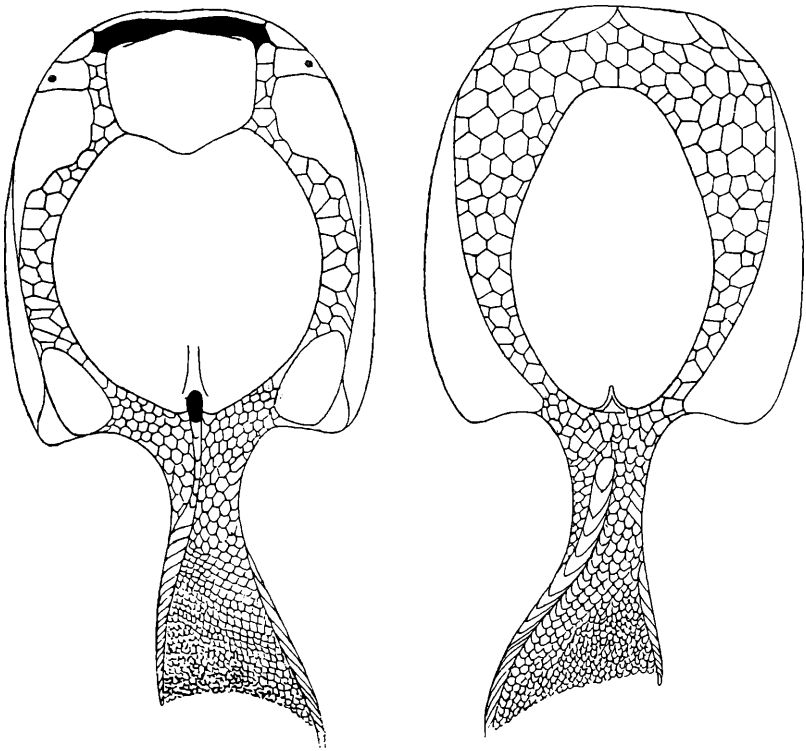

Fig. 4. Traquair's reconstruction of *Drepanaspis Gemündenensis* Traqu., much reduced, after compressed specimens. On the left from the dorsal, on the right from the ventral side. The small orifice behind the median dorsal plate, which of Traquair was explained as the anal opening, was in reality filled out by a small dorsal spine.

doubtful to me that this has actually been the case as figured in TRAQUAIR'S reconstruction. By the strong compression the softer under side with its many small plates may well have been pushed forward in front of the rostral plate of the dorsal side. The mouth may in this case have originally been terminal. The mouth opening is bounded as in Pteraspis on the upper side by the lower edge of the rostral plate, on the lower side by a number of oral plates. TRAQUAIR has drawn 4 of these oral plates in his reconstructions, but his photographic plates show that there has evidently also existed a central un-paired element. These oral plates are much shorter and broader, and are not found in so great a number as in Pteraspis Vogti (Plate II, TRAQUAIR), but the whole system of plates is, however, in acordance with this form in

its construction. Remarkably enough, TRAQUAIR accentuates further that this mouth has no teeth nor anything which can be called a mandible. In the specimen illustrated in fig. 5 may be seen, however, a peculiar ridge on the left side of the front edge of the rostral plate. This ridge may possibly be the left side of the maxillary plate which has been pushed forward. The mouth plates in this specimen also show strongly curved, tuberculated marginal rims, which may possibly be identified as lower tooth plates. This must be the subject of renewed investigations.

The other form which I shall mention is Tremataspis of which one may get a good conception in ROHON'S and PATTEN'S descriptions and

Fig. 5. The anterior part of *Drepanaspis Gemündenensis* Traqu., somewhat reduced copy after Plate III in the memoir of Traquair, showing oral-plates and probably the left side of the maxillary tooth plate. MDPl. Median dorsal plate. O. Orbita. OPl. Oral plates. RPl. Rostral plate.

reconstructions. It is, moreover, especially interesting because of its originating from the middle Ludlow and thus belonging to the very earliest known vertebrates.

When studying PATTEN'S description and no doubt excellent reconstruction (fig. 6), one undoubtedly gets the idea that the mouth, as also ROHON believed, lay directly behind the bent down edge of the dorsal shield, and was in front directly bordered by the latter. ROHON, however, assumed the mouth opening going too far back. The mouth must really be assumed to have been quite short, and at the back only bordered by the anterior mouth plates. Behind the mouth lies on each side a row of evidently 10 gill openings arranged in curve. Peculiarly enough PATTEN did not draw this conclusion, but assumed, however, that the mouth was situated centrally between the mouth plates. This he says despite his describing a number of interesting

details which definitely support ROHON'S conception as being the correct one. On the lower, beak-like rim of the front edge of the dorsal shield he points out the existence of two tooth-like processes, and just between them a peculiar arched, inwardly bent plate, which PATTEN calls „a remarkable keel-like ridge" (fig. 7). I cite here PATTEN'S description: „The keel stands vertically, with its thickened ventral end just protruding above the level of the oral plates. Its pointed dorsal end lies close to the inner surface of the dorsal

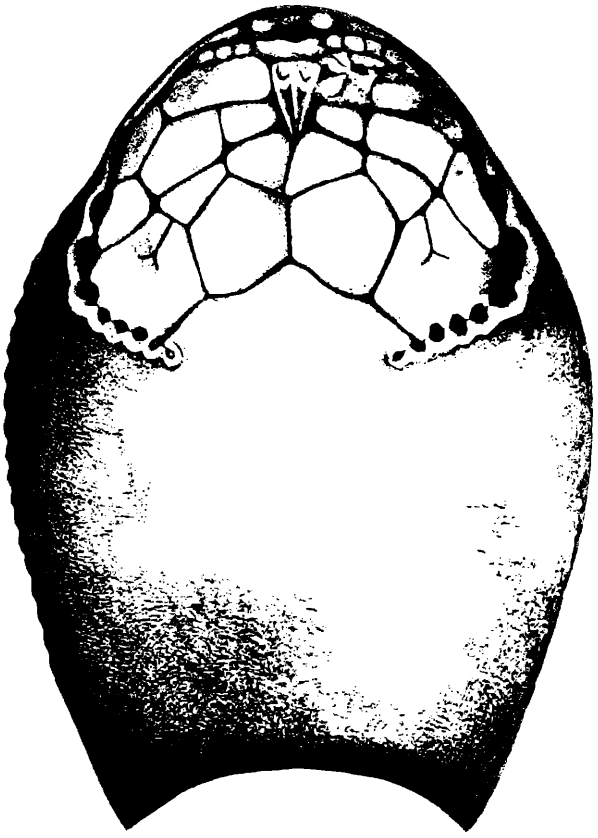

Fig. 6. Patten's reconstruction of the ventral side of *Trematapsis*, copy after Patten 1903.

shield. When seen from the side, or in sagittal sections, the crest of the keel is nearly circular in outline, with the convex surface directed backwards. When the limestone matrix is deeply excavated in this region, the keel is seen to lie on an indistinct plate, which in turn seems to fit into the angle formed by the under surface of the dorsal shield and the posterior surface of the flexed margin. The plate is somewhat irregular, but is distinctly triangular in outline, with the apex directed upwards and backwards. The surface of the keel, and of the keel plate, is similar in color and general appearance to the outer surface of the shield, but differs from it in being rougher and full of pores, which make it difficult to remove the matrix."

PATTEN'S figure and description give — as may be seen — a very good conception of this interesting formation, and also furnish reliable data for assuming it to be a peculiarly formed maxillary tooth plate. That it should be connected by a joint to the central oral plate — as PATTEN believes — I assume to be quite out of the question. If my opinion is right there has evidently also existed one or more tooth plates on the under side of the mouth. Possibly the peculiar, small plates pictured by ROHON in Pl. I, fig. 12—13, represent these tooth plates.

As is known, only one of the specimens described by ROHON and PATTEN shows the oral area in good preservation, but even here many details are still uncertain. It would therefore be of the greatest interest if more completely preserved specimens of this remarkable form could be found.

Fig. 7. The anterior, beak-like lower border of the head shield of *Trematapsis*, after the opinion of the author building the upper border of the mouth. Copy after Patten 1903. a) median maxillary tooth plate. b) Large tooth-like process.

General remarks.

The observations reported above seem to be a sufficient proof of the following statements in regard of the structure of the mouth in the earliest known Vertebrates.

I. In Pteraspis the mouth was a transverse slit lying on the under side of the snout. On the upper side of the mouth was a long maxillary tooth-plate just within the lower edge of the rostral plate. On the under side the mouth was bordered by a row of long narrow oral-plates on the inner sides of which in front were developed some small tooth plates. Also the Palaeaspids had a similar mouth apparatus and also Drepanaspis clearly shows points of agreement. I think I may assume that the mouth in the whole group (the Pteraspidomorphi) has been developed according to the same principle, though undoubtedly with variations.

II. In the Cephalaspids also the mouth was a transverse slit-like opening, which in front was bordered by the curved edge of the dorsal shield, on the inner side of which there was one (or more?) maxillary tooth plate differently developed in the different genera. The lower border of the mouth opening consisted generally of larger or smaller oral-plates or of a softer dermal skeleton, and must also in this case be assumed to have been provided with one (or more) inner tooth plates with a similar construction as in the upper side.

III. Judging from the existing conditions these hard mouth skeletons on the upper and lower sides of the mouth have worked against each other and corresponded in function to the elements of the upper and lower jaws in the higher-standing fishes. As also in this case the mouth was bordered by hard edges, this mouth in the earliest known vertebrates was not a soft, protractile, or a suctorial one, as has previously been maintained, but in its function a sort of biting or crushing mouth according to the development of the teeth.

To this summary I shall attach a few short remarks.

The relations of the Pteraspids to the Cephalaspids.

In my earlier work on the Anaspids I came to the result that the Pteraspids and the Cephalaspids were two very different groups. While the Cephalaspids together with the Anaspids were closely related to the Cyclostomes of the present time, I assumed the Pteraspids to be extremely primitive Elasmobranchs.

STENSJÖ has, however, in his study of the system of lateral lines in the Pteraspids, believed that he has found great accordances with the Petromyzontids and maintains that the Pteraspids also must be related to the Cyclostomes of the present time. This fact will further be proved in his large work on the Cephalaspids of Spitsbergen.

By the help of the large material of Pteraspids now in my possession I have a much greater chance than before to reach a conclusion regarding this question.

It is, however, so complicated that I will not express myself more definitely regarding it until I publish my monography. I also first want to study the work of STENSJÖ which will be published in the nearest future. Meantime I do not regard it as absolute certain that STENSJÖ's opinion is the right one, but I must agree that the accordances existing between these two groups regarding the structure of the mouth seem to point in that direction. The two different opinions in this question, however, are actually not so divergent as one might suppose, as, according to my earlier conception, the Pteraspids might be believed to represent a primitive type of Diplorhines. It is not necessary to suppose that the Pteraspids were, in their organisation, greatly different from the old Monorhines.

The mouth structure in the Pteraspids and the Cephalaspids compared with higher forms.

The mouth structure has been hitherto most clearly discerned in Pteraspids. Here it appears in such a strange form, that it seems to be quite different from the type which characterizes the gnathostome vertebrates.

I shall try to throw a little more light on this matter in the following.

The difference does not consist so much in the form and construction of the mouth and tooth plates. Dermal skeleton plates of a similar nature also play the most important part in the mouth structure of the Gnathostomes; they, moreover, show in some of the most primitive groups a form and development which in some degree reminds one of the mouth plates in Pteraspis. Here I refer more particularly to the mouth structure in the Arthrodires which is described in such an interesting way by JAEKEL in many of his more recent papers. The spleniale (mandibulare) of the lower jaw thus shows cer-

tain similarities with a single oral plate in Pteraspis. Both are dermal skeleton elements, certain parts of which have been specialized into tooth plates. Of special interest is JAEKEL'S demonstration of the fact that the splenialia in front of the mouth opening are not connected with each other, but separated by a space filled out by the front elements of the hyoid arch. The latter, it is true, do not appear to be true dermal bones.

In this way the under side of the mouth in front has been formed by two pairs of parallel, for-stretched skeleton plates, which in a certain way remind one of the mouth area in Pteraspis. In the latter, however, the number of the long-drawn oral plates is much larger.

The splenialia of the Arthrodires work against two pairs of tooth plates situated on the upper side of the mouth, viz., the palatinalia (JAEKEL), lying in front and generally strongly developed, and the pterygialia, lying behind the former. These two are also dermal bones similar to the splenialia of the lower jaw. In the Holocephali these dermal skeleton elements are further reduced to isolated tooth-plates.

All these dermal plates which go to make up the mouth apparatus of these most primitive Gnathostomes are, however, clearly related to the cartilaginous endocranium with its mouth arches of which especially the mandibular arch is the most important part.

This does not appear to be the case in the earliest vertebrates mentioned here.

It may perhaps possibly be the case in Pteraspis. The oral-plates must then be interpreted as dermal plates in relation not only to the mandibular and hyoid arches, but also to the other branchial arches having been pushed forward right up to the mouth opening.

I do not, however, believe this to be the case at all, as all these oral-plates have the same form and structure. A further reason against it is, that the number and form of the oral-plates vary greatly in the different genera.

It seems much more probable that the mouth plates in these earliest forms were not in any way related to a possibly underlying cartilaginous skeleton of mouth arches which had not yet begun to play any important part in the function of the mouth, and I think this condition is the most important one in this earliest mouth structure which has now come to our knowledge.

The dermal skeleton around the mouth opening in these earliest forms became divided into smaller parts which then in form adapted themselves more closely to the functioning of the mouth.

The development of the dermal skeleton itself also played an important part here. This may be seen especially clear in the forming of those parts of the mouth apparatus which I have denoted as tooth plates. In Pteraspis, as we have seen, both the maxillary plate and the short tooth plates of the oral plates are covered with extremely fine tooth-like dentine denticles similar in nature to the dentine ridges of the dermal skeleton. On the maxillary plate they are arranged in regular rows, which outwards pass into the ordinary dentine ridges. They are either primary formations or else must have been brought into existence by the dentine ridges dissolving into single points. In Aceraspis, on the contrary, the maxillary plate is set with fine knotty dentine elements in accordance with the rest of the dermal skeleton

in this genus. In Trematapis again the surface of the maxillary plate possesses the same peculiar character as the other dermal skeleton of the head-shield. This is a remarkable thing which must assuredly be regarded as a very primitive character in these earliest forms.

In Pteraspis these tooth plates are much like fine raspes and one might believe that they rasped against each other. The curving of the surface is, however, against such an interpretation. More probably the mouth has been a biting or grasping one. In the Cephalaspids it looks as the mouth has functioned in a slightly crushing manner. The author assumes that the segmental myotomes could give by specialisation the necessary muscles for this mouth-apparatus.

It is an interesting question whether the tooth formation in the Cyclostomes of the present day may possibly be derived from the tooth plates in the Pteraspids and Cephalaspids, with whom the former must now be assumed to be closely related. The horny teeth in the Cyclostomes have, as is known, been the subject of many different opinions. H. HANSEN'S interesting study of these teeth (1920) makes it probable that they are rudiments of true teeth. One may, therefore, very well presume that the primary tooth plates have been transformed and degenerated in connection with the very peculiar transformation of the mouth and its function, which have taken place in the degenerated lines of recent Cyclostomes.

Comparison with the structure of the mouth of Anaspida.

Since my work on Norwegian Anaspida was published in 1924 the organisation, systematic position, and significance of these interesting forms, and their influence on the oldest development of vertebrata have been dealt with by a number of authors (STROMER 1926, RAYMOND 1925, SIMPSON 1926, STETSON 1927, JAEKEL 1927). This preliminary report is not the place in which to deal with these questions, the more so as STENSJÖ, on the basis of the wonderfully well preserved material of Cephalaspids from Spitsbergen has, in a far more thorough manner than I could do, arrived to results which, taken all round, agree with mine. I shall here merely draw a brief comparison with the mouth structure of Anaspida which, we may now confidently say, were closely related to Cephalaspids and the recent Cyclostomata.

In the Anaspida the mouth was terminal. This was certainly the case in Pharyngolepis and Rhyncholepis, and, therefore, also in all probability in the other genera, in which it is more difficult to determine. In Pterolepis the slit of the mouth is bounded by fine scales, in Pharyngolepis and Rhyncholepis, on the other hand, by larger dermal skeleton plates. Particularly in the latter genus they have a form and arrangement that appear to indicate that they are developed in relation with an underlying cartilaginous mandibular arch. If this would be the case and the author would be right in his opinion that Rhyncholepis is the most specialized of these genera, this would seem to point to the fact that the structure of the mouth has undergone a gradual development, the mandibular arch in this group having played an increasingly important part in the function of the mouth.

The structure of the mouth of the oldest known vertebrates does not appear to give any clew to the development of the inner visceral skeleton, which a number of investigators, e. g., JAEKEL, SEWERTZOFF, NAEF and others, have endeavoured to elucidate in recent years. I have therefore not dealt with the various views that have been advanced on this question.

The facts I have given in this short paper show how these oldest known primitive forms by a specialization of the dermal skeleton of the mouth region, have developed a mouth skeleton that after the opinion of the author is not homologous with the mouth structure in the lower gnathostome vertebrates, but which nevertheless shows certain points in agreement with it. This must be founded upon the interaction between form and function, which so often develops the most remarkable convergences in the evolution of the organic world.

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Erklärungen zu Tafel XII.

Pteraspis Vogti nov. sp. (manusci.), Red Bay series, Downtonian, Spitsbergen. Collector A. Heintz on Th. Vogts Spitsbergen expedition 1925. Original in Pal. Mus. Univ. Oslo.

Fig. 1. Ventral side of the head with the mouth, oral area and lateral plates, ×4. For explanation see textfigure 3. On the ventral shield only a few of the lateral line pores are seen. A. Heintz phot.

Fig. 2. Longitudinal section through the rostral and oral area, ×10. No. 87 of section series A. MPl. Maxillary tooth plate. OPl. Oral plates. OTPl. Oral tooth plate. RPl. Rostral plate. VS. Ventral shield. In this section four oral pletes have been cut through; the left one shows the tooth plate with the fine dentine denticles. A. Heintz phot.

Erklärungen zu Tafel XIII.

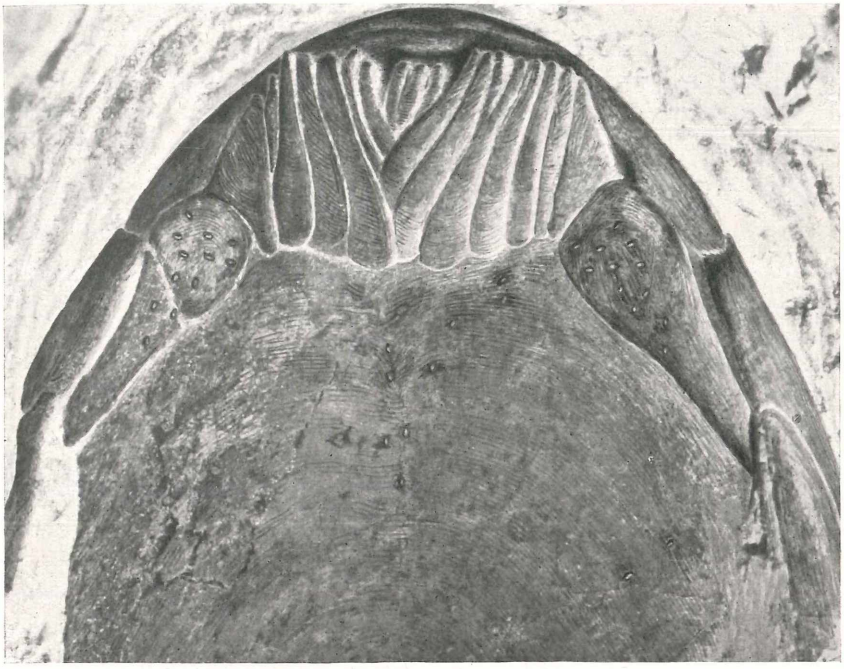
Micraspis gracilis Kiaer, Lower Downtonian, Ringerike, Norway Collector J. Kiaer. Original in Pal. Mus. Univ. Oslo.

Fig. 1. Ventral side of the head, ×4. M. Mouth. OPl. Oral plates. On the front is the right side reconstructed. A. Heintz phot.

Aceraspis robustus. Kiaer, Lower Downtonian, Ringerike, Norway. Collector J. Kiaer. Original in Pal. Mus. Univ. Oslo.

Fig. 2. Head shield seen from the inside, ×1,5. Etching preparate with fluoric acide. A. Heintz phot.

Fig. 3. The central part of the lower side of the marginal border of the same specimen, ×5,5. MDPl. Maxillary tooth plate. The asterisk shows the left limit of the mouth. A. Heintz phot.



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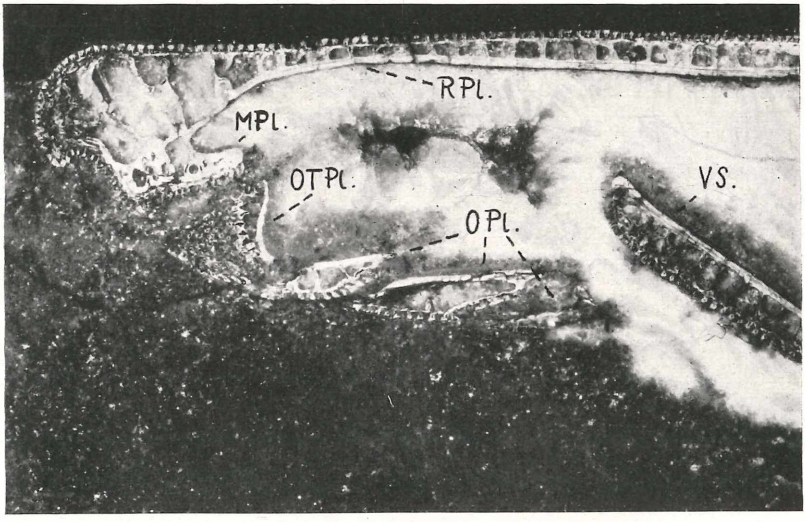

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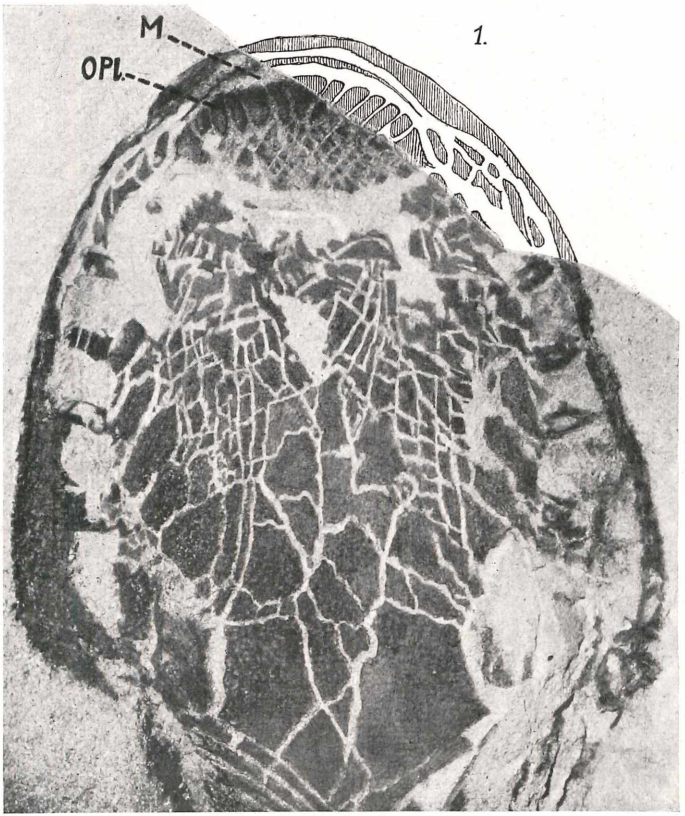

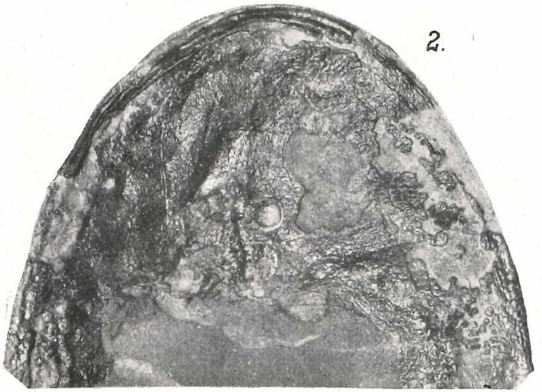

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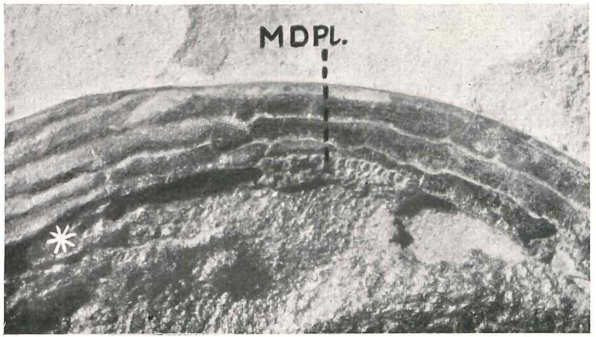

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