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NORGES SVALBARD- OG ISHAVS-UNDERSØKELSER  
LEDER: ADOLF HOEL

# SKRIFTER OM SVALBARD OG ISHAVET

Nr. 40

THE DOWNTONIAN AND DEVONIAN  
VERTEBRATES OF SPITSBERGEN

V

SUBORDER *CYATHASPIDA*

PART I

TRIBE *PORASPIDEI*

FAMILY *PORASPIDAE* KIÆR

BY

JOHAN KIÆR† AND ANATOL HEINTZ

WITH 1 MAP, 3 TABLES,  
57 FIGURES IN THE TEXT AND 40 PLATES



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I KOMMISJON HOS JACOB DYBWAD

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RESULTS OF THE NORWEGIAN EXPLORATIONS TO SVALBARD  
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ISACHSEN, GUNNAR, Première Partie. Récit de voyage. Fasc. XL. 1912. Fr. 120.00.

With map: Spitsberg (Côte Nord-Ouest). Scale 1:100 000. (2 sheets.) Charts: De la Partie Nord du Foreland à la Baie Magdalena, and Mouillages de la Côte Ouest du Spitsberg. ISACHSEN, GUNNAR and ADOLF HOEL, Deuxième Partie. Description du champ d'opération. Fasc. XLI. 1913. Fr. 80.00.

HOEL, ADOLF, Troisième Partie. Géologie. Fasc. XLII. 1914. Fr. 100.00.

SCHETELIG, JAKOB, Quatrième Partie. Les formations primitives. Fasc. XLIII. 1912. Fr. 16.00.

RESVOLL HOLMSEN, HANNA, Cinquième Partie. Observations botaniques. Fasc. XLIV, 1913. Fr. 40.00.

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ISACHSEN, GUNNAR, Rapport sur l'Expédition Isachsen au Spitsberg. 1912, No. 15. Kr. 5,40.

ALEXANDER, ANTON, Observations astronomiques. 1911, No. 19. Kr. 0,40.

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With chart: Waters and anchorages on the west and north coast. Publ. by the Norw. Geogr. Survey, No. 198.

HOEL, A. et O. HOLTEDAHL, Les nappes de lave, les volcans et les sources thermales dans les environs de la Baie Wood au Spitsberg. 1911, No. 8. Kr. 4,00.

GOLDSCHMIDT, V. M., Petrographische Untersuchung einiger Eruptivgesteine von Nord-westspitzbergen. 1911, No. 9. Kr. 0,80.

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HOLTEDAHL, OLAF, Zur Kenntnis der Karbonablagerungen des westlichen Spitzbergens. I. Eine Fauna der Moskauer Stufe. 1911, No. 10. Kr. 3,00. II. Allgemeine stratigraphische und tektonische Beobachtungen. 1912, No. 23. Kr. 5,00.

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With map: Spitsberg (Partie Nord-Ouest). Scale 1:200 000 (2 sheets).

GUNNAR ISACHSEN has also published: Green Harbour, in *Norsk Geogr. Selsk. Aarb.*, Kristiania, 1912—13, Green Harbour, Spitsbergen, in *Scot. geogr. Mag.*, Edinburgh, 1915, and, Spitsbergen: Notes to accompany map, in *Geogr. Journ.*, London, 1915.

All the above publications have been collected into two volumes as *Expédition Isachsen au Spitsberg 1909—1910. Résultats scientifiques. I, II. Kristiania 1916*.

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The following topographical maps and charts have been published separately:

Maps:

Bear Island. 1:25 000. 1925. Kr. 10,00.

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East Greenland. Eirik Raudes Land from Sofiasund to Youngsund. 1:200 000. 1932. Kr. 5,00.

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A. W. BRØGGERS BOKTRYKKERI A/S

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## PREFACE

Professor Dr. Johan Kiær, during the last 20 years of his life, had intensively studied the fossil fishes collected by Norwegian expeditions to Spitsbergen. He had hoped to be able to describe the forms belonging to the group *Heterostraci*, and had planned to publish 3 or 4 monographs about these remarkable vertebrates. During his last years he concentrated his investigations on the first group of *Heterostraci*, which he called *Cyathaspida*. A manuscript of about 200 pages text, with more than 100 plates and 75 figures in the text, was written and he had hoped to finish the whole work in the autumn of 1931. Unfortunately, a painful illness destroyed his plans and prevented him from finishing his great work. After his death on October 31st, 1931, only an unfinished manuscript was found.

As Professor Kiær's pupil, collaborator and friend, and as a specialist in the paleozoic fishes, I have undertaken to finish his paper on the *Cyathaspida*. A study of the manuscript has shown me that unfortunately, only the systematical part, is more or less finished, the introduction and the general part not having been written at all. But there has been so much to alter, compare, add and correct in the systematical part, that I have been unable to get it ready quickly enough. As, in the meantime, it was very desirable to publish the results of Professor Kiær's investigations as soon as possible, I prepared, after consultation with Docent A. Hoel, a short abstract from the systematical part of the manuscript, which abstract was published in November 1932. (Kiær 1932, 1).

In a list of contents found among Professor Kiær's effects he divides the paper into three parts: I) General and stratigraphical introduction, II) Systematical part, classification of the *Heterostraci* and III) General part (structure and organization of *Cyathaspida*, systematical position of *Cyathaspida* and *Heterostraci*).

As mentioned, of these three parts only the second is more or less ready written. Of the first, only some short remarks and sketches have been found, while the material for the third is completely absent, except some few drawings without explanations.

I have therefore determined to complete as thoroughly as possible the first and second parts, but not, in this publication, to attempt to reconstruct Professor Kiær's opinion upon the systematical position of the *Heterostraci*.

It has, however, proved during the preparation of the manuscript, that it will be more practical not to publish the whole paper at once, but to divide it into several parts. The first, which is presented here, includes the introductory part and the description of the Fam. *Poraspidae* — the first and largest family of the Tribe *Poraspidei*. In the second, the other families belonging to the Tribe *Poraspidei* will be dealt with and, finally, the third will contain the description of the Tribe *Cyathaspidei*.

Paleontologisk Museum, Oslo, May 1935.

*A. Heintz.*



## INTRODUCTION

In the huge material of fish remains collected by Norwegian expeditions from the Downtonian and Devonian formations of Spitsbergen, the *Heterostraci* are the most important, particularly in the two oldest series pertaining to the Downtonian and the Lower Devonian. Here in certain horizons the fossils are found in enormous quantities and often in an excellent state of preservation (Pl. I). They also occur in such considerable numbers of partly known, partly new and richly varying forms, that one might be tempted to consider these arctic regions as being the very centre of distribution with regard to this remarkable group of fishes.

It is, without doubt, the largest and best preserved material of the *Heterostraci* which has ever been brought together. Unfortunately, most of the forms here, as in previously known regions from more southern latitudes, have been found only as isolated shields and scales. Still the considerable number of specimens, which have enabled a thorough examination, and a few particularly good finds in a more or less complete state of preservation, have made it possible to get a better insight than before, into the structure of these surely very primitive vertebrates. The examination of this enormous material, containing more than six thousand rock pieces, each often with many specimens of different forms, has necessarily taken a long time. In fact, it has cost the authors many years work. And yet, in this first part there will be described a few groups, named the *Cyathaspida*, of the Order of the *Heterostraci*. These are forms related to the previously-known Genera *Cyathaspis* and *Palaeaspis*.

## COLLECTION OF THE MATERIAL. (A. H.)<sup>1</sup>

The material of the *Heterostraci*, described in this paper, has been collected exclusively in Red Bay, a small bay on North Spitsbergen. Here we find the beds of Downtonian age. The mighty Red Bay Series begins with conglomerate, continuing with yellow, red and green sandstones and shales. It measures about 3000 meters of which the uppermost 1500 m contain a great quantity of fossils.

This series was discovered and explored by Norwegian expeditions (Hoel 1929, Vogt 1926, 1929) and all the enormous material collected here, is now preserved in the Paleontological Museum in Oslo.

The discovery of the fossil-bearing strata in Red Bay, was made in 1906 by an expedition fitted out by Prince Albert I of Monaco and led by G. Isachsen (Hoel 1910). On a mountain, called "Mt. Pteraspis" situated between Liefde Bay and Red Bay, Lieutenant Staxrud, in a horizon 800 m above sea-level, collected some concretions containing fragments of fishes. These first fossils from Red Bay were determined by Kiær as specimens of a small *Pteraspis* and fragments of a *Cephalaspis* (Kiær in Hoel's 1910, 1914, Kiær 1916, Stensiö 1927, Hoel 1929).

The next exploration of the strata in Red Bay and collection of fossils were undertaken during Isachsen's great expeditions in the summers of 1909 and 1910. In 1909 Docent Hoel systematically collected fossils on Frænkelryggen and on Mt. Ben Nevis, new localities discovered by him. The next summer Hoel continued the collection on Frænkelryggen and G. Watnelie on Ben Nevis. In both these localities more than 30 fossiliferous horizons containing a great number of fossils were found and immense collections of these were brought home. This material comprises the nucleus of the collection of the Downtonian fossils from Red Bay, preserved in Oslo, and is of particular great value as it consists of fossils collected in many

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<sup>1</sup> (A. H.) — after the title of the chapter indicates that it is wholly written by A. Heintz. (J. K. & A. H.) — after the title of the chapter indicates that more than a half has been written by A. Heintz.

exactly determined horizons through practically the whole Red Bay Series, and thus gives the best material for a stratigraphical division of this formation.

The next expeditions visiting the Red Bay Series, was Hoel's and Staxrud's in 1911 and 1912. The most important work these years was done round Wood Bay and Wijde Bay. The only collection in the Red Bay Series was gathered on Frænkelryggen by Hoel and Holtedahl in 1911 and around Mt. Pteraspis by Hoel in 1912.

During the succeeding 13 years no expeditions visited Red Bay, and not before 1925 was a new collection made in this interesting locality. The Spitsbergen expeditions of Professor Th. Vogt in 1925 and 1928 was initiated by Vogt and planned and arranged by the Professors Kiær and Vogt. The expedition in 1925 also received valuable help from Hoel's expedition to Spitsbergen that year. The special object of these two expeditions was a study of the Downtonian and Devonian formations of central and northern Spitsbergen.

In 1925 (Vogt 1926) the expedition, with Dr. A. Heintz and Docent Fr. Isachsen as scientific members, worked, as planned, one week in Red Bay. The good finds, on this short visit, involved a longer stay in this area next time.

In 1928 (Vogt 1929) a party of three paleontologists Dr. A. Heintz, Dr. T. Strand and Dr. L. Størmer with one assistant — spent more than a month in Red Bay and undertook a systematical collection of fossils from different localities. Frænkelryggen and Ben Nevis were very carefully explored and a number of new fossil localities were found. In addition, they also made some excursions to Mt. Wulff and collected fossils on different smaller ridges, moraines and on the shores of Red Bay.

The material gathered by these two last expeditions was a very welcome addition to the older, collected by Hoel. It partly completed the material from older localities, and partly consisted of excellently preserved specimens, showing not only the finest details in the structure of the dorsal and ventral shields, but also the structure of the hind, scale-covered part of the body.

As we have seen, seven different Norwegian expeditions, have worked in Red Bay (1906, 1909, 1910, 1911, 1912, 1925 and 1928), (Table I). The material of fish fossils collected on these expeditions is really enormous. About 6 000 rock pieces are now preserved in the museum in Oslo, many, containing a great number of specimens. The greatest part of this collection consists of different *Heterostraci*, of *Cephalaspida*, already partly described by Stensiö (1927), and, finally, of *Lammelibranchiata* (partly described by Quenstedt (1926)), *Ostracoda* (described by Solle 1935) *Merostomata* (described by Størmer, 1934) and badly preserved plants.

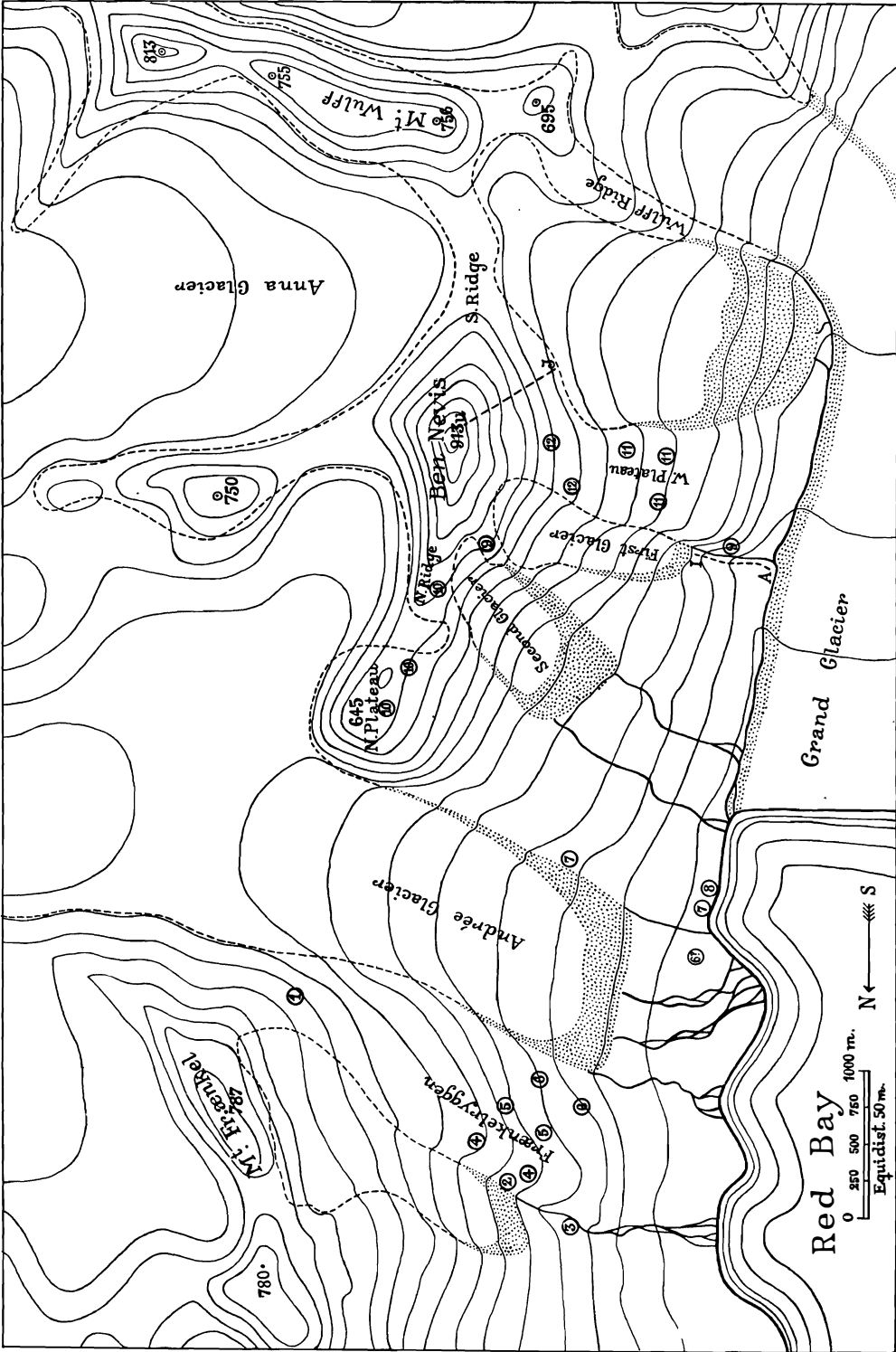
Of the immense material of *Heterostraci*, those belonging to the Fam. *Poraspidae* Kiær (Sub-Order *Cyathaspida*) will be described in this paper.

Table I.

Expedition	Leader	Collectors	Localities
1906 . . . . .	G. Isachsen	Staxrud	Mt. Pteraspis
1909 . . . . .	G. Isachsen	Hoel	Frænkelryggen Mt. Ben Nevis
1910 . . . . .	G. Isachsen	Hoel Watnelie	Frænkelryggen Mt. Ben Nevis
1911 . . . . .	Hoel and Staxrud	Hoel Holtedahll	Frænkelryggen
1912 . . . . .	Hoel and Staxrud	Hoel	Mt. Pteraspis
1925 . . . . .	Th. Vogt	F. Isachsen A. Heintz Th. Vogt	Frænkelryggen E shore of R. B. Mt. Ben Nevis
1928 . . . . .	Th. Vogt	A. Heintz T. Strand L. Størmer	Frænkelryggen E shore of R. B. Mt. Ben Nevis Mt. Wulff

## THE GENERAL STRATIGRAPHY OF THE FOSSILIFEROUS PART OF THE RED BAY SERIES. (A. H.)

The description of the stratigraphy of the Red Bay Series, will be given later by Professor Th. Vogt, in his paper on the stratigraphy of the Devonian rocks in Spitsbergen. In this place, chiefly based on the previously published descriptions of the stratigraphy of the Red Bay Series (Hoel 1910, 1914, 1929; Holtedahll, 1913, 1914, 1926; Stensiö 1927), will only be given a summary of the stratigraphical division of that part of the Red Bay Series, where the greatest portion of the fossils has been collected. Such a description is necessary for the understanding of the relative stratigraphical position of the different fossilbearing horizons mentioned later in this paper. A map of the innermost part of the east side of Red Bay (pag. 11) where the best fossil localities occur, and a panoramic view of the same part (fig. 1), show the position of the different localities and horizons. The map, a somewhat altered, enlarged copy of Isachsen's maps of NW Spitsbergen, is worked out by Heintz and Størmer. The panorama is based on a sketch made by Heintz. The heights on this panorama are greatly enlarged, thus displaying a quite distinct relief.



Explanation of the numbers as in fig. 1.

Nr "9" placed between the Second and First Glacier, is meant to be nr "13".

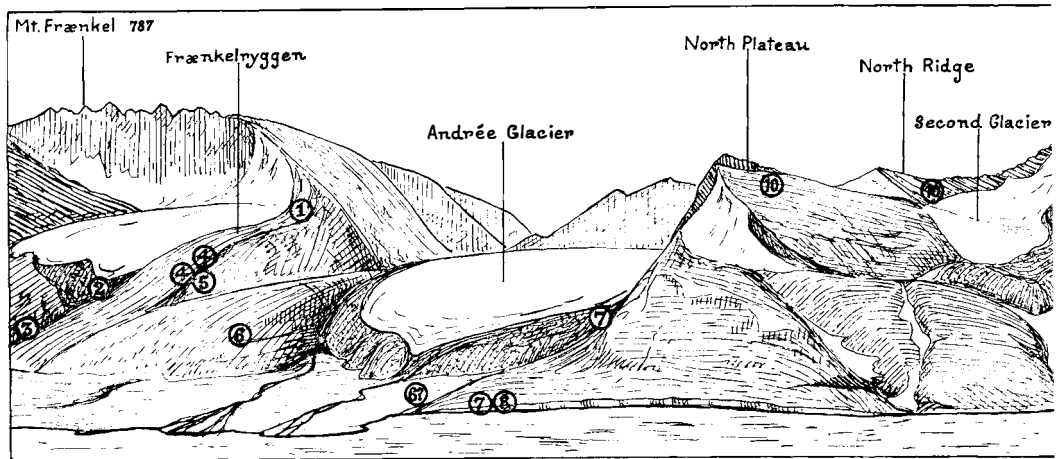


Fig. 1. Panoramic view of a part of the east shore  
 1. *Psammosteus* Horizon. 2. *Corvaspis* Horizon. 3. Plant Horizon. 4. *Primaeva* Horizon. 5. *Polaris*  
 11. *Ctenaspis* Horizon. 12. *Benneviaspis* Horizon. 13. Tunge. A—I Hoel's

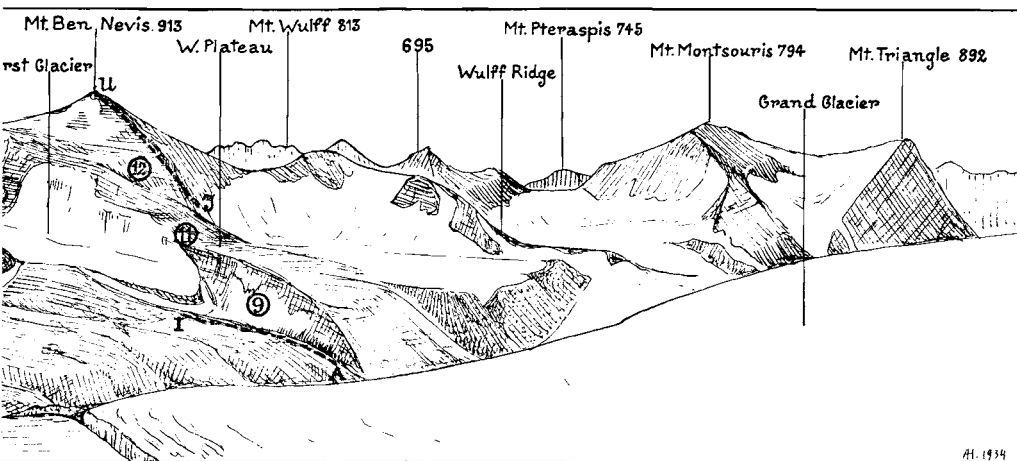
As is known, the oldest part of the fossil-bearing deposits was found on Frænkelryggen. As the striking of the sandstone in the Red Bay Series is about NNW—SSE with the dip towards the west, it is natural that we find the oldest deposits on the top and north side of Frænkelryggen.

In reality, the oldest known fossil horizon is placed on the very top of the ridge in a yellow-grey sandstone, about 550 m above sea-level. This horizon, which was discovered by Strand in 1928, was called the “*Psammosteus* horizon” as the most abundant fossil in the layer are fragments of an interesting new *Psammosteus*-like form.

The second horizon, called the “*Corvaspis*” horizon, was discovered by Heintz in 1928, on the north side of Frænkelryggen. Here was found a large number of big shield plates, covered by a remarkable structure, reminiscent of that in *Tolypaspis*. It is, of course, evident that the form from Spitsbergen has nothing to do with the Estonian; it is probably a *Psammosteus*-like form. It was recently described by Woodward (1934) from England as *Corvaspis kingi*.

The third horizon, was also found in 1928 by Strand and Størmer, on the north side of Frænkelryggen, somewhat lower down than the *Corvaspis* horizon. Here, in addition to the fish fossils, was found a number of badly-preserved plants, and the horizon is therefore named the Plant horizon.

The fourth horizon, found in 1909—10 by Hoel, is situated higher up and more to the south nearly at the edge of Frænkelryggen. It was termed the “*Primaeva* horizon” after a small *Pteraspis* — *Pt. primaeva*



the Red Bay. After a sketch by A. Heintz.

horizon. 6. Anglaspis Horizon. 7. Red Horizon. 8. Rotundatus Horizon. 9. Cliff. 10. Vogti Horizon. section. (Horizons from A to I). J—U Hoel's Section. (Horizons from J—U).

n. sp. — found very abundantly in this deposit. Hoel in 1909 gave this horizon, which consists of a red fine sandstone, the name “300 m above sea-level”.

The fifth horizon, the “Polaris horizon”, named after the very common fossil — *Poraspis polaris* n. sp., which occurs in thousands of species in the grey-green fine sandstone (Pl. I) was also discovered in 1909—10 by Hoel and called “250 m above sea-level”. It is situated immediately on top of the red “Primaeva horizon” and can be found somewhat lower down at the edge of Fränkelryggen.

The last horizon, the sixth, known on Fränkelryggen is the “Anglaspis horizon”. The beautiful small forms of *Anglaspis* are very common in this nearly grey sandstone. This horizon was also already known by Hoel, who collected fossils from this locality and called it “200 m above sea-level”. On the expedition in 1928, however, especially rich portions of this horizon were discovered by Heintz lower down on the south side of Fränkelryggen.

The next section was explored on the expeditions in 1925 and 28. It was deposited along the East shore of Red Bay, on both sides of a stream running from the south corner of the Andrée Glacier. Here, only three horizons containing fossils were found: The first was placed on the N side of the stream, where in grey, quite coarse sandstone, a large number of badly-preserved fossils was found, and among them a small *Anglaspis* species was common. It is, therefore, quite probable that this horizon corresponds more or less with the “Anglaspis horizon” on Fränkelryggen.

The next is named the "Red horizon" because of the red colour of the sandstone. It is situated on the S side of the stream, about 100 m away from it. It can be traced running parallel to the stream into the country, towards the foot of the northern part of Ben Nevis. Here in 1928, in a very steep cliff, a red horizon containing a quantity of badly-preserved fossils was discovered. Probably this horizon corresponds to the "Red horizon" on the shore.

The third horizon, lying on the shore, is the so-called "Rotundata horizon" (after *Pteraspis rotundata* n. sp.). In the green-grey fine sandstone a number of relatively well preserved black fossils was found already in 1925. This horizon was not re-found on the N cliff.

The great section through all the Ben Nevis deposits, which we shall now discuss, was chiefly explored by Hoel in 1909—10. The collections from different localities gathered during the expeditions in 1925 and 28, were of a more occasional character, but it is not particularly difficult to find the correct place of the new localities among the 20 horizons determined by Hoel.

The first part of Hoel's section is placed along a stream running from the "First glacier" on Ben Nevis. This stream does not reach the sea, but falls into a larger stream, running along the west side of the Grand glacier.

The first horizon in this section lying about 57 m above sea-level is called "Horizon A". After this, follow with short intervals 8 other horizons, termed with the letters from B to I.

"Horizon B" is situated 65 m, C—75 m, D—81 m, E—88 m, F—90 m, G—110 m, H—135 m, and, finally, I—167 m above sea-level. All these horizons are petrographically somewhat alike and represent a very hard, grey, often micaceous sandstone. The fossils are neither especially well preserved, nor richly represented. The horizons A, B, F and I are relatively richer than the others. In 1925 and 28, some fossils were collected in these horizons, and also on the W side of the northern part of Ben Nevis, which part corresponds to the different horizons in the above mentioned profile A—I.

The next horizons determined by Hoel are placed on a very steep cliff on the south side of the above-mentioned stream from the First glacier. This cliff forms the northern limit of a relatively flat plateau on the W side of Ben Nevis. On the cliff, fossils have been collected from two horizons — 260 and 290 m above sea-level respectively. In addition, both on the expeditions in 1909—10 and 1925—28 a number of fossils was collected in the boulders found beneath and on the cliff.

A horizon very probably corresponding with one or another of the horizons on this cliff is "Vogti horizon". The horizon, consisting of a fine red and grey sandstone with very well preserved white fossils,



is named after a short and broad *Pteraspis* — *Pt. vogti* n. sp. collected there. It is widely distributed and was for the first time found in 1928 on the N ridge of Ben Nevis, and it was pursued to the northern plateau of Ben Nevis.

We find the continuation of the section made by Hoel on the SW side of Ben Nevis, where he has determined 12 horizons, from J to U. Horizon J lies 490 m, K—497 m, L—532 m, M—577 m, N—623 m, O—627 m, P—653 m, Q—675 m, R—690 m, S—713 m, T—840 m and U—900 m above sea-level respectively. All these horizons, composed of finer and coarser grey, and green-grey sandstones, partly contain a large quantity of fossils, horizons K, L, N, O and R being particularly rich.

On the expedition in 1925 no fossils were collected in this section, but a relatively rich material was brought together on the above-mentioned W plateau, about 300—400 m above sea-level. This horizon, which had been more extensively explored in 1928, contained a number of different fossils, and as especially the *Ctenaspis* forms were very abundant, this horizon has been called the "Ctenaspis horizon". It probably corresponds to the horizons J, K and L in Hoel's section. Higher up, on the W side of Ben Nevis, a number of fossils was collected in 1928 mostly from the horizon between 500 and 600 m above sea-level (Benneviaspis horizon). This comparatively rich horizon may correspond to the O, P, Q and R horizons in Hoel's section. Another locality discovered in 1928, was a narrow, long tongue, situated on the NW side of Ben Nevis between the First and Second glaciers ("Tunge"); also the horizons found here may correspond to the O—R in Hoel's section.

Besides all these systematically undertaken collections on Fränkelryggen and Ben Nevis, a great number of fossils was gathered in different moraines and debris beneath different steep cliffs and ridges. An excursion along Wulffs Ridge to Mt. Wulff undertaken in 1928 and, further, to the south ridge of Ben Nevis, did not give any particularly interesting palæontological results. The deposits on Mt. Wulff may correspond to those on Fränkelryggen.

On Mt. Pteraspis, fossils have only been gathered in 1906 and 1912 from 4—5 different horizons, and it seems not improbable, that the lowest horizon here corresponds to Anglaspis horizon on Fränkelryggen, and the uppermost, round the Vogti horizon on Ben Nevis.

As we have seen, the section through the Red Bay Series is very complete. The lowest part is found on Fränkelryggen, the youngest deposit at the top of Ben Nevis. The following table (pag. 16) gives the probable relationship between the different horizons of the Red Bay Series.

Table II.

Fränkelyggen Group		E. Shore	Mt. Pterasp.	Ben Nevis Group	
1909—1910	1925—1928	1928	1912	1909—1910	1925 1928
				Hor. U (900 m ) » T (840 » ) » S (713 » ) » R (690 » ) » Q (675 » ) » P (653 » ) » O (627 » ) » N (623 » ) » M (577 » ) » L (532 » ) » K (497 » ) » J (490 » )	Benneviasp. Hor. (500—600 m) Tunge.
			? 760—825	Cliff under W. Plateau: (290 m ) (260 » )	? Vogti Hor.
			? 650	Hor. I (167 m ) » H (135 » ) » G (110 » ) » F ( 90 » ) » E ( 88 » ) » D ( 81 » ) » C ( 75 » ) » B ( 65 » ) » A ( 57 » )	
		Rotunda Hor. Red Hori- zon			Red Hor. on N. cliff.
200 m	Anglaspis Hor.	Anglaspis Hor.	? 50		
250 »	Polaris Hor.		?		
300 »	Primaeva Hor. Plant Hor. Corvaspis Hor. Psammost. Hor.		Lowest by Erik Glacier		

## MATERIAL AND METHODS. (A. H.)

As is mentioned above, the rocks where the fossils are found in the Red Bay Series, consist of different kinds of sandstone. The most abundant is a somewhat hard, often micaceous grey sandstone, where the fossils in freshly-broken stones are dark, often almost black, in more weathered parts, of a lighter colour, white-grey to nearly white. The preservation varies: in micaceous sandstone it is as a rule bad, in finer sandstone, on the other hand, it can be very good. These grey sandstones of greatly varying structure and outline are especially characteristic of the horizons on Ben Nevis, but they are also found in the uppermost part of Frænkelryggen (Anglaspis horizon). Beyond that, on Frænkelryggen, is the shaly grey-green sandstone, almost without mica, more characteristic. Especially the darker, green-grey fine shaly sandstone from the Polaris, and partly from the Plant horizons contain excellently preserved fossils, which, as a rule, are rather dark, but never black, with a fine glossy surface, displaying the finest details in the structure of the dentine ribs, and in the pores of the sensory canal system. The microscopical sections, however, show no finer details. The red sandstone occurs comparatively seldom and only in the lower part of the Red Bay Series. On Frænkelryggen the Primaeva horizon is red, the sandstone is very fine, compact and rich in fossils, which here are nearly white, often with a faint rose or light-blue colour. The preservation is very good, the surface is glossy, and in some cases, nearly transparent, the inner structure of the shield showing indistinctly through it. The Red horizon in the "short section" and on the north cliff is more coarse. The fossils, which in some parts occur in enormous numbers, are badly preserved. They are also here of a white colour, but the surface is not glossy, and the macroscopical and microscopical structures are difficult to see. Finally, on Ben Nevis on the north plateau and north ridge occurs a red, almost shaly, fine sandstone with a large number of concretions. These concretions are mostly blank, and of many hundreds which were crushed during the expeditions in 1925—28 only very few contained fossil remains, while, on the contrary, the red and grey-red sandstone found in their immediate neighbourhood, contained a number of fine fossils. Apparently the fine slab with 6 complete specimens of *Pteraspis vogti* Kiær, described by Kiær in 1927, is from this horizon. It seems also very probable that the red concretion horizon found on Mt. Pteraspis, corresponds to that on Ben Nevis.

A specific kind of rock represents the lowest horizon on Frænkelryggen (the Psammosteus horizon), which, at the same time, as mentioned

above, is the oldest fossil-bearing horizon in the Red Bay Series. The sandstone is here a rather coarse, yellow-grey. The fossils are nearly black, except on the weathered surface where the sandstone becomes almost yellow, the fossils are whitish, often with a tone of blue. They are badly preserved and only seldom display some finer details.

The preparation of the fossils was carried out by hand, with the help of chisels, and the finest details were cleared out with the thinnest needles. Often they could with advantage be prepared in alcohol. All preparations were done under binoculars magnifying from 5 to 50 times. Besides the chisels, a dentist's boring machine and gold hammer were often used with very good results. The very fine, small grindstones used by dentists in the boring machines, were especially favourable for the preparation of the sensory canals in the shields of the *Cyathaspida*. A number of fine preparates of the sensory canals were carried out in this manner (Pl. VII; VIII). The gold hammer was more useful for the excavation of different tender parts of the fossils. The corrosion with HCL was sometimes applied, for instance, to get a more distinct relief of the structure of the inner layers of the shields, when the outer layer had been ground off with the help of a boring machine (Pl. VII; VIII).

The serial sections were used only to a very limited degree chiefly for the study of the front part of the head shield; some small models were also prepared.

All the preparations were made either by Professor Kiær himself, or under his direction. A relatively large number of fossils have also been worked out by Dr. Heintz. All the photographs illustrating this paper were prepared in the Paleontological Museum in Oslo, and taken, under the direction of Professor Kiær and Dr. Heintz, by Miss L. Monsen, Miss Torbjørnsen and Mrs. Zachariassen. The microphotographs were partly done by Dr. Heintz and partly by Dr. Størmer, and the retouch of the photographs chiefly by Miss Barstad, Miss Torbjørnsen and Mrs. Zachariassen. The drawings were made from sketches of Professor Kiær by Miss Barstad and Mrs. Zachariassen, a few by Dr. Heintz. The serial sections and wax models were constructed by Cand. real Knaben.

All the numerous microscopical slides have been made by the preparator of the Paleontological Museum, Oslo, Mr. Sveen.

The authors will here express their best thanks to all who have helped with the preparation of this paper.

## CLASSIFICATION OF THE HETEROSTRACI. (J. K. & A. H.)

The first forms, belonging to the *Heterostraci* were described as early as in 1833 by Agassiz. He united them with the *Cephalaspida* and regarded them only as different species of this genus (*C. rostratus*, *C. lewisii* and *C. lloydii*). Together with other "armoured fishes" he considered them as belonging to the Ganoida.

In 1847, Kner described a new form from Upper Silurian of Gallicia, which is strongly reminiscent of *C. lewisii* Ag. and *C. lloydii* Ag. He regarded them, however, not as belonging to fishes at all, but as fragments of the internal skeleton of a Cephalopod related to *Sepia*, and proposed for them the generic name *Pteraspis*.

Some years later, Roemer (1856) described remains from the Devonian of Eifel shale as *Palæoteuthis*. This form was in reality closely related to *C. lloydii* Ag., but Roemer expressed the opinion, that his form, together with Kner's *Pteraspida*, was neither the remains of fishes nor *Cephalopoda*, but represented the armour of a *Crustacea*.

In opposition to Kner and Roemer, Huxley (1858, 1) wrote that, in fact, there was no foundation for the supposed resemblance between *Pteraspida* on one hand and *Sepia* or *Crustacea* on the other. He also proposed to adopt the name Gen. *Pteraspis* for the type of fishes described by Agassiz as *Cephalaspis lewisii*, *C. lloydii* and *C. rostrata*. He regarded both the Gen. *Cephalaspis* Ag. and Gen. *Pteraspis* Kner as related to *Chondrostei*, but considered that they formed a very distinct family (Huxley 1858, 2).

It was, however, Lankester, who in the first part of his "The fishes of the Old Red Sandstone of Britain" (1868) introduced the name *Heterostraci*. He proposed to divide the "Familia vel. Sub-Order *Cephalaspidæ*" Huxley, into two sections: A) *Heterostraci* — in view of the special characteristic of their test, and B) *Osteostraci* — in reference to the occurrence of the bony structure in their cephalic shields. The first section, *Heterostraci*, was divided into three Genera: *Scaphaspis*, *Cyathaspis* and *Pteraspis*. Concerning the relationship of the Fam. *Cephalaspidæ*, Lankester agreed with Huxley, that it is nearest related to *Chondrostei*.

In the later parts of the same "Monograph" Lankester, however, is more doubtful with regard to the near relationship between the *Heterostraci* and the *Osteostraci*. He also changed his opinion about the systematical position of the whole group and is very much in doubt to which forms among the fishes they are related.

Schmidt (1873, 3) also expressed the opinion, that *Heterostraci* and *Osteostraci* cannot be united into one family.

Zittel in his well-known "Palæozoologie", (Vol. III, 1887) also pointed out the great difference between *Heterostraci* and *Osteostraci*, giving them the range of an independent Orders. He did not, however, accept the above-mentioned names proposed by Lankester, but suggested to call the *Heterostraci* as Order *Pteraspida* and *Osteostraci* as Order *Cephalaspida*. Both these Orders, together with a number of others (*Placodermi*, *Chondrostei*, *Acanthodii*) he reunited as "Unterklasse *Ganoidei*". In the description of the Order *Pteraspida* (= *Heterostraci*) he mentioned only four different Genera: *Pteraspis*, *Cyathaspis*, *Lophostracon?* and *Holaspis*.

A wholly new classification principle of the oldest vertebrates was introduced by Cope (1889, 1891). He established a new class of Craniata Vertebrata, the Class *Agnatha* (Heckel) characteristic of the absence of the jaws, pectoral arches and ossified inner skeleton. The Class *Agnatha* constitutes two groups: The *Cyclostomi*, comprising the living lampreys and hag-fishes and the *Ostracodermi*, which combines the *Pteraspida*, *Cephalaspida* and *Pterichtyida* (in 1891, Cope altered the name *Ostracodermi* to *Ostracophori*).

The new name *Ostracodermi* was adopted by Woodward in "Catalogue" (1891). He regarded the *Ostracodermi* as "a primitive Piscine sub-class of uncertain affinities" and divided it, corresponding to Cope, into three Orders: *Heterostraci*, *Osteostraci* and *Antiarchi*, Order *Heterostraci* containing only one Family *Pteraspidae* with three Genera: *Pteraspis*, *Palaeaspis* (= *Holaspis*) and *Cyathaspis*.

The next year Rohon (1893) in his paper "Die Obersilurischen Fische von Oesel II", also discussed the relationship of the oldest vertebrates. He is almost of the same opinion as Woodward, but considers that "*Antiarchi*" does not belong to the same group as *Heterostraci* and *Osteostraci*. He therefore proposed a new name Sub-Class *Protocephali*, which combined the Orders *Heterostraci* and *Osteostraci* only. Some years later (1896) Rohon discussed more in detail the systematical division of the oldest vertebrates, and suggested two new names: Order *Aspidorhini* instead of *Heterostraci* and Order *Aspidocephali* for the *Osteostraci*. The first Order comprises only one Family *Pteraspidae* with three Genera: *Pteraspis*, *Palaeaspis* and *Cyathaspis* and one Sub-Genus *Tolypaspis*.

In a text-book published in 1895 Dean mentioned a division of the primitive vertebrates, nearly corresponding to that given by Cope, only with the difference that, instead of the name "Class *Agnatha*", he proposed "Class *Marsipobranchii*" which, however, comprises the same forms as Cope's "*Agnatha*": The *Cyclostomi* and *Ostracodermi*.

In the first edition of the "Grundzüge der Palæozoologie", Zittel (1897) adopted the name "*Heterostraci*", instead of *Pteraspidae* used

in 1887, but instead of *Osteostraci* he re-introduced the name *Aspidocephali* — a name for the first time proposed by Brandt in 1866 including both *Pteraspida* and *Cephalaspida*, and, as mentioned above, later accepted by Rohon but only referring to *Osteostraci* (= *Cephalaspida*). Zittel connected the Orders *Heterostraci*, *Aspidocephali*, *Antiarchi* and *Arthrodira* in an independent Sub-Class of fishes “*Placoderma*”, a Sub-Class co-ordinated with the “*Ganoida*” and “*Teleostei*”. He remarked, however, that the systematical position of the “*Placoderma*” is uncertain.

In “Outline of Vertebrate Paleontology” (1898), Woodward followed the division of the primitive vertebrates, proposed by Cope, only with some small alterations. The Class *Agnatha* was divided into two Sub-Classes *Cyclostomi* and *Ostracodermi*, the latter with three Orders: *Heterostraci*, *Osteostraci* and *Antiarchi*.

On the contrary, Lankester (1897) pointed out that the *Ostracodermi* are not related to the *Cyclostomi*, and probably do not compose a natural group, because the *Heterostraci*, *Osteostraci* and *Antiarchi* can hardly be regarded as closely-related forms. In his opinion: “concerning the closer relationship of these groups judgment must be suspended”.

As we have seen, since Lankester introduced the name *Heterostraci* (1867), all later authors have in general accepted his limitation of this group. The differences lay first in the names, which were proposed by different investigators, and, secondly, in the various opinions concerning the relationship of “*Heterostraci*” (= *Pteraspidae* = *Aspido-rhini*) to other “*Ostracodermi*” and other fishes. The epochal papers by Traquair, have in many respects changed and enlarged our knowledge of these remarkable forms (1899, 1, 2; 1900, 1, 2; 1902; 1903).

When studying the material of Coelolepid-like forms collected in the upper Silurian rocks in Scotland, Traquair came to the result, that the microscopical structure of the scales of *Coelolepis* (known already from the investigations by Pander, Schmidt and Rohon), *Thelodus* and *Lanarkia*, in many respects are similar to those on the shield of *Heterostraci* (*Pteraspis*). Moreover, he has shown, that *Psammosteus* and *Drepanaspis* also must be regarded as closely related to *Pteraspis*, as the general shape of the body and the single shields (in *Drepanaspis*), and the microscopical structure of the shield (in *Psammosteus*), are quite similar to those in *Pteraspis*. Thus Traquair has greatly extended the limits of the “*Heterostraci*”. Besides the previously known Family *Pteraspidae*, he now added three new Families: *Coelolepidae*, *Drepanaspidae* and *Psammosteidae*. He remarks, however, that the last two Families are closely related and perhaps can be joined in one.

Contrary to the opinion of Cope, Woodward and Dean, Traquair did not regard the *Heterostraci* as *Agnatha* forms, but emphasized its

relationship with the *Elasmobranchii*. According to him, the *Coelolepida*, with its fine placoid scales and flat "pectoral" fins, are most primitive forms, which in many respects are closely related to the primitive *Elasmobranchii*. *Drepanaspis* shows the next stage in the development. The single placoid scales have here melted together into smaller and larger scales and plates, covering the whole body, and the "pectoral" fins (posterior lateral corner) protected by solid plates (= cor-nale) have become unmovable. In *Psammosteus* the fusion is probably still stronger, and, finally, in *Pteraspis*, the whole head and front part of the body are covered with solid, thick plates, and the "pectoral" fins have completely disappeared.

Nevertheless, Traquair kept the name Sub-Class *Ostracodermi* Cope, which he divided into three Orders: *Heterostraci*, *Osteostraci* and, finally, a new Order *Anaspida*, but excluded the Order *Antiarchi* from the *Ostracodermi*.

Later authors generally acknowledged that the *Coelolepidae*, *Drepanaspidae* and *Psammosteidae*, were combined into the Order *Heterostraci*. On the contrary, Traquair's opinion about the *Elasmobranchii*-nature in the *Heterostraci*, provoked a great deal of controversy.

In a review of Traquair's paper, Woodward (1900) strongly criticized his opinion, and considered that Cope's theory about the agnatha character of the *Heterostraci* "is for the present, the less beset with difficulties".

Also Dean, in a paper published in 1900, did not accept Traquair's proposition, and introduced a new, quite diverging classification of the Paleozoic vertebrates. He erected six independent classes for the fish-like forms. The first, — Class *Ostracophori* (a name proposed by Cope in 1891 instead of *Ostracodermi*), contained three Sub-Classes: *Osteostraci*, *Heterostraci* and *Antiarchi*. The second, Class *Arthrognathi* is new, and contained two Sub-Classes *Anarthrodira* and *Arthrodira*. The next, Class *Cyclie* is erected for the *Palaeospondylus* only, the Class *Protochordata* for *Tunicata* and *Amphioxus*, Class *Marsipobranchia* for *Cyclostoma* and, finally, the Class *Pisces* unites all other fishes.

In this place may also be mentioned a series of papers, published by Patten (1890, 1901, 1903), also partly dealing with *Heterostraci*. As is well known, Patten regarded all *Ostracodermi* (*Pteraspidae*, *Cephalaspidae* and *Asterolepidae*) as representing different transitional forms between *Archnoids* and the vertebrates. This opinion, which Patten later discussed more in detail in his paper: "The evolution of the Vertebrate" (1912), met with great scepticism from all other authors, and can hardly be accepted.

In 1902, Jaekel published a short paper "Über *Cocosteus* und Beurteilung der *Placodermen*". He reunited all the armoured primitive vertebrates in one group "*Placodermen*" which, according to him, con-



stituted: *Pteraspiden*, *Tremataspiden*, *Cephalaspiden*, *Coccosteiden*, *Macropetalichthyiden* und *Asterolepiden*, and "scheint die echte Fische zu sein". He pointed out, however, that "Die einzelnen Typen der *Placodermen* befinden sich offenbar auf sehr verschiedener Ausbildungshöhe". Thus *Pteraspiden* "haben einen larvalen Charakter ziemlich rein bevahrt", and *Coccosteiden* "eine ancestrale Stellung gegenüber den *Ganoiden* und nämlich *Chimeriden* einnehmen". He remarked, finally, in connection with the opinion he expressed as early as in 1896, that the *Placodermi* show some tetrapod characteristics. As is known, in all his papers, Jaekel advocated the opinion that all fishes are derived from very primitive terrestrial animals, which have in different periods passed into an aquatic life, where their essential structures have been changed and adapted to their new life.

In another short paper published the succeeding year (1903), Jaekel proposed a new division of the armoured paleozoic fishes. For the forms where the head is sharply divided from the body-armour (e. g. *Arthrodira* and *Antiarchi*), he introduced the name *Temneuchenia*. The *Pteraspida*, *Tremataspida* and *Cephalaspida*, on the contrary, he proposed to unite in another group *Holauchenia*; about the relationship of these two groups to each other and to other fishes he did not express any distinct opinion, but only remarked that "Zu einer Verteilung des *Placodermata* im weiteren Sinne in getrennte Klasse liegt meiner Erachtens noch kein zwingender Grund vor". Of greater interest are the general remarks about the development of the skeleton in the vertebrates, which we find in this paper. Jaekel here for the first time expressed clearly that: 1) "stammesgeschichtlich eine Zerlegung oder Auflösung der anfangs zusammenhängenden Körperbedeckung eingetreten ist", 2) "Innerhalb der historischen Entwicklung . . . zeigt sich eine schrittweise Reduktion der Verknöcherung". Both these opinions were in striking contrast to the prevalent meaning of that time. Later investigation, however, has shown, that Jaekel — in general — has expressed a thoroughly correct view.

In two short papers Kemna (1903, 1904) gives a critical review of the papers published about the *Ostracodermi*, and draws the conclusion that it is most likely that the *Ostracodermi* must be combined with the *Cyclostoma* into the group *Agnatha*. He regards as unacceptable Traquair's theory that the *Heterostraci* are related to the *Elasmobranchii*.

Dollo on the contrary (1903), in a short paper about "Le *Pteraspis* dans l'Ardenne" writes more reserved. He considered the *Heterostraci* certainly as agnatha forms, but is not quite sure that they are related to the *Cyclostoma*, as it seems not improbable that the latter group secondarily can change to become agnatha. Regarding their relation with the *Elasmobranchii*, Dollo also agrees with Traquair, maintaining that it is not impossible that "les *Ostracodermes* les plus primitive

(*Coelolepidae*) pourraient représenter les ancêtres pregnatostomes des *Elasmobranches* typiques, comme ils seraient ceux des *Ostracodermes* très évolués (= *Pteraspidae*)".

Bridge (1904) in the "Fishes in Cambridge Natural History" prefers to deal with all armoured paleozoic fishes as an "independent group". He divided *Ostracodermi*, corresponding to Traquair into three Orders: *Heterostraci*, *Osteostraci* and *Anaspida*, but excluded *Antiarchi* from this Group.

The next and very important contribution to our knowledge of the structure and affinity of the *Heterostraci* can be found in Goodrich well-known "Vertebrata Craniata" (1909). He divided the craniata into two branches, I. *Cyclostomata* and II. *Gnathostomata*. The first "Grade" of the last branch is the "Class *Pisces*", which again is divided into three "Sub-Grades": 1) *Chondrichthyes* (*Elasmobranchii* etc.), 2) *Ostracodermi* and 3) *Osteichthyes* (*Dipnoi* and *Teleostomi*). He furthermore divided the *Ostracodermi* into 4 Orders: 1) *Pteraspidomorphi* (a name he proposed instead of *Heterostraci*), 2) *Cephalaspidomorphi* (instead of *Osteostraci*), 3) *Anaspida* and 4) *Pterichthyomorphi* a new name for *Antiarchi*. As is seen, Goodrich separated the *Ostracodermi* sharply from the *Agnatha*, but in the text, however, he pointed out that "this is merely a provisional group, in which are gathered some of the oldest and least satisfactorily-known paleozoic fishes". But he agrees with Traquair, that "the affinities of the *Pteraspidomorphi* (= *Heterostraci*) to the *Elasmobranchii*, through the *Coelolepida*, seem to be now well established". In a very clear and interesting drawing, he tries to illustrate the evolution from a single scale in *Coelolepis* to the complete armour in *Pteraspis*. According to him, however, it is not certain that the 4 Families, *Coelolepidae*, *Drepanaspidae*, *Psammosteidae* and *Pteraspidae*, really form a phylogenetic series. The relationship of *Cephalaspidomorphi* (= *Osteostraci*), *Anaspida* and *Pterichthyomorphi* (= *Antiarchi*) to each other and to *Pteraspidomorphi* "remains" according to Goodrich "as obscure as ever".

In the second edition of Zittel's "Grundzüge der Paläontologie" Vol. II, Koken (1911) proposed the name "*Placodermi*" for the Orders *Anaspida*, *Heterostraci* and *Osteostraci*. Thus, in reality, he used this name nearly to the same extent as Cope, Woodward, Dean and Goodrich had used the name "*Ostracodermi*". Koken could not accept the affinity between the "*Placodermi*" and *Cyclostoma*, but placed them as a Sub-Order of the *Pisces*.

The same year Jaekel (1911) published a text-book "Die Wirbeltiere" wherein he introduced a new systematical division of the vertebrates, and used a number of new names. He based the new system on his above-mentioned opinions that fishes as all other water-living vertebrates, descend from land-living forms. The unknown land-living

ancestor-form of fishes he called *Eotetrapods*. The different representatives of this "Class", had, according to him, at different times adapted themselves to an aquatic life, thus giving rise to the different groups of fishes, which, however, can hardly be regarded as closely related, natural groups of animals. Jaekel divided the group "*Pisces*" which he named "Nebenstamme der zweite Wirbeltierstufe" into three Classes: I. *Malacostomata*, II. *Hypostomata* and III. *Teleostomata*. The first, Class *Malacostomata* — or "Weichmäuler" almost corresponds to the Group "*Agnatha*" by Cope and Woodward, and is divided as follows:

- |  |  |
|--|--|
| <p>I. Un.kl. <i>Palaeostraci</i>.<br/>         1. Ord. <i>Heterostraci</i>.<br/>             Und. Ord. <i>Palaeaspidi</i>.<br/>             "    " <i>Pteraspidi</i>.<br/>         2. Ord. <i>Goniaspidi</i>.<br/>             Und. Ord. <i>Tremataspidi</i>.<br/>             "    " <i>Cephalaspidi</i>.<br/>             "    " <i>Drepanaspidi</i>.<br/>             "    " <i>Thelodonti</i>.<br/>         3. Ord. <i>Anaspidi</i>.<br/>         Neben Ord. <i>Pterichthyi</i>.</p> | <p>II. Un.kl. <i>Cyclostomata</i>.<br/>         Ord. <i>Palaeospondyli</i>.<br/>             " <i>Hypospondyli</i>.<br/>             " <i>Myxini</i>.<br/>             " <i>Petromyzontes</i>.</p> <p>III. Un. kl. <i>Leptocardia</i>.</p> |
|--|--|

The most remarkable in this system is the division of the *Palaeostraci* into two Orders *Heterostraci* and *Goniaspidi*. According to Jaekel, the *Heterostraci* had no gill-openings (primitive character). Its gills were only represented by blind pouches of esophagus. For the first time he divided this group into two Sub-Orders *Palaeaspidi* and *Pteraspidi* — a division, which is completely in accordance with the investigations of recent years. The second Order *Goniaspidi* had gill-openings. It combines quite divergent forms, as *Tremataspis*, *Cephalaspis*, *Psammosteus*, *Drepanaspis* and *Thelodus*. In reality, it is remarkable that Jaekel has united all these forms. The differences between the *Cephalaspida* and *Tremataspida* on one hand, and *Psammosteida*, *Drepanaspida* and *Thelodonti* on the other, are quite striking, and the investigations of Traquair have also clearly shown that the last three forms are closely related to "*Heterostraci*". It is interesting to notice the more independent position of the *Thelodonti* which Jaekel proposed. According to him, the *Thelodonti* are forms where the carapace "in Dornen aufgelöst ist".

Our recent and better knowledge of the old paleozoic vertebrates makes it difficult for us to accept the systematical division, proposed by Jaekel, but in two points he was right: in the division of the "*Heterostraci*" into *Palaeaspidi* and *Pteraspidi*, and when introducing a more independent position of the *Thelodonti* (formerly *Coelolepidae*).

In "Lehrbuch der Paläozoologie" Stromer (1912) reunited all the armoured "fishes" from Paleozoicum as "Pisces incertae sedis". He proposed only two Orders: *Arthrodira* and *Ostracodermi*. The latter containing the Sub. Ord. *Heterostraci* (*Drepanaspis*, *Theلودus* and *Pteraspis*) the Sub. Ord. *Aspidocephali* (= *Osteostraci*) and the Sub. Ord. *Antiarchi*.

Pompeckj (1913) divided "Und.kl. *Placodermi*" (= *Ostracodermi*) into the usual 4 Orders: *Anaspida*, *Heterostraci* (to which belong *Coelolepida*, *Drepanaspida* and *Pteraspida*), *Osteostraci* and *Antiarchi*.

In 1915 Kiær in an investigation about the fish fauna collected in upper Devonian from Ellesmereland, gave an interesting account of the relationship between different *Heterostraci*. He had studied the microscopical structure of *Psammosteus* and *Drepanaspis*, and thus supplementing Traquair's investigations showed that these two forms were closely related. He therefore connected them into one Family *Psammosteidae*, where "we find, of course, several lines of development, which have evolved independently of each other from *Theلودus*-like forms". The co-ordinated Family *Pteraspidae* containing *Palaeaspis*, *Pteraspis* and others "constitutes a related group with a similar origin".

Schlosser (1918) in the third edition of Zittel's "Grundzüge" adapted nearly the same division as was proposed in the second (1911). He regards "*Placodermi*" and "*Arthrodira*" as two first Sub-Orders of the Class *Pisces*. The *Placodermi* he divided, as usual into *Anaspida*, *Heterostraci* (with. Fam. *Coelolepidae*, *Gemündenidae*, *Drepanaspidae* and *Pteraspidae*), *Osteostraci* and *Antiarchi*. He was, however, of the opinion that for all armoured forms "später wird wohl . . . der name *Ostracodermi* zur Geltung kommen müssen". As seen, the new point in Schlosser's classification is only that he included *Gemündina* in the *Heterostraci*. He pointed out, that "die drei Familien *Coelolepis*, *Drepanaspis* und *Gemündina* in engerem Zusammenhenge stehen" and that "Die *Coelolepiden* und *Gemündiniden* Vorläufer von *Elasmobrancher* sind". Exactly the same division is proposed in the IV edition of Zittel (Schlosser 1923) with the only difference that, to the *Heterostraci*, he added a new Family *Astraspidae*.

Abel in "Stamme der Wirbeltiere" (1919) as also in both editions of "Lehrbuch der Paläozoologie" (1921, 1924) divided "Klasse *Pisces*" into 7 independent Sub-Classes. The 4 first correspond to the "armoured fishes" of the older authors, and are 1 *Anaspida*, 2 *Osteostraci*, 3 *Antiarchi* and 4 *Arthrodira*. The Sub-Class *Osteostraci* does, however, not in any case correspond to the definition given originally by Lankester and used later by the majority of other investigators. Abel united in this Sub-Class the Families *Coelolepidae*, *Cephalaspidae*, *Tremataspidae*, *Drepanaspidae* and *Pteraspidae*. He quite agrees with Traquair that "durch Verschmelzung von Einzelschuppen zu Platten entsteht bei speziali-

sierteren Gattungen zuerst ein mosaikartige Panzer, und schließlich können sich diese Mosaikplatten zu großen, scheinbar einheitlichen Plattenkomplexen vereinigen".

A very important review of the *Heterostraci* is given by Woodward (1920). He also agrees with Traquair as to the development of the *Heterostraci*, and remarks that "through *Kallostracon* and *Tolypolepis* or *Tolypaspis* the primitive *Heterostraci* (= *Coelolepis*, *Theلودus*, *Lanarkia*) seem to pass into *Cyathaspis*, *Palaeaspis* and *Pteraspis*, in which the shagreen grainless on the head are united into a few symmetrically arranged plates by fusion with the underlying calcified tissue".

Jordan in "A Classification of Fishes" (1923) proposed to divide the Class *Osteacophori* (= *Ostracodermi*) into 5 Orders: *Heterostraci*, *Osteostraci*, *Antiarchi*, *Anaspida* and *Cycliae* (= *Palaeospondylus*). He is, however, not certain that these 5 Orders really are related. Also the affinities of the whole class is unclear "It may be" he said "that the group is a mailed variant of the Lampreys, that it is ancestral to the sharks, that it is derived from primitive sharks or that it is a variant of primitive Crustaceans".

The next year (1924) appears Kiær's fundamental paper about the *Anaspida*. In a chapter about the systematical position of these forms, he gives a very interesting review of the older opinions according to the systematical divisions of the primitive vertebrates and puts forward a new theory. According to him "the most important and remarkable characteristics in *Anaspida* are beyond doubt the unpaired nasal opening, and also the numerous small openings for the branchial apparatus at the sides of the head region". In all other Craniata, on the contrary, we have a double nasal opening. "If we remember" says Kiær "the extreme constancy with which the latter feature (double nasal opening) occurs in all higher craniata . . . , it appears fully justifiable to regard it as a fundamental feature, whereby Craniata can be divided into two natural branches: *Monorhina* and *Diplorhina* (Haeckel 1895)."

The *Ostracodermi* in Kiær's opinion "comprise groups of a very different nature and origin". The *Anaspida*, *Osteostraci* (= *Cephalaspida*) and recent *Cyclostoma* are *Monorhina*, while on the other hand the *Heterostraci* are *Diplorhina* and must be classified as real fishes. Thus in spite of the circumstance that "there are certain points of agreement between *Pteraspidae* and *Cephalaspidae*, it appears scarcely probable that there is any phylogenetical connection between these groups".

According to the development of the dermal skeleton, Kiær pointed out that "from forms without skeleton there developed others with small isolated placoid scales or other small dermal formations. These formations had a tendency to fuse together in various ways into dermal plates or scales . . . . This dermal skeleton was then further specialized

in various ways. On the one hand there might arise more or less armoured forms like the palæozoic "*Ostracodermi*" and recent *Silurida* and *Ostracionida*, on the other, the dorsal skeleton might be reduced and disappear entirely".

As is seen, Kiær proposed a new classification of *Ostracodermi*, which, according to him, cannot be regarded as a "natural group". The whole vertebrate-stem must be divided into two branches *Monorhina* and *Diplorhina*. To the first belong *Anaspida*, *Osteostraci* and *Cyclostoma*, to the latter all other vertebrates and thus also *Heterostraci*. The absence or presence of real jaws is, according to Kiær, not of so great a value, as the lack of jaws "need not be a primary feature".

The systematical division proposed by Kiær, was discussed and criticized by many authors. Stromer (1926), Sewertzoff (1928) and Stensiö (1926) pointed out that the division of the vertebrates into *Monorhina* and *Diplorhina* can hardly be accepted. Stensiö, moreover, tried to show that the sensory canal-system in *Pteraspis* "is undoubtedly very different from that in fishes" but "to some extent shows several important agreements with that in the *Petromyzontids*". Together with several other facts it "seems to indicate with a high degree of probability that *Pteraspids* really are closely related to, and must be referred to, the same larger branch of the vertebrate-stem as the *Anaspids*, *Cephalaspids* and *Cyclostomes*".

In a short paper about the structure of the mouth of the oldest known vertebrates, Kiær (1927) remarked that according to the relation of the *Pteraspida* to the *Cephalaspida* "I will not express myself more definitely. Meantime I do not regard it as absolutely certain that Stensiö'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".

In the same year (1927) the important paper of Stensiö about *Cephalaspids* from Spitsbergen was published. In the general part Stensiö also gives a most interesting and detailed description of the *Heterostraci*. We shall not here refer to this well-known paper as it will be done later in a separate publication. We can only point out that Stensiö here advances the opinion he mentioned in his earlier paper (1926) and tries to prove the near relationship between *Osteostraci*, *Anaspida*, *Heterostraci* and *Cyclostoma*. He regards them all as Agnatha forms and proposes to connect them in one Class *Ostracodermi*. This Class he divided into two Sub-Classes. The first *Pteraspidomorphi* with three Orders: 1) *Heterostraci* (containing, *Pteraspidae*, *Drepanaspidae* and *Coelolepidae*), 2) *Palaeospondyloidea* and 3) recent *Myxinoidea*. The second Sub-Class *Cephalaspidomorphi* contains also three Orders: 1) *Osteostraci* (*Cephalaspidae* and *Tremataspidae*), 2) *Anaspida* and 3) recent *Petromyzontia*. This division is based on very careful and

accurate studies of the anatomy, and especially of the development of the sensory canals in both fossil and recent forms.

In a monograph on British *Cephalaspids*, Stensiö (1932) adds a number of new arguments in favour of the proposed systematical division. In the same paper he describes in detail the microscopical structure of the dermal skeleton of the *Pteraspids* and "*Palaeaspids*". We shall return to this description in a later part of this paper. It may only be mentioned, however, that Stensiö's systematical division, and especially the circumstance that he separates the recent *Cyclostoma* into two not closely related groups, has partly met with criticism (Goodrich 1931, and De Beer, 1931).

We have now only to refer to a few of the most recent papers. First, mention may be made of two papers by Zych (1927, 1931) describing the *Heterostraci* from Podolien. In the former the author tries to show that the division of the "Family *Pteraspidae*" into three Genera, *Palaeaspis*, *Cyathaspis* and *Pteraspis*, is in reality incorrect, as these three Genera, in fact, are only "etapes d'évolutions de cette Famille" — a conclusion which can hardly be accepted in such a form and is to be discussed in a later paper. His second paper, discussing, so far as it can be judged, the structure and development of different forms belonging to *Heterostraci*, is, unfortunately, written in Polish only, without an abstract.

In Kær's paper on *Ctenaspis* (1930) as also in two of Kær's posthumous papers (1932, 1, 2) edited by Heintz the following division of the primitive vertebrates is proposed. The *Agnatha* is divided into two branches I *Monorhina* and II *Diplorhina*. The former consists of the Orders: *Osteostraci* and *Cyclostomata*, the latter of the Orders: *Heterostraci* and *Thelodonti*. The *Heterostraci* is further divided into three Sub-Orders *Psammosteida*, *Cyathaspida* and *Pteraspida*. Unfortunately, it has been impossible to find among Kær's posthumous manuscripts any clear account of the reasons for such a division, especially regarding the division of the *Agnatha* into *Monorhina* and *Diplorhina*, a division criticized by different scientists after the publication of the "*Anaspida*" (1924).

In some points, however, the new systematical division now proposed by Kær differs, from that advocated in *Anaspida*: he now regards *Monorhina* and *Diplorhina* as closely allied forms, and unites them as *Agnatha* forms, in contrast to all other higher vertebrates, which must be regarded as *Gnathostoma*.

In the new (second) English edition of Zittel's "Text-Book of Palæontology", Woodward (1932) maintained the old division, and regarded the *Ostracodermi* and *Cyclostoma* as the two first independent Sub-Classes of the *Pisces*. *Ostracodermi* being divided into four Orders: *Anaspida*, *Heterostraci* (containing *Coelolepida*, *Pteraspida* and *Drepanaspida*), *Osteostraci* and *Anthiarchi*.

In three short papers recently published by Brotzen (1933, 1, 2; 1934) he proposes a somewhat diverging nomenclature. According to him, the *Heterostraci* must be divided into two Orders: *Aspidophorida* (new name) containing all really armoured *Heterostraci* and another Order containing *Coelolepida* and all its allies, which means, forms having the body covered with small scales (He proposed no new name for this group). In reality also Brotzen's division of *Heterostraci* and its allies is the same as Kiær's they differ in the names only. Kiær's Order *Heterostraci* Brotzen called "Ord. *Aspidophorida*". Kiær's *Thelodonti* corresponds to his *Coelolepida*. He regards "*Heterostraci*" as a higher systematical category, connecting "*Aspidophorida*" and *Coelolepida*. Otherwise Brotzen agrees with Stensiö and divides Agnatha into *Cephalaspidomorphi* and *Pteraspidomorphi*, the latter being divided into *Heterostraci*, *Palaeospondyloidea* and *Myxenoidae*.

Roemer in "Vertebrate Paleontology" (1933) gives a short but interesting review of the oldest vertebrates. According to him the *Cyclostomata* are the only recent representatives of the *Agnatha* Class, and must be regarded as descendants from the paleozoic *Ostracodermi*. This Group he divided into *Osteostraci*, *Anaspida* and *Heterostraci*. *Palaeospondylus*, according to him, perhaps, "was intermediate between an early armoured ancestor and the modern degenerated types". Roemer considered, that "armour, probably bony in nature, and some ossification of the internal skeleton were developed at a very early stage in the vertebrate history, and that the cartilaginous skeleton of the lower existing types represents a degenerated, rather than a primitive, condition. *Heterostraci* may represent comparatively late survivors of the primitive stock, which gave rise to single-nostril forms. Further, *Thelodus* and *Lanarkia* appear to demonstrate the degenerative process by which the shagreen skin may have arisen from a primitively armoured condition".

In a diagram of distribution of *Agnatha*, Roemer pictured the whole *Agnatha*-stem as divided, during Ordovician (?), into two branches. The first, containing *Osteostraci* and *Anaspida*, gives, according to him, probably rise both to *Palaeospondylus* and the recent *Cyclostoma*. The other branch is represented by *Heterostraci*. From this, perhaps, higher *Gnathostoma* vertebrates have arisen, probably already in Ordovician time. Roemer, thus to some degree, connects both Stensiö's and Kiær's opinions.

In this and following papers we shall follow a systematical division, closely corresponding to that proposed by Kiær, with the only difference that the names "*Monorhina*" and "*Diplorhina*" will be replaced by *Cephalaspidomorphi* and *Pteraspidomorphi* — names for the first time proposed by Goodrich and accepted to some extent by Stensiö and



Brotzen. The *Pteraspidomorphi*, (Kiær's *Diplorhina*) is divided into two Orders *Heterostraci* and *Thelodonti*. The name *Aspidophorida*, proposed by Brotzen in 1933, in reality corresponds to the definition given to the *Heterostraci* by Lankester in 1868, and to the re-definition given by Kiær in 1930. Therefore it must be regarded only as a synonym. The systematical division of *Ostracodermi* is thus as follows:

### Branch Agnathi.

Class *Ostracodermi*.

Sub-Class *Cephalaspidomorphi* (= *Monorhina* Kiær).

Ord. *Ostracodermi*.

Ord. *Anaspida*.

Sub-Class *Pteraspidomorhi* (= *Diplorhina* Kiær).

Ord. *Heterostraci* (*Aspidophorida* Brotzen).

Sub-Ord. *Cyathaspida*.

Sub-Ord. *Pteraspida*.

Sub-Ord. *Psammosteida*.

Ord. *Thelodonti*.

Gen. *Thelodus*.

Gen. *Coelolepis*.

According to the systematical position of *Palaeospondylus*, which Stensiö regards as a representative of the *Pteraspidomorphi*, and Roemer, for instance, as a representative of the *Cephalaspidomorphi*, nothing can be said with absolute certainty at present. The position of the recent *Cyclostoma* is also quite problematical. They are, without doubt, closely related to the *Ostracodermi*, but their relation to the different Sub-Classes and Orders in this Group is not as yet clear. Stensiö's opinion, however, that *Myxinoidea* are related to the *Pteraspidomorphi*, and *Petromyzontia* to the *Cephalaspidomorphi*, seems to be the most probable.

In this paper will only be described, the general structure of the Sub-Order *Cyathaspida* and a detailed description given of the forms belonging to the Fam. *Poraspidae*. The other Families and Genera belonging to the Sub-Order *Cyathaspida* as well as all theoretical questions about the possible affinities of *Agnathi* to other vertebrates, and the relation between different Groups of *Ostracodermi*, will be discussed in other papers.

## HISTORICAL REVIEW OF THE *CYATHASPIDA*.

The first form pertaining to the *Cyathaspida* was found by Mr. Banks in the Downtonian sandstone near Kington in Herefordshire and was described in 1856 by Huxley and Salter and in 1858 by Huxley (1858, 2), as *Pteraspis banksi*, Lankester some years later (1865, 1) separated it as a distinct Genus *Cyathaspis*, of a more simple structure than *Pteraspis* and finally, described it somewhat more in detail, and figured it in Part I of his great monograph of 1868—70. This is a quite singular type not found in the material from Spitsbergen. It is easily distinguished by the fact that the dentine layer of the dorsal shield shows a division into four portions, a median part (median disc), a rostral, and two brim-like lateral parts, which in front bound the orbital notches. Lankester also places another form in the Genus *Cyathaspis*, though with hesitation, the so-called *Cyathaspis* (?) *symondsi*. As later pointed out by Traquair, it is a form belonging to the *Psammosteida*, and he described it more in detail as *Psammosteus anglicus*.

The next discovery of a *Cyathaspid* was made in the vicinity of Berlin. Near Schöneberg in a railway section through quarternary deposits in a small erratic boulder of so-called graptolite-limestone, a specimen was found in an unusually good state of preservation. A. Kunth in 1872 described it as *Cyathaspis integer*. It showed for the first time the dorsal and the ventral shields in their natural position separated by an elongated lateral plate. The significance of this plate, however, was not realized until many years later by Jaekel (1911). On account of the circumstance that the ventral shield was similar to that in *Scaphaspis*, Kunth drew the important conclusion that Lankester's Genus *Scaphaspis*, was based on the ventral shields of *Pteraspis* and *Cyathaspis*. Thus in his opinion *Cyathaspis banksi* and *Scaphaspis truncatus* constituted the dorsal and ventral shields of one and the same form. Moreover he advanced, in the same small paper, the remarkable hypothesis that these fossils were not remains of armoured fishes, as the English investigators had tried to prove, but they represented the head shields and tail of some sort of *Crustacae* related to trilobites.

Kunth's publication made a great sensation among English scientists who, due to Huxley's and Lankester's excellent papers, were highly interested in these primeval, still mysterious vertebrates, and, in the subsequent year, in the "Geological Magazine" there ensued an animated discussion with regard to Kunth's conclusions. Lankester (1873, 1, 2)

wrote an article, where, in a very clear and convincing manner, he proves the vertebrate nature of these forms, of which he certainly was the best judge of his time. He also very strongly maintained that *Scaphaspis* formed the shields of a separate Genus of a more simple structure than that of *Pteraspis*. Unfortunately, Kunth was killed during the German-Franco war, but his interpretation of *Scaphaspis* was advocated by Friedrich Schmidt (1873, 1, 2, 3), the later, so famous Russian Silurian-paleontologist. The discussion was carried on with some vehemence on the part of Lankester (1874), who finally, however, had to submit to the fact that the editor of Geological Magazine in a foot-note was most inclined to join Kunth's party. As is well known, subsequent researches have proved that Kunth was right concerning the *Scaphaspis* problem, to the solution of which the Berlin specimen of *Cyathaspis integer* afforded the first contribution.

Later, in the vicinity of Berlin some new discoveries have been made of this interesting form — finds which in an excellent manner, add to Kunth's original. On the basis of one of these, a very well-preserved dorsal shield, there have later been published various sketches by Jaekel (1919, 1926, 1, 2, 1927, 1929), who mentions this form in several of his papers.

Kunth was of the opinion that *C. integer* almost agreed with *C. banksi*. In fact, it is without doubt closely related to the latter, but however, deviates from it in many respects. Jaekel, therefore in one of his latest papers without explanatory statements proposed to establish it as a new Genus *Archegonaspis* (1926, 1).

In the above-mentioned volume of Geological Magazine in which appeared the *Scaphaspis* discussion, Lankester (1873, 2) under the term of *Holaspis sericeus* described a new *Cyathaspis*, which had been found in Cornstone from the Lower Old Red near Abergavenny, Monmouthshire.

The plate and a sketch showing the fossil in profile, illustrating the paper convey a correct idea of this splendidly preserved dorsal shield. It shows a type wholly different from *C. banksi*, while its general outline is slightly reminiscent of *Pteraspis*. It deviates from the latter by the circumstance that the surface does not show any limits of the rostral and the lateral parts, and the orbital openings are seen as incuts on the sides only. A characteristic linear system of impressed dots is most distinctly apparent on the surface. According to Lankester they must have been "the sites of soft tegumentary structures, in all probability of those characteristic sensory fallicles of fishes, with which they agree in disposition."

Lankester points out that *H. sericeus*, with regard to the structure of its dorsal shield, occupies an intermediate position between *Pteraspis* and *Scaphaspis*. But remarkably enough, he does not compare it more

closely with *Cyathaspis banksi*, with which, in reality, it is most in accordance.

The following year A. von Alth (1874) in his paper "Die palaeozoischen Gebilde Podoliens und deren Versteinerungen", described a single dorsal shield from the Silurian limestone under the name *Cyathaspis sturi*. The specimen shows the interior side of the shield and the well preserved cast with good impressions of the various internal organs. According to our recent knowledge this form comes nearest to *Holaspis sericeus*. As Lankester's work, however, was evidently not yet known to von Alth, he places the specimen in the same Genus with *Cyathaspis banksi*, to which in his opinion, it is very close related.

Many years elapse before any new discoveries of *Cyathaspids* are reported in literature. It is not until the middle of the eighties that the knowledge of these forms is again extended. F. E. Geinitz in 1884 reports a new *Cyathaspis* which had been found in Rostock in a boulder of so-called "Graptolithengestein" thus, on the same horizon, where *C. integer* was found. The specimen, now in the museum of Rostock, consists of a fragmentary dorsal shield with well preserved surface on its anterior part. Geinitz was of the opinion that this new form most resembles *C. banksi*, but is even more closely related to *C. integer*. It deviates, however, from the latter and he therefore establishes it as a new species *Cyathaspis schmidtii*.

The same year appears E. W. Clappole's (1884, 1, 2, 3) interesting communications of the occurrence of Pteraspidian fishes in the Upper Silurian of North America. His more detailed account of it was published in Quart. Journal the following year (1885). Here he describes some comparatively rich discoveries *Cyathaspids* from Bloomfield sandstone (uppermost member of the Onondaga variegated shales) in Perry County, Pennsylvania and distinguishes two species *americana* and *bitruncata*, both pertaining to his new Genus *Palaeaspis* of which, however, he does not give any precise generic diagnosis. The figures are merely sketched and the description is so brief that it is difficult to get a correct idea of these forms. The preservation is also bad. They give, however, an impression of being most in accordance with *Holaspis sericeus*.

In the year 1886 G. F. Matthew in "Canadian Record of Science", Vol. II reports having found remains of a *Pteraspis* fish in Upper Silurian (Division 2) near Westfield in New Brunswick, Canada. In 1887 he describes it more closely under the name *Diplaspis acadica*. This is a separate type nearest related to *Cyathaspis* but remarkable by the circumstance that the dorsal shield consists of several wholly isolated portions.

Some years later in 1891 appeared the second volume of A. Smith-Woodward's well-known Catalogue of the fossil fishes, which became

of fundamental importance by reason of the author's extensive and superior knowledge and by his prominent judgment. Also with regard to the system of the Pteraspid fishes, his critical review was of the greatest significance.

As is known, the *Scaphaspis*-problem was solved in a paper by von Alth (1886 1, 2), in favour of Kunth's opinion. According to this, Smith-Woodward in "Catalogue" tried to determine to which *Pteraspis* or *Cyathaspis* forms, the different "*Scaphaspis*" shields belong. The so-called "*Scaphaspis truncatus*" is thus supposed to represent the ventral shields pertaining to *Cyathaspis banksi*, although, according to Smith-Woodward it is not excluded that certain specimens may be detached median discs of the dorsal shield, in the same form. To *Cyathaspis*, according to the same author, there also belong a few ventral shields from the Lower and Upper Ludlow. They were first described by Salter as *Pteraspis ludensis* and later by Lankester introduced as "*Scaphaspis ludensis*". It is a form with coarse ridges, and, according to Lankester, widely different from "*Scaphaspis truncatus*".

Smith-Woodward, moreover, in his catalogue gives a new contribution to our knowledge of the *Cyathaspids* by quite briefly describing a new form *Cyathaspis maccolloughi*, which had been found as a single incomplete dorsal shield near Bodenham in Herefordshire. This is a new and very remarkable type, which for the first time we become acquainted with here. This form is characterized by its flat, elongated shape and coarse dentine ridges. Smith-Woodward assigns it to *Cyathaspis*. As we shall see later, this form (called *Anglaspis*) occurs most abundantly in Spitsbergen and will be dealt with in detail in the next part of this work.

The following year a new contribution treating with the American *Palaeaspis* forms was afforded by Claypole (1892). The main part of this work, however, deals with an historical review of our knowledge of the *Pteraspis* fishes and their structures, especially the *Scaphaspis* question, which had already been finally settled in a paper by von Alth (1886). Claypole now assumes that the species *bitruncata* of 1884 represents the ventral shield of his type species *Palaeaspis americana*. He supposes that he has found both the shields in their natural connection. He also believes to have discovered in this form an unattached elongated plate situated on each side posteriorly between the dorsal and the ventral shields. His idea in this respect is most clearly pointed out in his reconstruction of the entire animal where, in addition, he pictures a most remarkable lateral fin, which protudes from the dorsal shield just in front of the supposed lateral plate. We shall later discuss these remarkable structures. Finally, he gives an otherwise very incomplete diagnosis, of the Genus *Palaeaspis*, which in his opinion,

is identical with Lankester's Genus *Holaspis*. Lankester's name therefore, ought to be maintained, but as this term already was occupied, he, with Smith-Woodward, decided that the generic designation *Palaeaspis* could be used with regard to both the American and the English species.

J. V. Rohon in 1893 in the second volume of his important work, "Die obersilurische Fische von Oesel", gives a thorough description of a remarkable *Cyathaspid* from the upper marine Ludlow layer in Estonia. Small fragments of this form had already been described by Pander in 1856 under the name *Tolypelepis undulatus* and was supposed to be a scale. Fr. Schmidt in 1893 mentions a find of an almost complete shield of the same form from Okkesaare Pank at Oesel. He then understood that it must belong to a new Genus of *Pteraspids* and proposed for it a new generic name *Tolypaspis*, as Pander's name *Tolypelepis* referred to a scale. Schmidt considered the specimen to be a ventral shield (*Pteraspiden* Bauchschilde); and so does Rohon also in his above-mentioned paper. This form, which is well known through Rohon's beautiful drawing, is distinguished by its short elliptical shape and its very unusual surface sculpture. The dentine ridges, which most anteriorly on the rostral part have a transverse course, in other places, have been partitioned into small areas where sometimes the ridges show a concentric development. Rohon interprets the scales that have been described by Pander under the term *Oviscolepis* as probably pertaining to this or closely related forms, and further states that also in the Ludlow Bone bed in Shropshire minute remains have been found agreeing with *Tolypaspis*.

Shortly afterwards (1894, 1896) appeared G. Lindström's splendid paper on the interesting *Cyathaspid* find made in the median part of Ludlow at Lanbacker, Gottland. A dorsal and a ventral shield were found lying close together and partly covering each other, besides a few body scales and a piece of an elongated plate. This latter, which according to Lindström's supposition might possibly be a piece of an arm, in reality, was one of the lateral plates originally placed between both shields. The body carapace is rather flattened but displays the surface in an excellent state of preservation. This is, without doubt one of the finest *Cyathaspid* discoveries made up to that date, and therefore this piece has always been justly estimated as being one of the treasures in the Stockholm Riksmuseum. Liljeval's unusually beautiful and clear figures both of the surface of the shields with their complex pattern of dentine ridges, as well as of the microscopic sections, are the best published about these forms and convey a good idea of their structures. Lindström was of the opinion that his *Cyathaspis* from Gottland was closely related both to *C. integer* Kunth and to *C. schmidti* Geinitz, particularly to the latter. In the author's opinion, however,

Lindström's species shows a specific difference from both these. A new term must be applied for it and the author thus proposes the name of *Cyathaspis lindströmi* (Lindström).

During the years from 1884 to 1895 the range of our knowledge of the *Cyathaspida* became widely extended, quite a number of new forms being found in various horizons. Then again for some years there was stagnation, until 1906 when a new contribution to our knowledge was published by Leriche, who describes *Cyathaspis barroisi* from the Upper Silurian near Lievèn and *Cyathaspis* sp. from Gedinien near Terne-en-Artois (Pas de Calais). The former was represented by a number of good specimens of both dorsal and ventral shields. The preservation was quite good, notwithstanding the fact that the sculpture of the surface with its fine dentine ridges could not be made out in detail. According to Leriche the dorsal shield most closely agrees with *Palaeaspis sericea*, but as the natural moulds display similar impressions to those in *Cyathaspis banksi*, he takes it as an indication that these two genera cannot be separated but must be joined together. As we shall see later, this supposition cannot be maintained. According to the author's researches, the French form is very closely related to *Holaspis sericeus* Lank. and *Cyathaspis sturi* von Alth and also to several forms from Spitsbergen.

Many years elapse without any new finds of *Cyathaspids* — until 1913 when R. Campbell in his paper on the Downtonian series of southeastern Kincardineshire, Scotland, reports a new *Cyathaspis* of which a single specimen was found. A quite brief diagnosis was given by Traquair of this interesting form, which had not yet been figured and described in detail. Its most characteristic feature is the fact that the surface of the dorsal shield is not provided with the usual dentine ridges but with small elevations or tubercles. In this respect it deviates from all other previously known forms. This remarkable form will be described anew in the next part of this work.

We now come to the publications dating from the last few years. In the first instance we must mention the communications of new discoveries of *Cyathaspids* found in W. Wickham King's papers on the development of the Downtonian and Devonian series of south-western England. This author, as is well-known, has undertaken very extensive investigations of strata and brought together large new collections. In "Notes on the Old Red Sandstone of Shropshire" 1925 he thus mentions from the Downtonian a long series of various fishes among which are *Cyathaspis macculloughi* and *C. leathensis*. The latter, after an examination of the specimens sent to Prof. Kiær from the British Museum of Nat. Hist., proves to be a *Pteraspid* form. *Tolyaspis* is also mentioned. These are fragments of large *Heterostrace* forms also found in considerable numbers in the Red Bay Series.

They have nothing to do with the Estonian Genus *Tolypaspis* but are most closely allied to the *Psammosteida* (cfr. Woodward 1934.)

The following year appeared an important paper by W. K. Bryant "On the structure of *Palaeaspis* and on the occurrence in the United States of fossil fishes belonging to the family *Pteraspidae*" (1926). He here re-describes the previously known forms of *Palaeaspis* on the basis of new collections and reports the finds of two new *Cyathaspis* forms from still more ancient layers, that is, from the uppermost of the Guymard quartzite near Guymard, south-west of Otisville, Orange County, New York. The age of these layers has been determined as Medina, the two *Cyathaspis* forms *C. wardelli* and *C. van ingeni* are thus the oldest remains of *Cyathaspids* that have up to now been found. They are of the greatest interest and it is a matter of regret that the material is not more complete and better preserved. The descriptions, therefore, are not particularly thorough. The same applies to the *Palaeaspis* forms, which, however, are here much better characterized than in Claypole's papers. Bryant again places *Palaeaspis americana* and *bitruncata* as two separate species, but, unfortunately, it is not possible on the basis of his descriptions and figures to form a quite correct idea of these forms.

Finally, there must be mentioned a paper by W. Zych on "Old Red de la Podolie" (1927), in which he partly gives a stratigraphical summary, partly a revision, of the fish fauna especially of the *Pteraspidae* on the basis both of v. Alth's older material and of his own new quite big collections. The work is of considerable interest. We shall not here enter in detail upon his theoretical conclusions on the evolution of the *Pteraspids*. It may be pointed out, however, that he figures a new dorsal shield of *Cyathaspis sturi* Alth and a ventral shield presumably pertaining to the same form. He places them under the name *Pteraspis* (=*Cyathaspis*) *sturi* Alth believing to be able to ascertain that this form transmigrates into a *Pteraspis* form, with a quite brief rostrum, which he calls *Pteraspis sturi* Alth sp. mut, *brevirostrata* Zych. Moreover, he supposes *Cyathaspis barroisi*, described by Leriche, to be synonymous with the Polish form.

These Polish series seem to contain a very rich fish fauna, especially of *Heterostraci* from the passage-beds extending from the Silurian to the Devonian. These beds are here very completely developed and will therefore most certainly be of increasing interest as the investigation of them proceeds.

In a second paper of W. Zych (1931), is depicted a number of different *Poraspida*. However, as this paper is in Polish only, it is very difficult to understand the author's opinion and we are thus, unfortunately, unable to discuss his results.



We must mention next the paper on *Ctenaspis* published in 1930 by Kiær, and the preliminary abstract of "*Cyathaspida*" published in 1932. A smaller paper discussing the fragments of *Cyathaspis* from an erratic block found in Germany was published by Heintz (1933).

Finally, in a short paper published in 1933, Brotzen described two new species from Podolien: *Palaeaspis simplex* and *Palaeaspis pompeckji* and in a paper published in 1934 Bryant described and depicted a new form *Cryptaspis ellipticus*, which according to him, is closely related to *Poraspidae*.

As is seen, a fairly large number of forms have previously been described of the *Cyathaspida* from different horizons in Europe and North America. Most of them, however, have been found in only one or a few specimens and, frequently, they have been very briefly and incompletely described. Nobody has previously, tried to give a synopsis of all these forms. Therefore in this and following papers we have attempted to undertake a thorough revision of the whole group, with new descriptions of the known, older forms, the original material of which Prof. Kiær contrived to obtain the loan.

## I Sub Order *Cyathaspida*.

The numerous forms of *Heterostraci* from the Silurian and Devonian, which have naturally been grouped with the previously known forms as *Cyathaspis*, *Holaspis* (= *Poraspis* in this paper) *Palaeaspis* and *Diplaspis*, are here connected in one Sub Order *Cyathaspida*. This name has been chosen, as *Cyathaspis* was the form first described and must therefore be regarded as the type genus.

It is quite difficult, however, to give an exhaustive and distinct diagnosis of the Sub Order *Cyathaspida* because this Sub Order, during its phylogenetical development differentiated considerably in various directions.

A few characteristics, however, which are common for all *Cyathaspida* and separate them from the somewhat younger Sub Order *Pteraspida*, can be stated here. Among these features the following may be particularly pointed out:

1. The orbits are not as in the *Pteraspida* entirely surrounded by the dorsal shield (orbital plate), but they only form roundish notches in the sides of the dorsal shield (see for instance Pl. II).

2. The large oblong branchial plates situated between the dorsal and ventral shields are quite detached, whereas, in the *Pteraspida* they coalesced firmly with the dorsal shield (e. g., Pl. XXX, 1).

3. The dentine ridges, forming the surface of the dermal skeleton, are smooth, not crenated as in the *Pteraspida* (e. g., Pl. X). This characteristic, however, is not found in all the *Cyathaspida*, some genera of which having the dentine ridges transformed in a Psammosteid-like direction. In addition it must be pointed out that a few of the later *Pteraspida* had quite smooth ridges.

Most of the other features which may be mentioned, are not characteristic for all the *Cyathaspida*. For a further division of the Sub Order *Cyathaspida* it is of particular importance to know the division or non-division of the dorsal shield, into several parts. According to the divergent developments in this respect the *Cyathaspida* have been divided into two tribes. In the one, the *Poraspidei*, comprising *Palaeaspis*, *Poraspis* (= *Holaspis*), *Anglaspis* and several new genera from Spitsbergen, the dorsal shield is completely undivided and the diverse parts of the shield are merged without defined lines of demarcation (fig. 2; Pl. II). In the other, the *Cyathaspidei*, including *Cyathaspis* and several other previously known forms, the surface of the dorsal shield is divided into four portions by distinct limits in the dentine layer: one rostral part, one central disc and two lateral parts (fig. 4), which even in some genera form quite detached plates. (This feature is reminiscent of that in *Pteraspida* and is, moreover, often accompanied by other more or less *Pteraspid*-like characteristics.) In a later paper will be discussed more in detail which of these tribes constitutes the primary stage of development but it may be pointed out here that these two tribes in most of their other characteristics completely agree with each other and may in several respects show a parallel development.

The *Cyathaspida* appear for the first time in the upper part of the Silurian, then continue throughout the Downtonian and disappear with this series. In most of the localities where the *Cyathaspida* have previously been found, they are very scarce and several species are only known from one or a few specimens. Only two of the other European localities the Downtonian Sandstone near Kington and Old-Red in Podolia, Poland are relatively rich. Still richer are the known American occurrences of *Palaeaspis americana* in the Bloomsbury red shale of Pennsylvania and in the Vermon red shale of New York State, both pertaining to Salina. But the state of preservation in these richer localities, particularly the American ones, is rather bad.

All the formerly known localities are widely surpassed by the new ones of the Red Bay Series in Red Bay in the northern Spitsbergen, where many layers are astonishingly rich in well preserved remains of *Cyathaspida* (cf. Pl. I). As mentioned above, from these huge occurrences, an enormous material has been gathered by the Norwegian expeditions, and the Paleontological Museum in Oslo has now possession of more than 3000 rock-specimens many of which contain remains

of numerous *Cythaspida*. It is without doubt the largest and best collection of this group, which has ever been brought together. It contains, however, only forms pertaining to the *Poraspidei*.

With regard to the *Cythaspidei*, we have still only the few collections from older localities.

## THE TERMINOLOGY OF THE DERMAL SKELETON.

Before entering into the systematical description of the *Cythaspida* we shall here state the terminology of the different parts of the dermal skeleton used in this paper. There will thus be given a short description of the structure of the Genus *Poraspis*, which is the type genus for the *Poraspidei*, now being particularly well-known on the account of the rich discoveries in Spitsbergen. The main differences, which can be seen in other *Cythaspida*, are also to be shortly mentioned.

The armour of the front part of the body consists in *Poraspis*, as in the other *Cythaspida*, chiefly of two large more or less vaulted and elongated plates covering the dorsal and the ventral sides (fig. 2). They are often the only plates preserved and the systematical classification, therefore, must accordingly be essentially based on their structure. In this paper will be used the old well-known terms dorsal and ventral shields not the names epitegum and hypotegum proposed by Jaekel (1926, 1). The dorsal and ventral shields are joined by means of two intermediate elongated detached plates, one on each side, the so-called branchial plates. (Fig. 2, c; 51; Pl. XXXIII, 4, 5, 6).

The dorsal shield (fig. 2, A, B; 3, a; Pl. II; V, and others) forms in *Poraspis*, a large entirely undivided, elongated more or less vaulted plate, which covered the head and the front part of the body. It can be divided into three portions, which however, in all *Poraspidei* pass into one another without any sharp limits or sutures. Most in front the short rostral part is situated (fig. 2, A; Pl. X; XII, 1; XXIV). It covers the snout and, ventrally, shows impressions of the large paired nasal sacs, which in *Poraspis* and other closely related forms are placed near together behind the anterior rostral margin and are strongly marked (ns, fig. 3, a; Pl. XI; XXX, 3). In other forms they may be more indistinct or placed farther towards the sides. The rostral part is difficult to define in the *Poraspidei*, as the dentine ridge pattern of the surface runs continually backwards to the pineal macula (Pl. X; XII, 1; XXIV). The latter forms, as a rule, a clearly limited dentine covering (Pl. V; XIII; XVI; XXIV; XXXI, 2; XXXIV) above the large interior impression of the pineal organ (Pl. VII; IX, 2; XI, p; XV, 1; XXVI, 2; XXVIII, 2, p; XXIX, 1, 2; XXX, 3; XXXV, 1, p; XL, 1, p). In the American

Genus *Palaeaspis* and the, probably, related new Fam. *Irregularaspidae*, however, the pineal macula (not the impression of the pineal organ) is indistinct or seems to be missing. It is, therefore, most practical in all *Poraspidei*, to use the diverging pineal branches of the lateral line system as the posterior limit of the rostral part, especially as these branches with their distinct pores are also clearly seen on the surface (fig. 2, A; 3, a, pb; and e. g. Pl. II, 1; V; VII; XI, 2, pb; XXXI, 2).

The median portion of the shield is called the branchial part (fig. 2, A, B; fig. 3, a), as it covers the branchial apparatus with its seven gill chambers. They have in the interior side of the shield, usually left very distinct elliptical branchial impressions (Fig. 3, a; Pl. IX, 2; XI, 1, 2; XXVI, 2; XXIX, 1; XXX, 3). Between the two rows of the branchial impressions, more or less distinct impressions of the brain and the angularly placed semi-circular canals of the auditory organ are seen (fig. 3, a; Pl. IX, 2; XI, 1, 2; XXVI, 2; XXIX, 1; XXX, 3). The margin of the branchial part is slightly curved outwards on the sides and somewhat within this margin is seen, on the interior side of the shield, a series of small often angular impressions corresponding to the gill impressions. They are called the marginal branchial impressions (fig. 3; Pl. IX, 2; XI, 1, mbi; XXVI, 2; XXVIII, 1). All these impressions are better shown on good natural casts.

Just behind the branchial part, the lateral margin of the shield shows a distinct incurvation which has composed the uppermost limit of the branchial opening and therefore is called the branchial sinus (fig. 2, B; Pl. II, 2).

Behind the branchial sinus follows the post-branchial part of the dorsal shield which, however, can be more or less strongly developed (fig. 2, A, B; 55, A, B; e. g. Pl. II; V). This hindmost portion of the dorsal shield curves downwards with the lateral sides and thus often forms very distinct side-lobes, the post-branchial lateral lobes (fig. 2, B; 55, B; Pl. II, 2).

In *Poraspis* and most of the other *Poraspidei* these lobes follow closely the sides of the body, but in the strongly differentiated Genus *Anglaspis* they project somewhat at the sides and may even form small rearwardly directed lateral spines (Kiær 1932, 1).

In the *Cyathaspidei*, these three portions of the dorsal shield may also be discovered, but here are found in the dentine layer more or less distinct limits in the sculpture which more naturally divide the surface into four distinct parts (fig. 4).

1. A rostral division comprising the anterior portion only of what is called the rostral part in the *Poraspidei*.

2. A median part, reaching quite back to the posterior margin and comprising both the median portion of the branchial part and the whole post-branchial part. It can be named the central disc.

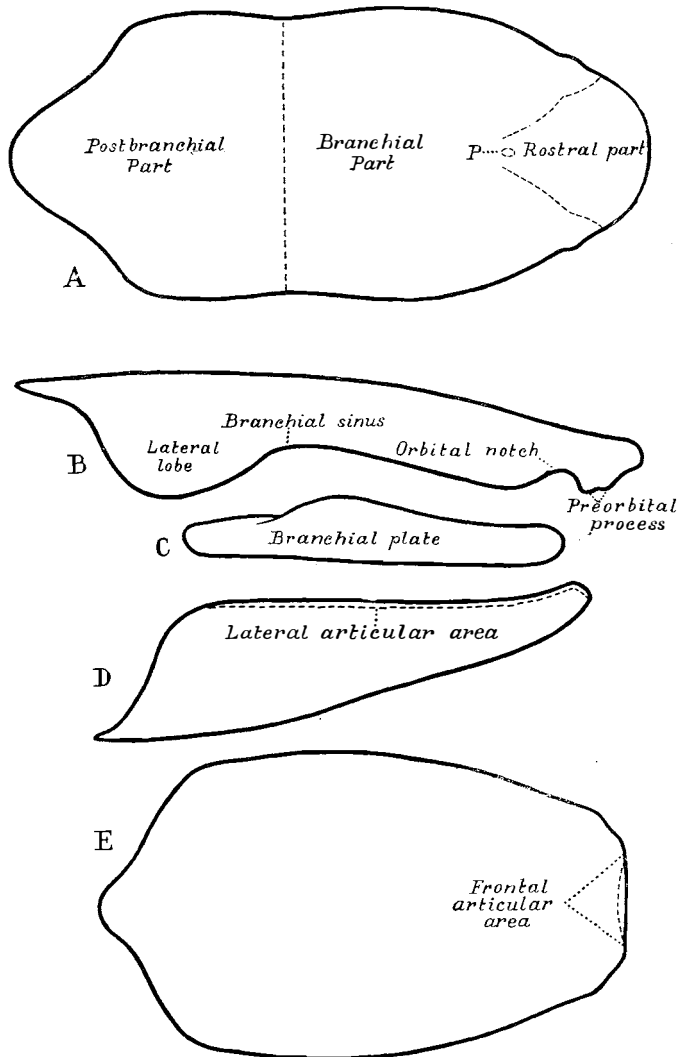


Fig. 2. *Poraspis polaris* Kiær. An outline drawing, showing the nomenclature of the different parts of the dermal skeleton. Ca.  $\times 2,5$ . A=Dorsal shield from above; B=Dorsal shield from the side; C=Branchial plate; D=Ventral shield from the side; E=Ventral shield from above.

3. The two elongated lateral divisions which vary in size in the different forms enclosing anteriorly the orbital notches.

It is obvious that the posterior portion of the rostral part in the *Poraspidei*, forms only a portion of the central disc in the *Cyathaspidei*. This triangle-shaped portion is often marked by a diverging surface-sculpture. In the posterior corner of this area is found the pineal organ often covered by a distinct pineal macula, surrounded by concentric dentine ridges. This area is called the pineal area.

This division of the surface of the dorsal shield in the *Cyathaspidei* is reminiscent of that in the *Pteraspida*. Corresponding to the condition in some later *Pteraspida*, in some *Cyathaspidei* the dorsal shield along these lines can even be divided into quite detached plates (*Traquairaspis* Kiær 1932, 1).

We shall now come back to *Poraspis*, where on each side behind the rostral part, the semi-circular orbital notches are situated. They limited the orbits from above (fig. 2, B; orb, Pl. II; V; IX; X; XIII; XIV; XVI; XVII; XIX; XXX, 2; XXXI, 1; XXXII, 2). Inferiorly the orbits were probably bounded by small sub-orbital plates, which are only very seldom preserved.

Just in front of the orbital notches the dorsal shield bends downwards into the strongly developed somewhat thickened pre-orbital processes (fig. 2, B; Pl. II; XXXI, 1; XXXII, 2). Between these processes is developed below the anterior margin a distinct maxillar brim, forming the upper boundary of the mouth-opening. The superficial dentine layer continues to this brim and the dentine ridges are here partly broken up into fine tooth-like tubercles (Pl. IX, 2; XXVI, 1; XXXVIII, mb). Also along the margin of the branchial part the dentine layer goes on to the interior side and forms a narrow internal marginal dentine area with uniform dentine ridges which are called the intern marginal ribs (imr. Pl. XI, 1; XXXVI, 4, 5; XL, 1).

In the *Cyathaspidei* the orbital notches, the pre-orbital processes and the maxillar brim are developed quite identically.

The ventral shield is entirely undivided and, corresponding to the dorsal shield, has a more or less elongated form (fig. 2, D and E; Pl. III; IV; VI; XV, 3, 4; XX; XXI, 1; XXV; XXVI, 3; XXVII, 2; XXIX, 3, 4; XXX, 1; XXXII, 1). The lateral margins are mostly slightly curved and the posterior margin more or less distinctly truncated, in *Poraspis*, however, without any indication of a spine (Pl. III; VI; XV, 3; XXV). In front, the ventral shield is abruptly truncated with a median faint incurvation (e. g., Pl. VI; XX, 3). In this place a distinct narrow area is developed without any dentine layer, to which originally the mouth plates were attached. This marginal articular area continues round the somewhat marginated front-corners and along the whole lateral margins of the shield (fig. 2, D, E; Pl. III; IV; VI; XV, 3, 4; XX). To this last part of the articular area the sub-orbital plates (?) and the long branchial plates have been attached (Pl. XXX, 1). The inside of the shield shows anteriorly 4—5 pairs of longish impressions of the branchial sacs (fig. 3, b; Pl. XII, 2, 3; XXVI, 3; XXVII, 2; XXXII, 1). In other forms these impressions are either indistinct or quite wanting. In front of these branchial impressions is commonly seen a median impression

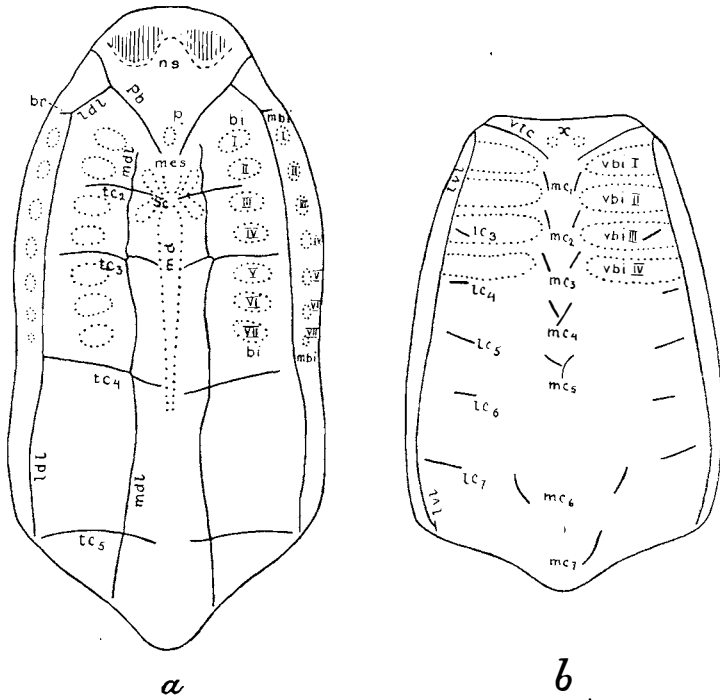


Fig. 3. *Poraspis polaris* Kiær. An outline drawing, showing the position of the impressions on the inside of the dorsal (a) and ventral (b) shields and the course of the sensory canals.

*br* = branch from *ldl* canal. *bi I-VII* = branchial impression. *ldl* = lateral dorsal lines, *lvl* = lateral ventral line. *lc<sub>3</sub>-lc<sub>7</sub>* = lateral portions of ventral transverse commissures. *mbi* = marginal branchial impressions. *md* = medulla oblongata. *mdl* = median dorsal lines. *mc<sub>1</sub>-mc<sub>7</sub>* = median portions of the ventral transverse commissures. *mes* = mesencephalon. *ns* = nasal sacs. *Pb* = pineal branch. *p* = impression of the pineal organ. *Sc* = impressions of the anterior and posterior semicircular canals. *vbi<sub>I</sub>-vbi<sub>IV</sub>* = ventral branchial impressions. *vlc* = ventral transverse commissure. *x* = anterior median impression.

often of an angular shape (anterior median impression) (fig. 3, b; Pl. XII, 2, 3; XXVII, 2).

In addition we shall mention here the measures used for the description of the dorsal and the ventral shields (fig. 5). The measurements of the length (L) and the breadth (B) need no further explanation. It must, however, be pointed out that by the breadth of the dorsal shield, where nothing else is stated, is always meant the breadth of the branchial part of the shield. The orbital breadth (OB) is the distance between the orbital notches. By the pineal length (PL) is meant the distance from the anterior margin of the shield either to the impression of the pineal organ or to the middle of the pineal macula. The rostral length (RL) is, in the *Poraspidei*, the distance from the

anterior margin to a line between the orbital notches (=Orbital breadth), which corresponds to the length of the rostral part in the *Cyathaspidei*. This length is often more characteristic than the pineal length.

Still more elucidative than these direct measurements, is, however, the relationship between them. For these proportionate numbers or indexes is calculated in the first instance the breadth-length index (B.L. Ind.)

$$= \frac{\text{breadth}}{\text{length}} \times 100.$$

This index gives at once a clear idea of the proportions of the shields, if we remember that it is like 100 when the breadth equals the length, and that it is 50 when the breadth constitutes half of the length. Another important index is the rostral index (R.Ind.)

$$= \frac{\text{rostral length}}{\text{total length}} \times 100.$$

The accuracy of these measurements and indexes is of course influenced by the different degree of pressure to which the shields have been exposed. If we, however, are able to measure a greater number of specimens, the faults may be almost adjusted.

As already mentioned, the shields are joined by means of the elongated branchial plates, one on each side. The lower margin on these plates is quite even and has been tightly fitted into the marginal articular area of the ventral shield (fig. 2, C; 52; 53). The upper margin fitted into the lateral margin of the dorsal shield, however, without being closely connected to it. In the posterior portion is seen an incurvation, which bounded the gill opening below (fig. 2, C; 51; Pl. XXXIII, 4, 5, 6).

These detached branchial plates, which in the *Pteraspida* closely coalesced with the dorsal shield, are particularly characteristic of the *Cyathaspida*. They are seldom preserved and were formerly little noticed although Jaekel long ago described them in *Archegonaspis integer* and called them paratega (1926, 1). They have now been refound and are more exactly described below with regard to several forms both of the *Poraspidei* and the *Cyathaspidei*.

The mouth plates have not yet been found in *Poraspis*, but as these have been ascertained in the closely related Genus *Anglaspis* they must be supposed to have been present similarly developed also in the other *Cyathaspida*. The system is reminiscent of that which Kiær has described in *Pteraspis vogti* (1927), and will be more particularly mentioned in another paper.

Behind the above described armour of the head and the front part of the body the hind part of the body was covered by relatively large scales. Known hitherto in the Genus *Poraspis* are only isolated scales (fig. 41; 42; 43; 44; 45; 46; 47; 48; 49; Pl. XXXIII, 2, 3), but judging by the more completely preserved specimens belonging to the closely allied Genera *Irregularaspis* (= *Dictyaspis* Kiær 1932, 1) and *Anglaspis*



(Kiær 1932, 1), it may be considered as certain that the scales have formed marked segmentally arranged circles each one consisting of six scales: one median dorsal scale, two lateral scales on each side and one median ventral scale (fig. 50). Of the symmetrical median scales there have been found in *Poraspis* two kinds: some long pointed ones and others more rounded. The lateral scales are very large, elongated, almost rectangular plates though not quite symmetrical. Like the median scales they have to a considerable degree covered the subsequent ones with their thinner posterior portions. This scale-cover is exceptionally strong and massive. In most of the *Cyathaspida* it seems to have been constructed in the manner described here, however, with variations in the development of the above-mentioned different scale types. Some *Cyathaspidei*, however, seem to begin a development of a scale system more conformable to that of the *Pteraspida* with smaller and more numerous lateral scales.

Most behind on the caudal fin, the large lateral scales have been broken up into smaller ones. The fin itself according to *Anglaspis* and *Pteraspis* has had a hypocercal form (Kiær 1932, 1). Other unpaired fins have certainly not been developed and also the paired fins are entirely missing.

The shape of the body in *Poraspis* and closely related forms has been almost cylindrical and rather elongated. From this original body type there have in both tribes been developed forms with more or less broadly widened body armours (*Anglaspis*, *Cyathaspis*).

The dermal skeleton has a similar structure as in the *Pteraspida* and the same skeletal layers can be discerned: the basal layer, the cancellous layer, the reticular layer and the dentine layer (Pl. XXXV; XXXVI; XXXVII; XXXVIII; XXXIX; XL). Some variations, are found, however, in the different genera. The dentine layer consists in almost all forms of fine, even, flat or faintly vaulted dentine ridges, which in some parts of the shields may be broken up into shorter pieces or even into small tubercles. In most cases the ridges are not crenated (as they are, for instance, in the *Pteraspida*), the only exceptions are the ridges on the maxillar brim (Pl. XXVI, 1; XXXVIII). The dentine ridges as a whole have a longitudinal course,

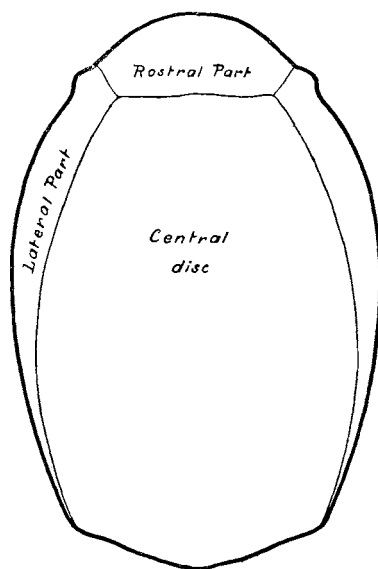


Fig. 4. *Archegonaspis* sp. An outline drawing, showing the position of the different parts of the dorsal shield in a *Cyathaspis*. Ca.  $\times 2$ .

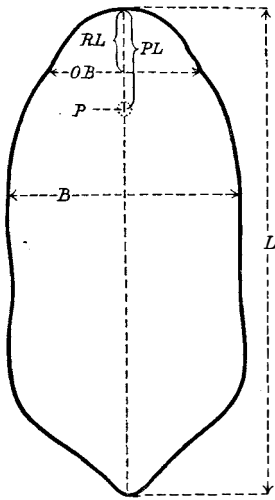


Fig. 5. *Poraspis* sp. An outline drawing of the dorsal shield, showing the measures for the dorsal shield.

B = breadth. L = length  
OB = orbital breadth. P =  
pineal macula. PL = pineal  
length. RL = rostral length.

however, with many slight deviations and variations. In the later forms of the *Cyathaspidei*, the ridges on the median disc of the dorsal shield and those on the ventral shield are arranged more elliptically similarly to the pattern in the *Pteraspida*. In most of the *Poraspidei* they have a longitudinal course also in the rostral part, which is often marked by a characteristic ridge pattern (e. g., Pl. X; XII; XXXI, 2). In some genera in the same tribe (*Palaeaspis* and *Irregularaspis* (= *Dictyaspis* Kiær 1932, 1)) the ridges run transversally archwise, often in whirls, and in the *Cyathaspida*, this transverse course is an established rule (Kiær 1932, 1).

The lateral line system in the *Poraspidei* is very strongly developed and shows a more primitive stage than that in the *Pteraspida*. The lateral lines in most genera form fine cylindrical canals in the cancellous layer (Pl. VII); they open into numerous fine pores on the surface.

The system consists of parallel longitudinal canals and transverse commissures, which have a fixed relation to the internal organ systems (brain, sense organs and gills (fig. 3, a; Pl. XI, 2)). On the dorsal shield there are two pairs of longitudinal lines, namely, the median dorsal lines and the lateral dorsal lines, and five transverse commissures, which can be more or less complete (*mdl*, *ldl*, *tc*<sub>2</sub>—*tc*<sub>5</sub>, fig. 3, a; Pl. VII; XI, 2; XXVIII, 2; XXIX, 2). The first one of these commissures, lying just behind the pineal organ, is most often indistinct. A portion of it has coalesced with the anterior part of the median dorsal lines and has formed the two strongly marked diverging pineal branches (*Pb* fig. 3; Pl. VII; XI; XXVIII, 2; XXIX, 1), which are distinguished by particularly conspicuous pores (Pl. XII; XIV; XXXI). These branches reach the border in front of the orbits and continue downwards into the pre-orbital processes. The connection of these pineal branches with the median dorsal lines is often interrupted (e. g., Pl. VII). The lateral dorsal lines send out a short branch just behind the orbits, (*br* fig. 3; 12) and then continue on the inner side of the orbits to the pineal branches (fig. 3; Pl. VII).

On the ventral shield we have one pair of longitudinal lines, the lateral ventral lines, along the sides of the shield and then a series of transverse commissures (*lvl*; *lc*<sub>1</sub>—*lc*<sub>5</sub>, fig. 3, b; Pl. VIII; XXIX, 4). The foremost of these going from the anterior

corner in a median direction, is abruptly in its median part (*vtc*, fig. 3, b). The others are even more reduced, being dissolved into short lateral transverse lines ( $lc_1$ — $lc_5$ , fig. 3, b) and short median lines ( $mc_1$ — $mc_7$ , fig. 3, b), lying in pairs in the median part of the shield. Six pairs of lateral transverse lines have been found in this form. The median lines, however, are more numerous and it can be proved that originally 10 transverse commissures have been developed in the ventral shield.

The lateral line system shows a rather rich variation in the other families of the *Poraspidei*. In the *Cyathaspidei*, the system is not yet quite ascertained due to the scarce material. It looks as if it is faintly developed or reduced in this latter tribe.

### Tribe I. *Poraspidei*.

The dorsal shield in this tribe is always pronouncedly entire and never divided into the four portions, characteristic of the *Cyathaspidei*. The surface of the dorsal shield shows, however, in many cases, smaller areas with a diversified dentine rib pattern (Pl. V; X; XVI; XVII; XXXI, 2; XXXII, 2) but these areas are bounded in a quite different way, mostly by the rows of pores of the lateral line system. One also sees that they do not only change from species to species, but may even be subject to a strong, individual variation within one and the same species. The rib pattern of the rostral part is often characteristic and reaches quite back to the pineal branches, which are often marked out by especially distinct pores (Pl. X; XII; XIII; XVII; XXIV; XXXI, 2). The rostral part is therefore here limited differently from that in the *Cyathaspidei* as it reaches quite back to the pineal branches (fig. 2 A).

Another important trait in the *Poraspidei* is the strong development of the lateral line system with very distinct and numerous pores. Thus, in specimens with well preserved surface, the course of the sensory canals is distinctly marked by these pores (e. g., Pl. III; V; IX, 3; XIV; XVII; XXX, 2; XXXI, 2). The system has already been briefly described in the introduction (pag. 48). It varies, however, in the different genera. In some (*Irregularaspis* = *Dictyaspis*, Kiær 1932, 1) it may be complicated and reticularly developed, in others more or less reduced (*Anglaspis*, Kiær 1932, 1).

The previously described species belonging to the tribe *Poraspidei* have been placed under the Genera *Holaspis* (= *Poraspis*), *Palaeaspis*, *Cyathaspis* and *Anglaspis*. The species, that have been referred to *Cyathaspis*, must be separated from this genus, which is the type of the *Cyathaspidei*.

The first species belonging to the Tribe *Poraspidei* is Lankester's *Holaspis sericeus* (1873, 2) (fig. 6). As this name was preoccupied and

thus not available, A. S. Woodward (1891) later on placed it under Claypole's Genus *Palaeaspis*. According to Prof. Kiær's investigations, however, it pertains to a widely different and distinct type for which the new name: *Poraspis* has been applied. It is thus the type genus for the Tribe *Poraspidei*.

The numerous species, now known, will be described in the following. They may be assigned to four Families, each with one or more genera, namely the *Poraspidae*, the *Palaeaspidae*, the *Irregularaspidae* (= *Dinaspidae*) and the *Anglaspidae*.

The *Poraspidei* occur in European regions solely in the Downtonian. Thus they have here a more recent geological occurrence than the lower part of the *Cyathaspidei*, which are known from the Upper Silurian and the Downtonian. In N. America on the other hand, there have been found some forms of *Poraspidei* in Silurian horizons (Salina), but also here anticipated by the *Cyathaspidei*.

### Family *Poraspidae* KIÆR.

This family will be treated as the first as it comprises the first described form pertaining to the *Poraspidei*, and therefore must be considered as the type Family. To this may be added that it occurs in the Red Bay Series in such a great number both of species and of specimens (Pl. I), that it furnishes particularly good material for studying the question of the species-limitation in the *Cyathaspida*.

The *Poraspidae* comprises forms with, most often, elongated, faintly vaulted dorsal and ventral shields from quite small to comparatively large (ca. 60—70 mm, fig. 6; Pl. XXVIII; XXIX). The rostral part of the dorsal shield is mostly somewhat narrowed in front of the orbits (fig. 2, A; Pl. II; V; IX; X; XIII; XVIII; XIX; XXII; XXIV; XXVIII) with a well developed, often very broad, flat maxillar brim (Pl. XXVI, 1). The post-branchial part is, as a rule, long with well developed end even downwardly bent, lateral lobes, which anteriorly, towards the branchial sinus, are uniformly rounded (fig. 2, B; Pl. II, 2; XXX, 2). The shield is posteriorly distinctly drawn out, but does not end in a point but in a rounded, flat lobe (fig. 2, A; Pl. II, 1; V; VII; IX; XIII; XV, 1, 2; XVIII; XIX; XXIII, a; XXVII; XXVIII, 1; XXX, 2). The branchial plates are elongated and flat (fig. 2, C; 51; 52; Pl. XXXIII, 4, 5, 6). The ventral shield has slightly curved sides (fig. 2, D; Pl. IV; XX, 2; XXV, 3) and farthest back is less drawn out, but somewhat more pointed than the dorsal shield (fig. 2, E; Pl. III; VI; XV, 3, 4; XVIII, b; XXV). The dentine ridges of the surface are fine to comparatively broad, always pronouncedly flat and run on both shields in the main longitudinally (e. g., Pl. II; III), in the details, however, with lesser but often strongly varied diviations (e. g., Pl. XXXII, 2). The pattern on the

rostral part has longitudinally or faintly fan-shaped arranged ridges, in front, often with a broader or narrower marginal area, with ridges following the anterior margin and often broken up into smaller portions and flat tubercles (fig. 7; 8; 9; Pl. II; X; XII, 1; XIII; XIV; XVI; XVII; XIX; XXII; XXIV; XXVII, 1; XXX, 2; XXXI, 2). The pineal macula is most frequently strongly marked out (Pl. XXXIV).

The interior sides of the shields show very distinct impressions of the nasal sacs, the semi-circular canals, several portions of the brain and the branchiae (Pl. IX, 2; XI; XXVI, 2; XXIX, 1; XXX, 3).

Only isolated body scales have been found. The median scales are comparatively short, rounded (fig. 41, 42, 43, 44), to more or less pointed (fig. 42, a). The lateral scales are very long, rectangular (fig. 45, 46, 47). The lateral line system is regularly and normally developed in both shields (fig. 3; 55; Pl. VII; VIII; XXVIII, 2), with marked pineal branches and numerous regularly arranged pores (e. g., Pl. IX, 3; XII). Some of the longitudinal lines of the shields continue on the lateral body scales, only they are here broken up into quite short lines (fig. 49, a).

The *Poraspidae* is the family of the *Cyathaspida* that has the widest distribution. It is known in numerous forms from different Downtonian regions in Europe, and also in N. America (?).

It comprises the two Genera *Poraspis* and *Homaspis*, which differ particularly with regard to the structure of the dentine ridges and to the development of the lateral line system.

The third Genus *Cryptaspis* is newly described by Bryant (1934) from N. America. It is, however, not absolute certain, that it really belongs to the Fam. *Poraspidae*.

### 1 Gen. *Poraspis* KIÆR.

*Holaspis*, E. R. Lankester, 1873, 2.

*Palaeaspis*, Claypole, in part. Woodward 1891.

*Cyathaspis*, Alth. 1874.

*Cyathaspis*, Leriche. 1906.

*Pteraspis*, in part. Zych. 1927.

*Poraspis*, Kiær. 1930.

*Poraspis*, Zych. 1931.

*Poraspis*, Kiær. 1932, 1.

*Palaeaspis*, Brotzen. 1934.

Generic characteristics. Small to comparatively large forms. The rostral part somewhat narrowed in front of the orbital notches. The branchial part faintly arched. The post-branchial part comparatively long, with well-developed lateral lobes. Fine dentine ridges. The dermal skeleton with faintly-developed reticular layer, most often with comparatively narrow openings from the cancellae upwards into the pulpa canals. The lateral line system distinguished by particularly large and

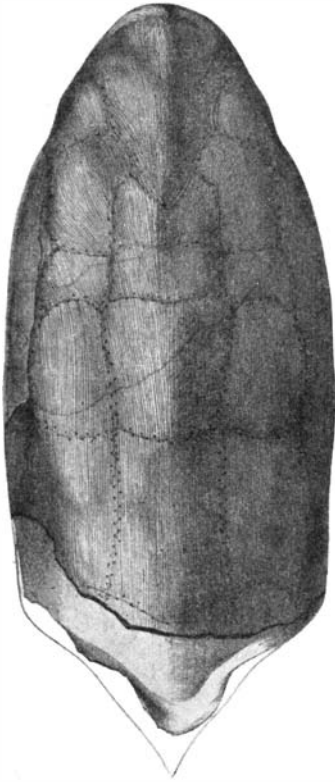


Fig. 6. *Poraspis* (= *Holaspis*) *sericea* (Lankester). Dorsal shield.  
Ca.  $\times 1.4$ . From Lankester.  
1873, 2.

conspicuous pores on the pineal branches and by the fact that the median lines in the ventral shield are as a rule not coherent. Further, reference may be made to the description of the Family.

The genotype is *Holaspis sericeus*, described by Lankester in 1873 (fig. 6). As mentioned, A. Smith Woodward ascribed it to the Genus *Palaeaspis* Claypole. (1891) Most writers have subsequently followed him, whereas some have placed it under the Genus *Cyathaspis*. None of these views can be accepted. *Cyathaspis* is widely different and must be even regarded as a type genus of quite another tribe of the *Cyathaspida*. *Palaeaspis* is much nearer related to Lankester's form, but, as we shall see later on, deviates from it in many important characteristics, thus these forms cannot be united.

For this and for closely related forms, is therefore established a new generic name *Poraspis*, thereby indicating, one of the pronounced characteristics of this genus, namely, the numerous conspicuous and regularly arranged lateral line pores. Besides the genotype (*Palaeaspis sericea* (Lank.)) many other previously described forms belong to this genus as: *Cyathaspis sturi* Alth., *C. barroisi* Leriche, *Palaeaspis pompeckji* and *P. simplex* Brotzen. To these are now joined a number of new species from Spitsbergen. Many of these, unlike the previously known species, are very common in several horizons in the Red Bay Series, indeed one (*P. polaris*) is found in abundance and have therefore been very closely investigated. Unfortunately, none has been found in a complete state of preservation, but besides the dorsal and ventral shields so many of the other plates and scales are known, that the animals can be reconstructed in the main features by means of the complete specimens found of *Anglaspis*.

The Genus *Poraspis* is present throughout the Red Ray Series in a number of forms characterizing very well the different portions of this mighty series.

However, before passing on to the description of both these new and the formerly known species of *Poraspis*, we shall discuss in a special section the principles for specific definition, which are used in this paper.

### Specific definition.

The concise specific definition of the *Poraspidei* from the Red Bay Series has shown to be relatively difficult. The first disadvantage appearing consists in the incomplete state of the preservation of the material. In fact, it is extremely rare to find the dermal skeleton preserved as a whole; in most cases the various portions of the armour are found isolated. With regard to the specific description the difficulty is to decide what parts pertain to one and the same species, that is, what dorsal and ventral shields belong to each other.

The most simple case is when in an horizon, of one Genus, only one type of each of the shields has been found. We may then be justified in assuming that these shields pertain together if no particular facts point in another direction. It is more complicated if, in one and the same horizon, there are found shields of several closely related forms. In that case, the matter is more difficult to solve especially as the ventral shields are less characteristic than the dorsal, and the diverse features may vary considerably within the same species. We must then decide particularly according to the respective lengths and breadths of the shields. This has been tried, for instance, for three closely related species of *Poraspis* (*P. polaris*, *P. elongata* and *P. brevis*), which have been found intermingled in the rich fossil layers of the Polaris horizon (pag. 13). With regard to the smaller plates and to the body scales it is generally still more difficult, and even impossible, to decide to which dorsal shields they belong.

Still greater difficulties as to the specific definition are due to various other features: First by the secondary sexual characters, which are distinctly expressed in the *Cyathaspida*; then by the strong individual variations; and, finally, by the phylogenetical changes which different lines have undergone during the long periods, in which the mighty layers of the Red Bay Series have been deposited.

Secondary sexual characters. That such characteristics really exist in the *Cyathaspida* has been realized by researches of the rich *Poraspis* material from the Polaris horizon of Frænkelryggen. As early as in 1912 Patten, when studying the *Palaeaspis* forms from America, expressed the opinion that the narrow and broad form of *Palaeaspis* was probably only the female and male of one and the same species. In the Polaris horizon is found a great number of comparatively small *Poraspis* which have been called *P. polaris*. The holotype of the species is the comparatively elongated dorsal shield figured on Pl. II. Beside such narrow dorsal shields, somewhat shorter and considerably broader ones (Pl. V) occur quite commonly, which, however, in the majority of other features, agree closely with the narrow

forms. An examination of the B. L. Ind. (breadth—length—index) of a considerable number of specimens showed that the variations of this index number gave quite separate curves of variations. This fact indicates that although the number of specimens may be too small to give quite decisive results, these two forms are not joined by continuous variations. At first, this led to the supposition that there were here present shields of two, no doubt, closely related, but yet separate, species. But as these two forms in other respects closely agree and seem to vary in the same respects, this interpretation did not strike one as being very natural. Further researches, if the material at hand was relatively rich, showed that it was a common phenomenon to find in the various horizons, a narrow and a broad form of the same type. This applies not only to the Genus *Poraspis* but also to the other genera of the *Cyathaspida* and to the *Pteraspida*. The difference between these two forms is not always equally great but usually quite considerable.

We may thus expect that this difference is due to secondary sexual characteristics.

Such characteristics are strongly developed in the primitive forms and essentially consist in a different length—breadth proportion of the head and of the front part of the body. Among recent fishes, as is well known, secondary sexual characteristics occur quite often. They mostly cause the development of different colours in the two sexes or the variation in the size and shape of their fins. Not infrequently there is also present a difference with regard to the size of the body and to the shape of the head. There might here be recorded a long series of examples to this effect. We shall, however, confine ourselves to mentioning a few cases, in which the size of the body and the proportions of the head are different in the two sexes.

In the northern fish fauna in the Genus *Cottus*, the female is mostly larger than the male, a fact which seems to be usual in the fishes. Numerous exceptions are, however, found in these features. Thus the male is larger than the female in *Cottus gobio* L., the same being pronouncedly the case with regard to the pretty *Callionymus lyra* L. In this latter species the head is also comparatively broader in the male, which, as is known, is distinguished by larger and differently shaped fins. Also in *Trigla gundarus* L. and in *Agonus cataphractus* L., the front part of the head between the eyes is broader in the male than in the female. Distinctive secondary sexual characteristics of similar kind are found in many tropical forms. A known example is here the siluroid fish *Plecostonus barbatus* from South America, which has been mentioned and figured by Darwin in his work "The descent of man." In this species the male has its mouth and inter-operculum fringed with a beard of stiff hairs of which the



female shows hardly a trace; this male is also larger than the female and has a broader head.

In the *Elasmobranchii* the female is most often larger than the male, but with regard to the shape of the body, no difference between the two sexes can be noticed. The same is the case with the *Cyclostomata*.

These facts confirm the interpretation that the mentioned differences in the *Cyathaspida* are caused by secondary sexual characteristics. It seems impossible at present to decide which sex is represented by the narrow, and which by the broad form, and we shall therefore only call them the "angusta" and the "lata" forms. It is, however, reasonable to assume that the angusta form with its larger and more elongated shield has been the female.

Variation of the characteristics. Researches on the continuous variations of diverse characteristics is very important for the specific definition. Otherwise it is often difficult to decide how much attention ought to be paid to a different development of one or another certain characteristic. Most often, however, the material available is far too scarce to enable such investigations. Even from the horizons most rich in fossils, the Polaris- and Anglaspis horizons of Frænkelryggen, the material of complete or fairly complete dorsal and ventral shields, is not sufficiently large to give continuous and definite curves of variation. The curves that may be obtained cannot, therefore, give anything more than indications in one or another direction, but such hints may also be of importance and ought to be considered in establishing the species.

We shall give an example from the Polaris horizon. Here is a quantity of the Genus *Poraspis*, plainly present in several forms (Pl. I). The most common one is the form called *P. polaris* (Pl. II; V) with the distinct sexual dimorphism which was dealt with above. Besides this, there is found a more elongated form called *P. elongata* (Pl. XVIII). It mostly appears as an angusta form. When comparing this with the angusta form of *P. polaris* we realize that the length is almost the same in both forms, but that their B. L. Ind. deviates considerably. Trying the statistical method, we shall find that the numbers of complete dorsal shields, particularly of those of *elongata*, are too inconsiderable to give certain results. A greater number of specimens would probably give a two-topped curve definitely indicating two species. These two forms differ, however, not only in their B. L. Inds. but also with regard to other characteristics.

In addition, there have been found, in the Polaris horizon, two specimens of a minute *Poraspis* form, called *brevis* (Pl. XV). It is more common in the older Primaeva horizon. The B. L. Inds of these two shields correspond to the B. L. Ind. of the lata form of *P. polaris* their total lengths, however, are considerably smaller and apparently

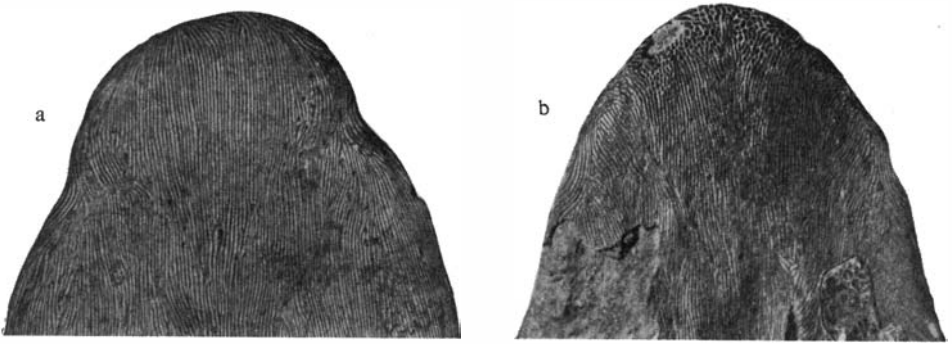


Fig. 7. *Poraspis polaris* Kiær. Variations in the rostral pattern.  
 Ca.  $\times 5$ . a. Frænkelryggen. Polaris horizon. Specimen D 2165. Pal. Mus., Oslo.  
 b. Frænkelryggen. Polaris horizon. Specimen D 209. Pal. Mus., Oslo.

come outside the range of variation of this form. As in other respects they are in close accordance with each other it seems natural to suppose that the short and small specimens were representing individuals of a younger age of the same species. As it is doubtful, however, how the growth of the dermal skeleton has proceeded in the *Cyathaspida* it is after all better to establish a separate species for this short form. The same three forms also occur in the older Primaeva horizon. The material from this horizon, which is still more scarce than that from the Polaris, gives, however, essentially the same results according to the establishment of three species.

As will be seen, the statistical treatment of the material gives poor results owing to the far too insufficient number of specimens available. One fact of importance is, however, obvious; the range of variation of the different characteristics is rather wide. Therefore, with a scarce material at hand, one must not limit the species too restrictively.

As a second example of variations may be mentioned researches of the pattern of the dentine ribs, particularly of the rostral pattern in *P. polaris*.

The most ordinary rostral pattern of this species is seen, for instance, in the holotype (Pl. II, 1). It is characterized by the fact that the ribs in the median portion of the rostral part run parallel to each other, that is, without any perceptible outward spreading towards the sides. Laterally, the ribs curve conformably to the margin and most anteriorly a narrow marginal area is developed with more or less dissolved ridges going uniformly with the arched anterior margin (Pl. X, 1). This pattern with slight changes is found in the great majority of specimens. Examples of such alterations are to be seen in figs. 7 a & b. In the left figure (a) is pictured a rostral part with strongly pronounced parallel arrangement of the ridges but with a rudimentary

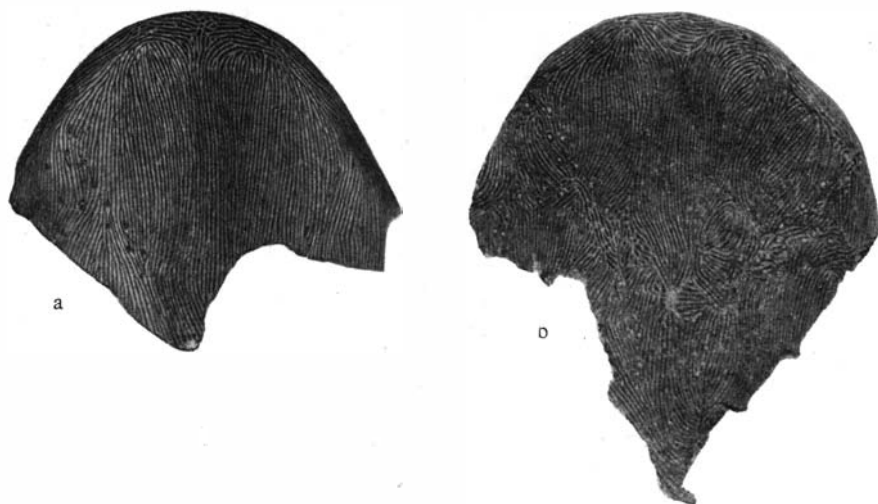


Fig. 8. *Poraspis polaris* Kiær. Variations in the rostral pattern.  
 Ca.  $\times 5$ . a. Frænkelryggen. Polaris horizon. Specimen D 1898. Pal. Mus., Oslo.  
 b. Frænkelryggen. Polaris horizon. Specimen D 008. Pal. Mus., Oslo.

development of the anterior marginal area. The right figure (7, b) shows a very striking dissolution of the ridges in the most anterior portion. Otherwise the ridges are almost parallelly arranged, but run laterally outwards in the direction of the margin instead of curving conformably to this.

Further, two variations of interest are seen in figs. 8, a & b. Unusually fine is the pattern in the left figure (a). The ridges here, behind the well developed marginal area, form two symmetrical curves and the pattern is strikingly reminiscent of that which fairly constantly occurs in the much younger form *P. rostrata* (Pl. XXIV). An additional variation of this type is seen in the right figure (8, b). Here the pattern is furthermore complicated by the development of small whirls in the posterior portion.

Most remarkable is a variation seen in fig. 9, a. One might call it a bipolar type as the ridges here radiate from two points situated one on each side in the posterior portion of the rostral part. This type presumably is very rare.

More common is a rostral pattern, as is the one shown in the right figure (fig. 9, b) with a slightly fan-shaped arrangement of the ridges. In front of the pineal branches of the lateral line system, the ridges run outwardly in the direction of the lateral margin. Most in front, a narrow marginal area with dissolved ridges is seen. This variation is interesting as it seems to be the usual one in the older form of *P. polaris* of the Primaeva horizon (Pl. XIII). It may also be pointed out that a similar pattern is found in the majority of older forms of other *Poraspis* species (Pl. XIV; XXII).

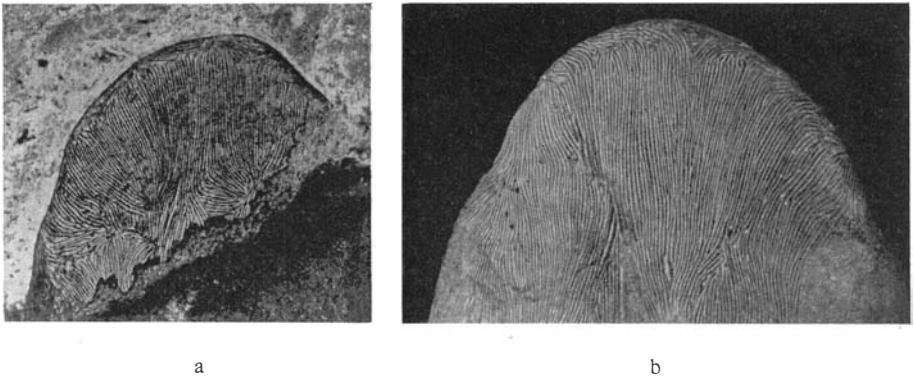


Fig. 9. *Poraspis polaris* Kiær. Variations in the rostral pattern.  
 Ca.  $\times 5$ . a. Frænkelyggen. Polaris horizon. Specimen D 1899. Pal. Mus., Oslo.  
 b. Frænkelyggen. Polaris horizon. Specimen D 0017. Pal. Mus., Oslo.

We have here only mentioned a few of the more considerable variations. They can be divided into several main types. The principal ones are the typical polaris type (fig. 7, a, b; Pl. II, 1; V; IX, 1; X, 1; XII, 1), the rostrata type (fig. 8, a, b) and the primitive type (fig. 9, b; Pl. XIII; XIV; XXII). If one goes further into detail it becomes apparent that the pattern in all individuals deviates in one or another small feature similar to the papillary pattern of man.

The variations of the rostral pattern in *Poraspis polaris* are of interest in many respects. Several of these, mentioned above, deviate very considerably from each other and, therefore, one should in the case of a limited material of a certain species, be very careful in using a particular pattern as a specific characteristic. There are, however, indications suggesting that the range of variation of this characteristic is not equally important in all forms, and that a special type of pattern may thus, in another species, be more constant than is the case in *Poraspis polaris*.

This applies both to *P. elongata* (Pl. IX, 3; X, 2; XVIII; XIX) and to *P. rostrata* (Pl. XXIII; XXIV). The material available, particularly with regard to the latter species, is, however, too scarce to allow this question to be decided with certainty.

The pattern of the dentine ridges more posteriorly on the dorsal shield also varies. The ridges may here have a most regular, longitudinal course without being noticeably deflected by various lateral lines. In other specimens again, a more or less pronounced change can be seen in the course of the ridges between the lateral lines, into the extreme development of the pattern seen in fig. 2, Pl. XXXII.

Also the shape of the pineal macula varies greatly in *Poraspis polaris*. Figs. 1—5, Pl. XXXIV show several interesting variations of this characteristic. As a rule, the pineal macula is shortly elliptical

(figs. 1—2). Some of the variations are quite similar to the pattern in closely related species. Thus the figs. 3—4 are reminiscent of the shape of the pineal macula in *P. elongata* (Pl. XIX). A most aberrant development is seen in fig. 11, where no macula at all has been formed. There, where this macula should have been according to the rule, is seen a transversally arranged elliptical system of ridges. This pattern must, however, be regarded as a quite abnormal one.

The dentine ridge-pattern on the ventral shields vary also quite strongly, without showing, however, any concisely developed pattern-types (Pl. III; IV; VI; VIII; XV, 3, 4; XX; XXI, 1; XXV).

*Poraspis polaris* KIÆR.

*Poraspis polaris*. Kiær 1930.

*Poraspis polaris*. Kiær 1932, 1.

(Pl. I—VIII; IX, 1, 2; X, 1; XI—XIII; XXVI, 1; XXXI, 1; XXXII, 2; XXXIV, 1—5; XXXV; XXXVI; XXXVII; XXXVIII, 1; figs. 2, 3, 5, 7, 8, 9, 10, 11, 12, 13, 14).

Specific characteristics. The dorsal shield with a total length from 30 to 40 mm somewhat varying in the different horizons and also deviating in the angusta and the lata forms, which are particularly distinctly expressed. The breadth-length-index (B. L. Ind.) in the first about 50 or somewhat less, in the last, about 60 to 65. The rostral part short, often faintly contracted in front of the orbits and often slightly flattened, particularly in the lata-forms (Pl. XII, 1). Rostral index (R. Ind.) from 15 to 16. The post-branchial part comparatively long with rather long lateral lobes (Pl. II, 2). The maxillar brim broad (Pl. XXVI, 1). The pattern in the rostral part most often shows almost parallel ridges, which near the anterior margin are broken up into small tubercles (e. g. Pl. X, 1). Not infrequently, however, is seen a faintly fan-like arrangement. The pineal macula is marked and is of a short elliptical or rounded shape (Pl. XXXIV, 1—5). The ventral shield comparatively short and broad with a total length from 27 to 31 mm and varying in shape corresponding to the dorsal shield (Pl. III; IV; VI; VIII; XII, 2, 3). The breadth-length index (B. L. Ind.) can be divided into two groups, one from 58—61 (the angusta-form), the other from 66 to 71 (the lata-form).

As holotype has been chosen the specimen D 665 (Pl. II; XXXI, 1; XXXIV, 2).

Occurrence and material. *Poraspis polaris* is one of the chief forms in the upper part of the Frænkelyggen group. It is comparatively common in the Primaeva horizon, is found in abundance in the Polaris horizon and also occurs, even if rarely, somewhat above this horizon and in the Anglaspis horizon. It changes, however, somewhat through these layers, as we shall see later. The species was first found by A. Hoel, but only in a few specimens. Not until the

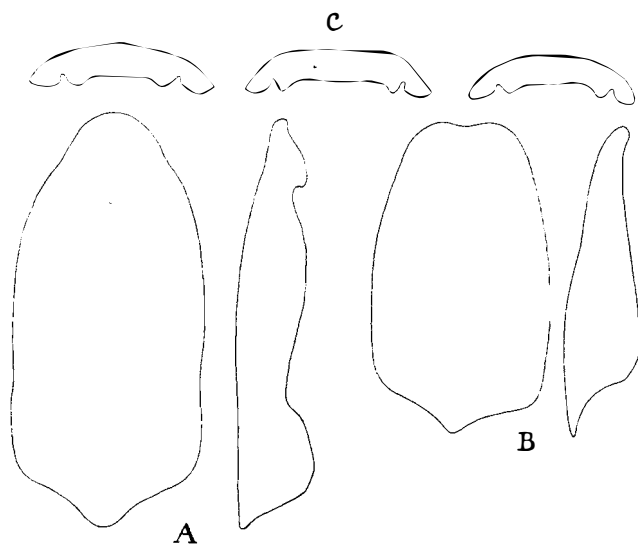


Fig. 10. *Poraspis polaris* forma *angusta* Kiær. An outline drawing of the dorsal shield from above and side (A), from front (C) and ventral shield from above and side (B). Ca.  $\times$  1,5.

careful examination of Frænkelyggen, carried out by the expeditions in 1925 and 1928, was its common and partly numerous occurrence ascertained in the upper part of Frænkelyggen, and the splendid material that we now possess brought together. The enormous number of this form in the Polaris horizon is particularly remarkable. The thin greenish layers are almost covered with dorsal and ventral-shields and other plates and scales in an excellent state of preservation (Pl. I). In most cases these plates and shields become more or less broken before the embedment, but many are complete or almost so. Unfortunately, all these remains are always isolated and there have never been found specimens with all parts of the armour in a natural connection. Also from the Primaeva horizon a very good material has been collected, although far less than in the Polaris horizon. Of these species about 300 rock-specimens have been found, many containing remains of a good deal of individuals.

**General description.** As mentioned above, we must distinguish between two forms of *P. polaris*: the *angusta* and *lata*, and these two forms must be kept apart in the description. Furthermore, the species change somewhat through the horizons in which they occur, but, as this only concerns the size, the oldest form is not separated as a distinct variety. The following detailed description refers to the form abounding in the Polaris horizon. Finally, the forms from the other horizons will be briefly described.

**Forma angusta.**

(Pl. I—IV; VII; IX, 1—2; X, 1; XI, 2; XII, 2; XIII; XXVI, 1; XXXI, 1; XXXII, 2; figs. 2, 3, 5, 7, 8, 9, 10, 11, 12.)

The variations of the dorsal shield regarding the total length and breadth-length index (B. L. Ind.) have been dealt with in a previous chapter (pag. 59). The total length in the Polaris horizon is mostly 36—39 mm. It may in some case increase to 40,5 (the holotype) and go down to 35; the B. L. Ind. is usually somewhat below 50 (45—51). The shield is thus comparatively elongated and having a faintly and evenly vaulted dorsal side. The rostral part is short and uniformly curved, with rostral index (R. Ind.) from 15 to 16. It is mostly somewhat contracted in front of the orbital notches and often slightly compressed compared with the rest of the shield; but specimens with a quite evenly curved lateral margin have also been found.

The branchial part is arch-wise widened, and when well preserved, constitutes the broadest portion of the shield. The post-branchial part has about the same length as the branchial; it is only somewhat narrower than the latter and is provided with long, strongly downwardly bent lateral lobes. Farthest back, the dorsal shield is quite strongly drawn out and ends in a flat, rounded lobe. Often the shields are pressed and more or less deformed, the posterior portion thus becoming very broad, as the lateral lobes have been pressed outward.

As a result of the strong development of the lateral lobes the branchial sinus is distinctly marked (fig. 2, C; 10, A; Pl. II, 2). The orbital notches are also deeply incised (fig. 2, C; 10, A; Pl. II, 2; XXXI, 1; XXXII, 1) and can just be seen in dorsal view of the shield (Pl. II, 1). The pre-orbital processes are strong and very broad (fig. 2, C; 10, A; Pl. II, 2; XXVI, 1; XXXI, 1). Between them lies the margin of the mouth, which is flat and slightly bent downward in its median portion (fig. 10, C; Pl. XXXI, 1). The maxillar brim is strongly developed (*mpl*, Pl. XXVI, 1; *mb*, Pl. XXXVIII, 1) and forms a flat border about 1,5 mm broad, within the margin of the mouth. It narrows at the sides and is here limited by the pre-orbital processes (Pl. XXVI, 1). Innermost, the maxillar brim projects freely (Pl. XXVI, 1; XXXVIII, 1).

The dentine ridges of the surface are fine (7—8 on 1 mm) and have mostly a regular longitudinal course. The lateral ridges, however, run conformably to the outside margin of the shield, thus having a somewhat deviating course, where the margin is more or less strongly curved, as, for instance, round the branchial sinus (Pl. II, 2). Still more pronouncedly arched are the ridges, which in a number of 5—6, encircle the orbital notches. In front, they curve either downwards into the pre-orbital processes, or, in an anterior direction, along the margin (orb. Pl. II, 2; XXXI, 1). Sometimes seen here are more or

less distinct rib-whirls. Along the curved margin of the rostral part, some ridges running conformably to it are often developed (Pl. XXVI, 1; XXXI, 1).

The mouth-margin is always limited by one or two strongly arched ridges (Pl. XXXI, 1). To these, the ridges of the internal maxillar brim are joined (Pl. XXVI, 1). The uttermost of these is comparatively broad whereas the others become more and more sharp with tuberculated margins. The inmost ridges have possibly been broken up into rows of tooth-like dentine tubercles (Pl. XXVI, 1; XXXVIII, 1). The dentine layer continues also along the sides of the branchial part round the margin forming a narrow marginal area on the internal side of the shield. The area attains a width of 0,8 mm and shows 7—8 fine, longitudinal ridges (Pl. XI, 1). As is seen in the microscopical sections, these internal marginal ridges are widely different from the usual dentine ridges on the surface of the shield. They are quite narrow with uniform margins and placed at a great distance from each other (*imr.* Pl. XXXVI, 4, 5). This area disappears behind the branchial sinus. On the other hand, there is developed below the posterior margin of the shield a similar, but still narrower dentine area showing quite short, faintly converging ridges. These internal dentine areas are not without interest as they must be supposed to have been formed in the skin-folds.

In other respects a great many trifling variations of the course of the dentine ridges are found, these variations being most marked in the rostral part. As mentioned above (pag. 56—57), the most common pattern of the rostral part is that with parallel dentine ridges. Most anteriorly they are broken up into quite short ridges and flat tubercles, which are generally arranged conformably to the anterior margin. The marginal area may be more or less strongly developed. This is the typical polaris-pattern seen, for instance, in the holotype (Pl. II, 1; XXXI, 1; in addition, see Pl. X, 1 and fig. 7, a). More rare is a distinct fan-like arrangement of the ridges which most in front are either dissolved into tubercles (fig. 7, b) or curved in an outward direction (fig. 9, b). The rostral pattern of this type is reminiscent of that in an older form *Poraspis elongata* found in the Primaeva horizon (Pl. IX, 3). Still more rare is the pattern seen in fig. 8 a. The median ridges form here most anteriorly two symmetrical loops, and in front of these there is developed a broad marginal area with ridges running conformably to the margin. This type is interesting, as, with regard to the rostral pattern, it is highly reminiscent of the far younger form *Poraspis rostrata* (Pl. XXIV). Of great interest is also the variation of the same pattern with partly whirl-like disposition of the ridges seen in fig. 8, b.

As is seen, the range of variation of the rostral pattern in *Poraspis polaris* is very large and comprises patterns, which seem to be more constant in other species.



Placed in the median line immediately behind the rostral portion is the pineal macula, the quite thin dentine covering of the large internal impression caused by the pineal organ (Pl. XXXV, 1). Most often this macula is of a short, comparatively broad shape, slightly vaulted (Pl. XXXIV, 1, 2). It commonly represents a strong widening of a single ridge, but the shape and the details vary considerably as shown in fig. 11 and Pl. XXXIV, 1—5.

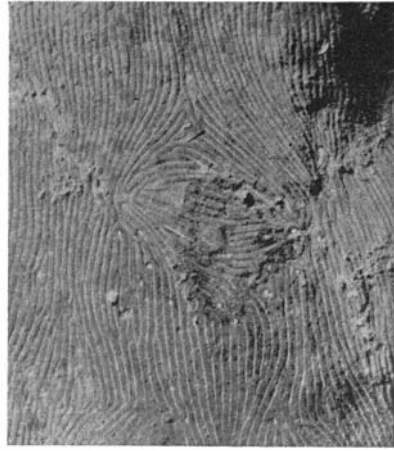


Fig. 11. *Poraspis polaris* Kær. Remarkable variation of the dentine ridges in the pineal region. Frænkelryggen. Polaris horizon. Ca.  $\times 10$ . Specimen D 1161. Pal. Mus. Oslo.

The arrangement of the dentine ridges in the median and the posterior portions of the shield is also subject to considerable variation, particularly in the anterior portion of the branchial part. In some specimens, as, for instance, in the holotype (Pl. II), we have a very regular longitudinal development nearly all over the shield, only somewhat diverging on the sides of the postbranchial part and behind the pineal branches. In others are found greater or smaller deviations in the different areas between the lateral lines. Particularly the longitudinal lateral lines seem to have great influence on the dentine ridge pattern. Occasionally this feature is very strongly pronounced as shown in Pl. XXXII, 2. Here the surface of the shield is distinctly divided into five longitudinal areas with different patterns. A differentiation so strongly developed seems, however, to be rare, while more moderate variations with regard to the details seem to have been present in all individuals.

All these variations with regard to the sculpture of the surface have been ascertained in dorsal shields to agree so well in shape, proportions and measurements that they all must be supposed to have belonged to the same species.

The ventral shield (fig. 2, B, C; 3, B; 10, B; Pl. III; IV; XII, 2) has only been found in isolated specimens in the Polaris horizon. As this shield, however, is less characteristic than the dorsal shield and as, in addition, there are found in the same horizon more closely related forms of *Poraspis* each one with both the angusta- and the lata-forms, it is often difficult to decide to which type of dorsal shields the ventral shields are to be referred. It is, therefore, of particular importance to know the relation between the length of the dorsal and the ventral shields. A clue to the solution of this question we find in a specimen

from the Primaeva horizon (D 383). Here the two shields are found in connection and show that the relation between the length of the ventral shield and the length of the dorsal shield is 1 : 1,3.

The ventral shields in the Polaris horizon may be divided into several groups. The most numerous of these attains a total length from 27 to 31 mm (average 29) a breadth from 16,5 to 19 mm (average 18) and a B. L. Ind. of about 60. Another less numerous group shows a somewhat more reduced total length (28—29 mm, average 28,2), considerably greater breadth (19,5—20,5, average 20) and B. L. Ind. of about 70. A third small group is of a considerable length, namely about 30 mm, a more reduced breadth 16,5—17 mm and a B. L. Ind. of 55—56. The first of these groups must apparently correspond to the *angusta* form of *P. polaris*. The total length of 27 to 31 mm corresponds to dorsal shields with a length of 35 to 40 — just the measurements usual for the *angusta* form. The breadth agrees also well, The fact of the B. L.; Ind. being considerably greater is a matter of course, as the ventral shield is always considerably shorter than the dorsal one, whereas the breadth is nearly the same. The second group corresponds obviously to the *lata* form, while the third pertains to the more elongated and narrow species *P. elongata*, which is comparatively rare. It must, however, be mentioned, that there is present in the material, ventral shields regarding which it is difficult to decide whether they belong to the *angusta*, or to the *lata* form.

A comparatively small but typical ventral shield of the *angusta* form is figured in Pl. III and IV with the total length 27 mm, breadth 16,5 mm and B. L. Ind. 61 mm. The maximum breadth is situated almost in the middle, and decreases more strongly forwards than backwards. The breadth just behind the anterior corners in the figured specimen is 11,5 mm whereas, most posteriorly, it amounts to 14,7 mm. The shield is anteriorly slightly vaulted but becomes more strongly curved in the posterior part as shown in Pl. IV, the difference, however, often not being so distinct as in the figured specimen. The anterior margin is abruptly truncated and slightly concave the anterior corners obliquely cut off and distinctly emarginated (Pl. III; IV). The lateral margin forms a uniform curve seen from below. By a lateral aspect it is faintly emarginated in its anterior portion (Pl. IV). The posterior margin is far more moderately drawn out than in the dorsal shield; the shield here ends in a short lobe, usually more tapering than in the dorsal shield (Pl. III). Along the anterior margins of the ventral shield runs a narrow but distinct marginal area without dentine ridges (Pl. IV; XXXVI, 3). This area has its largest width in the anterior emargination (0,6 mm). Laterally it is very narrow (0,2 mm) and then increases again somewhat in breadth backwards (0,4 mm).

This is an articular area to which have been fastened the mouth plates, the sub-orbital plates (?) and the branchial plates.

The dentine ridges of the ventral shield have a very regular longitudinal course; only most in front is seen a marked divergence outwards in the direction of the corners (Pl. III). Near the anterior margin the dentine layer is stopped by a few transverse dentine ridges, which often can be broken up into quite short pieces (Pl. III; IV; XXXVI, 3, *oaa*). Sometimes the ridges outside the lateral longitudinal lines of the lateral line system have a deviating direction, as can plainly be seen in Pl. IV. Smaller variations sometimes occur in other parts of the shield as well.

We have already in the introduction (pag. 48) given a short general account of the development of the lateral line system regarding this species. We must here give some additional details and also discuss the relation of the lateral line system to the inner organs, the impressions of which are left on the inside of the shields.

The lateral lines (=sensory canals) can often be seen in well-preserved surfaces as faintly expressed ridges. The fine round canals are placed in the cancellous layer (Pl. XXXV, 1, 4, *lc*). In some cases the skeleton is so transparent, that the canals are visible when the specimens are wetted in alcohol. This is, for instance, the case with specimens from the red *Primaeva* horizon, in which the skeletal substance is particularly light and clear of hue (Pl. XIII). On the other hand, however, in the rich *Polaris* horizon and in most of the other horizons the skeletons are always dark in colour and opaque. Most often we must therefore study the lateral line system either with the help of the fine pores, that are seen more or less distinctly on the surface of the shields (e. g. Pl. III; XIII; XXXII), or by working out the very canals. This last method gives, of course, the most certain result and can most easily be accomplished by grinding and etching (pag. 18). Sometimes, however, nature itself has taken over the business and in some weathered specimens the canal system is perfectly seen (e. g. Pl. XXVIII, 2). At first we thought that it was sufficient to work out only half of the shields (fig. 12; Pl. VII; VIII) but subsequent investigations showed that there is often some small differences between the right and the left side. It is better, therefore, to grind out the whole shield but also when using this method we are not always able to get out the whole system, as, for instance, in the ventral shield of *Poraspis polaris*, pores were found that do not pertain to the actual canals but seem to be openings for isolated sense organs (pits). Such pores are thus completely lost if the grinding method is used. The numerous preparations of the lateral line canals, undertaken with *P. polaris*, show some variations in details.

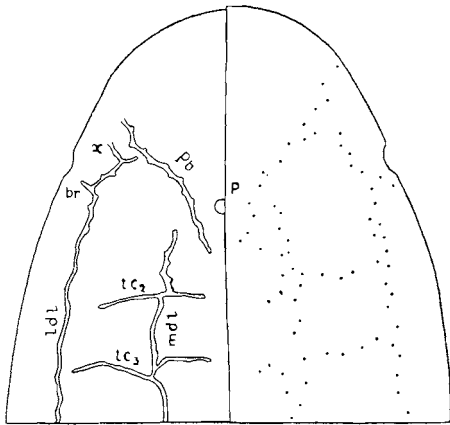


Fig. 12. *Poraspis polaris* forma *angusta* Kiær. An outline drawing, showing the variations in the course of the sensory canals in the front part of the dorsal shield. Explanations as in fig. 3. Right side shows the sensory canal pores, left — the course of the sensory canals. Frænkelryggen. Polaris horizon.

On the dorsal shield the two pairs of longitudinal lines are very regularly developed (fig. 3, a; 12; Pl. VII). The lateral dorsal lines run somewhat within the lateral margin and bend slightly in a downward direction into the post-branchial lobes (*ldl*, fig. 3, a; 12; Pl. VII; XI, 2). Just behind the orbits there issues from these a quite short branch in an outward direction (*br*). Inside the orbital notches the lines bend inwardly and coalesce with the pineal branches (*pb*). In rare cases a short branch running in an outward direction has also been found in front of the orbits (fig. 12, x).

The median dorsal lines are placed comparatively closely together in the middle of the shield (*mdl*, fig. 3, a; 12; Pl. VII; XI, 2). They often bend slightly inwardly, between the three most posterior transverse commissures, distinctly diverging farthest back, and near the commissures they are often somewhat deflected. They stop a little in front of the second transverse commissure and thus do not reach the pineal branches (fig. 3; 12; Pl. VII). These last begin just behind the pineal impression but without coalescing in the median line (*pb*, fig. 3, a; 12; Pl. VII; XI, 2). From here they go, strongly diverging, outwards, reaching the lateral margin a little in front of the orbital notches where they curve downwards into the preorbital processes. Judging from the condition in *Irregularaspis* (= *Dictyaspis* Kiær 1932, 1) these pineal branches represent the most anterior portions of the median dorsal lines and the remains of the pineal transverse commissure melted together.

Farther back, behind the pineal impression, are found four transverse commissures (*tc<sub>2</sub>*—*tc<sub>5</sub>*, fig. 3, a; 12; Pl. VII; XI, 2). They vary considerably. Most often they are discontinued in the median line and only rarely reach so far as to the lateral dorsal lines. Particularly the front commissure is often short (*tc<sub>2</sub>*).

As mentioned above, the pineal branches bend downwards into the preorbital processes and continue in the direction of the ventral shield which they reach at the anterior corners (fig. 3, b; Pl. VIII). The connection is here conducted through a little intermediate plate just behind the plate series of the oral area. These plates have not been

found in *Poraspis* but are known as isolated plates in the closely-related Genus *Homaspis* (Pl. XXX, 1, a; XXXIII, 1) and also in *Anglaspis* (Kiær 1932, 1). The plates in these forms have several line pores thus corresponding to the ventral lateral plates in *Pteraspis*, described in an earlier paper (Kiær 1927). From the anterior corners of the ventral shield, the lines continue backwards just inside the lateral margin similar to the dorsal lateral lines (*lvl*, fig. 3, b; 13; Pl. VIII). They are very constant in development, except at the extreme back where they may vary considerably, either reaching continuously the posterior margin of the shield, or being sometimes broken up in different ways. Both these ventral, and the above-mentioned dorsal, longitudinal lines stop short before they reach the posterior margin of the shields, as on their inner sides a quite narrow marginal dentine area is developed.

From the anterior corners of the ventral shield, besides the above-mentioned lateral ventral canals, some other lines run more or less transversally in an inward direction but without coalescing in the median line of the shield (*vtc*, fig. 3, b; 13; Pl. VIII). They probably represent the first ventral transverse commissure of the ventral shield and may possibly be combined with the short transverse branch (*br*) developed just behind the orbits on the dorsal shield (fig. 3, a, b; 12).

Seen behind the foremost branch, near the median line, are several pairs of short angularly arranged lines. The five first pairs of these ventral median lines ( $mc_1$ — $mc_5$ , fig. 3, b; 13; Pl. VIII) are placed closely together, and, after a somewhat larger interspace follow two-three similar pairs forming a posterior group ( $mc_6$ — $mc_7$ , fig. 3, b). These lines represent the median portions of the ventral transverse commissures, the short transverse canals inside the lateral longitudinal lines thus represent the lateral portions of the same commissures ( $lc_3$ — $lc_7$ , fig. 3, b; 13; Pl. VIII). Behind the first transverse commissure (*vtc*, fig. 3, b) there have been found by grinding, 5 pairs of these lateral portions of the transverse commissures, developed as quite short branches inside the lateral longitudinal lines but separated from them by short interspaces ( $lc_3$ — $lc_7$ , fig. 3, b; 13). The immediate connection between these lateral and median portions of the transverse commissures is broken, but can without difficulty be reconstructed, especially as these portions are partly connected by isolated pit-organs. The first pair of lateral transverse branches ( $lc_3$ ) is separated from the marked first transverse commissure (*vtc*) by a larger interspace and seems to correspond to the third pair of the short median lines ( $mc_3$ ). Further, the two ensuing pairs ( $lc_4$ ,  $lc_5$ ) may be combined with the fourth and the fifth pairs of median lines ( $mc_4$ ,  $mc_5$ ). The following pair of lateral transverse branches ( $lc_6$ ) seems to lack the corresponding median lines. On the contrary, to the posterior pair of the lateral transverse branches ( $lc_7$ ) corresponds a distinctly developed median lateral line ( $mc_6$ ). It is, therefore,

probable that several primary transverse commissures have become more or less reduced. In some cases the lateral parts of the transverse commissures have been lost, while in others, the median parts are missing and there are found, particularly in the posterior portion of the ventral shield, detached pits that may be supposed to represent the remains of such reduced lines. It is very probable, therefore, that, originally in the ventral shield were present ten such regularly segmentally arranged transverse commissures. This feature is particularly marked in the anterior portion of the shield, where impressions of the intersegmental branchiae have been found (*vbi* I—*vbi* IV, fig. 3, b; 13; Pl. XII, 2, 3). The ventral shield thus displays a more primitive feature than the dorsal shield where a far less number of the transverse commissures is preserved.

The lateral line pores are often very distinctly seen on the surface of the shields of well-preserved specimens (e. g. Pl. X, 1; XIII; XXXII, 2). They alternate most often on the right and the left side of the canals thus forming double series arranged particularly regular on the dorsal shield (Pl. XXXII, 2). In those cases when the surface is not to a certain degree eroded, the pores are more or less indistinct. They are very fine and situated partly in the middle of the ridges and partly between them, as can plainly be seen in several of the plates (Pl. III; X, 1; XIII; XXXII; XXXIV, 1—5). Sometimes the ridges are enlarged round the pores, and in a few cases the pores may be found in a small quite defined dentine area (e. g. Pl. XIII). Particularly marked are the pores of the pineal branches. The most anterior of these pores are very large and are often placed in such small dentine areas (Pl. X, 1). As is seen, the surface is here somewhat depressed round the opening, which is surrounded by a narrow elevated margin.

The impressions on the insides of the shields, particularly well-developed in the *Poraspidei*, give important information on the internal organisation of the animals. There occur in the Spitsbergen material not only a number of casts, that show more or less distinct moulds of these internal impressions (Pl. IX, 2; XXVI, 2), but also several shields displaying the inside in an excellent state of preservation (Pl. XI). Similar impressions have been found in several previously described forms of the *Cyathaspida* (Alth (1874), A. S. Woodward (1891), Jaekel (1926, 2), Leriche (1906), Stensiö (1926), Zych (1931) Brotzen (1933)).

The most numerous and important impressions in *Poraspis polaris* are seen on the inner side of the dorsal shield. Below the anterior portion of the rostral part just behind the maxillar brim are most often seen well marked impressions for the nasal sacs (*ns*, fig. 3, a; Pl. XI). They are very large extending far out at the sides, where they are often strongly widened. They are divided into two parts, right and left, the median border, however, may be rather indistinctly developed.

A very important question is, how these nasal sacs have opened outwards. As they are anteriorly bordered by the maxillar brim, which forms the upper mouth margin, there cannot here exist any opening unpaired or paired. The problem was solved when working out the ventral margin of the rostral part, distinct notches in the incurved preorbital processes (*n*, Pl. XXVI) became visible on both sides behind the maxillar brim. These notches, which are situated closely below the lateral portions of the nasal sacs, very probably represent the paired nasal openings lying widely apart.

Behind the posterior point of the rostral part is found the impression of the pineal organ (*p*, fig. 3, a;

Pl. IX, 2; XI). It is unusually large with almost the same width as the posteriorly situated impression of the brain. The outline of the impression is elliptical, most posteriorly it is quite shallow becoming deeper and deeper forwards. It gradually penetrates the different layers of the dermal skeleton, thus the anterior, deepest portion, showing a small, round, even area corresponding to the pineal macula of the surface, is only covered by a quite thin and originally wholly transparent dentine lamella (Pl. XXXV, 1, *p*). This fact in connection with the remarkable large size of the impression makes it not impossible that the pineal organ in these animals constituted a more or less well-developed unpaired eye.

Behind the pineal impression in the median line are often seen very distinct impressions of the posterior portions of the brain. First, a short brain-portion, which narrows strongly posteriorly (*mes*, fig. 3, a; Pl. XI) and then a very elongated rhombic impression (*md*, fig. 3, a; Pl. XI), that, gradually narrowing, can be traced backwards as far as the post-branchial part, sometimes even continuing into the latter. There can scarcely be any doubt as to these being the impressions of the

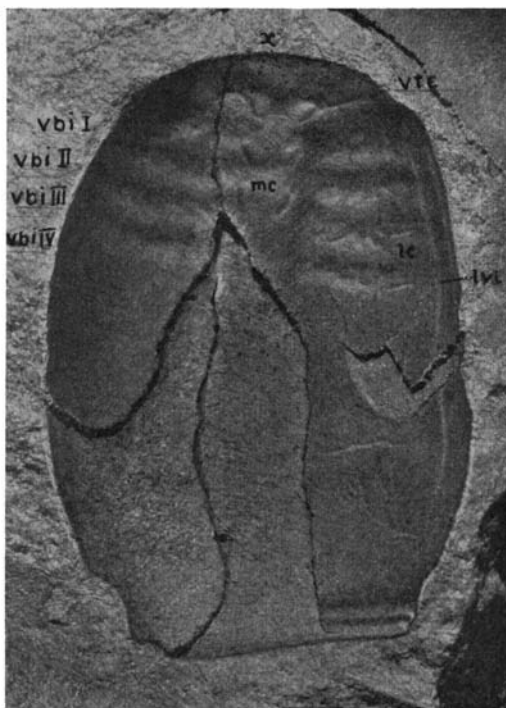


Fig. 13. *Poraspis polaris forma lata* Kiær. Natural cast of the ventral shield. Ca.  $\times 3$ . Explanations as in fig. 3. Frænkelryggen. Polaris horizon. Specimen D 067. Pal. Mus., Oslo.

mesencephalon and the myelencephalon (medulla oblongata). These impressions merge without any depression whatever, a fact indicating that no metencephalon has been developed.

For this interpretation of the brain impressions we have an additional support in the position of the large marked angular impressions of the anterior and posterior semi-circular canals (*sc*, fig. 3, a; Pl. IX, 2; XI). These are found on each side just outside the anterior narrow portion of medulla oblongata and are thus in relation to this posterior portion of the brain located likewise as in the other primitive vertebrates.

Outside all these impressions, are placed on each side seven elliptical impressions of the gills (*bi*, fig. 3, a; Pl. IX, 2; XI). These are most often arranged in a faint curve between the median line and the lateral margin. The most anterior ones are commonly directed somewhat forward and are large and deep, the posterior ones on the contrary, are directed slightly backward and are commonly smaller and less distinct. The breadth (in a longitudinal direction of the animal) is generally ca. 1,5 mm, the length about 3 mm. The impressions are not smooth. Distinct transverse or more irregular grooves are seen to be developed in well-preserved specimens.

Outside these branchial impressions just inside the margin of the branchial part, is found a series of small impressions, which have been called the marginal branchial impressions (*mbi*, fig. 3, a; Pl. IX, 2; XI). They are situated in a narrow border area, which, on the inside of the shield, is usually faintly depressed. To each one of the internal elliptical impressions corresponds either a single or a double one of the small marginal impressions. They may be more or less distinct in the anterior part of the shield, becoming less obvious in the posterior part.

On the inside of the ventral shield are also seen anteriorly four to five pairs of branchial impressions (*vbi*, fig. 3, b; 13; Pl. XII, 2, 3). They are much longer and not so elliptically formed as the dorsal ones and have a more straight transverse course, but are otherwise similarly developed. In front of these, near the median line, are seen two small often angularly situated impressions, that seem to be constant (*x*, fig. 3, b; 13; Pl. XII, 3). The interpretation of these small anterior median impressions is quite uncertain. In addition to the branchial impressions are often seen impressed lines corresponding to parts of the lateral line system (fig. 13). They are particularly interesting as they show that the lines have a fixed relation to the inner organs and to the body segments. On the dorsal shield the two median longitudinal lines are placed just inside the branchial impressions, where the lateral lines go between these and the small marginal branchial impressions (fig. 3, a; Pl. XI). In both places the dermal skeleton is thickened. The second transverse commissure goes always regularly across the semi-circular canals and farther outward between the second and the third pair of



the branchial impressions ( $tc_2$ , fig. 3, a; 12; Pl. XI). The third commissure runs between the fourth and the fifth pair and the fourth behind the seventh pair of the branchial impressions ( $tc_3$ ,  $tc_4$ , fig. 3, a; Pl. XI). This last commissure runs to the branchial sinus and thus corresponds to the limit between the branchial and the post-branchial parts of the dorsal shield (fig. 2 A).

On the ventral shield the foremost commissure runs just in front of the first pair of the branchial impressions ( $vtc$ , fig. 3, b; 13; Pl. VIII; XII, 2, 3). To each of these corresponds a pair of the short median lines which, therefore, must be segmentally arranged ( $mc_1$ - $mc_4$ , fig. 3, b).

Of the short transverse lateral branches the two foremost pairs are seen to correspond to the third and fourth branchial impressions ( $lc_3$ ,  $lc_4$ , fig. 3, b), while the two foremost pairs of the latter lack the corresponding transverse lines, which, apparently, must have been reduced.

Altogether, these conditions seem to indicate that the transverse commissures of the lateral line system have originally been pronouncedly segmentally developed and have only later become more or less reduced.

Finally, it may be mentioned that, below the posterior margin of both the dorsal- and ventral shields, a narrow, but distinct marginal furrow is developed to which probably the first series of the body scales was attached (Pl. IX, 2; XI, 1; XII, 3).

The structure of the skeleton has been closely studied in this species (Pl. XXXV; XXXVI; XXXVII; XXXVIII, 1). Unfortunately, the rich material from the green rock (Polaris horizon) is not well adapted for a microscopical examination. It has undergone considerable transformations, the finer details have disappeared and the substance of the skeleton is often seen to have been corroded, the basal layer in particular having been destroyed.

The state of preservation is better in the red calcareous rocks of the Primaeva horizon. In the first instance microscopical sections were examined, and, in addition, excellent information on the structure was obtained in studying the strongly weathered pieces of the dermal skeleton.

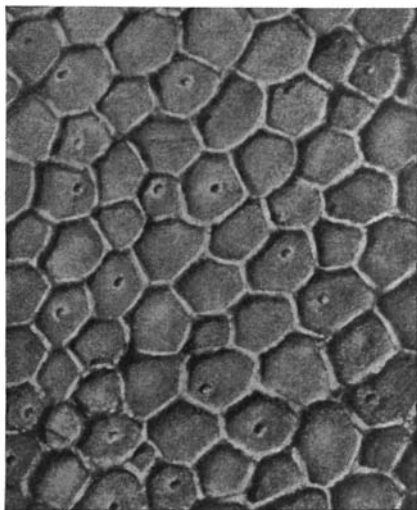


Fig. 14. *Poraspis polaris* Kær. A weathered part of the shield, showing the floor of the concellae with the pores running through the basal layer. Ca.  $\times 40$ .

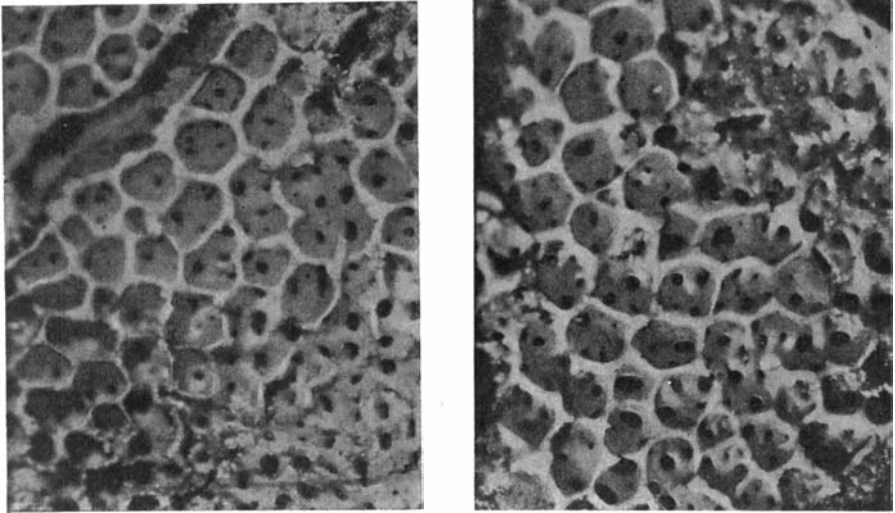


Fig. 15. *Poraspis polaris* Kiær. A weathered part of the shield from the inside, showing the roof of the cancellae with the pores running to the pulpa cavities of the dentine ridges. In the upper left corner — a sensory canal in longitudinal section. Ca.  $\times 40$ .  
 Fig. 16. *Poraspis polaris* Kiær. A part of the rostral division of the shield, weathered, from the inside, showing the roofs of the cancellae and the pores running to the pulpa cavities in the dentine ridges. Ca.  $\times 40$ .

The thickness of the dermal skeleton varies considerably in the different portions of the shield (from 0,4—0,65 mm) and attains its maximum in the middle of the dorsal shield. The post-branchial lateral lobes and the lateral areas of the branchial part on the other hand display a marked thin skeletal covering (Pl. XXXVI, 4, 5).

The basal layer (Pl. XXXV; XXXVI, 3) is comparatively thin even where it is not corroded (0,05—0,08 mm). The lamellar structure may now and then be seen. The cancellous layer is very mighty and regular (fig. 14, 15, 16, 17; Pl. XXXV; XXXVI; XXXVII). Along the margins only it becomes thinner and more irregularly constructed (Pl. XXXV, 3; XXXVI, 3). In all other places it consists of the remarkably regular cancellae of a more or less hexagonal prismatic form (Pl. XXXVII) with flat floor and most often with vaulted roof (fig. 14, 15, 16; Pl. XXXV, 2, 3, 4; XXXVI, 1). The cancellae are comparatively very regular but, of course, not nearly as regular as the cells of a honeycomb. Their shape and size exhibit some degree of variation as, among the common cancellae with a size of 0,3—0,4 mm, there are some considerably smaller ones, which may sometimes be quadrangular, pentagonal or of a more rounded shape (fig. 14, 15, 16; Pl. XXXVII) seen in cross-section. The thickness of the walls is about 0,04—0,05 mm (Pl. XXXV; XXXVI; XXXVII). From the cancellae vertical canals go downwards



Fig. 17. *Poraspis polaris* Kiær. The cross-section of the ventral shield. Frænkelryggen. Ca.  $\times 10$ . Stensiö phot.

throughout the basal layer. A few strongly eroded pieces (fig. 14) show these very distinctly. There seem only to be one such canal in each cancella and for many cancellae such canals are completely missing. There are also connecting-canals between the single cancellae, they seem mostly to perforate the upper portions of the walls (Pl. XXXV; XXXVI). The cancellous layer occupies the largest portion of the skeleton. In a section of the dorsal shield with a thickness of 0,56 mm the cancellous layer measures 0,4—0,44 mm, whereas the corresponding dimensions of the basal layer are merely 0,04—0,05 mm and the thickness of the reticular layer and the dentine layer is 0,085—0,12 mm. Another section through a ventral shield with a thickness of 0,56 mm displayed a thickness of the cancellous layer of 0,35 mm, while that of the basal layer was only 0,087, and of the two upper skeletal layers, 0,13 mm together.

Uppermost in the cancellous layer are found the canals for the lateral line system (*lc.* fig. 15; Pl. XXXV, 1, 4; XXXVII, 2). These have a rounded form in cross-section, with a diameter of about 0,3 mm and are mostly supported by one of the cancellae walls (Pl. XXXV, 1, 4). The pores, that in great number go from the canals upward to the surface, are sometimes to be seen in microscopical sections (Pl. XXXV, 1; XXXVII, 2, *po*).

As already mentioned, the cancellous layer has changed along the margin of the shields, where the skeleton grows thinner. This feature is particularly clearly seen along the margin of the branchial part. Here is developed a system of more crowded vascular canals irregularly arranged (Pl. XXXVI, 3, 4, 5). This is equally the case along the posterior margin of the shields.

The cancellous layer is covered by the reticular layer and this again by the dentine layer with its dentine ridges that form the surface (Pl. XXXV; XXXVI; XXXVII).

The reticular layer is quite thin, the thickness being only 0,04—0,05 mm. This layer is perforated by rows of vertical short canals,

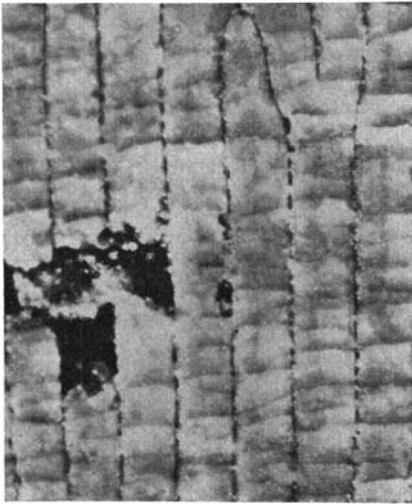


Fig. 18. *Poraspis polaris* Kiær. Surface of the dorsal shield, showing the openings between the dentine ridges. Ca.  $\times 40$ . Frænkelryggen. *Poraspis* horizon. Specimen D 618. Pal. Mus., Oslo.

openings upwards into the pulpa canals of the dentine ridges. These canals are easily seen both in vertical, longitudinal, transverse and horizontal microscopical sections (Pl. XXXV; XXXVI; XXXVII). The best pictures, however, are obtained from shields weathered out by erosion by nature itself (fig. 15, 16). The width of these canals varies considerably. Finer canals going in other directions, horizontally or obliquely, are sometimes found. The walls of this reticular layer has a lamellar structure similar to the walls in the underlying skeletal parts. No traces of bone cell lacunes have ever been observed. The substance of the skeleton goes continuously into the dentine ridges, which are very

regular. The thickness of this superficial layer exceeds in most cases somewhat that of the underlying reticular layer. The ridges are, as we have seen, exceedingly regular with almost flat surface (Pl. XXXV; XXXVI). They join together uppermost, where the breadth is largest and grow narrower downwards. There are in this manner formed between them fine tubular canals of a pear-shaped transverse section, the so-called intercostal grooves (Stensiö's "mucous grooves" 1932), (Pl. XXXV, 1, 2, 4; XXXVI, 1, 2, 4, 5; XXXVII, 2, *ig*). The dentine ridges have a marked pulpa canal which, as mentioned, is connected with the cancellae by numerous openings arranged in series (Pl. XXXV, 1, 2, 3, *pc*, 4; XXXVI). From the pulpa canals there run many fine dentine tubules upwards into the upper portions of the ridges, which seem uppermost to have a quite thin transparent covering probably consisting of enamel (Pl. XXXVI, 1, 2), which, however, is usually difficult to discern. In this manner the ridges in cross-section are quite similar to the dentine formations (teeth and scales), we know in the *Elasmobranchii* and in the higher fishes. The pulpa canals are by numerous, regularly arranged, fine transverse canals connected with the intercostal grooves (Pl. XXXVII). These grooves again open upwards between the dentine ridges by means of fine, narrow pores, usually invisible in the common state of preservation, but often easily seen in favourably weathered surfaces (fig. 18). The cancellae, as will be understood, are much broader than the dentine ridges and do not show any definite relation to the latter.

In the dorsal shield to each cancella corresponds 2—3 ridges (Pl. XXXV), in the ventral shield apparently less, 1—2 (Pl. XXXVI, 1, 2). In the latter, the vertical canals going from the cancellae upwards into the pulpa grooves, seem, as a rule, to be slightly wider.

The structure of the maxillar brim has already been briefly mentioned (pag. 44). From fig. 1 Pl. XXXVIII will be seen, that the outermost dentine ridges of the maxillar brim, are more normally developed, but grow quite sharp and tooth-like in cross-section. In working out the brim we find, however, that the ridges are not dissolved but have got strongly tubercular margins. Innermost, however, they are possibly broken up into fine tooth-like tubercles arranged in rows. The intercostal grooves are quite open. In the figured longitudinal section (Pl. XXXVIII, 1) the inner skeletal layers have been crushed, but from other microscopical sections can be seen, that the cancellous layer is here irregularly vacular with large cavities.

The structure of the skeleton with regard to the marginal areas has already been sufficiently dealt with (pag. 44). The structure of the pineal covering has also been briefly mentioned (pag. 41). The deep pineal impression is, as is shown in Pl. XXXV, 1, merely covered by a quite thin and transparent lamella which corresponds to the upper portions of the dentine ridges. There have not been developed any dentine tubules here.

#### Forma lata.

(Pl. V; VI; VIII; XI, 1; XII, 1, 3; fig. 19).

In specific characteristics (pag. 59) have already been pointed out the main features distinguishing the lata form of *P. polaris*. It is particularly the B. L. Ind., which is considerably greater than in the forma angusta: 60—65 for the dorsal- (Pl. V) and 66—71 for the ventral shields respectively (Pl. VI). Further, it must be emphasized that the total length is in most cases somewhat less: 29—36 mm. The anterior portion of the dorsal shield is comparatively very broad and the orbital

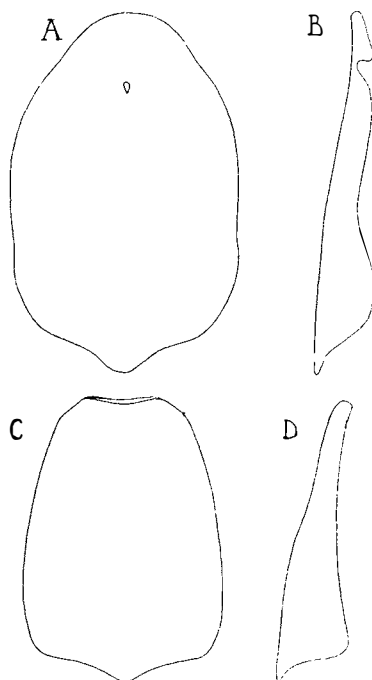


Fig. 19. *Poraspis polaris* forma lata Kiær. An outline drawing of the dorsal shield from above (A) and side (B) and ventral shield from above (C) and side (D). Ca.  $\times 1,5$ .

breadth thus considerably larger than in the *angusta* form. The rostral part conveys an impression of being short and flat (Pl. XII, 1). As for the other structural features they are the same as those described for the *angusta* form. The superficial sculptures agree closely, and the dentine rib pattern seems to vary similarly in both forms. It is, therefore, very natural to regard these differences as secondary generic characteristics, an interpretation which was treated more detailed in a previous chapter (pag. 53). It must, however, be pointed out, that in the *Polaris* horizon there have been found a few dorsal shields for which it is not easy to determine whether they pertain to the *angusta* or to the *lata* form. As an example can be mentioned the specimen D 084 with a length of 36,5 mm and a B. L. Ind. of 57, thus to a certain degree occupying an intermediate position.

#### **Other Portions of the dermal Skeleton.**

In addition to the large shields there have, particularly in the *Polaris* and the *Primaeva* horizons, been found other portions of the dermal skeleton as, for instance, the elongated branchial plates and various body scales. As, however, it cannot be determined with certainty, which of these pertain to the *P. polaris* and which pertain to the closely related forms *P. elongata* and *P. brevis* occurring in the same horizons, these skeletal remains will later on be described in a separate chapter (pag. 108).

#### **The Forms of *Poraspis polaris* from the other horizons of the upper part of the Frænkelyggen Group.**

As already mentioned, this species occurs also in other horizons of the upper part of the Frænkelyggen Group. Of particular interest is the form of which there has been found a series of well preserved specimens in the somewhat older *Primaeva* horizon (Pl. XIII). It is mostly somewhat smaller than the leading form of the *Polaris* horizon. The total lengths of six specimens of the *angusta* form thus being from 31 to 32,5 mm, (average 32), whereas the corresponding measurements of the specimens from the *Polaris* horizon are from 35,5 to 50,5 mm (average 38), as will be seen, not a slight difference. There is also present a specimen of the *lata* form with total length 31,5 while the *lata* form of the *Polaris* horizon is mostly somewhat larger. Further, the rostral pattern is constantly somewhat fan-shaped (Pl. XIII), whereas the most common pattern of the leading form is distinguished by almost parallel ridges. As, however, there have been found a few specimens with equally short total length in the *Polaris* horizon also, and, further, as a fan-shaped rostral pattern is now and then occurring in this younger horizon as well, there cannot be attached

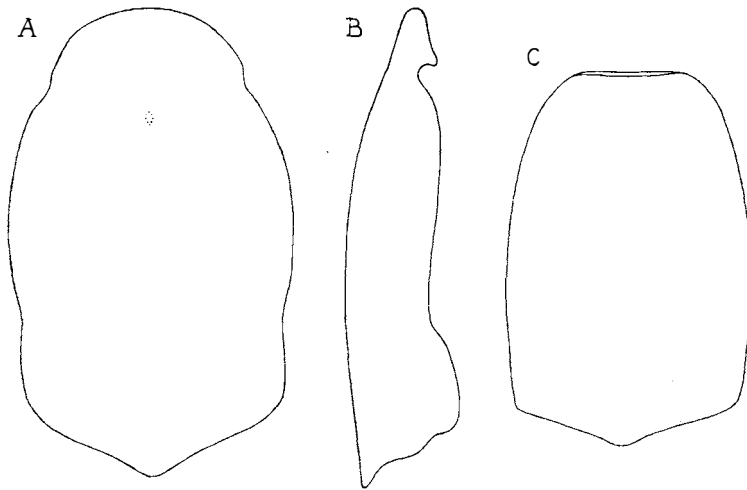


Fig. 20. *Poraspis brevis* n. sp. An outline drawing of the dorsal shield from above (A), from side (B) and ventral shield from above (C). Ca.  $\times 2$ .

a very great importance to these facts, particularly as the B. L. Inds. and the R. Inds. as well as the general morphological features closely agree. This form therefore, has neither been established as a separate species, nor as a variety.

The figured specimen shows a finely-developed elliptical pineal macula (Pl. XIII; XXXIV, 1). Of special interest is the previously mentioned specimen with the dorsal and the ventral shields preserved in a natural connection (pag. 64), which thus allows us to determine the relation between the length of these shields.

*Poraspis polaris* also occurs, although seldom, in the higher horizon (Anglaspis horizon). The few representatives, found in this horizon do not, however, seem to deviate from the leading form.

Remarks. *Poraspis polaris* is, as mentioned, one of the leading forms from the upper portion of the Frænkelryggen Group. It is closely related to the small *Poraspis brevis*, which is not very seldom found in the Primaeva and the Polaris horizons. *Poraspis intermedia* is also a closely allied form. More deviating is *Poraspis elongata*, which most often appears together with *P. polaris*. This *P. elongata* pertains to another line having a more elongated and a narrower rostral part. In the Ben Nevis Group all these small *Poraspis* forms have disappeared and in their place are found larger forms of more elongated shape. Of these latter *Poraspis cylindrica* seems to be most closely related the *polaris* form, although the ventral shields are quite diverging.

Of previously described Central-European *Poraspis* forms, *P. barroisi* Leriche (1906) is without doubt closely allied to *P. polaris*. There

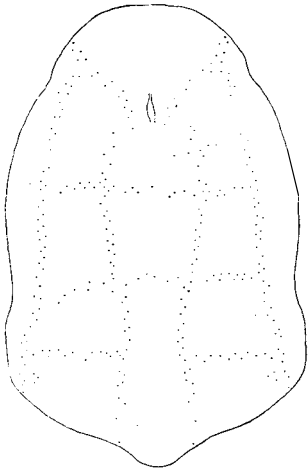


Fig. 21. *Poraspis brevis* n. sp. An outline drawing of the dorsal shield, showing the pores of the lateral line system. Ca.  $\times 2,5$ .

is a possibility that *P. barroisi* Leriche is an intermediate form between *P. polaris* and *P. cylindrica*.

Moreover, some of the *Poraspis* forms from Podolien, depicted and described by Zych (1931) are certainly also closely related to our form.

*Poraspis brevis* nov. sp.

(Pl. XIV; XV; fig. 20; 21; 22).

Specific characteristics. A minute form with total length of dorsal shield merely reaching 25–28 mm. The angusta and the lata-forms have nearly the same B. L. Inds. as *P. polaris*. The rostral part very short and broad with a R. Ind. somewhat surpassing 14. The ventral shield short and broad (the lata form) with a total length of 21,5–24,5 mm. The course and pattern of the dentine ridges, the development of the lateral line system (fig. 21) and other morphological features nearly as in *P. polaris*.

The holotype is the specimen D 304; it is a dorsal shield pertaining to forma lata (Pl. XIV).

Occurrence and material. This small form has been found in the Primaeva horizon of Frænkelyggen, where it is fairly common. From this horizon a well preserved material of dorsal and ventral shields has been brought together, nearly all these shields pertaining to the broad form (forma lata). *P. brevis* is also found in the Polaris horizon, but here it is rare. Altogether there are found fifteen dorsal and ventral shields in our material.

General description. Any thorough general description is not required, as *P. brevis* in most relations agrees closely with *P. polaris*, only displaying a few conspicuous differences between them. In the first instance with regard to size, which is considerably smaller in *P. brevis* than in *P. polaris* this fact being most pronounced in the Polaris horizon. All the well preserved specimens of *P. brevis* which were measured belong to the lata form; for comparison, we may, therefore, have to deal with the lata form of both species.

I	Total length of <i>P. brevis</i> in the Primaeva horizon..	25,5–28,5	mm
	» » » <i>P. polaris</i> (f. lata) » »	31,5	mm
II	» » » <i>P. brevis</i> in the Polaris horizon....	25–26	mm
	» » » <i>P. polaris</i> (f. lata) » »	.....	33,5 (average)



Another difference consists in the fact that the rostral part of *P. brevis* is much more broadly rounded than in *P. polaris* (forma lata) (compare Pl.V and XIV). This rostral part therefore strikes one as being considerably shorter, and the R. Ind., in fact, is only 14,3. In other respects the structure is of an astonishing conformability in both species, which

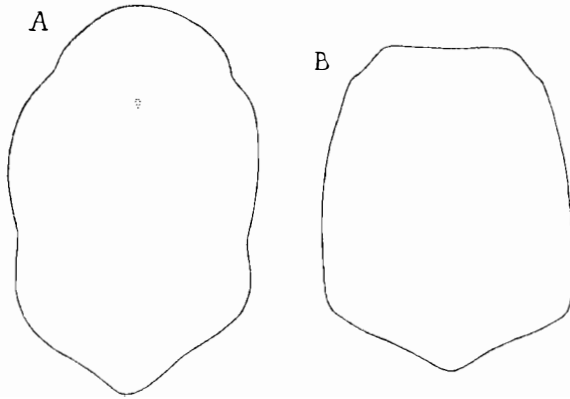


Fig. 22. *Poraspis brevis* n. sp. An outline drawing of the dorsal (A) and ventral (B) shields, collected by Hoel 1909–10. Ca.  $\times$  3.

fact applies both to the B. L. Ind. and to the other morphological features. The B. L. Ind. of the dorsal shield in the Primaeva horizon is thus 56–65 and in the Polaris horizon 60–66, while that of the ventral shield is 69–70. A dorsal shield and a ventral shield brought together by A. Hoel 1909–10 convey an impression of being still shorter (fig. 22). The last of these even with a B. L. Ind. of 77.

Remarks. *P. brevis* is, as will be seen, so highly reminiscent of *P. polaris*, that one would be apt to consider it as a juvenile form of the latter, the more so as it occurs in the same two horizons in which *P. polaris* is particularly prevailing. As it is still, however, a subject of great doubt, how the shields have been growing in the *Cyathaspida*, this form must be placed as a separate species, particularly marked by its minute size.

### *Poraspis intermedia* nov. sp.

(Pl. XVI; XVII.)

Specific characteristics. A comparatively minute form with a total length of the dorsal shield 26–28 mm. Probably also here an angusta and a lata form are known the former with B. L. Ind. 53 (Pl. XVI), the latter with B. L. Ind. 65 (Pl. XVII). The rostral part very short (R. Ind. about 14,5), not compressed in front of the orbital notches. The branchial part comparatively long, whereas the post-branchial part is short with short post-branchial lobes. In other respects this form is most reminiscent of *P. brevis*. The ventral shield is unknown.

The holotype is specimen D 1308, a dorsal shield, which is interpreted as an angusta form (Pl. XVI).

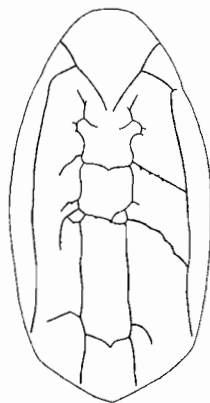
Occurrence and material. Of this species there have only been found two dorsal shields in the Anglaspis horizon of the Frænkelryggen, the species thus pertaining to the upper portion of the Frænkelryggen Group.

General description. The one of the two dorsal shields (holotype) found is an angusta form (Pl. XVI), the other a lata form (Pl. XVII). As the specimens deviate considerably from each other particularly with regard to the shape of the body, they ought to be dealt with separately.

The angusta form is represented by the holotype figured in Pl. XVI. It is a posteriorly imperfect dorsal shield with a very well-preserved surface. On the concave cast the total length can be estimated at 28 mm. The breadth being 16 mm, we have a B. L. Ind. of 53, thus somewhat exceeding that of *P. polaris*. The shield is evenly vaulted and is particularly distinguished by the rostral part being very uniformly rounded and not contracted in front of the orbital notches. The lateral margin of the shield thus forms a very evenly curved line only with a slight contraction in its posterior portion near the branchial sinus. The sculpture of the surface does not deviate very much from that which may be found in *P. brevis* and *P. polaris*. The rostral pattern is faintly fan-shaped with numerous interpolated ridges; most anteriorly, is seen a narrow curved area with partly dissolved ridges, running conformably to the margin. The pineal macula is short and continues in a forward direction with a single ridge, a feature, that may also be found in *P. polaris*.

The lata form. Another dorsal shield (Specimen D 293) from the same horizon may probably be interpreted as being the lata form of the species (Pl. XVII). This dorsal shield is somewhat shorter and considerably broader than that of the holotype namely 26 and 17 mm respectively, the B. L. Ind. consequently being 65; the specimen is, however, more flattened than the holotype, and the index number is thus somewhat too high. The species is otherwise very similar to the angusta form, particularly with regard to the even curve of the lateral margin and the short post-branchial lobes. The rostral part, in consequence of its large width, is getting a slightly different shape and is not quite as evenly curved. The rostral pattern strikes one as being rather different from that in the angusta form. It is more strongly fan-shaped with more continuous ridges and shows an unusually broad anterior area with transverse ridges. To judge by the strong variation, which has been ascertained with regard to the rostral pattern in *P. polaris*, this special pattern need not, however, be taken for anything else than an individual variation. The lateral line pores are very well preserved and show that the 3rd and 5th transverse commissures are well developed and reach the lateral longitudinal lines (Pl. XVII).

Fig. 23. *Poraspis subtilis* n. sp. An outline drawing of the dorsal shield, showing the course of the lateral line system. Ca.  $\times 2$ . Frænkelyggen. Plant horizon. Specimen D 1904. Pal. Mus., Oslo.



Remarks. These two dorsal shields display great similarities, and as they are also known from one, and the same horizon, it seems most natural to interpret them as being an angusta and a lata form of the same species. One must remember in comparing the figures, that the one in Pl. XVII has, unfortunately, been somewhat more enlarged than the figured of the holotype in Pl. XVI, while in an equal enlargement the conformability would be more conspicuous. The species is very closely related to *P. brevis* and may possibly be taken as a descendant of this latter occurring in the younger Anglaspis horizon.

*Poraspis subtilis* nov. sp.

(Pl. XXI, 1; XXII; fig. 23).

Specific characteristics. A small and comparatively elongated form. Total length of the dorsal shield 26 mm, maximum breadth (in the middle) 13,5 mm, B. L. Ind. 52. This shield has an even elliptical shape and narrows fairly strongly in a forward direction towards the narrow rostral part. The rostral pattern is distinguished by a pronouncedly fan-shaped development of the dentine ridges running conformably to the margin (Pl. XXII). The rostral line system is marked by peculiar curvatures and branchings of the median longitudinal lines (fig. 23). The ventral shield shows anteriorly an unusual faint diverging of the dentine ridges.

The holotype is specimen D 1904 representing a dorsal shield of probably an angusta form (Pl. XXII).

Occurrence and material. Of this species there has merely been found a single very fine dorsal shield in the Plant horizon of Frænkelyggen. This pertains to the lower portion of the Frænkelyggen Group. A fragment of a ventral shield from the same horizon probably also belongs here.

General description. The holotype is very finely preserved. The dermal skeleton is almost transparent, so much so that one may in alcohol see many features of the interior structure: thus without preparation, it has been possible to ascertain the development of the lateral line system (fig. 23).

The usual shape of the dorsal shield has been sufficiently determined under specific characteristics, the most characteristic

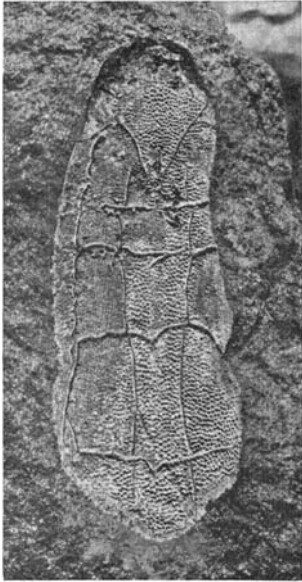


Fig. 24 A. *Poraspis* cf. *elongata* n. sp. Dorsal shield weathered, from the inside and showing the course of the lateral lines. Ca.  $\times 1,7$ . Frænkelryggen. Primaeva horizon. Specimen D 1877. Pal. Mus., Oslo.

feature being the uniformly elliptical shape and its comparatively narrow rostral part. Moreover, the rostral pattern seems to be rather characteristic of this species. The fan-shaped arrangement of the ridges also continues behind the pineal branches. In the median portion of the shield is seen a marked curve of the ridges in an outward direction, thus interrupting the regular longitudinal arrangement of the dentine ridges usual in this portion of the shield. The pineal macula is elongated and anteriorly pointed. The lateral line system strikes one as being the most pronounced feature. As shown in fig. 23, it is particularly the median longitudinal lines that display traits diverging from the general type in *Poraspis*. These lines are seen to have in their anterior portions peculiar out-curvings somewhat reminiscent of certain variations in *Irregularaspis* (= *Dictyaspis* Kiær 1932, 1). The transverse commissures are also distinguished by their irregularities.

The fragmentary ventral shield from the Plant horizon (Pl. XXI, 1) must in all probability be assigned to this species. The dentine ridges show an uncommonly uniform

longitudinal course with very faint divergences of the most anterior portions.

Remarks. *P. subtilis* is interesting by the fact that it is the oldest species of *Poraspis* in a good state of preservation from the Red Bay Series. It occupies an exceptional position by its peculiar lateral line system of which some features are reminiscent of *Irregularaspis* (= *Dictyaspis*). The development of the pineal branches in relation to the median longitudinal lines, however, is widely different from *Irregularaspis* and agrees with *Poraspis*. The shape of the dorsal shield is most suggestive of that in the later and larger form *P. elongata*. It is, however, with our scarce material, impossible to ascertain if there has been any closer relation between these two forms.

#### *Poraspis elongata* nov. sp.

(Pl. IX, 3; X, 2; XVIII; XIX; XX; XXI, 2; XXVII, 1; fig. 24 A; 24 B; 25; 26).

Specific characteristics. A comparatively small form with total length of the dorsal shield 36—40 mm. With absolute certainty, it is hitherto known only in the angusta form. The dorsal shield more

elongated than that in *P. polaris*, forma angusta, and narrower in a forward direction. The B. L. Ind. most often between 44 and 46. The post-branchial part long. The dentine ridges show as a rule a pronouncedly longitudinal course, often, however, with some whirls in the anterior portion of the shield. Most characteristic is the faintly fan-shaped rostral pattern with slightly curved lateral ridges (Pl. X, 2). The pineal macula elongated and often very narrow (Fig. 24, B).



Fig. 24 B. *Poraspis elongata* n. sp. The pineal pattern. Specimen D 141 (Holotype). Pal. Mus., Oslo. ca.  $\times 10$ .

The ventral shield more elongated and elliptical than in *P. polaris*. The total length usually about 30, B. L. Ind. from 54 to 56. The ridge pattern nearly similar to that in *P. polaris* (Pl. XVIII, b; XX).

The lateral line system as in *P. polaris* (fig. 24, A).

The holotype is the specimen D 141 a (fig. 24, B; Pl. X, 2; XVIII, a; XIX).

**Occurrence and material.** This species is quite common in the Polaris horizon of Frænkelyggen, where a very good material, particularly of dorsal shields, has been collected. All in all, there have been collected here during the expeditions of 1925 and 28 17 dorsal and 10 ventral shields. The species has also been found in the Primaeva horizon, although it seems here to be very rare (2 specimens from the expedition of 1928).

**General description.** To the features given under specific characteristics may be added some details. The species may most often be distinguished from the nearly equally sized *P. polaris* by the more elongated shape of the shields. The dorsal shield thus shows a B. L. Ind. of 43,5—47 (most often 44—46) whereas that of the dorsal shield in *P. polaris* is 45—51 (average about 50). The corresponding number with regard to the ventral shield is 54—56, while, for the ventral shield in *P. polaris*, it is about 60. Further, the dorsal shield is narrower in a forward direction, and the rostral part is much longer with a R. Ind. of as far as 18, whereas the corresponding measurement of this part in *P. polaris* does not exceed 15—16. The rostral pattern seems to be more constant and quite characteristic (Pl. X, 2; XXI, 2). In cases when this pattern is typically developed, which is the fact in the holotype, it is easily discernible from the general *polaris* pattern (Pl. X). This typical pattern is faintly fan-like, the ridges growing more and more curved towards the sides, where they go conformably



Fig. 25. *Poraspis elongata* n. sp. The variations in the rostral pattern. In front the maxillar brim (MB) is clearly seen. Ca.  $\times 5$ . Frænkelryggen. Polaris horizon. Specimen D 266. Pal. Mus., Oslo.

to the margin. Most in front is seen a narrow area with more or less dissolved ridges. The pineal macula is narrow and often faintly marked (holotype Pl. X, 2; fig. 24 B). Behind this macula there is in the holotype developed characteristic whirls (Pl. XIX). The material shows, however, that there are present considerable variations, also with regard to the configuration of the ridge pattern. In some individuals the course of the ridges is more regular, nearly as in *P. polaris*; in others, the whirls may be more marked and may be found developed even in

the rostral part (fig. 25). The rostral pattern is also seen to vary somewhat, yet apparently not so much as is the case in *P. polaris*.

The most typical ventral shield is the one figured in Pl. XVIII, b. The shape of this one agrees well with that of the dorsal shield, as it also narrows considerably in a forward direction. The specimen figured on Pl. XX is of a more equal breadth, in spite of the fact that it must be regarded as belonging to this species. The anterior portion with the anterior articular area is unusually well preserved (Pl. XX, 3). The ridges of the ventral shield are of a very regular, longitudinal course faintly diverging near the anterior margin. The general structure is in other respects very similar to that described in *P. polaris*. Also the development of the lateral line system closely agrees with that in this species (fig. 24 A, 26). Remarkably enough, no wholly typical lata form has been found. There is, however, a possibility that the dorsal shield figured on Pl. XXVII, fig. 1, is a representative of such a form. Its shape agrees well with *P. elongata*, but it must be pointed out that both the rostral pattern and the pineal macula are more in accordance with those in *P. polaris*.

Two representatives of *P. elongata* have also been found in the Pri-maeva horizon (fig. 24A). From the still older Corvaspis horizon is present a cast of a dorsal shield which possibly also belongs here (Pl. XXI, 2).

Remarks. *Poraspis elongata* with its comparatively slender shape and with its elongated rostral part is the species in the Frænkelryggen Group, which is most suggestive of the larger elongated forms found in the upper Ben Nevis Group.

*Poraspis rostrata*, nov. sp.

(Pl. XXIII; XXIV; XXV; XXXIX;  
fig. 27; 28 A; 28 B).

## Specific characteristics.

A comparatively large and elongated form. Only the angusta form is known. It is, however, not impossible that a specimen from horizon J (D 126) represents a fragment of a lata form belonging to this species. The dorsal shield has a total length of 45—51 mm with branchial breadth 20—23 mm, thus a B. L. Ind. of 44—45. The rostral part very elongated and anteriorly evenly bounded with R. Ind. about 20. The branchial part faintly developed, the post-branchial part very long with long lateral lobes (Pl. XXIII). The rostral



Fig. 26. *Poraspis elongata* n. sp. The course of the lateral lines in the front part of the dorsal shield. Ca.  $\times$  4,5. Frænkeiryggen. Polaris horizon. Specimen D 144. Pal. Mus., Oslo.

pattern of the dentine ridges seems to be rather constant (Pl. XXIV), and consists of regular somewhat fan-like arranged ridges, which near the lateral margin, curve more and more conformably to this and form, most in front, two symmetrical curves just behind the narrow area of the transverse marginal ridges. Pineal macula varying, most often longishly elliptical (fig. 28 B). The ventral shield very elongated with a total length of 38—42,5 and a B. L. Ind. of 45—47. The anterior portion of the shield is very flat and its maximum breadth is situated somewhat behind the middle (Pl. XXV). The lateral line system is distinguished by the fact that the median longitudinal lines on the dorsal shield coalesce with the pineal branches, which are also nearly united in the middle of the shield (fig. 27, A).

The holotype is the specimen D 124, figured on Pl. XXIII and XXIV, 2.

Occurrence and material. This form occurs commonly in the lower part of the Ben Nevis Group, particularly in the horizon A. A rostral fragment is also found in the horizon J, and several fragments have been brought together from the layers lowest down in the Mt. Pteraspis. The material consists of a few complete specimens of dorsal and ventral shields and a quantity of fragments, most of which being collected during the expedition of 1909—10.

General description. The dorsal shield seems to have been very uniformly vaulted with a faintly developed branchial part. The

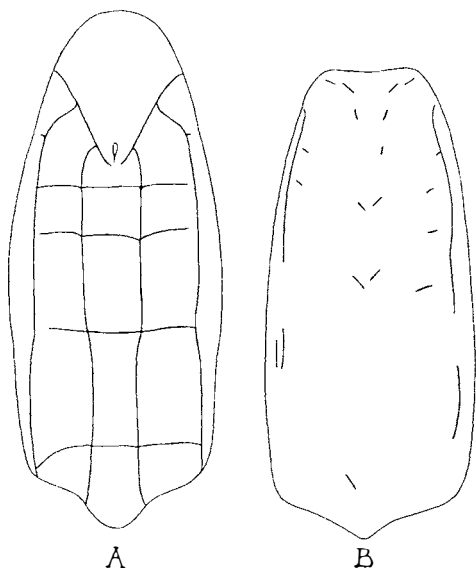


Fig. 27. *Poraspis rostrata* n. sp. An outline drawing of the dorsal (A) and ventral (B) shields, showing the course of the lateral lines. Ca.  $\times 1,5$ .

profile is even and flat. Sometimes the shield has been strongly flattened by pressure, which is the case in the specimen the rostral part of which has been figured in Pl. XXIV, 1. The measurements have been given above under specific characteristics. From the lower layers of the Mt. Pteraspis a portion of a very large dorsal shield is in hand, where the distance from the pineal macula to the rear end is 45 mm, corresponding to a total length of about 60 mm. That this should actually be a *P. rostrata* is, however, uncertain, the specimen may also be derived from higher horizons and may belong to *P. magna*,

which often displays a corresponding size. Under specific characteristics have also been described the general rostral pattern of this species. Pl. XXIV conveys a better idea of this pattern than any description can give. It seems to be constant in the essential features. The material, however, is too scarce to decide the breadth of variations. As previously pointed out, we have in *P. polaris* found a variation which almost entirely agrees with regard to this pattern, but here the rostral part is, of course, much shorter (fig. 8, a). This regular pattern continues also behind the pineal branches of the lateral line system and gradually passes into the regular longitudinal ridge-pattern of the median and posterior parts of the shield. Slight variations are, of course, also seen here.

The ventral shield is, as mentioned, very elongated (Pl. XXV). The anterior margin is faintly emarginated and the anterior corners somewhat truncated. At first, the shield increases very quickly in breadth, later on, however, more slowly, reaching its maximum breadth behind the middle part. In the hinder part, as is usual in the Genus *Poraspis*, the shield is somewhat more tapering than the dorsal shield (Pl. XXV, 2). The most anterior portion is very flat; backwards, it becomes more and more vaulted. Seen in profile the lateral margin displays a distinct incision for the branchial plate (Pl. XXV, 3). On the figured specimen this incision stops somewhat in front of the posterior corner, a condition which is not constant, however. The dentine ridges are



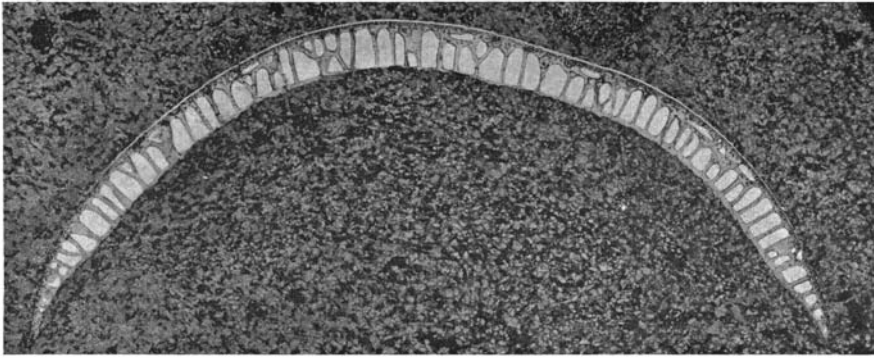


Fig. 28A. *Poraspis rostrata* n. sp. Cross-section of the dorsal shield in the post-branchial region. Ca.  $\times 7$ .  
Specimen D 1975. Pal. Mus., Oslo.

of a strikingly regular, longitudinal course. Only anteriorly, in front of the most anterior transverse commissure, they diffuse towards the corners.

The lateral line system has, as usual, been studied by means of grindings (fig. 27). The lateral lines of the dorsal shield (fig. 27, A) give an impression of being more completely and regularly developed than in the previously described forms: The first transverse commissures behind the pineal branches are more complete, and the median and lateral longitudinal lines, most in front, curve slowly inwardly and coalesce with the pineal branches. The pineal branches come more closely together in the median part of the shield than in the above described, older forms, but do not coalesce with each other.

The lateral lines of the ventral shield (fig. 27, B), on the other hand, are comparatively faintly developed. Thus the lateral longitudinal lines are most often interrupted in their posterior parts and the lateral and median portions of the transverse commissures are very short and often incomplete; they seem to be also present in a similar number, as, for instance, in *P. polaris*.

The structure of the dermal skeleton is seen in fig. 28 A, and Pl. XXXIX showing various portions of transverse sections through the post-branchial portion of the dorsal shield. As will be seen, the skeleton is considerably thicker and more massive than that in *P. polaris* (Pl. XXXV). The reticular layer is more strongly developed, particularly so about the lateral lines; this feature is distinctly seen in Pl. XXXIX, 1, 2, where they are cut obliquely. The openings from the cancellae upwards into the pulpa canals are of about the same size as in *P. polaris*. The pulpa canals on the contrary are generally more narrow. From fig. 3, Pl. XXXIX and fig. 28 A will be seen that the internal marginal ridges here, similar to other *Poraspis* forms, are not developed under the margins of the post-branchial lobes.

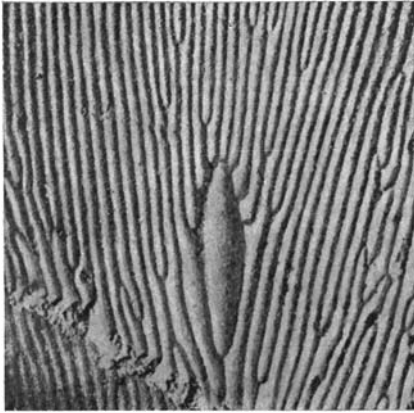


Fig. 28 B. *Poraspis rostrata* n. sp. The pineal pattern. Ca.  $\times 15$ . Ben Nevis horizon A. Specimen D 128. Pal. Mus., Oslo.

Remarks. *Poraspis rostrata* is the oldest of the *Poraspis* forms characterizing the Ben Nevis Group. These forms are of a particular outline and clearly diverge from those found in the older Frænkelryggen Group. They are larger, more elongated, with a comparatively long rostral part and also show differences in the lateral line system of the dorsal shield in that the median longitudinal lines coalesce with the pineal branches, which is never the case with the older forms. In addition, the pineal branches show a tendency of being united in the median line of the shield, a

feature which becomes realized in some of the previously described, closely related Central European forms. The only one of the Frænkelryggen Group *Poraspis* forms, which comes nearest to *rostrata* is, without doubt, *P. elongata*. This applies particularly to the general shape and the development of the rostral part whereas the lateral line system is still at the same stage as in the older forms.

#### *Poraspis cylindrica* nov. sp.

(Pl. XXVI, 2; XXVII, 2; XXIX, 1; fig. 29; 30).

Specific characteristics. A comparatively large form with the total length of the dorsal shield reaching from 46 mm to 53 mm. A forma lata can probably be separated, it is relatively short and broad with B. L. Ind. 47–50 and a longer and narrower angusta form with B. L. Ind. about 43. The dorsal shield is most often slightly contracted near the orbital notches. The rostral part which has a R. Ind. of 17 is narrow posteriorly as the pineal branches curve in an inward direction (fig. 29). The rostral pattern is characterized, firstly by its fan-shaped arranged longitudinal ridges, which on the sides curve along the margin, and secondly is particularly distinguished by the fact that the transversally going ridges along the anterior margin are very faintly developed. Pineal macula relatively broad, posteriorly somewhat tapering. The lateral line system (fig. 29) is characterized similarly, as in *P. rostrata*: the dorsal median longitudinal lines coalesce with the pineal branches, which do not join in the median line. The transverse commissures on the contrary are less complete than in *P. rostrata*; not one of these seems to reach the lateral median lines, and the two posterior ones are bent more backwards than is the case in *P. rostrata*. The ventral

shield with a length from 38—45 mm, is relatively narrow with a B. L. Ind. from 42—50. The slender form (42) (fig. 30, A) probably pertaining to *forma angusta*, the broad one (50) (fig. 30, B) to the *lata*. In the anterior portion, the ventral shield is more strongly vaulted and its anterior margin more rounded than is usually the case (Pl. XXVII, 2; fig. 30, B, C). Seen from above it looks almost semi-cylindrical.

As the holotype, has been chosen the specimen D 205 found in the *Benneviaspis* horizon, Ben Nevis collected during the expedition of 1928 (Pl. XXVI, 2).

**Occurrence and material.** Of this form a fairly rich but badly preserved material is present from the upper portion of the Ben Nevis Group. The species was found by A. Hoel during Isachsen's expedition 1909—10, in several horizons from L upwards to U, but, on the whole, its occurrence is scarce. A supplementary collections was brought together particularly during Vogt's expedition in 1928. The state of the preservation is nearly always rather bad, which is usually the case with regard to these upper layers. The greater part of the specimens are inferior casts, with scanty remains of the dermal skeleton. A few specimens show a better preservation, especially a somewhat incomplete dorsal shield from the locality "Tunge" Ben Nevis.

**General description.** The forms of *Poraspis*, occurring in the upper portion of Ben Nevis are very difficult to determine. There seem to be two closely related species; but as these to some degree are found in the same horizons and as the material is relatively scanty and the preservation most frequently bad it is often very difficult to decide to which species the specimen will have to be referred, the more so as both species must be supposed to occur in the shapes of longer — *angusta* — and shorter — *lata* — forms. Of the dorsal shield, which have been referred to *P. cylindrica*, by far the greatest number pertains to a relatively broad type with a total length of 46 mm to about 50 mm and with a B. L. Ind. 47—50. This form has been regarded as the *lata* form. A typical specimen is the dorsal shield which has been chosen as the holotype (Pl. XXVI, 2). Chosen as the *angusta* form for this species is a somewhat incomplete dorsal shield (D 140), found by A. Hoel during Isachsen's expedition 1909—10 (Pl. XXIX, 1). Its length reaches 53 mm with a B. L. Ind. of 43 only. As will be seen, these *lata* and *angusta* — forms differ distinctly from each other with regard to size and to B. L. Ind. In other respects they seem to agree closely. The rostral part, as mentioned, has a R. Ind. of about 17 and is thus considerably shorter than in *P. rostrata*, which is greatly reminiscent of the *angusta* forms. As the shield is commonly somewhat contracted near the orbital notches the rostral part becomes projected snoutlike and in front is rather narrowly rounded. The rostral pattern cannot be distinctly seen in any of the specimens, but it is, however, possible

to reconstruct it in its principal features. As the pineal branches of the lateral line system curve relatively strongly inwardly (fig. 29) the rostral part becomes distinctly contracted farthest back. Owing to the circumstance that this posterior portion of the rostral part can be viewed in a single specimen (D 136 from the "Tunge" locality) it cannot, however, be decided with certainty whether this feature is constant or due to an individual variation only. The dentine ridges in the rostral part are spread slightly fan-shaped and, on the sides, curve forwards nearly in the same manner as in *P. rostrata*. The pattern is, however, distinguished from that in the latter by the fact that the transverse ridges along the anterior margin are very faintly developed and that these most frequently are strongly broken up into smaller portions. The pineal macula, which can be seen in specimen D 136 from "Tunge" only is comparatively narrow. It is rounded in front and pointed most posteriorly.

In the remaining part of the dorsal shield the dentine ridges run regularly longitudinally, yet, usually, with slight deviations. The branchial part is distinctly archedly widened, and the shield has here its largest breadth (Pl. XXVI, 2). The post-branchial part is of the usual length. The post-branchial lateral lobes are not particularly long. The shield posteriorly ends in a rounded lobe as usual.

The ventral shields (Pl. XXVII, 2; fig. 30), as mentioned, are partly narrow and elongated (fig. 30, A) partly shorter and broader (fig. 30, B, C). The measurements have been given under "Specific characteristics". The ventral shields are of a quite characteristic shape: their anterior portions are more strongly vaulted and their anterior margins more rounded than usual, as the anterior excisions are very short and the anterior corners more rounded than is commonly the case. The shape of the shield approaches the semi-cylindrical. In the broad forms the breadth, however, distinctly increases backwards (fig. 30, B).

The impressions on the insides of the shields are most frequently badly preserved, but in some specimens these can be fairly well discerned, as, for instance, in the holotype (Pl. XXVI, 2) where one sees clear casts of the dorsal impressions. Most in front are seen the huge nasal sacs, reaching to the outside of the shield. From both lobes, divided from each other by a distinct incurvation, projections run in a backward direction soon grow thinner and, finally, disappear. These projections must be regarded as impressions of the olfactory lobes. Further behind in the median line is seen an impression of the strong pineal organ as an oblong elliptical elevation. Then follow the two pairs of anterior and posterior semi-circular canals in the usual development, and, in the median line behind these, the impression of the medulla oblongata. On both sides are situated the strong elliptical impressions of the branchiae. In this specimen are seen on the right side 7, on the left side only 6, impressions. Along the margin are the

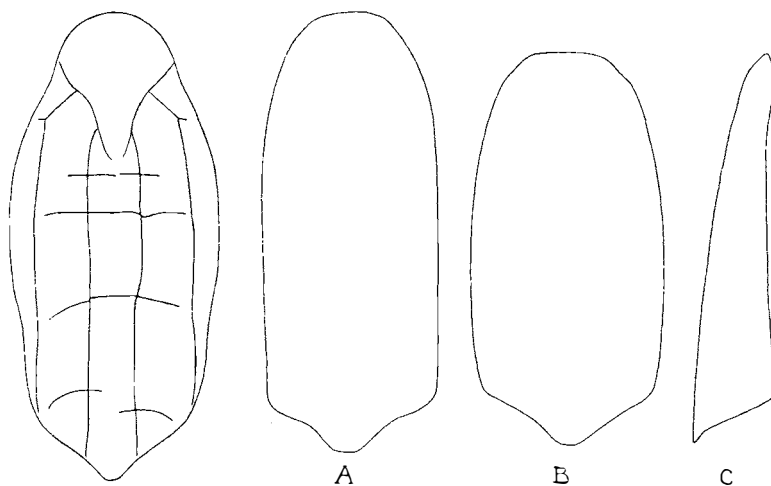


Fig. 29.

Fig. 30.

Fig. 29. *Poraspis cylindrica* n. sp. An outline drawing of the dorsal shield, showing the course of the lateral line system. Ca.  $\times 1,2$ .

Fig. 30. *Poraspis cylindrica* n. sp. An outline drawing of two types of the ventral shield: a long and narrow one (A, Specimen D 279. Pal. Mus., Oslo. Ben Nevis. horizon R) and a broad and short one (B, C, Specimen D 1798. Pal. Mus., Oslo. Ben Nevis). Ca.  $\times 1,2$

usual marginal branchial impressions but not so well preserved; they seem to have been double or angular for each branchia. The figured dorsal shield of the angusta form shows only very indistinct impressions (Pl. XXIX, 1). The variations found with regard to these impressions in different specimens do not seem to be due to the different degree of preservation only, but it seems much more likely that these interior organs in some specimens have left stronger, in others, fainter and more irregular, impressions.

The interior impressions of the ventral shield are seen in specimen D 1798 (Pl. XXVII, 2). Here are shown the marks after the very long impressions of the four first pairs of branchiae. In front of the branchiae is seen a strongly developed anterior median impression. Behind this is a distinct elevation in the median line of each branchia. The significance of these impressions is quite uncertain.

The development of the lateral line system is only very rarely seen in our material. In a single, somewhat incomplete specimen, from the locality "Tunge", Ben Nevis (D 136, exp. 1928) the main features of the lateral lines can be studied. The skeleton here is so transparent, that the lines can be seen without any grinding. From this specimen the reconstruction in fig. 29 has been made.

The lateral line system of the dorsal shield has already been briefly characterized (pag. 88). The longitudinal lines are very regular and they

both unite with the pineal branches, which curve in an inward direction making the posterior portion of the rostral part with the pineal macula very narrow. The two first post-pineal commissures have an almost rectilinear course. The first reaches only half-way out to the lateral longitudinal line, while the second almost coalesces with it. The third and fourth commissures curve strongly in a backward direction outside the median longitudinal lines and do not reach the lateral lines. Between the median longitudinal lines the commissures are rectilinear and regular except the last one, which is irregular and incomplete.

In all essentials the lateral line system of the dorsal shield is thus closely related to that in *P. rostrata*. Deviations appear in the commissures alone; it is possible, however, that these differences may chiefly be due to individual variations.

The lateral lines of the ventral shield are imperfectly known, yet it is probable, that they are somewhat more completely developed than those in *P. rostrata*.

As it has been impossible to make microscopic sections of the dermal skeleton, it can only be mentioned that the cancellae are large and regular and that 2—3 dentine ridges correspond to one cancella.

Remarks. The dorsal shield in this species — especially in the *angusta* form — is considerably reminiscent of that in *P. rostrata*, which occurs in the lower portion of Ben Nevis, but differs from the latter particularly in a smaller rostral index and in details with regard to the rostral pattern and to the lateral line system. The species is perhaps still more reminiscent of the previously described species *P. barroisi*, Leriche (1906), which, however, is somewhat smaller. This last-mentioned form, moreover, has a more longitudinal development of the dentine ridges in the rostral part. Unfortunately, the lateral line system of this French species is still entirely unknown. The most important feature, however, is that the ventral shield in *P. cylindrica* is widely different from those in the two mentioned species. In both these the anterior portion of the ventral shield is very flat, while in *P. cylindrica* this portion is vaulted.

*Poraspis magna* nov. sp.

(Pl. XXVIII; XXIX, 2, 4; XXXVIII, 2; fig. 31, 32).

Specific characteristics. A relatively very large form with the length of the dorsal shield reaching from about 52 to 62 mm. The longest specimen, which has a B. L. Ind. of 43,5 only and is very elongated probably represents the *angusta* form, while the shorter and somewhat broader specimens with a B. L. Ind. of about 50 can be regarded as *lata* forms. The lateral margin of the dorsal shield is evenly narrowing in a forward direction without any contraction in front

of the orbital notches. The rostral part has a R. Ind. of about 17,5 and is rather flattened with the anterior margin a little elevated. The rostral pattern (Pl. XXVIII, 1) is very slightly fan-shaped, the dentine ridges either reach quite out to the anterior margin or are sometimes broken up into small portions. The shape of the pineal macula cannot be determined with full certainty. On the remaining portion of the shield the dentine ridges are very regularly longitudinally arranged. The lateral line system (Pl. XXVIII, 2) on the whole seems to be quite similar to that in *Poraspis cylindrica*.

The ventral shield is incompletely known, reminiscent of that in *P. cylindrica*, only

it is larger and more widened in its median portion (Pl. XXIX, 4).

As the holotype has been chosen the specimen D 203, which was found on the expedition of 1928 in the second moraine, Ben Nevis and it is figured in Pl. XXVIII, 1.

**Occurrence and material.** This form is represented by a few specimens only from the upper part of Ben Nevis. A strongly eroded dorsal shield was found in the uppermost horizon U by A. Hoel during the expedition of 1909—10. On the expedition of 1925 a ventral shield, possibly belonging here, was found 620 m above sea level in a loose slab, and, finally, in 1928, four dorsal shields were brought together in debris from the second moraine of Ben Nevis, among these the holotype. The horizon from which these specimens are derived cannot be decided with certainty. Judging by the rock the species found in the second moraine all seem to belong to the same layer.

**General description.** As is previously pointed out it is often difficult to distinguish this species from *P. cylindrica* to which it is closely related. There can, however, scarcely be any doubt that we must here separate two species, what is obvious if, for instance, we compare the angusta form of *P. magma* (Pl. XXVIII, 1) with the corresponding one of *P. cylindrica* (Pl. XXIX, 1).

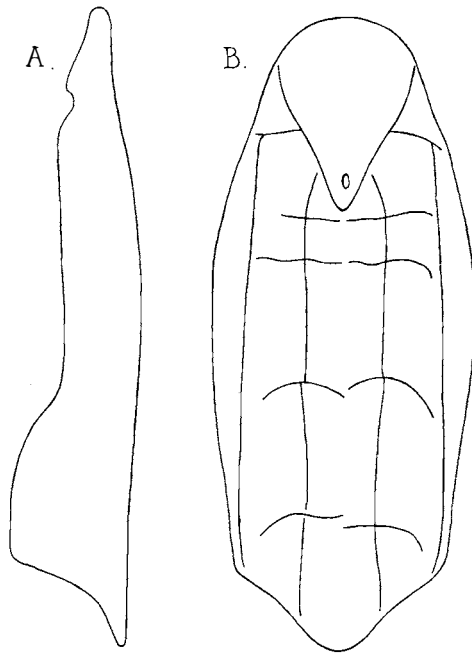


Fig. 31. *Poraspis magna* n. sp. An outline drawing of the dorsal shield, from above (B) and side (A) showing the course of the lateral lines. Ca.  $\times 2$ .

We start our description on the basis of the holotype (D 203) (Pl. XXVIII, 1), which must be regarded as the *angusta* form of this species. The length of this dorsal shield is 62 mm, the breadth 27, and the B. L. Ind. 43,5 only. It is thus an unusually large form, the largest *Poraspis* form in the Red Bay Series. The specimen is excellently preserved and probably shows its natural plastic form, but the dermal skeleton is partly missing in the median and the posterior portions. By this fact, however, excellent casts of some of the interior impressions are shown.

The shield narrows uniformly in a forward direction from the median portion of the branchial part and displays no marked contraction in front of the orbital notches. The rostral part is relatively long, nearly similar to that in *P. cylindrica*, with a R. Ind. of 17,5. It is thus considerably shorter than is the case in *P. rostrata*. The rostral pattern is characterized by an indistinctly fan-shaped arrangement of the dentine ridges, which, in reality, run nearly longitudinally, and by the fact, that the dentine ridges pass the pineal branches, almost without any deflection. Thus, as a whole, the dentine ridges of the dorsal shield are unusually regularly arranged. Along the anterior margin the ridges are broken up into smaller and irregular portions.

The rostral part is somewhat depressed with a distinctly elevated anterior margin. This is probably due to the circumstance that the maxillar brim has here resisted the pressure more strongly than the posteriorly situated portion of the rostral part. The fact is that the maxillar brim in this form is uncommonly broad and solid as is shown in the figured longitudinal section in Pl. XXXVIII, 2.

The pineal macula cannot be distinctly seen, the surface being here somewhat defect. The post-branchial part is slightly more elongated than in *P. cylindrica*. The lateral lobes are very strong and deep, but not especially long.

Where the dermal skeleton has fallen off, good casts of some of the interior impressions can be distinguished. There are seen the unusually long medulla oblongata, the six posterior branchial impressions on the right side and the corresponding marginal branchial impressions, which are here uncommonly small, and developed as faint, simple elevations only.

The lateral line system (fig. 31, B; Pl. XXVIII, 2; XXIX, 2) has been developed in a similar manner as that in *P. cylindrica*. The pineal branches, however, do not curve so strongly in an inward direction as in the latter. This circumstance, however, may only be due to an individual variation.

Together with the holotype in the same slab, was found a very well preserved snout-fragment. This fragment, being of the same type as the holotype, must also be regarded as belonging to *Por-*



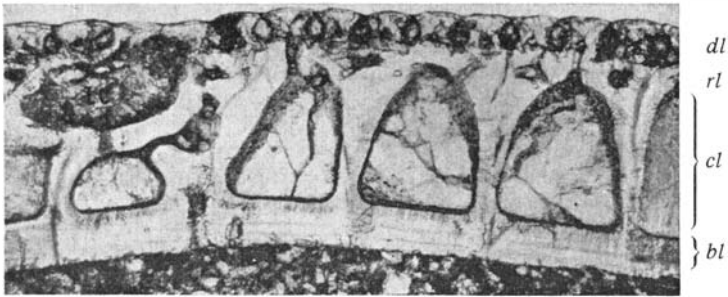


Fig. 32. *Poraspis magna* n. sp. Cross-section of the rostral division of the dorsal shield. *bl* = basal layer. *cl* = cancellous layer. *dl* = dentine ridges (on many "enamel" is clearly seen). *lc* = lateral line canal. *rl* = reticular layer. Ca.  $\times 50$ .

*aspis magna*. It was used for microscopical sections: one longitudinal showing the maxillar brim very clearly (Pl. XXXVIII, 2), and another the transverse (fig. 32). The microscopical sections show that the skeleton is relatively thin, but very solid. Both the basal layer and the walls of the cancellae are unusually thick, considerably thicker than, for instance, those in *Poraspis polaris* (cf. e. g., Pl. XXXV), and even more solid than in *Poraspis rostrata* (Pl. XXXIX). The basal layer shows very clearly the lamellated structure and the lamellae are also seen in the cancellae-walls. The relatively thin reticular layer is also unusually compact. The cross-section of the dentine ridges show quite small pulpa, and a clearly limited "enamel" layer at the top. To each cancella correspond from 2 to 3 dentine ridges. The longitudinal section shows an unusually broad and compact maxillar brim, with a relatively very large number of unchanged dentine ridges (Pl. XXXVIII, 2). In *Poraspis polaris*, for instance, (Pl. XXXVIII, 1) already the second ridge becomes thinner and more or less "tooth-like". In our form, on the contrary, the first 8 ridges are developed as ordinary "dentine ridges" and only from the 9th, they become more and more "toothlike" but of course, only the ridges 13, 14 and 15 can be called really "tooth-like".

From the second moraine, was derived a piece with two fragmentary dorsal shields and a few body-scales. As the rock of this piece is entirely conformable to that holding the holotype, this piece must be supposed to belong in the same layer. The individuals shown in this piece are of a shorter and broader shape than the holotype and can be regarded as the lata form of this species. The better of these dorsal shields (D 1309) has probably had a length of 52 mm and a B. L. Ind. of about 50. It narrows, like the holotype, evenly in a forward direction without any contraction in front of the orbital notches. The dentine ridges of the rostral pattern are more strongly fan-shaped

than in the described *angusta* form and reach the anterior margin without being broken up into smaller portions most in front. The ridges are more deflected near the pineal branches, which curve more strongly in an inward direction than is the case in the holotype. The circumstance is reminiscent of that in the *lata* form of *P. cylindrica*. A similar case is seen in another dorsal shield from the horizon U (Pl. XXIX, 2), it is so strongly eroded that the main features of the lateral line system are visible. The transverse commissures in this specimen seem to be somewhat deviating. As we must presume, on account of the size (length about 52 mm) and the shape, that both the shields pertain to *P. magna*, there is reason to conclude that many of these small deviations with regard to details of development of the dentine ridges and the lateral line system, are due to individual variations only. We find additional support for this opinion in the strong variation we have been able to ascertain in some older species of which a richer material is available. As it may be possible, however, that the breadth of variation is considerably less in the later forms, it is impossible with our scanty material, to know how important these deviations are for the specific definition. It is more natural to believe that details in the development of the transverse commissures and pineal branches are of less importance as specific characteristics, while more attention ought to be given to the arrangement of the dentine ridges near the anterior margin of the rostral part. As a matter of fact, the anterior margins with well developed transverse or more or less dissolved ridges in *P. cylindrica* and *P. magna* are both most frequently reduced or even entirely lost, whereas, in the older forms, this very rarely is the case.

Of ventral shields which, in all probability, can be referred to this species, only one is present (Pl. XXIX, 4). The species may correspond to the *lata* form. This shield appears to be vaulted in its most anterior portion, which is also the case in *P. cylindrica*. It is eroded from within and one can see a part of the lateral line system quite clearly. Remarkably enough, a few commissures seem to continue outside of the lateral longitudinal lines, a feature which is only refound in *Irregularaspis*. The piece is from a loose slab, Ben Nevis 620 m.

Remarks. This species is most closely related to *P. cylindrica*, but is considerably larger and thus probably evolved from the latter. The *angusta* form (the holotype) belongs to the largest *Poraspis* forms known from the Red Bay Series. The supposed *lata* forms are also comparatively very long, their length corresponding to that of the *angusta* form of *P. cylindrica*. It must be pointed out that it is only for one specimen that the horizon is known with certainty. This piece is Hoel's specimen from his horizon U in the upper portion of the Ben Nevis Group (Pl. XXIX, 2). The other pieces have been found farther down in loose slabs (620 m above sea-level) and from the second moraine.

As to these, it can merely be said that they must be supposed to be derived from the upper part of the Ben Nevis Group. As we have seen, *P. cylindrica* begins in older horizons but continues upwards reaching the uppermost ones, and here occurs partially together with *P. magna*. These two species are thus not strongly separated and both characterize the upper portion of the Ben Nevis Group. A richer material would probably display all transitions from the lesser *cylindrica* to the larger *magna*. But with our present knowledge these will have to be separated as being two closely related species the breadth of variation of which, however, we do not yet know.

Another form, which might be supposed to be a closely related one, is the large English *P. sericea* (fig. 6), which is the genotype. The length of its dorsal shield is 72 mm, thus exceeding that of the dorsal shield in *P. magna* by 10 mm. It is, however, not only by the size that this English form differs from *P. magna*, but also in a number of other not unimportant, characteristics, as, for instance, the concentric whirl of the dentine ridges in front of the orbital notches; further, the very elongated shape of the pineal macula and, finally, the more complete and more regularly developed lateral line system with the pineal branches probably entirely united in the median line. In addition, the post-branchial lateral lobes are much longer than in *P. magna* and the branchial part is more widened. It can, therefore, be presumed that *P. cylindrica* is much more closely related to *P. magna* than the English species, which, however, probably is of a fairly corresponding age.

*Poraspis* sp.

(Pl. XXIX, 3).

The ventral shield figured on Pl. XXIX, 3 cannot with certainty be referred to any of the species described above. It was found by A. Hoel at Mt. Pteraspis, locality 50 m. Here from the screes many forms have been brought together, forms which must be supposed to have originated from the layers corresponding to the upper horizons of the Fränkelryggen Group. Some forms, however, certainly belonging to higher horizons have also been found in this locality and it cannot therefore be definitely decided from which portion of the series this piece is derived. It may be supposed, however, that it belongs in the Ben Nevis Group.

The length of the shield is of about 54 mm and the B. L. Ind. is 47. It is accordingly a very large and comparatively narrow specimen. The anterior portion is flat, thus resembling neither *P. cylindrica* nor *P. magna*, it may be related to *P. rostrata*, but, on the other hand it does not agree with the ventral shields surely belonging to the latter. As only one specimen has been found in the shape of a rather badly preserved cast it has been established as *Poraspis* sp.

*Poraspis sericea* (Lankester).

(Fig. 6, 33, 34, 35).

*Scaphaspis* E. R. Lankester 1864.*Holaspis sericeus*, E. R. Lankester 1873, 2.*Palaeaspis sericea* (Lankester) Woodward 1891.*Poraspis sericea* (Lankester) Kiær 1932, 1.

Specific characteristics. A comparatively very large and elongated form with a total length of the dorsal shield somewhat exceeding 70 mm and with a B. L. Ind. about 44. The rostral part elongated with the anterior margin slightly curved upwards. Between the rostral part and the orbital notches the dentine ridges form a marked concentric whirl. The pineal macula extremely elongated, elliptical. The lateral line system very regular. The transverse commissures complete and the median longitudinal lines united with the pineal branches (fig. 33). The ventral shield unknown.

The holotype (fig. 6; 33) is the dorsal shield, figured by Lankester, present in the British Museum (P. 4117). This is the form of the Genus *Poraspis*, first described and depicted and, therefore, must be regarded as the genotype (pag. 52).

Occurrence and material. The holotype was given to Lankester for description by Dr. Mac. Cullough. It was found in Grey Cornstone near Abergavenny. From the same layers have been brought together specimens of *Pteraspis rostrata* and *crouchii*; the horizon thus, according to the classification of W. Wickham King (1925), pertains to the Dittonian (II, 2). The holotype is the only specimen, which has been better known. Lankester, however, mentions (pag. 243) having seen a fragment of another specimen from Herefordshire. Possibly this fragment is 'the piece, which belongs to Dr. Grindrod's Collection in Oxford Museum and which Prof. Kiær has had the opportunity of studying (fig. 34).

General description. This form is the first described of an entirely new type of *Heterostraci*, and Lankester, therefore, in his description quite naturally deals only with such characteristics which are common for all the *Poraspidei*. He looks upon it as a kind of intermediate form between the typical Genus *Pteraspis* and *Scaphaspis*, which he considered to represent the dorsal shield of a very simple type, but which, in reality, as we now know, represents only the ventral shields belonging to the different *Pteraspis* and *Cyathaspis* forms. Consequently, many of his statements with regard to this form are now of less importance. It must not be forgotten, however, that he very clearly points out the striking characteristics of the *Poraspidei*, the quite continuous dorsal shield and the distinct development of pores in regular lines, a feature very visible on his plate (cf. fig. 6 and 33) and which he very

correctly interpretes as openings for a lateral line system. "There is little doubt" he says "that they are the sites of soft tegumentary structures, in all probability of those characteristic sensory — follicles of fishes, with which they agree in disposition."

Now, as we have subsequently learnt to know a number of closely related forms it will be appropriate to try to determine the actual specific characteristics of this species which is the genotype.

Prof. Kiær has had the opportunity of studying the holotype-specimen in the British Museum and there was also placed at his disposal for examination another specimen, which he came across in 1929, when he studied the valuable Grindrod collection in the Oxford Museum. This undoubtedly pertains to the same form and is of similar dimensions but, unfortunately, quite fragmentary (fig. 34). The most important generic characteristics have been given above (pag. 51). We shall here report some further details in connection with Lankester's plate and sketch (fig. 6; 33; 35).

The dorsal shield is imposing in its size, having a total length of 72 mm and a branchial breadth of 33 mm. The fragment seems to have had the same dimensions. *Poraspis sericea* is thus the largest of all the known *Poraspidei*. The form is elongated, the B. L. Ind. being only 44. The rostral part is comparatively long with a R. Ind. of about 18. The anterior margin is somewhat curved upwards, but this may be the result of pressure, as the front-margin with the strongly developed maxillar brim has opposed more resistance than the more posterior thinner portion of the shield. The branchial part as usual curves somewhat behind the orbital notches. The post-branchial part is long, and the post-branchial lobes are very long and well developed (fig. 34, B; 35). The shield ends in a rounded lobe not in an acute point, as indicated by Lankester in his plate (fig. 6). The rostral pattern is distinguished by the fact that the faintly fan-like ridges run to the anterior margin, where they disperse to both sides. Thus there is not developed any marginal area with ridges going conformably to the anterior margin. The pineal macula is somewhat elliptical, nearly as in *P. rostrata*. Between the pineal branches and the orbital notches, the ridges are almost concentrically arranged. These very characteristic oval whirls are mentioned by Lankester and must in all cases provisionally be regarded as a specific trait, nothing corresponding having been found

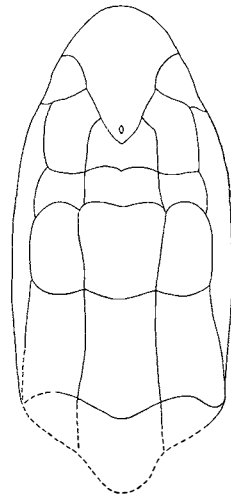


Fig. 33.

*Poraspis* (= *Holaspis*) *sericea* (Lankester). An outline drawing of the dorsal shield, showing the course of the lateral line system. Based on Lankester's drawing in *Geol. Mag.* 1873, Vol. X, Pl. X.

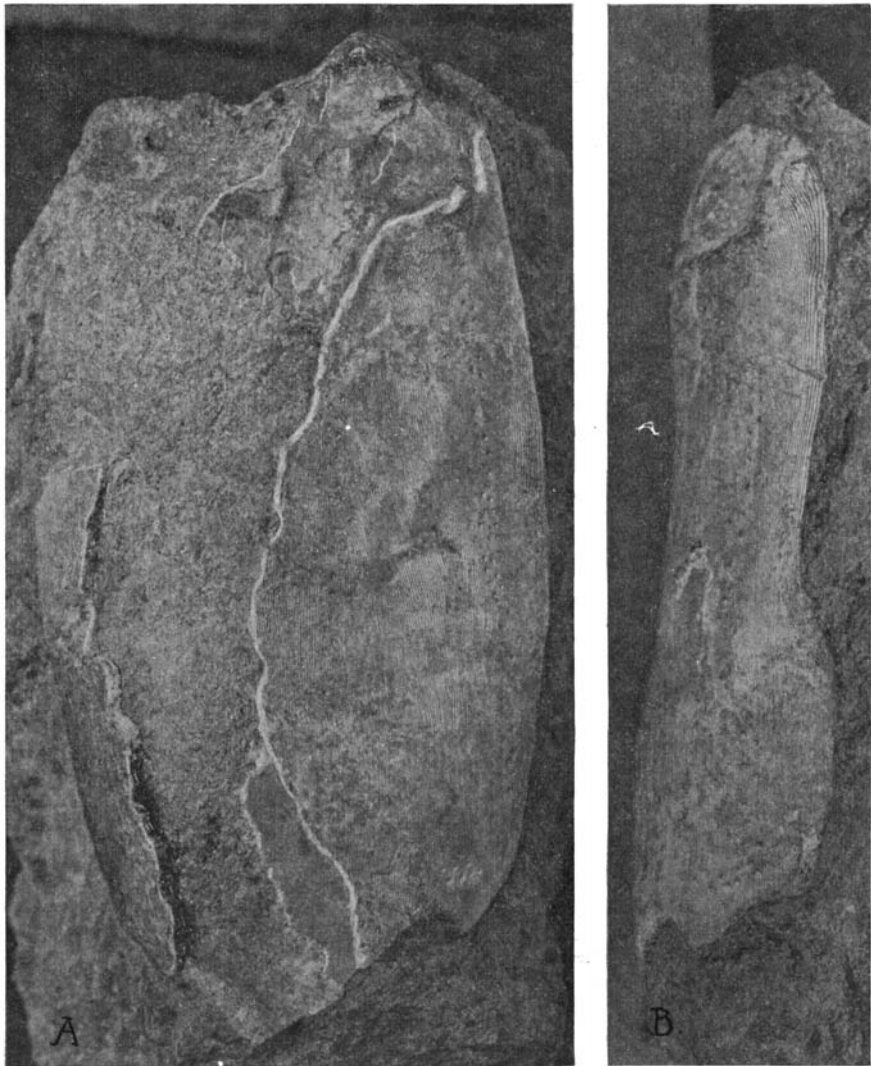


Fig. 34. *Poraspis* (= *Holaspis*) *sericea* (Lankester).  
 A fragment of a dorsal shield from above (A) and from the side (B). Grinrod collection.  
 Geological Museum, Oxford. Ca.  $\times 2$ .

in other species. Otherwise the ridges have a regular longitudinal course, only with smaller variations (fig. 6; 34). Thus the ridges just behind the orbital notches run somewhat differently in the holotype and in the fragment from Oxford Museum.

The lateral line system is very conspicuous in Lankester's plate (fig. 6; 33), where the development of the lines is, in the main, very well shown. The lateral line system in *P. sericea* has later on been sketched by Stensiö (1926, fig. 6) and by Jaekel (1927, fig. 31). These

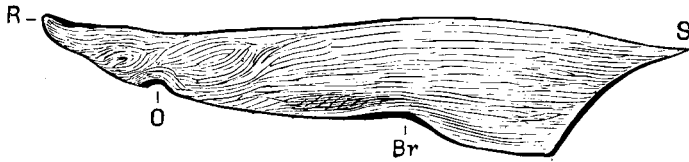


Fig. 35. *Poraspis* (= *Holaspis*) *sericea* (Lankester).

The side view of the dorsal shield. (After Lankester 1873). *Br* = branchial sinus.

*O* = orbital notches. *R* = rostral part.

*S* = hind point of the shield.

two sketches, however, give only the main features of the lateral line system, not being quite correct neither with regard to the outlines of the shield nor to the proportions between the different parts of the system. The pineal branches seem to coalesce in the median line behind the pineal macula, which cannot be seen in Lankester's figure. The median longitudinal lines running far forwards curve somewhat in an inward direction and, finally, join with the pineal branches. The longitudinal lines are otherwise very regular and all the transverse commissures are very completely developed. They reach the lateral longitudinal lines and do not seem to be abruptly in the median line. It must specially be pointed out that the second transverse commissure (here, as previously mentioned, the pineal branches are indicated as being portions of the first commissure) curves in a forward direction between the two pairs of longitudinal lines, while the third curves backwards and the fourth again forwards. The fragment from Oxford Museum shows, however, that this singular development of the transverse commissures is due to an individual variation (cf. fig. 6 and fig. 34). It will also be seen that the second and the third transverse commissures are placed unusually close to each other. This circumstance is probably of a systematical importance and may be considered as an actual specific characteristic besides the fact that the pineal branches apparently coalesce in the median line.

Remarks. *Poraspis sericea* is, undoubtedly, closely related to the *Poraspis* forms of the Ben Nevis Group, most closely to *P. magna*, which, however, neither attains the same size, nor shows the peculiar concentric whirls in front of the orbital notches.

#### *Poraspis barroisi* (LERICHE).

(Fig. 36, 37).

*Cyathaspis barroisi* Leriche 1906.

*Poraspis barroisi* (Leriche) Kiær 1932, 1.

Specific characteristics. A comparatively large form with a total length of dorsal shield 42—44 mm and with branchial breadth 21—22 mm B. L. Ind. thus about 50. The rostral part comparatively

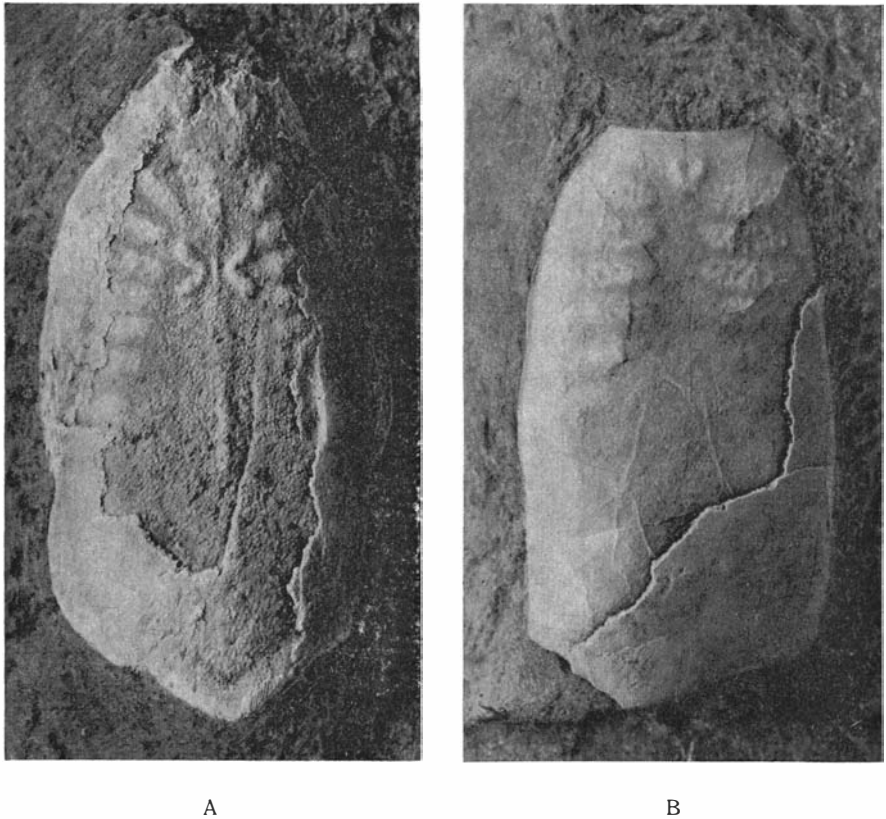


Fig. 36. *Poraspis (Cyathaspis) barroisi* (Leriche). A. Dorsal shield showing natural casts of the gills, semi-circular canals, pineal organ and medulla oblongata. B. Ventral shield showing natural casts of the gills and the anterior median impression.

Ca.  $\times$  2. Kiær photos.

elongated with R. Ind. 17—18. The rostral pattern is distinguished by longitudinally going ridges, which, near the anterior margin, become irregular and are apt to curve in an outward direction. The ventral shield has a total length of 38,5 mm, a breadth of 21 mm B. L. Ind. thus being about 54. The anterior portion of the ventral shield seems to be very flat.

Leriche has not chosen any holotype, but it is natural to take for a lectotype the specimen which is figured by Leriche on Pl. I, fig. 2.

Occurrence and material. Leriche states that this species is derived from "Puits No. 6 de la Concession de Liévin, Pas — de — Calais, Nord de la France". He indicates the horizon as "Niveau a *Cyathaspis barroisi*" belonging to the upper portion of the "passage beds" (Downtonian). Later on, Barrois, Prevost and Dubois referred this horizon to "Psammites bleus de Liévin," which forms the upper portion of the lower Gedinien. In other words, it should correspond to the upper part of the Downtonian of England. The material seems



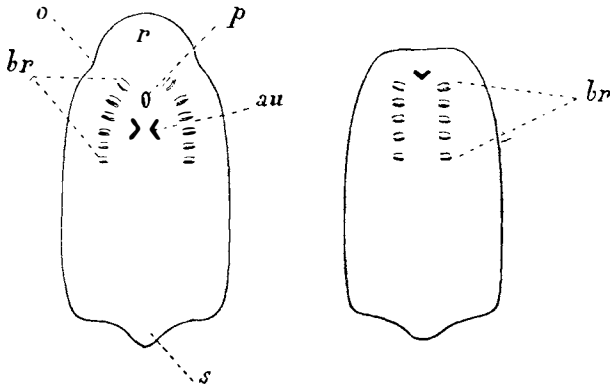


Fig. 37. *Poraspis* (= *Cyathaspis*) *barroisi* (Leriche). An outline drawing of the dorsal and ventral shields. After Leriche 1906.

to consist of a few dorsal shields and of one ventral shield preserved in Collection Musei Gosselet de l'Université de Lille.

**General description.** Evidently there was but a comparatively poor and incompletely preserved material available for Leriche's description of this species. His account of it, therefore, is very brief and his figures, good in themselves, give few details besides the shapes and proportions of the shields. More elucidative are his sketches, which are reproduced here (fig. 37). To get a sure conception of this species and of its relationship to other known forms on the basis of these alone was very difficult; it therefore was particularly interesting that by the great kindness of Prof. Leriche the original rock-specimens from the University of Lille for his figures were entrusted to Prof. Kiær for examination. The photographs of these specimens are reproduced in double size in fig. 36. They clearly exhibit the shapes of the shields and render good details of the interior impressions. By means of these two rock-specimens and by means of Leriche's description and figures the striking generic characteristics as reported above, have been determined. There cannot be added much more with regard to this form for the present, but some additional observations may be stated.

As will be seen from the photographs (fig. 36) the interior impressions, particularly those of the branchiae, are considerably larger than one could imagine, judging from the sketches by Leriche (fig. 37). As mentioned by Leriche, one can distinguish 6 pairs of branchial impressions on the dorsal, and 5 pairs on the ventral, shield, most in front on the latter is very distinctly seen the little angular median impression which is so characteristic for *Poraspis*. The lateral line system is entirely unknown. It must also be added that judging by the B. L. Ind. all the found specimens must be taken as belonging to the angusta form.

Remarks. *Poraspis barroisi* as to the sizes of the shields, ranges mid-way between *P. polaris* and *P. cylindrica* from Spitsbergen. It seems, however, to come nearer to the latter species, with which it agrees well with regard to the length and ridge-pattern of the rostral part. The ventral shield, however, deviates considerably from that in *P. cylindrica*; it is flat in its anterior portion almost as in *P. polaris*, whereas in *P. cylindrica*, it is fairly vaulted. *P. barroisi* cannot, therefore, be identified with any of the forms present in the Red Bay Series. In spite of the fact that the development of the lateral line system is entirely unknown, it seems as if this French form is closely related to the *Poraspis* forms from the upper portion of the Red Bay Series (the Ben Nevis Group).

***Poraspida* from Podolien (J. K.; A. H.).**

(Fig. 38, 39, 40).

The first species from Podolien, undoubtedly belonging to *Poraspis*, was described in 1874 by von Alth as *Cyathaspis sturi*. From the drawing given by Alth (reproduced on our fig. 38) it can be seen that *Poraspis* (*Cyathaspis*) *sturi* (Alth) is a comparatively large and very elongated form, with a total length of the dorsal shield of about 60 mm and with a B. L. Ind. of 39. The only known specimen (which also must be regarded as the holotype) was found near Doroszow on Dniestr in Poland. It comes from a horizon with marine fauna, which apparently corresponds to the Downtonian (passage beds) of England. As the original specimen was not available for re-studying the following description is based on von Alth's description and drawing.

*Poraspis sturi* (Alth) has a comparatively short rostral part, while the branchial and especially the post-branchial parts are long. The maxillar brim seems to be strongly developed (fig. 38, 1). Only 5 (or 6?) pairs of branchial impressions are seen, they are, however, probably not absolutely correctly depicted by Alth. The brain, the semi-circular canals and the nasal sacs have left very distinct impressions. As seen from Alth's figure 3, the shield is sculptured with fine quite irregularly(?) arranged flat dentine ridges. The rostral pattern is unknown. The same is the case with the lateral line system, and with the ventral shield also. In spite of such an incomplete diagnosis, it seems very probable that *Poraspis sturi* (Alth) must be regarded as a form quite closely related to the *Poraspis*-forms from the Ben Nevis Group.

During the last few years Zych and Brotzen, have intensively studied the Downtonian and Devonian formations from Podolien and collected a very great material of different *Ostracoderms* and *Placoderms*. This material is not as yet completely described, and three papers only are published, where some of the *Poraspida* are briefly described and depicted (Zych 1927, 1931 and Brotzen 1933). As both authors, as far

as is known intend to publish more detailed descriptions of the *Poraspida* from Podolien, only the already described forms are mentioned here.

In 1927 Zych briefly described and depicted only one *Poraspis*, which he determined as *Pteraspis* (= *Cyathaspis*) *sturi* Alth. He regarded this form as belonging to the same species as *Cyathaspis sturi* von Alth, and considered that *Cyathaspis barroisi* Leriche is also only a synonym for *Cyathaspis sturi* Alth. As can be seen from the descriptions of *Poraspis* (*Cyathaspis*) *barroisi* (Leriche) and *Poraspis* (*Cyathaspis*) *sturi* (Alth), given above, these two species cannot

be regarded as identical with each other. Judging by the photograph given by Zych of the new form (Zych, 1927, Pl. II, fig. 1), it is obvious, that this form is neither identical with *Poraspis sturi* (Alth), nor with *Poraspis barroisi* (Leriche). In all probability it is a new form. Zych's form is shorter and broader than *Poraspis sturi* (Alth), and longer and broader than *Poraspis barroisi* (Leriche). It measures in length ca. 55 mm and in breadth ca. 24 mm (the corresponding numbers for *P. sturi* and *P. barroisi* being respectively ca. 60 mm × 23 and ca. 44 mm × 22 mm). The B. L. Ind. is also different being 44 in Zych's form and 39 and 50 in *P. sturi* and *P. barroisi* respectively. The new form has a relatively short rostral part and long branchial and post-branchial parts. The impressions of the brain, the semi-circular organs and branchiae are quite clearly seen. The maxillar ridge also seems to be relatively broad. Nothing about the dentine pattern or the course of the lateral line system is known. The ventral shield is also unknown. This form comes from the layers with marine fauna supposed to correspond to the Downtonian (passage beds) of England and is thus the same horizon in which *P. sturi* has been found.

In a second paper, published in 1931, Zych depicted a number of different, partly very well preserved, *Poraspida* (Zych 1931, drawings 37, 38, 39, photographs 3, 4, 6, 7, 8, 9, 10, 12 and 13). The paper is, however, written in Polish only, what makes it very difficult to understand the text. As far as it is possible to judge, no exact diagnosis of

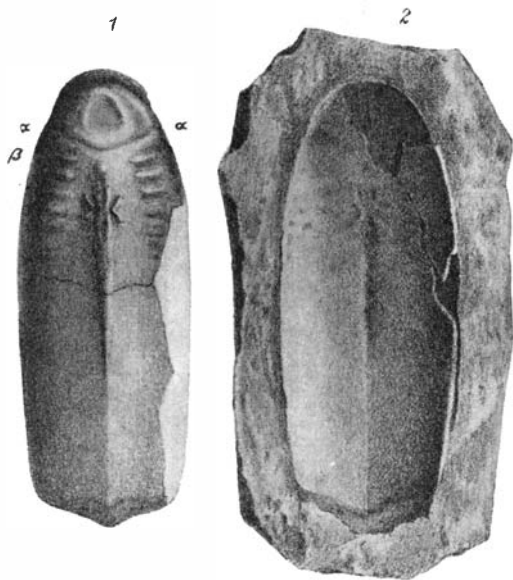


Fig. 38. *Poraspis* (= *Cyathaspis*) *sturi* (v. Alth)  
Natural cast and impression of the dorsal shield.  
After v. Alth 1874.

any new forms has been given. Only one new species is mentioned in the explanations of the plates and it is called *Poraspis siemiradzki* n. sp. It is a relatively big form, the length about 56 mm, and the breadth ca. 25 mm (measurements according to Zych's drawings), the B. L. Ind. thus being ca. 44. The rostral part is relatively short, the branchial, and especially the post-branchial, long. The maxillar brim is strongly developed (Zych's photograph 7). The dentine ridge arrangement is indistinctly seen. It may be observed, however, (Zych's phot. 4) that the rostral pattern is quite irregular, with small whirls in front of the orbits. The lateral line system, according to Zych's sketch (fig. 39), is very completely developed. The pineal branches melt together in the median line, the longitudinal canals coalesce with the pineal branches and all the transverse commissures run unbroken from one marginal lateral canal to the other. The impressions of the brain, the semi-circular canals, branchiae and the branchial marginal impressions are very distinctly seen (Zych's phot. 3 and 4). The ventral shield of this form is only depicted by Zych in one drawing (38 and 39. Our fig. 39, B). It is large, quite broad, but flat (ca. 49 mm long and 25 mm broad). The most interesting trait is the development of the lateral lines. The ventral longitudinal lines are very complete. The first transverse commissure is, as usual, strongly developed, and, according to Zych's sketch, even coalesces in the median line. The lateral parts of the other transverse commissures (7 in all) are clearly seen; they increase in size from front to rear, thus the second commissure is very short, while the last one almost reaches the median line. The median part of the transverse commissures can be seen only in the front part of the shield. They compose only two longitudinal relatively short branches, running from the median part of the first commissure backwards almost as far as to the third commissure. As is seen the development of the lateral lines in the ventral shield is quite unique. This form is in many respects reminiscent of the form described and depicted by Zych in 1926. They may be identical. It was found in the Jagielnica St. (from the marine beds corresponding to Downtonian?).

The other *Poraspida* depicted by Zych (phot. 8, 9, 10, 12 and 13) are only determined as *Poraspis* sp. They represent quite large forms (55 mm, phot. 8, 9, 10) with a very well developed lateral line system (phot. 12).

We must with great interest await the new papers by Zych describing all these remarkable forms more in detail. As far as can be judged from the localities, all these forms have been found in marine beds, corresponding to Downtonian.

At the present stage it seems apparent that none of the Podolien forms described and depicted by Zych are identical with any of the Spitsbergen forms. They represent, without doubt, new species.

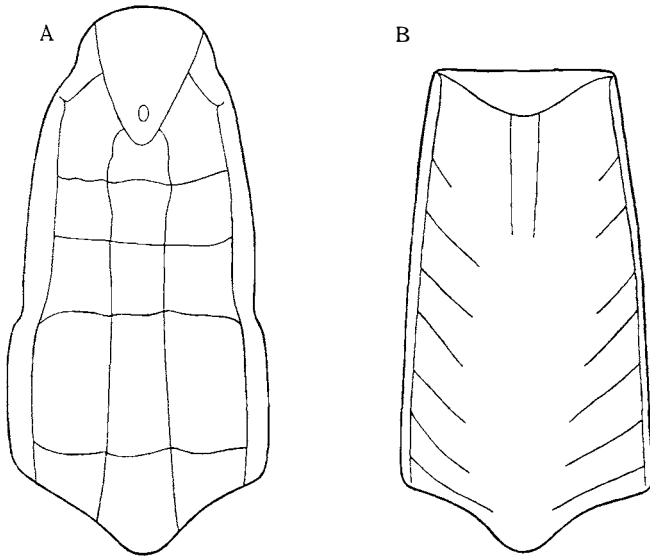


Fig. 39. *Poraspis siemiradzki* Zych.  
An outline drawing of dorsal (A) and ventral (B) shields,  
showing the course of the lateral line system. Ca.  $\times 1,5$ .  
After Zych 1931.

The last paper describing the *Poraspida* from Podolien is that of Brotzen (1933). He proposes two new species *Palaeaspis simplex* and *Palaeaspis pompeckji*. The material seems, however, to be too moderate and too badly preserved for a satisfactory description.

The first form is represented by a dorsal shield only. The length is 50 mm, the breadth 23 mm, the B. L. Ind. 46. The dentine ridges, the lateral line system and the impressions of the inner organs are unknown.

The second species is known from 3 dorsal and 2 ventral shields (fig. 40). It is somewhat larger (length 54—57, breadth 26—29 mm, B. L. Ind. 48). The dentine ridges are regularly longitudinally arranged. The rostral pattern is slightly fan-shaped, in front somewhat irregular, without distinct front marginal area (cf. Brotzen 1933, Taf. XXIV, fig. 4). The lateral line system is imperfectly known (fig. 40). It is very likely that the forms depicted and described by Zych and Brotzen are partly identical. Brotzen himself regards Zych's "*Pteraspis (Cyathaspis) sturi*" as probably belonging to *Poraspis pompeckji*.

*Poraspis simplex* was found by Zaleszczyki in marine beds corresponding to Downtonian in England, *Poraspis pompeckji* on the contrary was collected by Iwanie, Uscieszko and Zaleszczyki, in the lower and middle part of the Old-Red Group in Podolien, which corresponds to the lower Devonian.

The re-examination and re-description of the *Poraspida* from Podolien is a necessity. Only then can we obtain a clearer picture of the

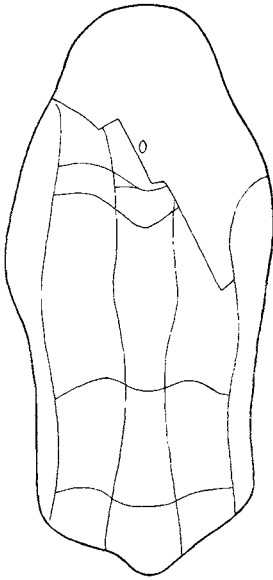


Fig. 40.

*Poraspis* (= *Palaeaspis*)  
*pompeckji* (Brotzen). An  
outline drawing of the  
dorsal shield, showing  
the course of the lateral  
lines. Ca.  $\times 1,5$ . After  
Brotzen 1934.

*Poraspis* forms from this district. As far as we can judge at the present, however, all the forms from Podolien are more or less closely related to the *Poraspida* from the Ben Nevis Group — that is to the younger stock of *Poraspida*. They are also related to *Poraspis sericea* (Lankester) and *Poraspis barroisi* (Leriche).

### The Body-Scales and Isolated Plates in *Poraspis*. (A. H.).

In practically all horizons in the Red Bay Series, in addition to the isolated dorsal and ventral shields of *Poraspis*, other *Cyathaspida* and *Pteraspida*, there have been found a number of isolated scales and plates which correspond in sculpture and microscopical structure exactly to the shields in *Poraspis*. It is, therefore, natural to regard these scales and plates as belonging to different *Poraspis* forms. To give a definition to the species, however, is only very seldom possible, and, as a rule, all these isolated portions of the body covering can only be determined as *Poraspis* sp. for which reason we shall here only give a general description

of different scales and plates of *Poraspis*, without trying to determine to which species they belong.

Unfortunately, no complete specimen of *Poraspis*, showing the relative position of the isolated plates and scales, is known, but, on the contrary, two specimens of *Anglaspis heintzi* Kiær (1932, 1) and one of *Irregularaspis* Zych (= *Dictyaspis*, Kiær 1932, 1) are more or less completely preserved and show the position of the scales and the isolated plates, thus giving us a possibility of reconstructing the scale covering in *Poraspis* as well.

As mentioned in the general part, we can, in all, distinguish between 4 different scale-types in the *Poraspidei*: the median-dorsal, the upper lateral, the lower lateral and the median ventral scales. These 6 scales (the lateral scales are represented by right and left ones) compose a closed scale-ring, probably corresponding to one metamere in the body. The scales in each ring are arranged in such a manner, that the median-dorsal with the hind side margin, covered the upper front margin of the upper lateral scale, the latter with the hind lower margin covered the upper front margin of the lower lateral scale, which, again, covered the front outside margin of the median-ventral scale (fig. 50). Each ring is thus,

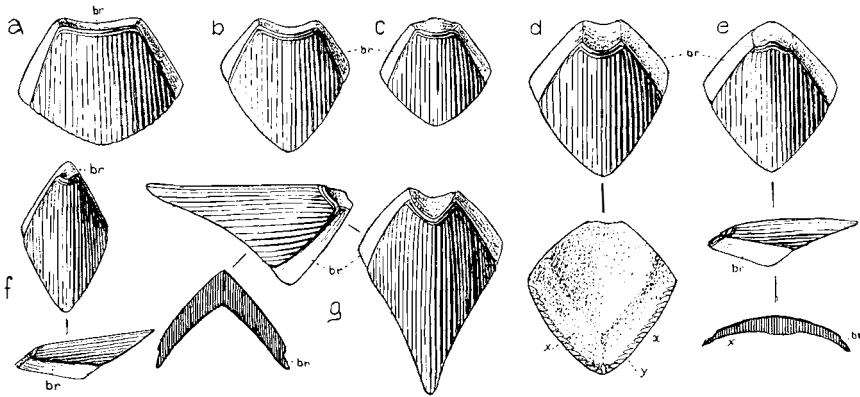


Fig. 41. *Poraspis* sp. The different median dorsal body scales from the Red Bay Series Spitsbergen. Ca.  $\times 4$ . *br* = overlapping-margin on the outside of the scale. *x* = overlapping-margin on the inside of the scale which overlaps the scale behind placed. *y* = the narrow brim of dentine ridges along the inside of the scale.

as usual in all scale-covered animals, constructed so that each overlying scale overlaps the underlying one. Furthermore, each ring overlaps the ring placed behind it, and is overlapped by the ring placed in front of it. (The first ring is overlapped by the hind margin of the dorsal and ventral shields and the branchial plates.) Thus on each scale can be seen clearly developed overlapping-margins both on the outside and the inside (fig. 41—50).

All the scales we know, can be divided into two groups: the symmetrical and the unsymmetrical ones. The former represents the median scales, the latter, the lateral scales.

The median scales have quite varying outlines — from flat, broad nearly pentagonal (fig. 41, a, b) to strongly curved along the median line, narrow, almost triangular-shaped (fig. 41, g).

Common for all these scales is the more or less broad, overlapping brim without sculpture developed, on the anterior and anterior-lateral margin on the outside of the scale (*br*, fig. 41; 42; 43). On the inside along the posterior-lateral margins are seen strong impressions; with these thinner parts the median scale overlaps the lateral scale lying behind (fig. 41, d; 43, b). From the outside, the scales are sculptured with dentine ridges, running more or less parallel to the median line, sometimes, however, somewhat fan-shaped. Along the anterior margin immediately behind the above mentioned overlapping brim, runs one, two, sometimes more, dentine ridges parallel to the anterior margin (fig. 41; 42; 43). They are thus placed more or less perpendicular to all the other ridges on the scale, and, together with the sculpture-free overlapping-margin, were covered by the posterior part of the lateral and median scales situated in front (fig. 50). The longitudinal dentine ridges, reaching the posterior margin of the scale, curve

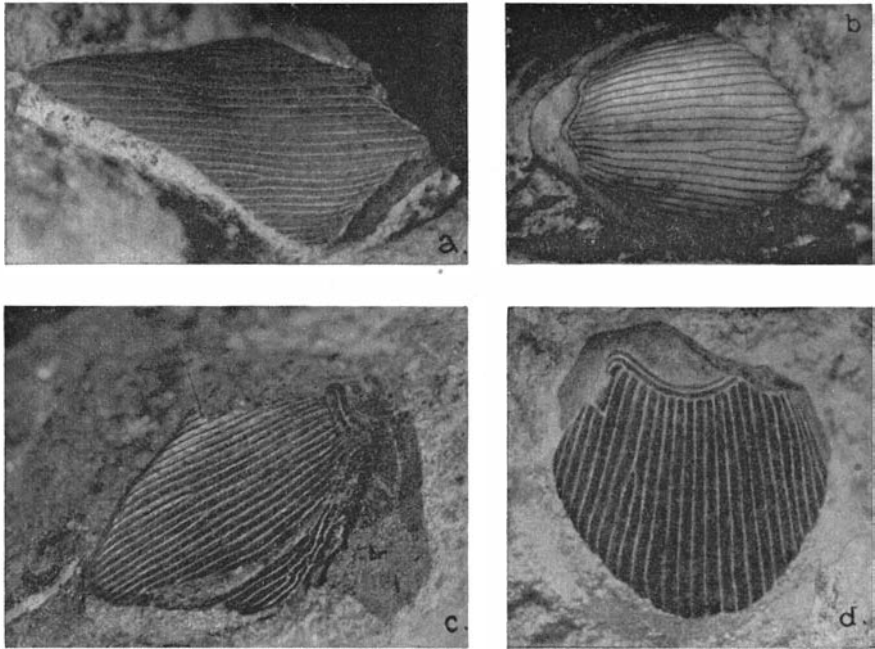


Fig. 42. *Poraspis* sp. Different median dorsal body scales from the Red Bay Series. All Ca.  $\times 7$ . a. A pointed, strongly bent scale (cf. fig. 41 g) oblique from above. Frænkelryggen. Polaris horizon. Specimen D 618. Pal. Mus., Oslo. b. A rounded, moderately bent scale (cf. fig. 41, e) from above. Frænkelryggen. Anglaspis horizon (?) Specimen D 642. Pal. Mus., Oslo. c. A large, flat scale, with very large overlapping-brim (*br*). S-side. Pteraspis Mt. 50. a. s. l. Specimen D 129. Pal. Mus., Oslo. d. A large, flat scale (cf. fig. 41 a and b). Frænkelryggen. Polaris horizon. Specimen. D 1265. Pal. Mus., Oslo.

sharply round the margin, and continue a very short distance on the inside of the scale. They thus form on the inside a narrow brim along the posterior margin of the scale (y fig. 41 d; 43, b). As mentioned above, corresponding "intern marginal ribs" can be seen, also from the inside, on the posterior margin of the dorsal and ventral shields (Pl. VI, IX, 2).

The shape of the scale varies strongly, principally according to the part of the body, where it is situated. The most anterior scales are more broad and flat, while the posterior ones are more curved, narrow and long. In the tail region they become typically fulcra-like.

The shape of the anterior margin of the median scales also varies strongly. In the most anterior ones it is long, only slightly concave (fig. 41, a, b; 42, d; 44, a), while, in the more posterior, it becomes shorter and more and more strongly concave (fig. 41, d, g; 42, a, c). Only in very few cases, was the anterior margin of the scales convex (fig. 41, e, 42, b).



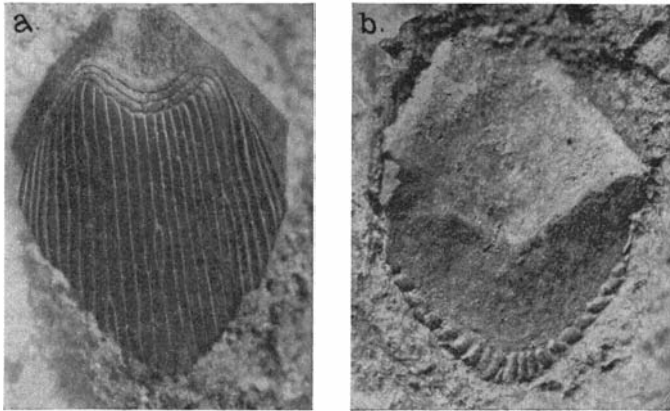


Fig. 43. *Poraspis* sp. A median dorsal scale from outside (a) and from inside (b). (cf. fig. 41 d.) Both Ca.  $\times 9$ . a. Frænkelyggen. Primaeva horizon, Specimen D 616. Pal. Mus., Oslo. b. Frænkelyggen. Primaeva horizon, Specimen D 627. Pal. Mus., Oslo.

Also the configuration of the posterior-lateral margins, forming the hind point of the scale varies considerably. In the most anterior scales they form an obtuse angle, and are relatively short (fig. 41, a, b, c; 42, d); in the more posterior, however, they gradually become longer, and the angle between them becomes more and more sharp (fig. 41, d, e, f; 42, c). In the most posterior ones, which become really fulcra-like, the hinder part of the scale protudes in a long point (fig. 41, g; 42, a). The really fulcra-scales, forming the upper and lower margin of the caudal fin have not been found.

The scale depicted in fig. 41, f and 44, b and c has an usual shape, its anterior margin being very short, only slightly concave, and the overlapping-margin very steep and broad (fig. 41, f, br; 44, c). The position of this scale in the body is as yet unknown.

Two other symmetrical body scales, or perhaps plates, must also be mentioned: one is depicted on Pl. XXXIII, 2, the other on Pl. XXXIII, 3. They are relatively large and flat, almost of a trapezoidal shape. Their anterior (?) margin is somewhat convex, 2—3 dentine ridges running conformably to it. No traces of the sculpture-free overlapping-brim can be seen. The posterior (?) margin is nearly straight, somewhat shorter than the anterior, thus the lateral margins run obliquely, not parallel to each other. The dentine ridges as a whole have a longitudinal course, but coalesce more or less complete anteriorly, thus forming a kind of a "centre". In another, somewhat broken, specimen, it can be seen that the anterior part of the scale is thicker, and the posterior thinner. This circumstance indicates that our scale with its posterior margin has overlapped another scale or

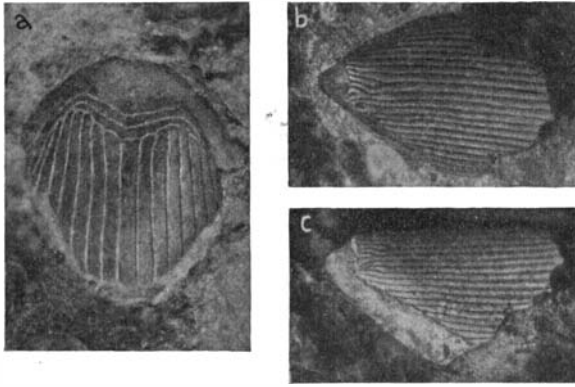


Fig. 44. *Poraspis* sp. Median dorsal scales. Ca.  $\times 6$ . a. A little scale from above. Ben Nevis W. plateau 600 m. Specimen D 438. Pal. Mus., Oslo. b, c. A scale very narrow in the front part (cf. 41, f) from above (b) and from side (c). Fr ankelryggen. Primaeva horizon. Specimen D638. Pal. Mus., Oslo.

plate, situated behind it. The position of this scale is unknown. It may represent the first dorsal or ventral scale, placed immediately behind the dorsal or ventral shields. It is, however, remarkable, that the sculpture-free overlapping-margin on the anterior margin is not developed.

The lateral scales represent two very different types. The first is large, more or less strongly bent, relatively narrow and

long, the other is small, roundish-pentangular. The first is the upper lateral scale, the other, the lower.

The upper lateral scale is the largest scale in *Poraspis*. The right and left together constitute about  $\frac{2}{3}$  to  $\frac{3}{4}$  of the whole "scale ring" while both the median dorsal and ventral scales and the lower lateral scales (right and left) form together the rest ca.  $\frac{1}{3}$  to  $\frac{1}{4}$  of the ring (fig. 50, A).

As mentioned, the single scales are long and relatively narrow (fig. 45—47). The relation between the length and breadth is from 2,5 to 3,5. The anterior and the posterior margins are somewhat curved — the anterior is concave, the posterior convex. They run parallel to each other. The dorsal and ventral margins, on the contrary, constitute two oblique limits — the anterior-dorsal and the posterior-dorsal, the anterior-ventral and the posterior-ventral (fig. 45). Thus in reality, dorsally and ventrally, the scales end in a point being, as a whole, more or less hexagonal.

From the outside, exactly corresponding to the condition in the median scales, we find along the anterior-dorsal, anterior and anterior-ventral margins, distinctly developed sculpture-free overlapping-margins (br fig. 45, a—c, e—f; 46; 47, a, d; 50). They are especially broad along the anterior dorsal and ventral margins (fig. 45, c, e, g, h, f). In one specimen, the anterior ventral margin was unusually large nearly triangle-shaped (fig. 46, b). This overlapping-margin was dorsally covered by the dorso-median scale, anteriorly by the upper lateral scale, ventrally by the lower lateral scale (fig. 50).

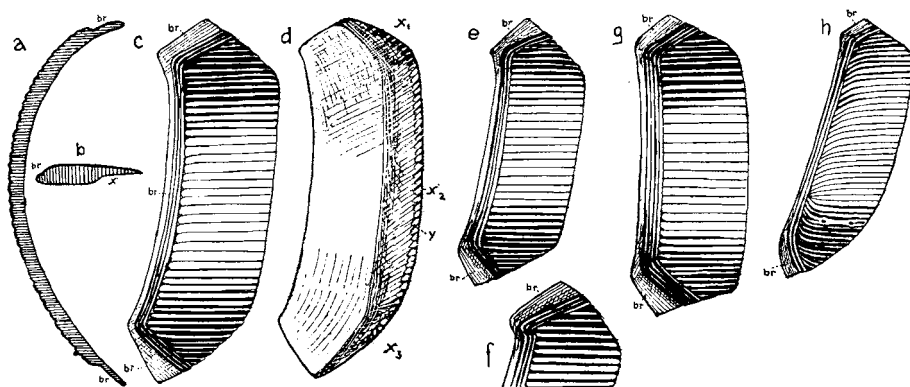


Fig. 45. *Poraspis* sp. Anterior-lateral scales of different forms. From the Red Bay Series. Ca.  $\times 4$ . a. Logitudinal section of a scale. b. Cross-section of a scale. c, e, g, h. Different scales from the outside. d. Scale from the inside. f. Upper part of a scale from the outside. br = overlapping-margin on the outside of the scale. x = overlapping-margin on the inside of the scale. y = a brim of dentine ridges from the inside of the scale.

Behind this overlapping-margin and conformably with it, corresponding to the condition in the median scales, run two, three, sometimes more dentine ridges, thus forming the anterior limit of the sculptured part of the scale (fig. 45, 46, 47). It seems apparent, that in the older forms of *Poraspis* (from Frænkelryggen Group) these anterior ridges are few in number and very regularly arranged (fig. 47, c, d, e), while on the contrary, in the younger forms, they become more numerous and irregular, often dissolved into smaller isolated portions (fig. 47, b). This development is common in scales from the Ben Nevis horizons, and also the scales from Podolien which have been studied, show the same structure.

The remaining part of the outside surface of the scale is covered with longitudinally arranged (e. g., running anterior-posteriorly), very regular dentine ridges (fig. 45, 46, 47). As a rule they run strongly parallel to each other, and only very seldom can be seen branchings of the single ridges (fig. 46, a). They are always more or less sharply divided from the above-mentioned transverse ridges, running conformably to the anterior margin of the scale (fig. 45, 46, 47). Thus, as a whole, the dentine ridges on the lateral scales in *Poraspis* are very regular, a trait which comparatively easily distinguishes them from the scales in *Irregularaspis*. Only in a relative few cases some deviations in the dentine pattern have been found: The longitudinal ridges are sometimes more or less strongly bent in the anterior portion, they may coalesce with the transverse ridges, or anteriorly become dissolved into smaller portions. This diverging pattern is reminiscent of the conditions found in the *Irregularaspis* scales, and is often found in the younger representatives of *Poraspis* (Ben Nevis Group).

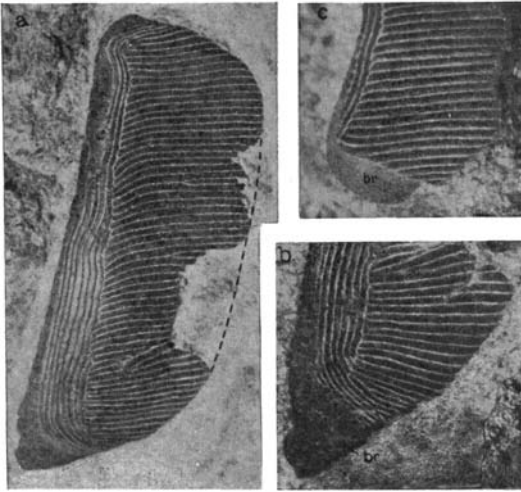


Fig. 46. *Poraspis* sp. Dorso-lateral scales from the outside. Frænkelyggen Polaris horizon. a. A large scale from the outside. Ca.  $\times 9$ . Specimen D 105. Pal. Mus., Oslo. b. The hind part of the same scale, showing the large hind overlapping-margin (*br*). Ca.  $\times 10$ . c. The hind part of another scale, showing clearly the overlapping-margin (*br*). Ca.  $\times 9$ . Specimen D 1632. Pal. Mus., Oslo.

The longitudinal (anterior-posteriorly) dentine ridges, as a rule, are neither placed perpendicular to the transverse (dorso-ventral) ridges, nor to the anterior margin of the scale, but form a more or less abrupt angle to them (fig. 45, 46, 47). This circumstance enables us to determine with full certainty the position of the single scales, and, further, whether we have to do with the right or the left scale. In fact, we know from the complete specimens of *Anglaspis* and *Irregularaspis*, that the upper lateral scales are placed with the anterior margin obliquely downwards and forwards (comp.

Kiær 1932, 1, fig. 5; 11; Pl. V). On the other hand we also know that the longitudinal dentine ridges on the scales always run horizontally (parallel to the longitudinal axis of the body). Taking these two circumstances into consideration it is not difficult to determine the exact position of the single scales: Placing the scale in such a manner that the longitudinal ridges run horizontally, and with the anterior margin to the left, all the scales, where the anterior margin runs obliquely downwards and forwards (to the left), belong to the left side of the body, while all those where the anterior margin runs obliquely downwards and backwards (to the right), belong to the right side of the body. It is obvious, however, that the right scales situated in this way are placed in an invert position — with the upper point down, and must be turned up-down, with the anterior margin to the right to be in their real position. Only in a very few cases are the longitudinal and transverse dentine ridges on the scales arranged practically perpendicular to each other (fig. 45, g). In that case it is impossible to determine whether we have a right or a left scale. There are, in addition, some other characteristics, although not so constant, which may help to define the position of the scales: often the anterior upper angle of the scale shows a more or less strong incurvation of the transversally arranged dentine ridges (fig. 45, f; 46, a). At the same

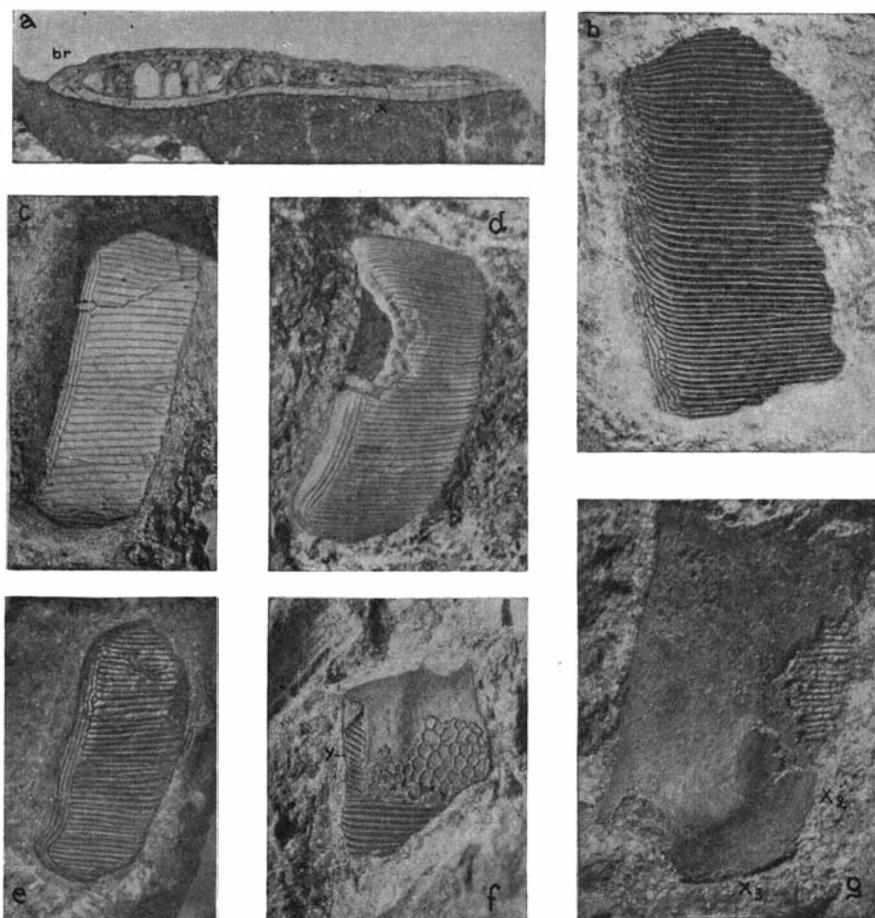


Fig. 47. *Poraspis* sp. Different dorso-lateral scales from the Red Bay Series. a. A cross-section of a scale, showing the overlapping-margin from the outside (*br*) and from the inside (*x*) and the strongly developed cancellous layer in the front part of the scale. Ca.  $\times 15$ . Mt. Pteraspis. Specimen D 2794. Pal. Mus., Oslo. b. A fragment of a scale with indistinctly developed transverse ribs. Ben Nevis horizon L. Specimen D 607. Pal. Mus., Oslo. c. A small scale with distinct pores of the lateral lines. Ben Nevis. Benneviaspis horizon. d. A scale with well developed transverse ribs. Frænkelryggen. Primaeva horizon. Specimen D 1276. Pal. Mus., Oslo. e. A very well preserved small scale. Ben Nevis W. plateau 600 m. Specimen D 438. Pal. Mus., Oslo. f. A fragment of the scale, showing the brim of the dentine ridges from the inside (*y*). Frænkelryggen. Anglaspis horizon (?) Specimen D 634. Pal. Mus., Oslo. g. The inside view of a scale, showing the overlapping-margin along the posterior ( $x_2$ ) and posterior-ventral ( $x_3$ ) margins. Mt. Pteraspis 650 m. Specimen D 630. Pal. Mus., Oslo. From b to g all ca.  $\times 4,5$ .

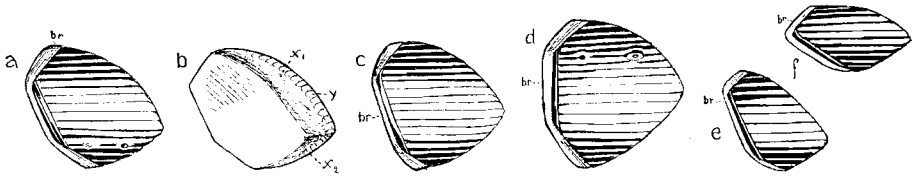


Fig. 48. *Poraspis* sp. Ventro-lateral scales from the Red Bay Series. Ca.  $\times 4$ . a, c, d, e, f. From outside. b. From inside. br = overlapping-margin on the outside of the scale. x = overlapping-margin on the inside of the scale. y = brim of the dentine ridges along the posterior margin of the scale from inside.

time, the posterior dorsal angle is, as a rule, sharper, while the posterior-ventral is more rounded (fig. 45, a, h; 46, a; 47, d).

The lateral-line pores are only very seldom found in the upper lateral scales. Of among 100 examined isolated scales only 3 were found with distinct pores (fig. 45, h; 47, c).

On the inside, the upper lateral scales show clearly three overlapping margins: the first placed along the posterior-dorsal margin ( $x_1$  fig. 45, d) the second along the posterior margin ( $x_2$  fig. 45, d; 47, a, f, g) and the last — along the posterior-ventral margin ( $x_3$  fig. 45, d; 47, g). The first of these margins covers the front part of the behind-placed median-dorsal scale, the second, the anterior margin of the behind-placed upper lateral scale and the third, the anterior-lateral margin of the lower lateral scale (fig. 50). Owing to the presence of these margins, the anterior part of the scale is much thicker than the posterior (fig. 45, b; 47, a, f, g). In a microscopical section of the scale it is distinctly seen that the cancellous layer in the scale becomes much thinner in the posterior part, while the basal, reticular and dentine layers are of the same thickness through the whole scale.

Corresponding to the condition in the median scales and in the shields we also find in the lateral scales that the dentine ridges from the outside, bend round the posterior margin to the inside where they form a narrow brim along the posterior-dorsal, posterior and posterior-ventral margins (y fig. 45, d; 47, f).

As mentioned above, the upper lateral scales are always more or less strongly bent, in side view. They are distinctly convex from the outside and correspondingly concave from the inside (fig. 45, a). They vary strongly, however, according to the degree of the curving: some are almost semi-circular, while others are nearly flat. These last types have obviously secondarily been deformed by pressure in the rock, after imbedding. Without doubt all the upper lateral scales must have been more or less strongly curved, and in specimens which have not been pressed it can clearly be seen, that the upper part of the scale is more strongly curved than the lower (fig. 45, a).

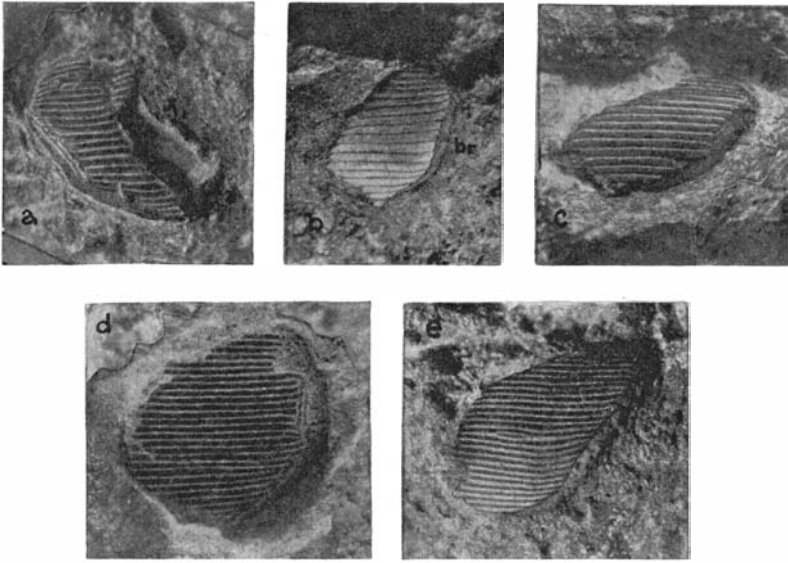


Fig. 49. *Poraspis* sp. Different ventro-lateral scales from the Red Bay Series. a. A left scale with impressions of the overlapping margin seen in the stone-matrix (*x*). Frænkelryggen. Anglaspis horizon (?). Specimen D 640. Pal. Mus., Oslo. b. A small right scale with well developed overlapping margin from the outside (*br*). Ben Nevis W. plateau 600 m. Specimen D 437. Pal. Mus., Oslo. c. A right scale from the hinder region of the body. Frænkelryggen. Polaris horizon. Specimen D 011. Pal. Mus., Oslo. d. A large right scale. Specimen D 1951. Ben Nevis horizon A (?). e. A large, narrow right scale. S. side. Mt. Pteraspis 50 m. a. s. l. Specimen D 129.

Pal. Mus., Oslo. All ca.  $\times 5$ .

The lower lateral scales are much smaller than the upper and have a more varying outline (fig. 48, 49). They are practically always more or less distinctly roundish-pentagonal. The three anterior margins (anterior-dorsal, anterior and anterior-ventral) are more or less straight, the two posterior ones (posterior-dorsal and posterior-ventral), on the contrary, convex (fig. 48, 49). Along the three anterior margins we again find developed the overlapping brim (*br*, fig. 48), which, however, is quite narrow, especially along the anterior margin. Also the transverse dentine ridge, which as usual, runs immediately behind the overlapping-brim, is only slightly developed: there is seldom more than one ridge, sometimes none at all. The dentine ridges are elsewhere longitudinally arranged and run strongly parallel to each other. The position of the single scales can be defined with more or less certainty, in the same manner as mentioned for the upper lateral scales. If the scales are placed with the anterior margin (with the overlapping brim) to the left and the longitudinal dentine ridges running horizontally, all the scales in which the anterior margin runs downwards and backwards (to the right) belong to the left side of the body and

are placed in their correct position with the dorsal margin up. While all the other scales, when the anterior margin runs downwards and forwards (to the left), are scales from the right side of the body and placed upside-down, with the dorsal side down. The position of the scale can often be easier determined, as the posterior-dorsal margin is, as a rule, longer, than the posterior-ventral (fig. 48, 49). On the inside, two overlapping margins are very obvious, one along the posterior-dorsal margin, the other along the posterior-ventral margin ( $x_1$ ,  $x_2$ , fig. 48, b; 49, a). The first overlaps partly the anterior-ventral part of the behind placed upper lateral scale and partly the anterior margin of the lower lateral scale also placed behind. The second covers the anterior margin of the median-ventral scale (fig. 50).

A relatively large number of the lower lateral scales have developed two pores for the lateral line system. In one weathered specimen is distinctly seen a short canal running from the anterior to the posterior margin of the scale.

Along the posterior margin is also seen a narrow brim of dentine ridges ( $y$  fig. 48, b).

In fig. 50 is given a reconstruction of the scale-covering of the body in *Poraspis*. It gives a probable picture of the more or less anterior portion of the body, not far from the dorsal and ventral shields. In the caudal region, as is known from *Anglaspis*, the median-dorsal and ventral scales get gradually more compressed and pointed and, finally, become really fulcra scales. The upper lateral scales become smaller, not so strongly bent, the lower long and narrow. In the caudal region and on the caudal fin — the lateral scales are broken up into numerous smaller ones. None of these have been found among the isolated scales from Red Bay. The scales depicted in fig. 48, e, f and 49, b, c, however, have certainly been situated in the posterior part of the body, perhaps close to the caudal fin.

The branchial plate (fig. 51; Pl. XXXIII, 4, 5, 6) has already been shortly described in the introductory part. It is a relatively long and narrow plate — about 6 to 7 times as long as broad — and is situated between the dorsal and the ventral shields (fig. 52). It begins immediately behind the orbital notch and runs practically to the posterior margin of the lateral lobe. Its length is thus somewhat shorter than the dorsal shield and as long as the ventral. Its lower margin (fig. 51, g—f), which comes almost in contact with the ventral shield, is nearly straight, only the most anterior and posterior portions are slightly bent upwards, thus forming the anterior and posterior margins of the plate (fig. 51, g—a, f—e). The upper margin, on the contrary, is strongly bent (fig. 51, b—c—d—e) and corresponds in configuration more or less to that of the lateral margin of the dorsal shield (fig. 2; 52). From the anterior dorsal corner (fig. 51, b) of the branchial plate, the upper margin runs first somewhat



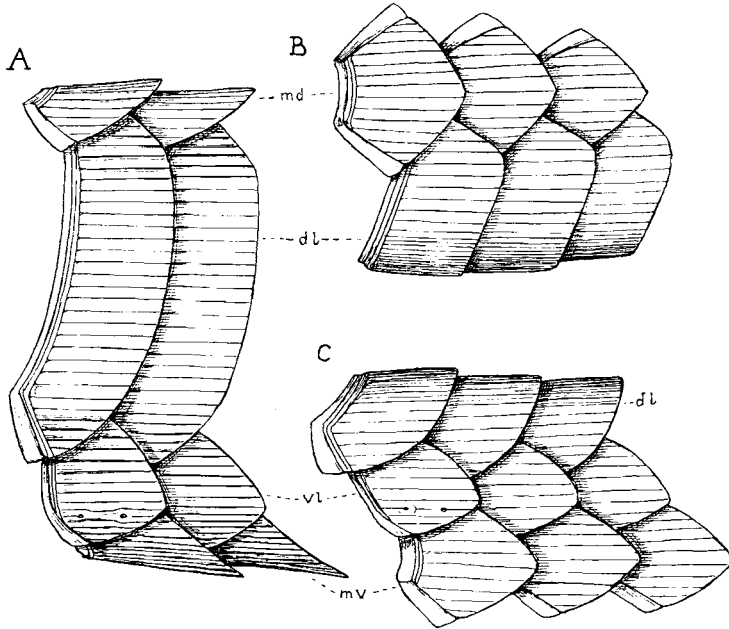


Fig. 50. *Poraspis* sp. Reconstruction of the scale-covering of the front part of the body (immediately behind the shields). Ca.  $\times 4$ . A. From the left side. B. From above (only the left-side lateral scales are depicted). C. From below (only the left-side lateral scales are depicted). *md* = median dorsal scale. *dl* = dorso-lateral scale. *vl* = ventro-lateral scale. *mv* = median ventral scale.

downwards and then gradually more and more upwards (fig. 51, b—c). About  $\frac{1}{3}$  from the hind point the branchial plate thus reaches its maximum breadth (fig. 51, c), and from this point the upper margin runs more rapidly downwards. It continues, however, not into the upper margin of the hind part of the plate, but disappears gradually in the upper portion of the hind part (fig. 51, c—e; Pl. XXXIII, 4). The upper margin of the hind part of the plate, runs from the hinder upper point (fig. 51, e) forwards and inwards (fig. 51, e—d), thus, when reaching the upper margin of the front part of the plate, it is placed far more inwardly in relation to the latter (fig. 51, c—d; 54, 3, C, 4, 5), and here it stops abruptly (fig. 51, d). From this point the upper margin makes a distinct curve running first downwards and forwards, then upwards and forwards and, finally, comes in contact with the inside of the front part of the plate. In this manner a distinct incut is formed in the upper part of the plate, an incut which continues backwards as an impression in the upper part of the plate (fig. 51, *br*). The mentioned configuration of the branchial plate is only seen in well-preserved not pressed plates (Pl. XXXIII, 4 here, however, the hind part of the plate is not worked out from the stone). In the more or less flattened-pressed plates the hinder part of the plate is almost on the level with the

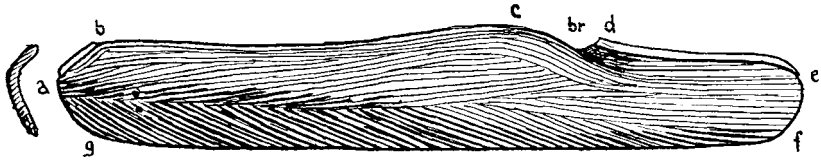


Fig. 51. *Poraspis* sp. Left branchial plate.  
*a—b* = the anterior overlapping-margin. *br* = branchial impression.  
*d—e* = the posterior overlapping-margin.

front part, and instead of the above mentioned incut and impression we find only a more or less distinct curve in the upper margin of the plate (Pl. XXXIII, 5, 6). The incut and the longitudinal impression in the branchial plate compose the lower limit of the branchial opening (fig. 52) and in form and configuration correspond perfectly to the condition we find in the *Pteraspida* (comp. Kiær 1927, Broili 1933, Gross 1933, Brotzen 1933, 2).

The relatively short posterior (fig. 51, *e—f*) and anterior (fig. 51, *g—a—b*) limits of the branchial plate are somewhat rounded. In the anterior margin we can clearly distinguish two parts: the lower, which is more or less curved and forms an immediate prolongation of the lower margin (fig. 51, *g—a*) and the upper, which is almost straight and placed at an abrupt angle to the lower part (fig. 51, *a—b*). In this part can be seen a sculpture-free overlapping-margin (fig. 51, *a—b*) clearly developed. Another part also showing an overlapping-margin is the posterior part of the upper margin of the plate (fig. 51, *d—e*). This margin is, however, not so easy to discover, and in all the branchial plates depicted on Pl. XXXIII it has not been worked out.

The dentine ridges in the branchial plate are mainly longitudinally arranged (fig. 51; Pl. XXXIII, 4, 5, 6). Two sets of ridges, however, can always be discerned, the one in the upper part of the plate running obliquely upwards and backwards, more or less parallel to the upper margin of the plate, especially in the posterior portion (fig. 51, *a—b—c—e*), the other, placed in the lower part of the plate running, on the contrary, obliquely, downwards and backwards and placed at a relatively very abrupt angle both to the lower margin of the plate and to the upper set of ridges (fig. 51, *a—f—g*). These two sets meet each other somewhat below the median line of the plate forming a distinct sculpture limit (fig. 51, *a—e—f*; Pl. XXXIII, 4, 5, 6). More to the rear, however, the ridges of the lower part are placed more and more horizontally and, finally, in the most posterior portion, the limit between the upper and lower sets of ridges practically completely disappears (fig. 51; Pl. XXXIII, 4, 5, 6). In addition to these two sets of ridges we find along the anterior dorsal and front part of the dorsal margin two-three ridges running continuously to the margin. Also on the inside of the

plate, along the front part of the dorsal margin are developed two-three dentine ridges, exactly corresponding to the intern marginal ribs, which are seen on the inside of the dorsal shield in the branchial region (Pl. XI, 1; XXVI, 2). As mentioned, the branchial plate is slightly bent from front to rear and from the upper to the lower margin, its outside being convex, the inside concave. The curvature from front to rear corresponds to that in the lateral margins of the dorsal and ventral shields. The dorso-ventral curvature is very distinct, the plate is more or less bent along the longitudinal line, which runs somewhat higher up than the above mentioned sculpture limit (fig. 51, a—e). The upper part is thus slightly narrower than the lower. This curvature, which is sharp in the front part, gradually disappears backwards, and is only very moderate in the most posterior part (fig. 52).

Two pores of the sensory canal system can practically always be found in the front part of the branchial plate. They are placed very near to each other (fig. 51; Pl. XXXIII, 4, 5, 6). The presence of a sensory canal, connecting these pores, cannot be recorded with certainty. We may here have only pit-lines, but it is, however, not improbable, that these pores in some way or other connect the sensory canal-nets in the dorsal and ventral shields.

As mentioned above, the branchial plate is situated between the dorsal and ventral shields connecting them together (fig. 2; 52), of course, not equally solidly in all places. The front  $\frac{2}{3}$  part of the upper margin of the branchial plate has, as we know, no overlapping-margins neither on the outside nor on the inside. On the contrary 2—3 dentine ridges run here along the upper margin also on the inside (the intern marginal ribs). Exactly the same is the case on the lateral margin in the dorsal shield, between the eye-notches and the branchial sinus (Pl. XI, 1). This may indicate that the dorsal shield and the branchial plate in this region do not touch each other, but on the contrary, were probably divided by a more or less narrow skin-portion, thus perhaps, these parts could move slightly in relation to each other (breathing?). It must not be forgotten, however, that this movement in all cases could only be of very minute dimensions. The hinder  $\frac{1}{3}$  part of the upper margin of the branchial plate shows, on the contrary, a very distinctly developed overlapping-margin from the outside. This part was covered by the post-branchial lobes of the dorsal shield, where the overlapping margin is clearly visible from the inside.

The lower margin of the branchial plate shows, as mentioned, a distinct overlapping-margin practically along the whole length on the inside. This margin covered the lateral margin of the ventral shield, where as we know, a relatively broad overlapping-margin is developed on the outside (Pl. IV). It is thus obvious that the branchial plate was solidly connected with the ventral shield.

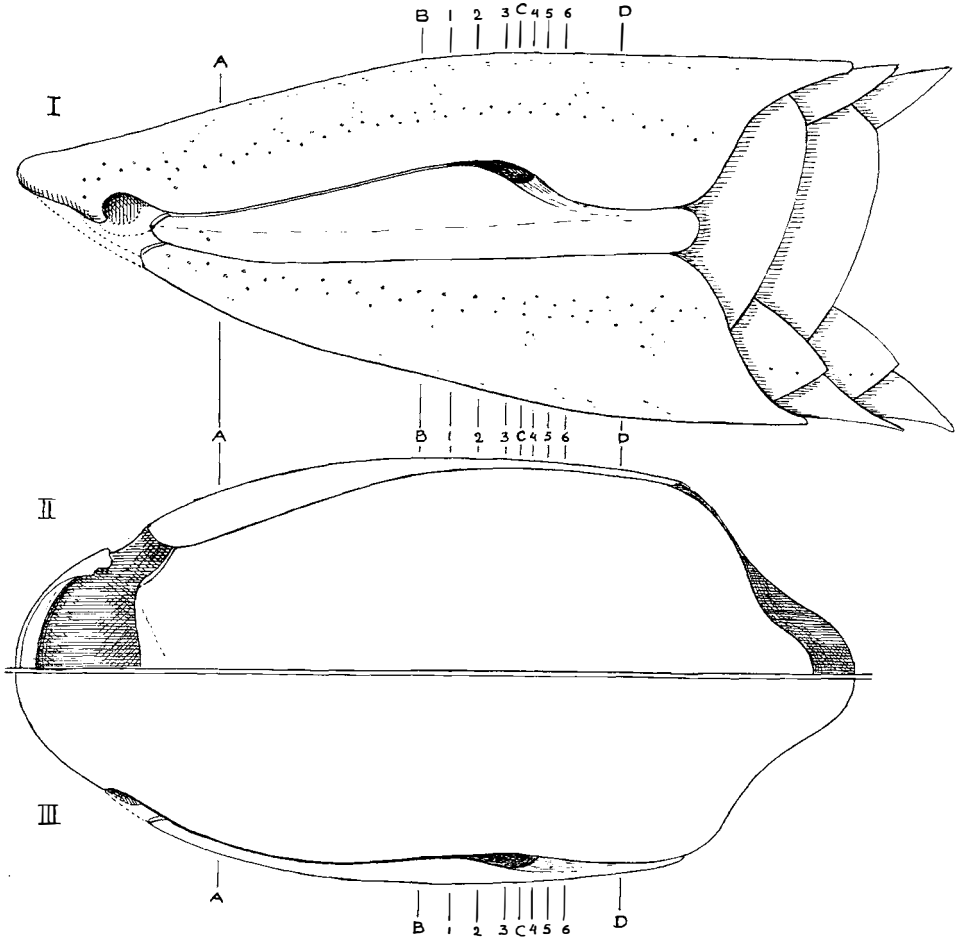


Fig. 52. *Poraspis* cf. *polaris* Kiær. The total reconstruction of the front part of the animal. I. From the left side. II. From the ventral side. III. From the dorsal side. A, B, C and D. The position of the cross-section depicted in fig. 53 and 54. 1, 2, 3, 4, 5, 6. The position of the cross-section depicted in fig. 54.

As we have heard before, another, short overlapping-margin is also found (from the outside) on the anterior dorsal margin of the branchial plate (fig. 51, a—b). At present we do not know which plate overlapped this margin of the branchial plate. Zych in his last paper (1931) gives a reconstruction of a *Poraspis* from Podolia (fig. 37, 39) where the branchial plate continues into the preorbital process of the dorsal shield. If this reconstruction is correct, the above-mentioned overlapping-margin in the front part of the branchial plate must have been overlapped by the preorbital process. It seems, however, that this reconstruction is not absolutely accurate. All the investigations which have been undertaken to compare the relative position of the

branchial plate and the dorsal shield in *Poraspis* show, that the branchial plate does not extend so far forwards, as expected by Zych. In addition, it may be mentioned that no overlapping-margin from the inside of the preorbital process has been observed. It is also improbable that if the branchial plate has, in reality, limited the orbits from beneath, no orbital impressions can be observed in its front part.

In *Anglaspis* has also been found the fragments of a minute plate placed in front of the branchial, and probable limiting the orbits on the inside (Kiær 1932, 1). It is possible that such a "sub-orbital" plate was also developed in *Poraspis*, and that it is this plate which overlapped the front part of the branchial plate. No trace, however, of such a plate has hitherto been found among the Spitsbergen material.

The same is also the case with the mouth plates — not one fragment indubitably belonging to the *Poraspis* mouth apparatus has been recognized among the Spitsbergen-collections. As, however, the mouth apparatus in *Anglaspis* is quite well known and as it is built very similarly to that in *Pteraspis* (Kiær 1927), we may assume that the mouth plates in *Poraspis* were developed more or less correspondingly to those in *Anglaspis* and *Pteraspis*: with two relatively large lateral plates, and a number of narrow oral ones.

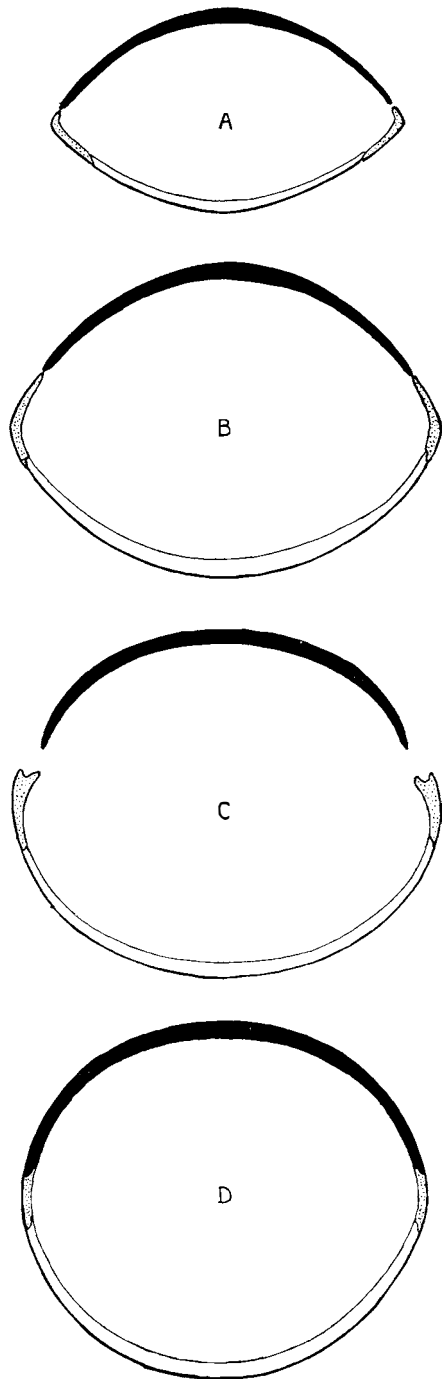


Fig. 53. *Poraspis* cf. *polaris* Kiær. Four cross-sections in different regions of the shield, shown in fig. 52 (A, B, C and D). Black = dorsal shield. Dotted = branchial plate. White = ventral shield.

### The total reconstruction of the *Poraspis* (J. K. & A. H.).

The more or less probable total reconstruction of *Poraspis*' dermal skeleton is given in fig. 52, 53 and 54. This reconstruction is chiefly based on the conditions and relations known from *Poraspis polaris* Kiær. The drawing is clear enough, some remarks only being necessary.

The branchial plate is placed in such a position that the surface of its upper part forms an immediate prolongation of the surface of the dorsal shield, and the surface of its lower part continues directly into that of the ventral shield (fig. 53, A, B, D). Thus the branchial plate forms the lateral margin of the whole carapace (fig. 52, II, III).

As is known, the dorsal and ventral shields are nearly equally broad in their hinder parts, but in the front part the dorsal shield is considerably the broader. The opening, which must thus be developed in the front part of the shield, is completely filled up by the branchial plate. This plate, as we know, is sharply bent in its front portion (fig. 51) and in such a manner, that the part placed above the curving line is narrower than that placed below (fig. 52, I, II; 53, A). In this manner, the variations in the breadth of the dorsal and the ventral shields become compensated, as the dorsal part of the branchial plate, which comes in contact with the dorsal shield, is considerably narrower than the ventral, which touches the ventral shield (fig. 52, II, III; 53, A). In the posterior part, where both the shields are equally broad, the branchial plate is only moderately and evenly bent (fig. 52; 53).

Especially interesting is, however, the development of the branchial opening. It is limited from above by the branchial sinus of the dorsal shield, from below by the branchial plate. The front ca.  $\frac{2}{3}$  part of the upper margin of the branchial plate follows in its configuration more or less the lateral margin of the dorsal shield (fig. 52). But somewhat in front of the branchial sinus, the upper limit of the branchial plate curves strongly downwards — thus forming here a relatively large opening. The post-branchial lobes in the dorsal shield are, as is known, much more strongly bent downwards than the branchial part of the shield. They come in contact with the hinder ca.  $\frac{1}{3}$  of the branchial plate, which they overlap, thus forming the hind limit of the branchial opening. The branchial opening becomes thereby shaped as a kind of a tube running obliquely backwards and outwards. The construction and configuration of the branchial opening can, however, be better understood, by studying the fig. 52 and especially 53 and 54, which show the cross-section through the branchial part of the shields.

The general outline of the body of a *Poraspis* is clearly seen in fig. 52 and 53. In the front part the body is more or less strongly dorso-ventrally compressed, with relatively sharply bent side edges (fig. 53, A). Backwardly, the body becomes more and more rounded,

and the sharp side edges gradually disappear (fig. 53, B, C). Finally, in the hinder part, the section of the shield is practically round without any edges (fig. 53, D). This, in section, round body continues certainly also into the front part of the scale-covered portion of the body. More to the rear, however, the body becomes more and more strongly compressed from the sides, and the sharp edges are again distinctly developed, but now not on the right

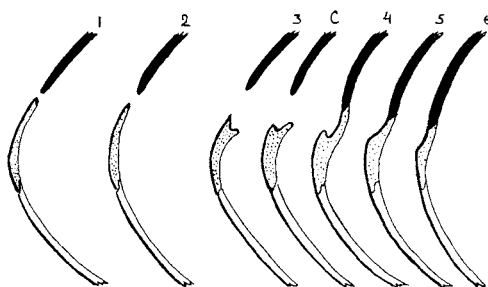


Fig. 54. *Poraspis* cf. *polaris* Kiær. Seven sections through the branchial region of the shield. The position of the sections shown in fig. 52 (1, 2, 3, C, 4, 5 and 6). Black = dorsal shield. Dotted = branchial plate. White = ventral shield.

and left sides, but on the dorsal and ventral sides. Finally, the caudal region of the body is completely flat, but now compressed not dorso-ventrally as the front part, but from the sides. No traces of the paired or unpaired fins or spines are known in *Poraspis*. It seems very improbable that such organs were developed at all in the *Cyathaspida*. The very well preserved complete specimens of *Anglaspis* known from Spitsbergen (Kiær 1932, 1) do not show any traces which can be regarded as fins or spines.

The only locomotion organ in *Poraspis* was the caudal fin. The construction of the body with the horizontally compressed front part and vertically flattened hind part must be regarded as a very primitive balance organ, which helped the animal, a typical benthic form, to keep a more or less stable position in the water when swimming.

### A retrospect of the evolution of the Genus *Poraspis*.

If we examine retrospectively both the numerous new species of *Poraspis* from Spitsbergen and the older known forms, it is not difficult to point out certain lawful changes undergone by the genus during its long life.

A circumstance which will be noticed in the first instance is that the species increase in size from the older to the younger forms. It can easily be shown graphically for the Red Bay Series (Table III).

This table shows just what we should expect with regard to the phylogenetic evolution of a genus if factors do not arise which may dwarf the individuals. Another difference will also be seen between the forms in the Frænkelryggen Group and those found in the Ben Nevis Group. The former Group, besides forms of a median size, also contains a number of small ones; such small forms are entirely lacking in the Ben Nevis Group, which is characterized by the occurrence of only comparatively large and very large forms.

This probably also applies to the other European areas in which *Poraspis* forms have been found, this at all events being the case in England. Here *P. sericea*, which particularly goes with the forms in the Ben Nevis Group and even exceeds these with regard to size, occurs in layers which must be regarded as corresponding to the upper part of the Red Bay Series.

Another feature which must also be pointed out is the change in the development of the lateral line system. In all older forms of the Fränkelryggen Group the dorsal median longitudinal lines end anteriorly freely, without being united to the pineal branches (fig. 3; 23). In the younger forms, on the other hand, belonging to the Ben Nevis Group a junction of these lines has occurred (fig. 27; 29; 31).

The same is the case with *P. sericea*, *Poraspida* from Podolien and probably also with the other *Poraspis* forms. In *P. sericea* we find a further development, as the pineal branches coalesce in the median line posteriorly of the pineal organ (fig. 33). At the same time the post-pineal commissures seem to grow more regular and to be completely developed.

As a third peculiarity can be mentioned that in the older forms we frequently find a strong development of transversally curving ridges behind the anterior margin of the rostral part, while such ridges are

Table III.  
Increase of dorsal shield in *Poraspis* through  
the Red Bay Series.

	Fränkelryggen			Ben Nevis		
	Lower part	Median part	Upper part	Lower part	Median part	Upper part
80 mm.....						I <sup>8</sup>
50 mm.....				I <sup>6</sup>	I <sup>7</sup>	I <sup>7</sup>
40 mm.....			I <sup>1</sup> I <sup>5</sup>			
30 mm.....		I <sup>1</sup>	I <sup>1</sup> I <sup>5</sup>			
20 mm.....	.4 I <sup>5?</sup>	I <sup>5</sup> I <sup>2</sup>	I <sup>2</sup> I <sup>3</sup>			

1 = *Poraspis polaris*.

2 = *Poraspis brevis*.

3 = *Poraspis intermedia*.

4 = *Poraspis subtilis*.

5 = *Poraspis elongata*.

6 = *Poraspis rostrata*.

7 = *Poraspis cylindrica*.

8 = *Poraspis magna*.



apt to be entirely lost in the younger forms in the upper part of the Ben Nevis Group. At the same time the dentine ridges of the dorsal shield seem to get a more and more regular longitudinal course. This, however, cannot be decided with certainty, as on account of the more scanty material of the younger forms we cannot have a correct notion of the breadth of variation of the dentine ridge-pattern in these, similarly to what we had of the older forms. Many circumstances will suggest, however, that the breadth of variations is considerably less in the younger than in the older forms. In other words, the pattern of the dentine ridges seems gradually to become more constant.

## 2. Genus *Homaspis* Heintz n. n.<sup>1</sup>

*Homalaspis* Kiær 1932, 1.

Generic characteristics. Small forms with a short, broadly rounded rostral part, faintly developed branchial part and very short post-branchial part with brief post-branchial lobes. The dentine ridges comparatively broad and the surface unusually glossy. The pineal macula broad and entirely flat. The dermal skeleton thin with almost wholly reduced reticular layer and with very broad openings from the cancellae upwards into the pulpa-canals. The development of the lateral line system of the dorsal shield is distinguished by rudimentarily transverse commissures. In the ventral shield, the anterior transverse commissure and the four succeeding brief median lines are united into one continuous line, whereas, in *Poraspis*, they form totally isolated parts. The pores of the pineal branches are not particularly large as is the case in *Poraspis*.

The genotype is *H. nitida*, which undoubtedly represents a separate type closely related to *Poraspis*. In most respects these two genera are homologous, but they also show a few pronounced differences. First may be mentioned the comparatively broad and flat dentine ridges, a feature, which, without doubt, furnishes the dermal skeleton with the unusually shining glossiness, so characteristic of this little form. Secondly, with regard to the interior structure of the skeleton the reticular layer is still more reduced than in *Poraspis* and the cancellae open upwards into the pulpa-canals with strikingly large openings in both shields (fig. 57). This simplification in the structure tends to make the skeleton thinner and lighter. The development of the lateral line system (fig. 55) of the dorsal shield shows a marked reduction of the transverse commissures. Still more important are the changes that the lateral lines have undergone in the ventral shield. Also this feature must be considered

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<sup>1</sup> Prof. E. Strand, Riga, has kindly pointed out, that the name *Homalaspis*, proposed by Kiær, is preoccupied I therefore introduce a new name *Homaspis*.

as representing a more advanced stage of the development of the lateral line system and justifies the establishment of a separate genus, which must be supposed to have specialized from some older *Poraspis*-forms.

This new type has not been found outside of Spitsbergen where it occurs abundantly in the Ben Nevis Group.

*Homaspis nitidus* (Kiær).

*Homalaspis nitida*. Kiær 1932, 1.

(Pl. XXX; XXXI, 2; XXXII, 1; XXXIII, 1; XXXIV, 6; XL; fig. 55; 56; 57).

Specific characteristics. A minute form with the length of the dorsal shield 20—23 mm. There may probably be separated an *angusta* and a *lata* form with a B. L. Ind. of about 42 and 52 respectively (fig. 56), with reference to other features apply to the generic characteristics given above.

The holotype is the specimen D 156, pictured in Pl. XXX, 2.

Occurrence and material. *H. nitidus* is a pronounced index fossil for the Ben Nevis Group and has been found in many of the horizons in this group both in its upper and lower portion. A. Hoel and G. Watnelie during Isachsen's expedition 1909—10 collected an excellent material, including the pretty holotype, from the horizons A, B, D, F, G, K, L, R and from the debris below the West plateau. It seems to be most common in the horizons A, F and L. A good supplementary material was obtained by the expeditions of 1925 and 28. The following localities may be mentioned: The north side of Ben Nevis, 50—80 m (= hor. A and B), Andrèe moraine, Ben Nevis 320 m, Vogti horizon, Cephalaspis moraine, Tunge, Ctenaspis horizon, Bennevisaspis horizon (= hor. 0). Moreover, it was found by A. Hoel 1912 on the east side (200 m) of Mt. Sigurd; situated to the west of the head of Wood Bay. We are thus in possession of a considerable, though most often fragmentary, material.

General description. The dorsal shield (fig. 55, A, B) of this small species does not exceed 20—23 mm in length, the branchial breadth being from 10,5—12 mm. In the very pretty holotype (Pl. XXX, 2) the length is 23 and the breadth 12 mm, the B. L. Ind. thus being 49—52,5. Yet there are also much more narrow representatives with B. L. Ind. 43. It is reasonable to presume, that these are *angusta* forms, whereas the former, somewhat broader specimens, which are the most common, are *lata* forms (fig. 56). In comparison with *Poraspis polaris*, *Homaspis nitidus* is a relatively slender form. The rostral part is short and broadly rounded and the branchial part slightly widened, thus the dorsal shield is of a fairly uniform breadth only narrowing somewhat far behind near the branchial sinus (fig. 55, A). The shield is often rather flat superiorly, but has originally been

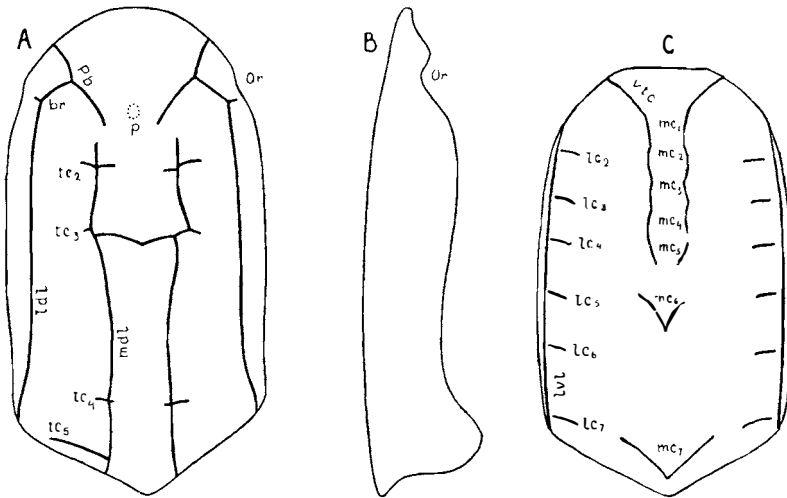


Fig. 55. *Homaspis nitidus* (Kiær). An outline drawing, showing the course of the sensory canals on the dorsal (A) and ventral (C) shields, and dorsal shield from the side (B). Ca.  $\times 3$ . *br* = branch from *ldl* canal. *ldl* = lateral dorsal line. *lvl* = lateral ventral line. *lc*<sub>2</sub>–*lc*<sub>7</sub> = lateral portions of ventral transverse commissures. *mdl* = median dorsal lines, *mc*<sub>1</sub>–*mc*<sub>7</sub> = median portions of the ventral transverse commissures. *Or* = orbits. *pb* = pineal branch. *p* = impression of the pineal organ. *vtc* = ventral transverse commissure.

faintly and evenly vaulted. It is, as usual, somewhat extended posteriorly and ends in a rounded lobe. The post-branchial part is strikingly short and the post-branchial lobes are slightly developed (fig. 55, B). The dentine ridges are of a regularly longitudinal arrangement and are somewhat broader than those in *Poraspis*, about 5 in 1 mm. They are strikingly plane and smooth which fact, presumably, causes the unusual strong gloss of the dermal skeleton in *Homaspis*.

The rostral pattern seems to be comparatively constant; it is distinguished by regular, longitudinal ridges, curving somewhat more on the sides (Pl. XXXI, 2). Along the anterior margin is developed a distinct area with ridges going conformably to the margin. Just behind this area the ridges converge more or less distinctly. The pineal macula is very large, broad, and flat (Pl. XXXI, 2). Unimportant variations with regard to the dentine-ridge-pattern of the surface are as usual found in all representatives.

The maxillar brim is developed nearly similar to that in *Poraspis*.

The ventral shield (fig. 55, C) is, similar to the dorsal shield, of a rather equal breadth with faintly curved margins (Pl. XXXII, 1). The anterior margin curves a little inwards and the anterior corners are distinctly truncated. Posteriorly, the shield is slightly extended and here ends in a rounded lobe (Pl. XXX, 1). The dentine ridges are of a regular longitudinal course, most in front with a dispersion of the ridges near the frontal transverse commissures.

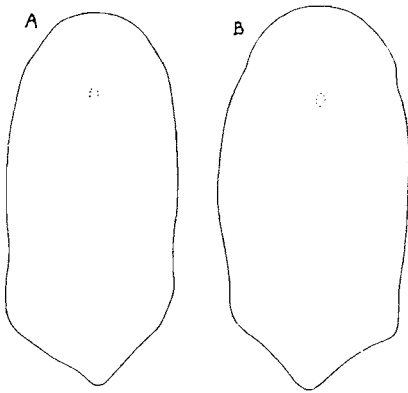


Fig 56. *Homaspis nitidus* (Kiær). An outline drawing of *angusta* (A) and *lata* (B) forms.

The main features of the lateral line system have already been briefly mentioned. The two pairs of longitudinal lines in the dorsal shield are similar to those in *Poraspis* (*ldl*, and *mdl* fig. 55, A). The transverse commissures, on the other hand, are much more indistinctly developed, particularly the three most posterior ones (fig. 55, A). The two most posterior of these lie close together, unusually far back on the dorsal shield, a consequence, probably due to the fact that the post-branchial part is uncommonly short. Still more unusual is the

development of the lateral line system of the ventral shield. (Fig. 55, C.) Here, as mentioned, the first long transverse commissure and the short median lines of the four succeeding transverse commissures are united into one continuous line, which, however, may be somewhat abrupted farthest behind. Then follow the median angularly arranged portions of the sixth and seventh transverse commissures. The latter, as usual, separated by a long intervening space, runs close to the posterior margin of the shield. The lateral longitudinal lines are developed as usual. By grinding, have been found six pairs of short lateral portions of transverse commissures, which, remarkably enough, is one more than in *Poraspis*. It seems as if the first pair of these represents the third and not, as in *Poraspis*, the fourth transverse commissure.

The interior impressions are often very clearly marked, especially on the dorsal shields, preserved in the horizons of finegrained sediment (Ben Nevis, A and L), often showing good natural casts (Pl. XXX, 3; XXXII, 1). The branchial impressions are very distinct with pitted surfaces. The first is very large, distinctly directed forward, the seventh, very faint and indiscernible. The marginal-branchial impressions are only faintly marked. The nasal sacs have left distinct impressions just behind the anterior margin. They lie close together, but are clearly divided into two portions and, similar to those in *Poraspis*, go far out to the sides. The impressions caused by the semi-circular canals are very big, but otherwise are of the usual shape and position. Between them are developed clear impressions of the posterior portion of the brain. Most in front is seen a distinct boundary of the mesencephalon and, farthest behind, the impressions caused by a strongly developed medulla oblongata. The connection between these brain portions is very narrow without any indications of the development

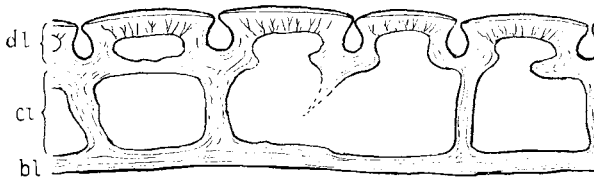


Fig. 57. *Homaspis nitidus* (Kiær). Cross-section of the dorsal shield. Ca.  $\times 75$ .  
*bl* = basal layer. *cl* = cancellous layer. *dl* = dentine layer.

of a metencephalon. In front of the mesencephalon is visible the impression caused by the very strongly developed pineal organ. The cast of this impression is unusually interesting. It becomes more and more elevated forwards with faint transverse wrinkles and, foremost, in its highest portion, there is a little smooth, round, flat place, which has been situated just beneath the thin skeleton of the pineal macula. The two diverging ridges, seen, on the cast, in front of the brain impressions correspond to the pineal branches of the lateral line system. On the cast, a marked longitudinal impression will be noticeable directly inside the marginal-branchial impressions. This impression corresponds to a strong thickening in the dermal skeleton.

Finally, the structure of the dermal skeleton of this species must be dealt with more in detail. As mentioned above, it is particularly distinguished by the uncommonly wide openings, by which the cancellae are in connection with the pulpa canals. This fact seems especially to appear in the dorsal shield (fig. 57). Here the pulpa canals are also unusually wide, whereas the structure of the ventral shield more resembles that in *Poraspis* (cf. Pl. XXXVI, 1, 2; Pl. XL, 3, 4). As mentioned, the reticular layer is also entirely reduced, a circumstance, which clearly simplifies the structure of the skeleton. Further, as the walls of the cancellae and the basal layer are finer, particularly in the dorsal shield, and as the skeleton as a whole is thinner than that in *Poraspis*, it is evident, that in our form the dermal skeleton is lighter than those in the other forms of the *Poraspidae*.

Of this form also the branchial plate is known in a few specimens. A particularly fine view of this is shown on the piece figured in Pl. XXX, 1. The plate here lies in connection with the ventral shield, though not in a wholly natural position as to some degree, it overlies the latter. It is very reminiscent of the branchial plate in *Poraspis polaris*, but more evenly thins out in its posterior portion and is devoid of the strongly marked branchial incision of this form. The lack of a branchial incision is apparently a characteristic of the genus.

On the same piece, in front of the ventral shield, is seen a small plate (a), which is reproduced greatly enlarged in Pl. XXXIII, 1. It does not seem to be altogether complete, it is of a nearly triangular

shape and shows two distinct pore-openings for the lateral line system. It is probably one of the lateral plates. This name refers to the two small plates that, ventrally, are situated just on the sides of the plates of the mouth-region (cf. Kiær 1927).

Behind the ventral shield is seen one of the body scales (*b*). This is in an incomplete state of preservation and comparatively small, but on the whole, of a similar structure as that in *Poraspis*. Most in front are seen three transverse ridges forming a striking contrast to the longitudinal ones, which cover the greatest part of the surface of the scale. Similar isolated scales are known from several horizons.

*Homaspis nitidus* var. *robustus* nov. var.

During Vogt's expedition in 1928 several dorsal and ventral shields of a more robust and a somewhat larger *Homaspis* form were found in the Vogti-horizon on the north plateau of Ben Nevis. As it was discovered in a red-brown stone the dermal skeleton had a whitish, faintly reddish colour, a striking contrast to the black colour, which is common for the skeleton of the greenish rocks. The total length of the dorsal shield is 23—26 mm, the B. L. Ind. somewhat exceeding the usual measure, being 54. In other respects it shows no other difference from the leading form which occurs in older and younger parts of the Red Bay Series. This form has therefore been designated as a variety only. As holotype has been chosen the specimen D 264.

**3. Genus *Cryptaspis* Bryant. (A. H.).**

This genus was described by Bryant (1934) from the lower Devonian beds of Bearthooth Butte, Wyoming, U. S. A. According to a letter from Prof. Bryant to Dr. Heintz, however, he is at present in possession of a much better and richer material of specimens belonging to this genus which he will soon describe. Therefore, we shall here only shortly mention some points in the structure of this new genus, otherwise referring to the detailed description and pictures given in Bryant's last papers (1932, Pl. III, 3; 1933, Pl. XVII, 2; 1934, fig. 7, 8; Pl. VIII, 4; XXVI, 1).

The only species known is:

*Cryptaspis ellipticus* Bryant. It is hitherto the largest known representative of the *Cyathaspida*. Its length measures ca. 90 mm and the breadth ca. 54 mm. B. L. Ind. being ca. 60 (all measurements are taken from photographs only). The orbital notches are quite indistinct, being situated very far forward. Thus the rostral part is unusually short, and the rostral index is only ca. 12 — the smallest rostral index known in *Poraspidei*. According to the development of the sensory canals, sculpture and others — see Bryant 1934, pp. 154—157.

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In the description of this form Bryant mentioned the "branchial plate." The picture of it is given in Pl. III in his paper of 1932, and fig. 7 and Pl. XXVI, 1 in the paper of 1934. According to Bryant it is a relatively short and broad plate, which does not show any trace of branchial impressions. After having studied Bryant's picture I am of the opinion, however, that the depicted plate is not a branchial plate, but the upper lateral body scale in *Cryptaspis*. It corresponds in form and in the development of the overlapping-margin to the similar scales in *Poraspis* and *Irregularaspis*. Unfortunately, no trace of dentine ridges is seen on the depicted plates. The well-preserved sculpture could solve this question at once: if the ridges run parallel to the longitudinal axis of the plate — it can hardly be a body scale. If, on the contrary, they run perpendicular to the longitudinal axis — it cannot be the branchial plate. The supposition, that these plates are body scales is supported by the fact, that, according to Bryant, there have been found a "goodly number of branchial plates of variable size and shape." Also in our material from Spitsbergen the body scales, as we know, are very abundant and vary greatly in shape and size.

The described form is, without doubt, closely related to the *Poraspidei*, but it is not absolutely certain that it belongs to the Fam. *Poraspidae*, as Bryant pointed out. A new description based on better material, will surely solve this problem, and show us the real systematic position of this interesting form.

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### Errata in the text of the plates.

As the majority of the plates were printed already in 1930 it was necessary to undertake the following alterations in the text of the plates.

Plate	Is printed	Shall be changed to
VII . . . . .	D 60 Pal. Mus., Oslo.	D 01 Pal. Mus., Oslo.
XI, fig. 2 . . . . .	im.	imr.
XXI, fig. 2 . . . . .	Upper Kallastracon	Corvaspis
XXVI, fig. 3 . . . . .	<i>Homalaspis</i> sp.	<i>Homaspis</i> sp.
XXX . . . . .	<i>Homalaspis nitidus</i> .	<i>Homaspis nitidus</i> (Kiær).
XXXI, fig. 2. . . . .	<i>Homalaspis nitidus</i> .	<i>Homaspis nitidus</i> (Kiær).

# PLATES

PLATE I.

*Poraspis polaris* nov. gen. & sp.

Rock specimen from the polaris Horizon, Frænkelryggen Group, Red Bay Series, to show the abundance of fossils in some layers in this horizon,  $\times 1/2$ . Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 241, Pal. Mus. Oslo.

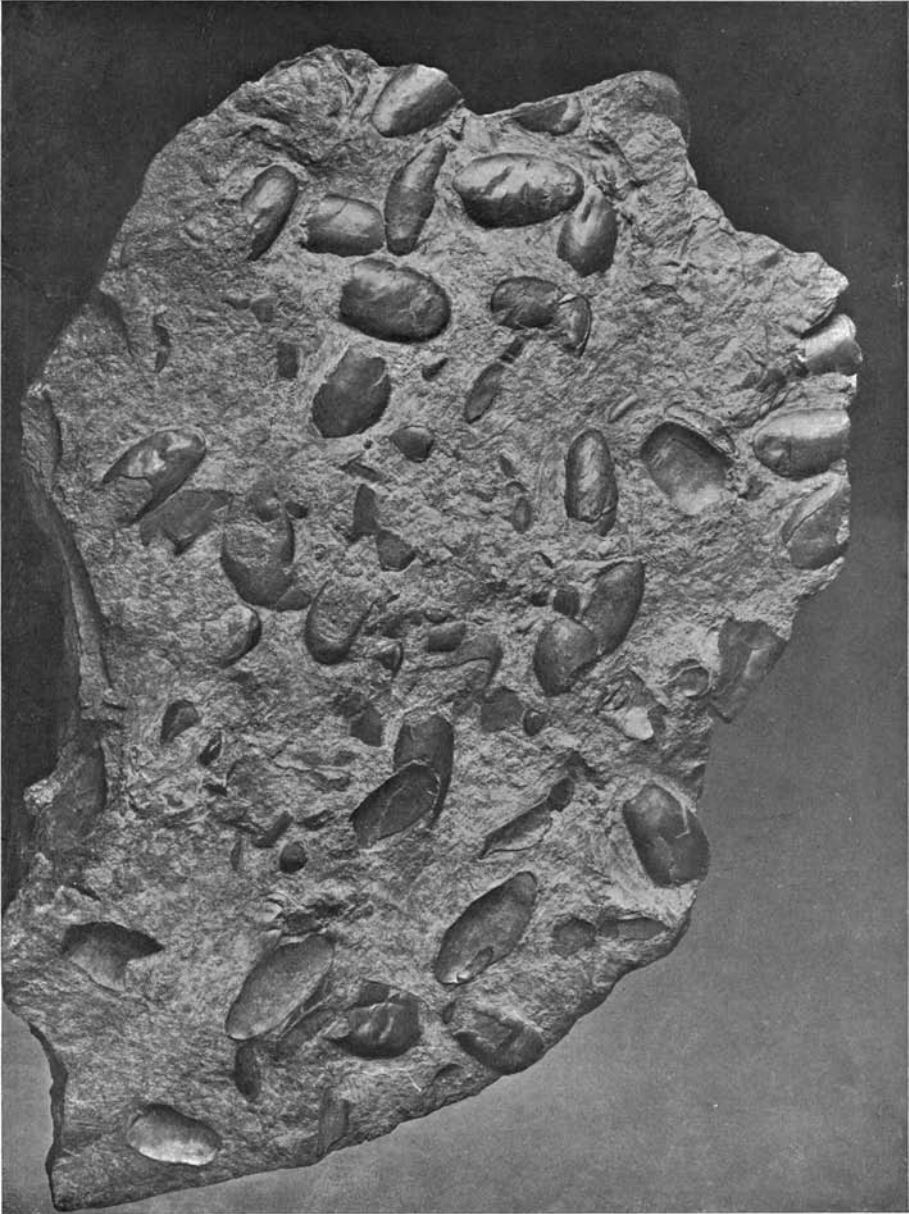


PLATE II.

*Poraspis polaris* nov. gen. & sp. Forma angusta.

Fig. 1. Dorsal shield,  $\times$  ca. 4. This typical specimen, with the dermal skeleton missing only on the left postbranchial lobe, is the holotype. Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 665, Pal. Mus. Oslo.

Fig. 2. Same specimen in lateral aspect,  $\times$  ca. 4.

Orb, Orbital notch.





PLATE III.

*Poraspis polaris* nov. gen. & sp. Forma angusta.

Ventral shield,  $\times$  ca. 5. Fine specimen, showing splendidly the dentine sculpture and the pores of the lateral line system. The dermal skeleton is only missing on the right anterior corner. Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 206, Pal. Mus. Oslo.



PLATE IV.

*Poraspis polaris* nov. gen. & sp. Forma angusta.

Ventral shield in lateral aspect, same specimen as in plate III,  $\times$  ca. 5. Lateral view of the shield with the marginal articular area, the dentine sculpture and the pores of the lateral line system in excellent preservation.

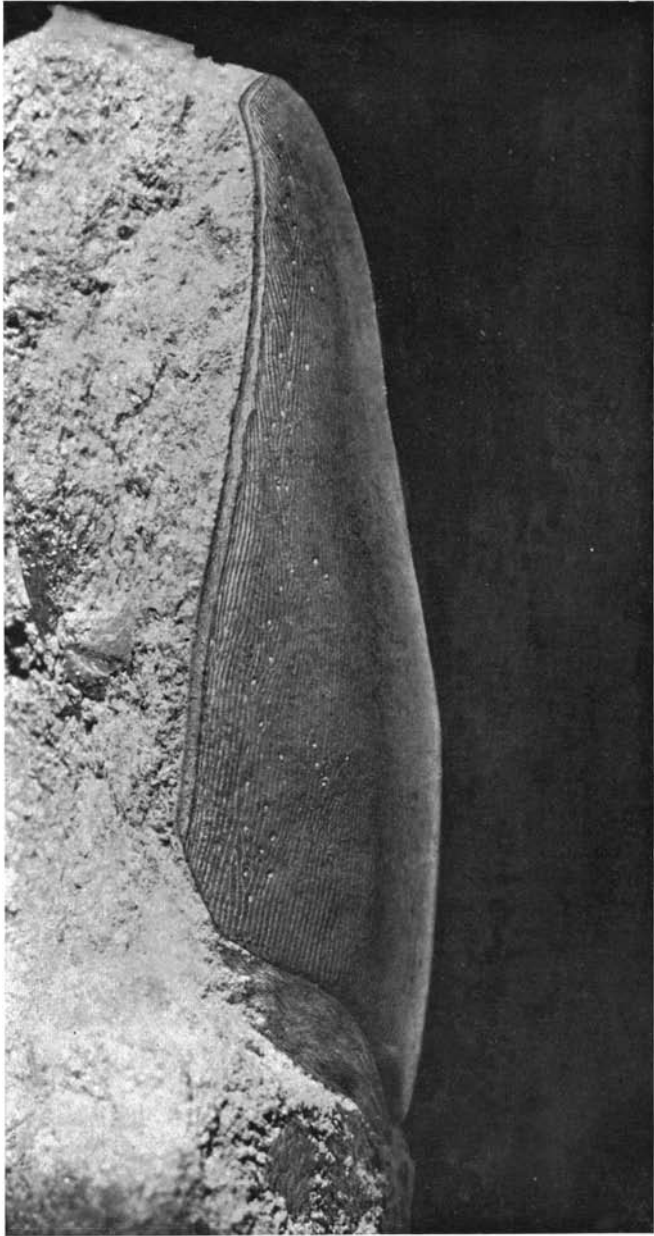


PLATE V.

*Poraspis polaris* nov. gen. & sp. Forma lata.

Almost complete dorsal shield,  $\times 5,4$ . Excellent preservation of the dentine sculpture and the pores of the lateral line system. Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 115, Pal. Mus. Oslo.

Orb, Orbital notch.



PLATE VI.

*Poraspis polaris* nov. gen. & sp. Forma lata.

Ventral shield,  $\times 5$ . Good specimen with the dermal skeleton missing in the right and left posterior part and with excellent preservation of the dentine sculpture and the pores of the lateral line system. Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 113. Pal. Mus. Oslo.





PLATE VII.

*Poraspis polaris* nov. gen. & sp. Forma angusta.

Dorsal shield,  $\times 5$ . Preparation by grinding to show the canals of the lateral line system on the left side. Polaris Horizon, Frænkelryggen Group, Red Bay Series, Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 60, Pal. Mus. Oslo.

Orb, Orbital notch.

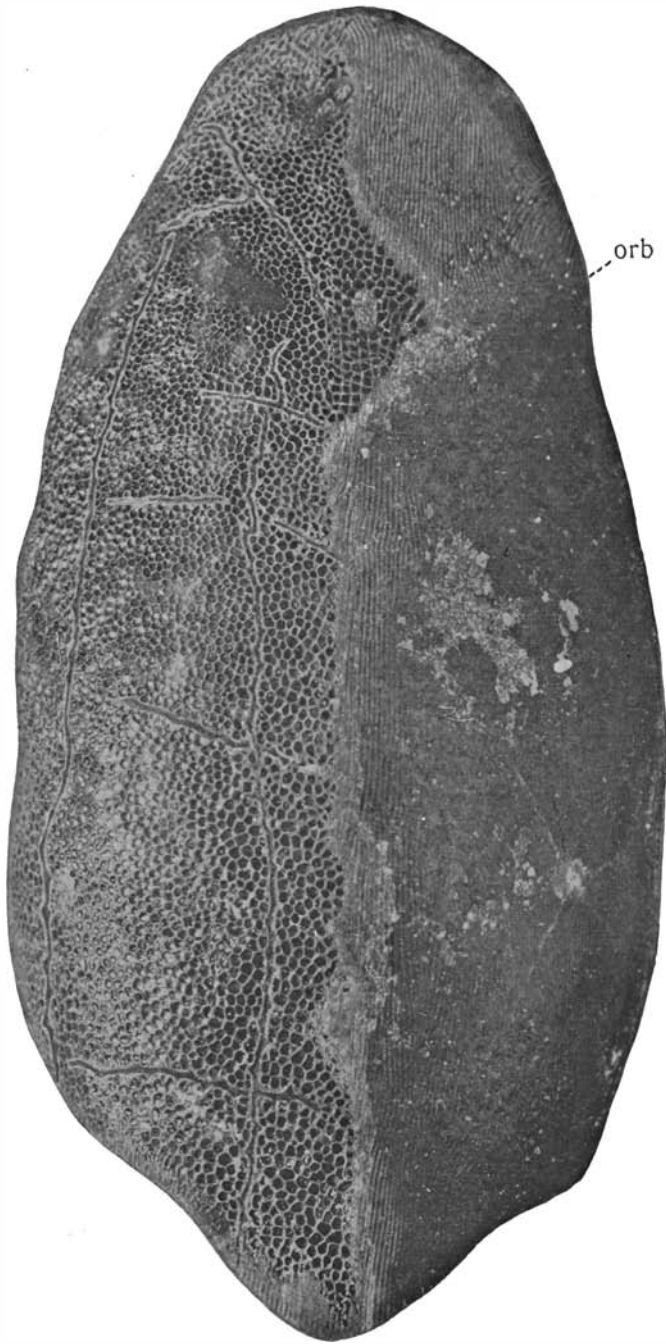


PLATE VIII.

*Poraspis polaris* nov. gen. & sp. Forma lata.

Ventral shield,  $\times 5$ . Preparation by grinding to show the canals of the lateral line system on one side. Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 38, Pal. Mus. Oslo.

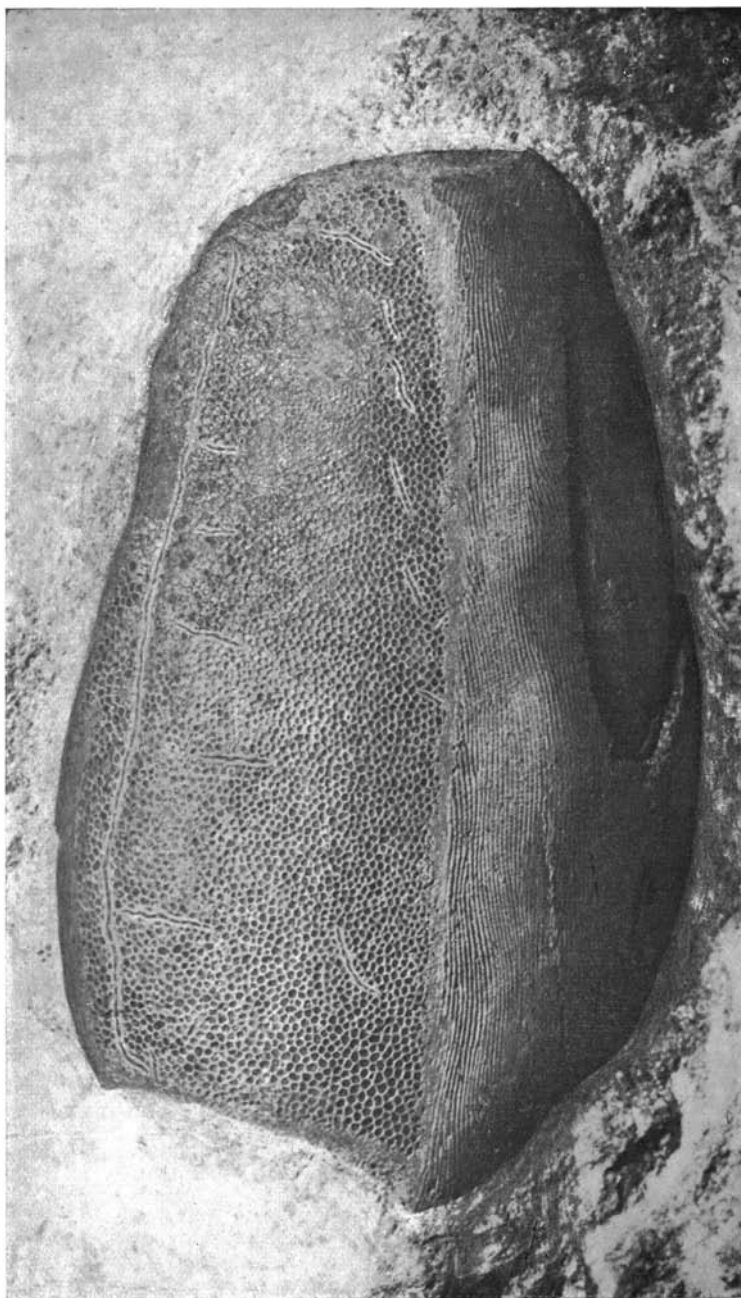


PLATE IX.

Fig. 1. *Poraspis polaris* nov. gen. & sp. Forma angusta.

Dorsal shield,  $\times 2.5$ . Well preserved, but somewhat deformed specimen. Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 204 a, Pal. Mus. Oslo.

Fig. 2. *Poraspis polaris* nov. gen. & sp. Forma angusta.

Dorsal shield,  $\times$  ca. 3. On the right side the dermal skeleton wanting, thus showing casts of the internal impressions. Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 2, Pal. Mus. Oslo.

Fig. 3. *Poraspis elongata* nov. gen. & sp. Forma angusta.

Dorsal shield,  $\times 3$ . Dermal skeleton crushed, but finely preserved, showing splendidly the pores of the lateral line system. Primaeva Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Adolf Hoel, Isachsen's Exp. 1909–10. Specimen D 147, Pal. Mus. Oslo.

Orb, Orbital notch.

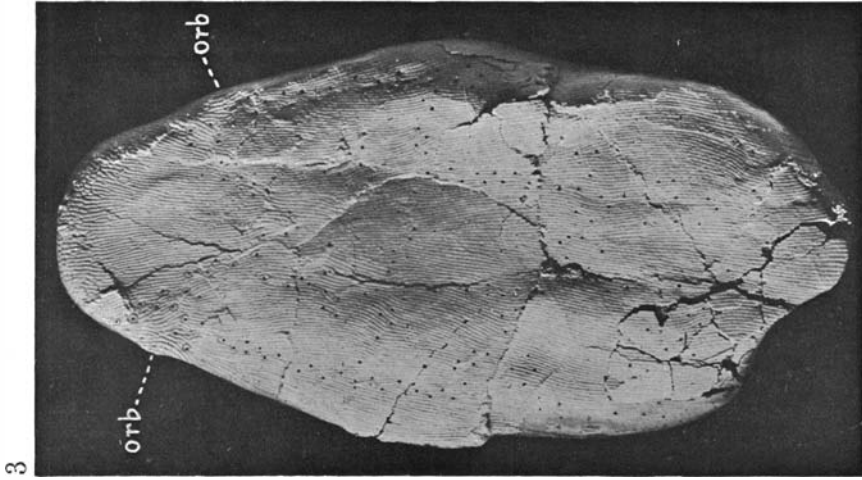


PLATE X.

Fig. 1. *Poraspis polaris* nov. gen. & sp. Forma angusta.

Rostral part of dorsal shield, showing the pattern of the dentine ridges,  $\times 6$ . Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 204 a, the same as figured in fig. 1, pl. IX, Pal. Mus. Oslo.

Fig. 2. *Poraspis elongata* nov. gen. & sp. Forma angusta.

Rostral part of dorsal shield, showing the pattern of the dentine ridges,  $\times 6$ . Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 141, Pal. Mus. Oslo.

Orb, Orbital notch.



1



2

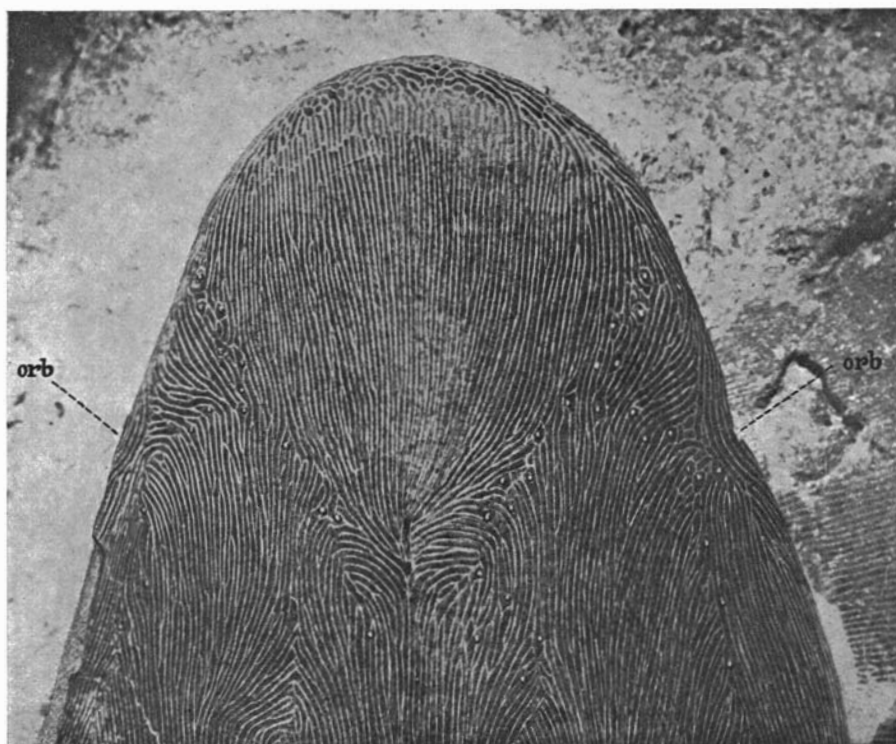


PLATE XI.

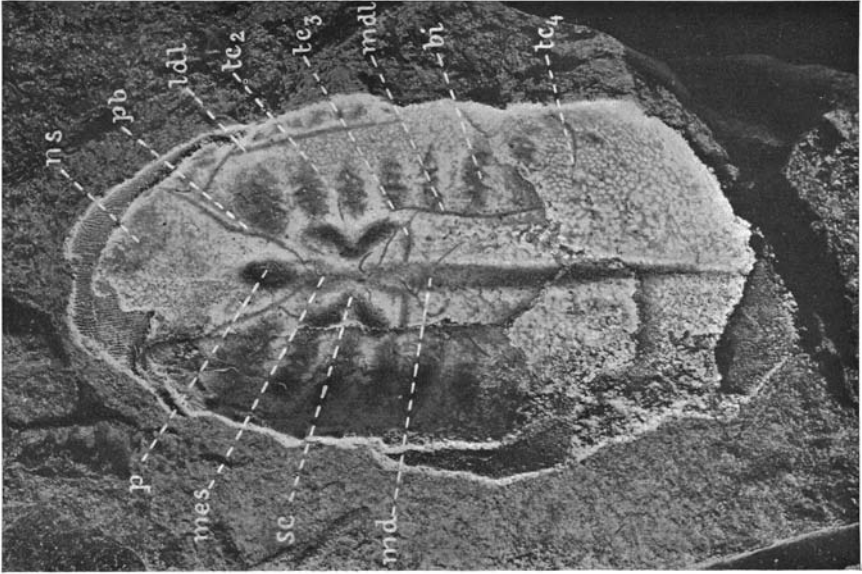
*Poraspis polaris* nov. gen. & sp.

Dorsal shields seen from the inside with impressions of several organs,  $\times 3$ . Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928.

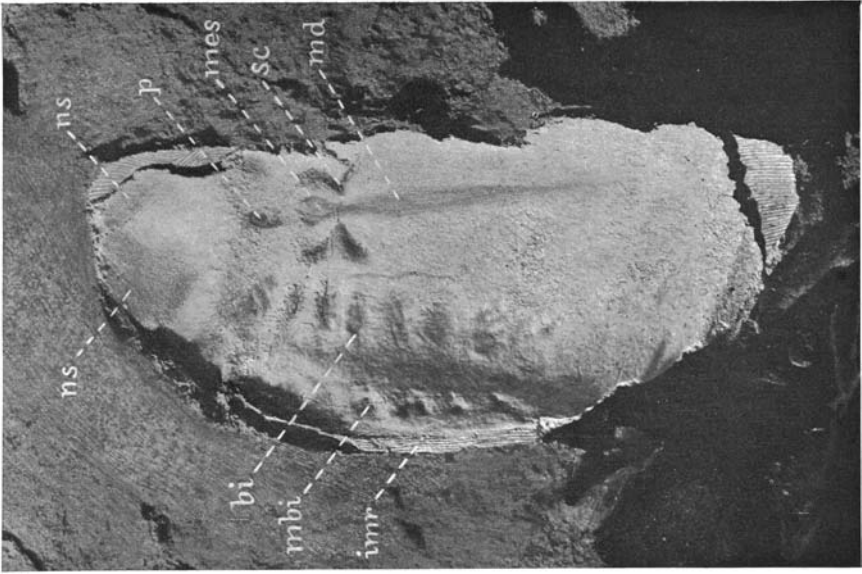
Fig. 1. Forma lata. Specimen D 66, Pal. Mus. Oslo.

Fig. 2. Forma angusta. Specimen D 68, Pal. Mus. Oslo.

*bi*, branchial impressions. *sc*, semicircular canals. *im*, intern marginal ribs. *mbi*, marginal branchial impressions. *md*, medulla oblongata. *mdl*, median dorsal line. *mes*, mesencephalon. *ns*, nasal sacs. *ldl*, lateral dorsal line. *p*, pineal organ. *pb*, pineal branch of lateral line system. *tc*<sub>2-4</sub>, second—fourth transversal commissure.



2



1

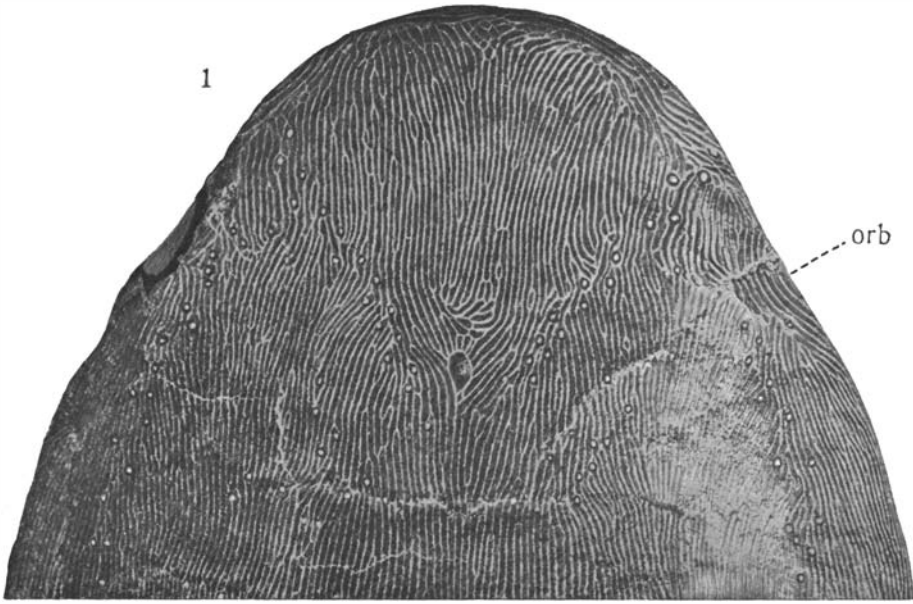
PLATE XII.

*Poraspis polaris* nov. gen. & sp.

Fig. 1. *Forma lata*. Rostral part of dorsal shield, showing the pattern of the dentine ridges,  $\times 5,5$ . Same specimen as in pl. V. *Polaris* Horizon, Fränkelryggen Group, Red Bay Series. Fränkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 115, Pal. Mus. Oslo. Orb, Orbital notch.

Fig. 2. *Forma angusta*. Imperfect ventral shield without dermal skeleton, showing fine casts of the internal impressions,  $\times 3$ . Same horizon and locality as in fig. 1. Th. Vogt's Exp. 1925. Specimen D 36, Pal. Mus. Oslo.

Fig. 3. *Forma lata*. Ventral shield without dermal skeleton, showing fine casts of the internal impressions,  $\times 3$ . Same horizon and locality as in fig. 1. Th. Vogt's Exp. 1925. Specimen 101, Pal. Mus. Oslo.



2



3

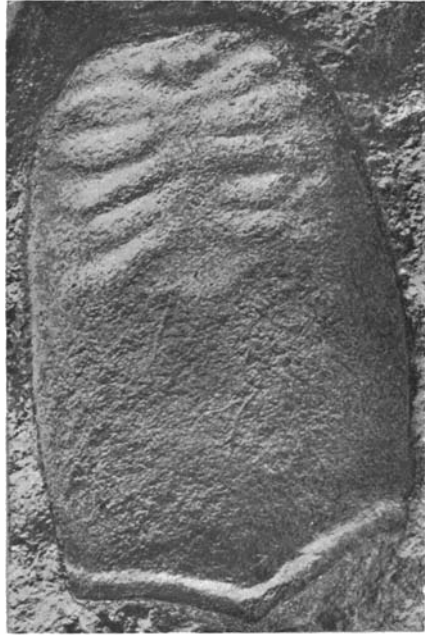


PLATE XIII.

*Poraspis polaris* nov. gen. & sp. Forma angusta.

Dorsal shield,  $\times 5$ . Finely preserved specimen of the oldest form of the species. Primaeva Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 198, Pal. Mus. Oslo.

Orb, Orbital notch.



PLATE XIV.

*Poraspis brevis* nov. gen. & sp. Forma lata.

Dorsal shield,  $\times 5,3$ . The holotype. Almost complete specimen with fine preservation of the dentine ridges and the pores of the lateral line system. Primaeva Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 304, Pal. Mus. Oslo.

Orb, Orbital notch.



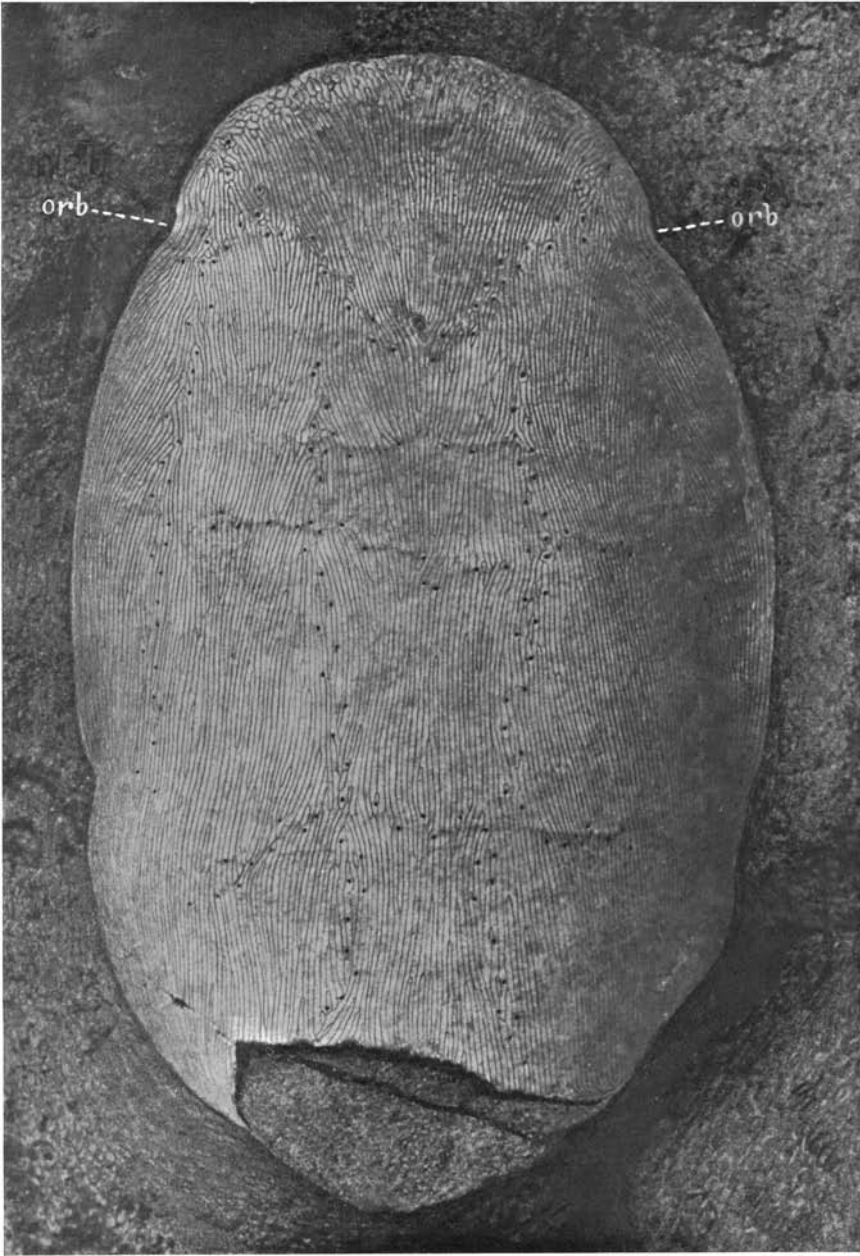


PLATE XV.

*Poraspis brevis* nov. gen. & sp.

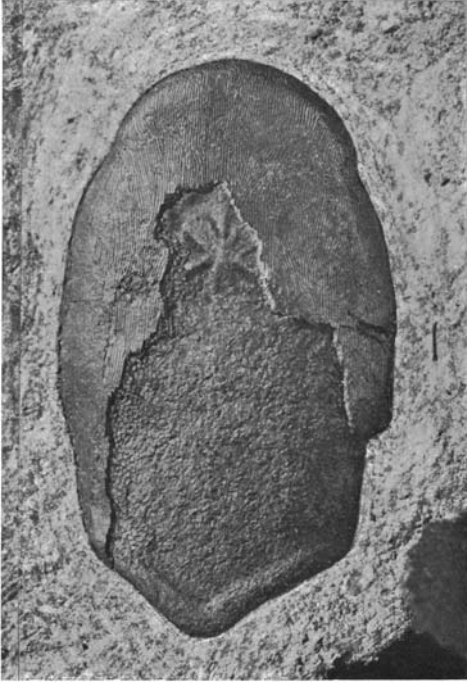
Fig. 1. *Forma lata*. Dorsal shield,  $\times 3$ . The dermal skeleton wanting in the middle and posterior part, here showing fine cast of the posterior marginal furrow. Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 1259, Pal. Mus. Oslo.

Fig. 2. *Forma lata*. Dorsal shield with the dermal skeleton wanting on the right side,  $\times 3$ . Same horizon and locality as in fig. 1. Th. Vogt's Exp. 1925. Specimen D 368, Pal. Mus. Oslo.

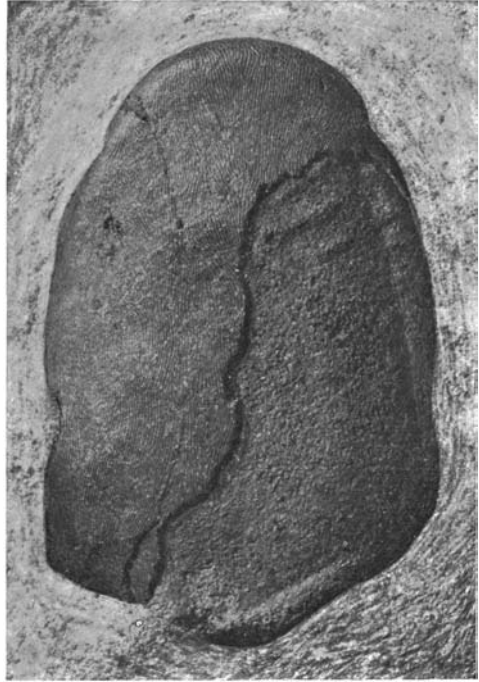
Fig. 3. Ventral shield,  $\times 3$ . Small specimen probably of *forma lata*. Same horizon and locality as in fig. 1. Th. Vogt's Exp. 1925. Specimen D 87, Pal. Mus. Oslo.

Fig. 4. Ventral shield,  $\times 3$ . *Forma angusta*. Fine specimen, showing the anterior articular marginal area. Primaeva Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 299, Pal. Mus. Oslo.

1



2



3



4



PLATE XVI.

*Poraspis intermedia* nov. gen. & sp. Forma angusta.

Dorsal shield, somewhat imperfect in the posterior part,  $\times 5$ . The holotype. Anglaspis Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 1308, Pal. Mus. Oslo.

Orb, Orbital notch.

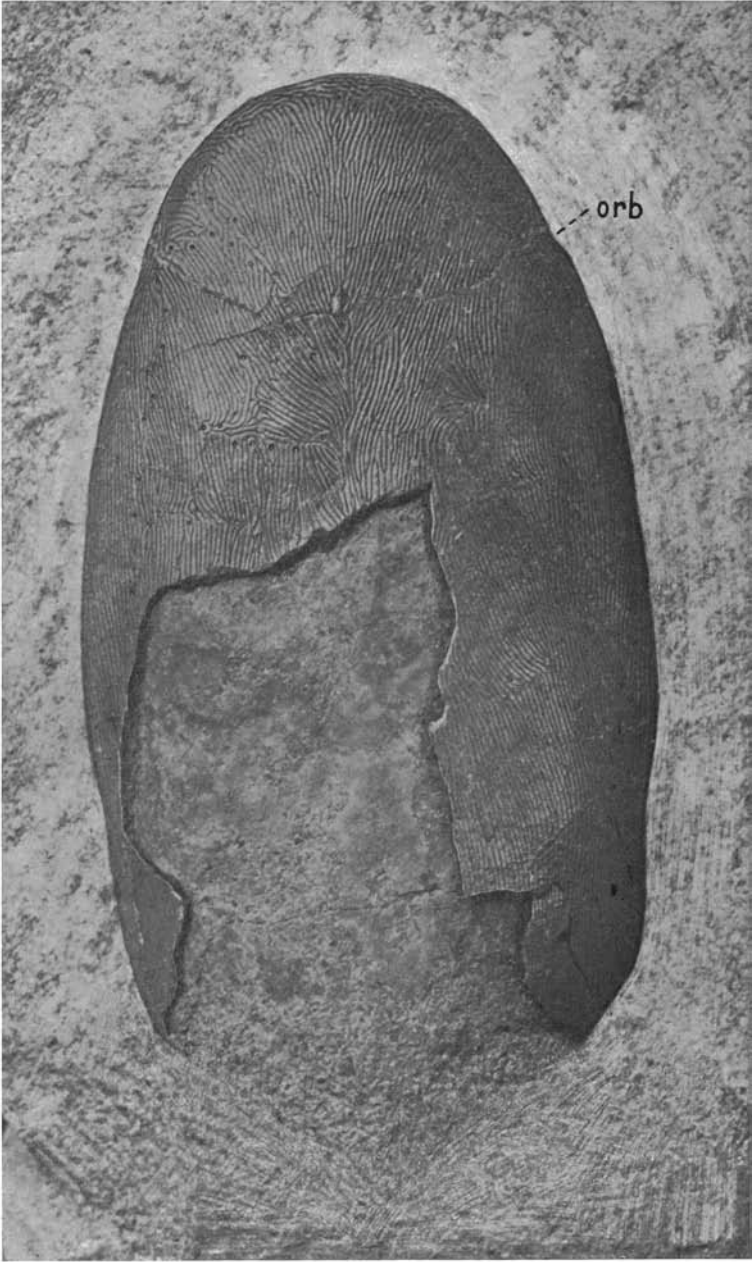


PLATE XVII.

*Poraspis intermedia* nov. gen. & sp. Forma lata.

Dorsal shield,  $\times 6$ . Well preserved, but flattened specimen, showing nicely the dentine sculpture and the pores of the lateral line system. Anglaspis Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 293, Pal. Mus. Oslo.

Orb, Orbital notch.



PLATE XVIII.

*Poraspis elongata* nov. gen. & sp. Forma angusta.

Rock specimen with two dorsal- (*a* and *c*) and one ventral-shield (*b*) of *Poraspis elongata* nov. gen. & sp.  $\times 2$ . *a* is the holotype. Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 141, Pal. Mus. Oslo.



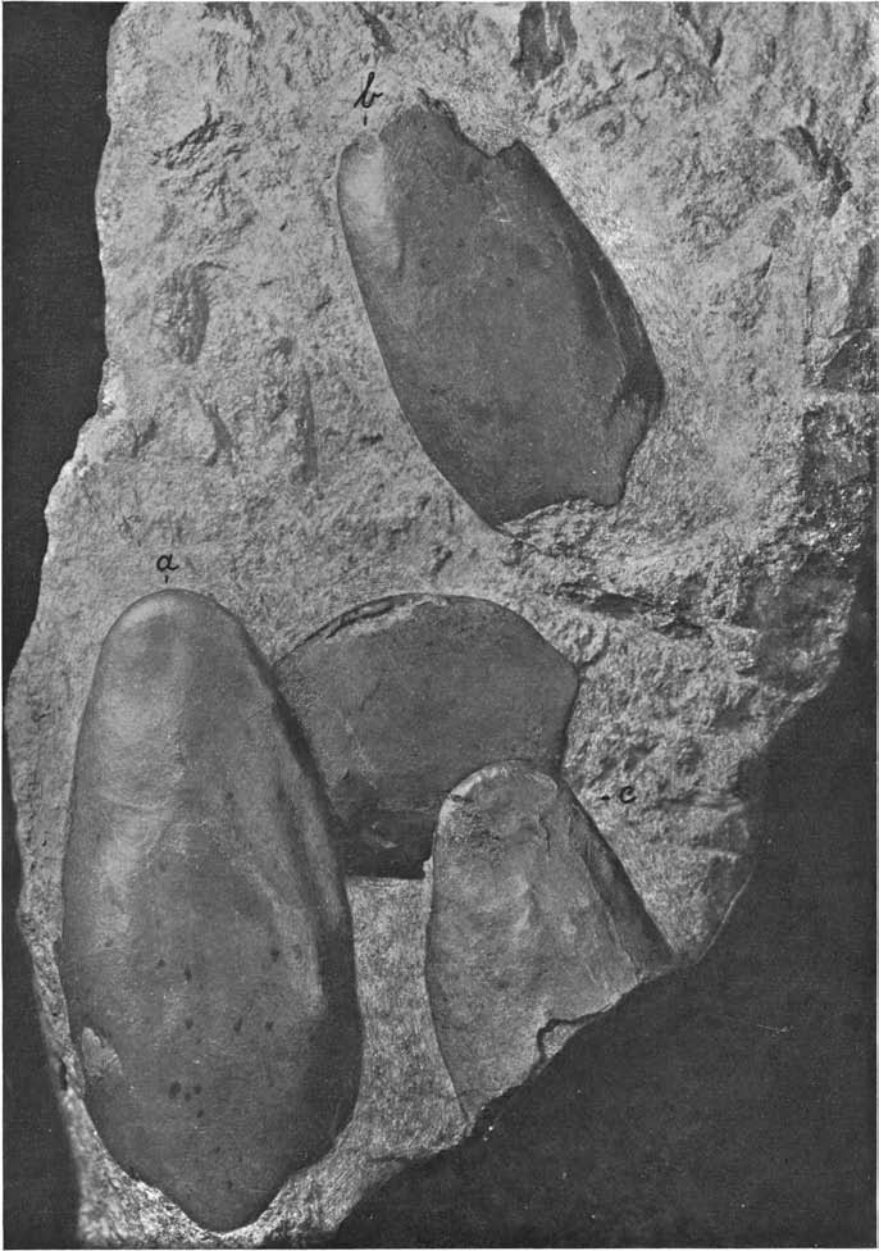


PLATE XIX.

*Poraspis elongata* nov. gen. & sp. Forma angusta.

Dorsal shield,  $\times$  ca. 4. This complete specimen is the holotype (*a* in plate XVIII). Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 141, Pal. Mus. Oslo.

Orb, Orbital notch.



PLATE XX.

*Poraspis elongata* nov. sp. & gen. Forma angusta.

Fig. 1. Ventral shield,  $\times$  ca. 3. Almost complete specimen with the right anterior part in good preservation. Polaris Horizon, Fränkelryggen Group, Red Bay Series. Fränkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 35, Pal. Mus. Oslo.

Fig. 2. Same specimen in lateral aspect,  $\times$  ca. 3.

Fig. 3. Anterior part of same specimen,  $\times$  ca. 7. The anterior articular area is here seen in excellent preservation.

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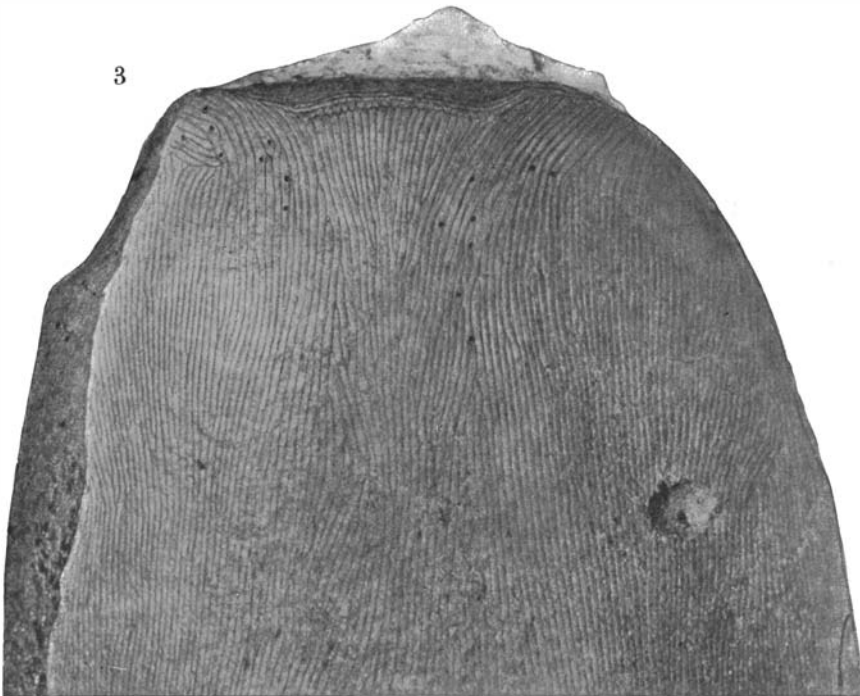
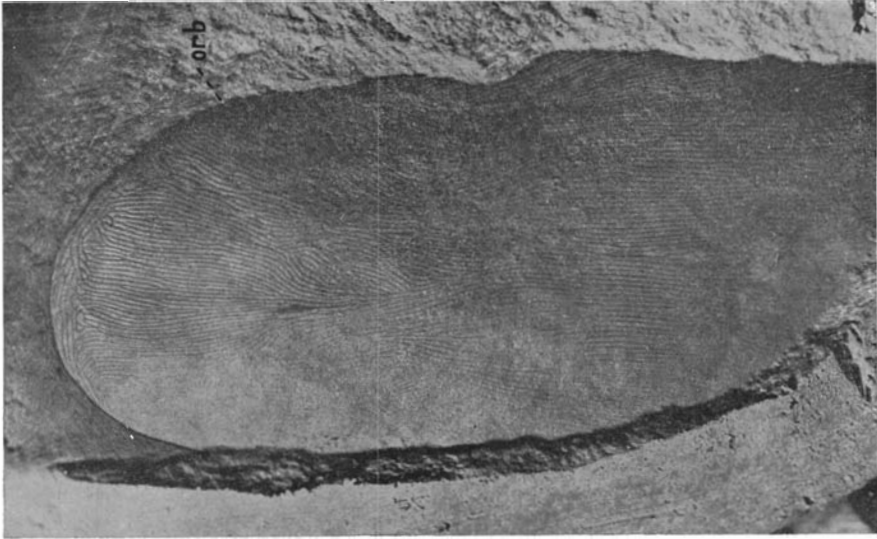


PLATE XXI.

Fig. 1. *Poraspis subtilis* nov. gen. & sp. (?). Incomplete ventral shield,  $\times 5$ . Plant Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 1903, Pal. Mus. Oslo.

Fig. 2. *Poraspis elongata* nov. gen. & sp. (?). Incomplete dorsal shield,  $\times 5$ . Upper Kallastracon Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 243, Pal. Mus. Oslo.



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PLATE XXII.

*Poraspis subtilis* nov. gen. & sp.

Almost complete dorsal shield,  $\times 6$ . The holotype. Plant Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 1904, Pal. Mus. Oslo.

Orb, Orbital notch.



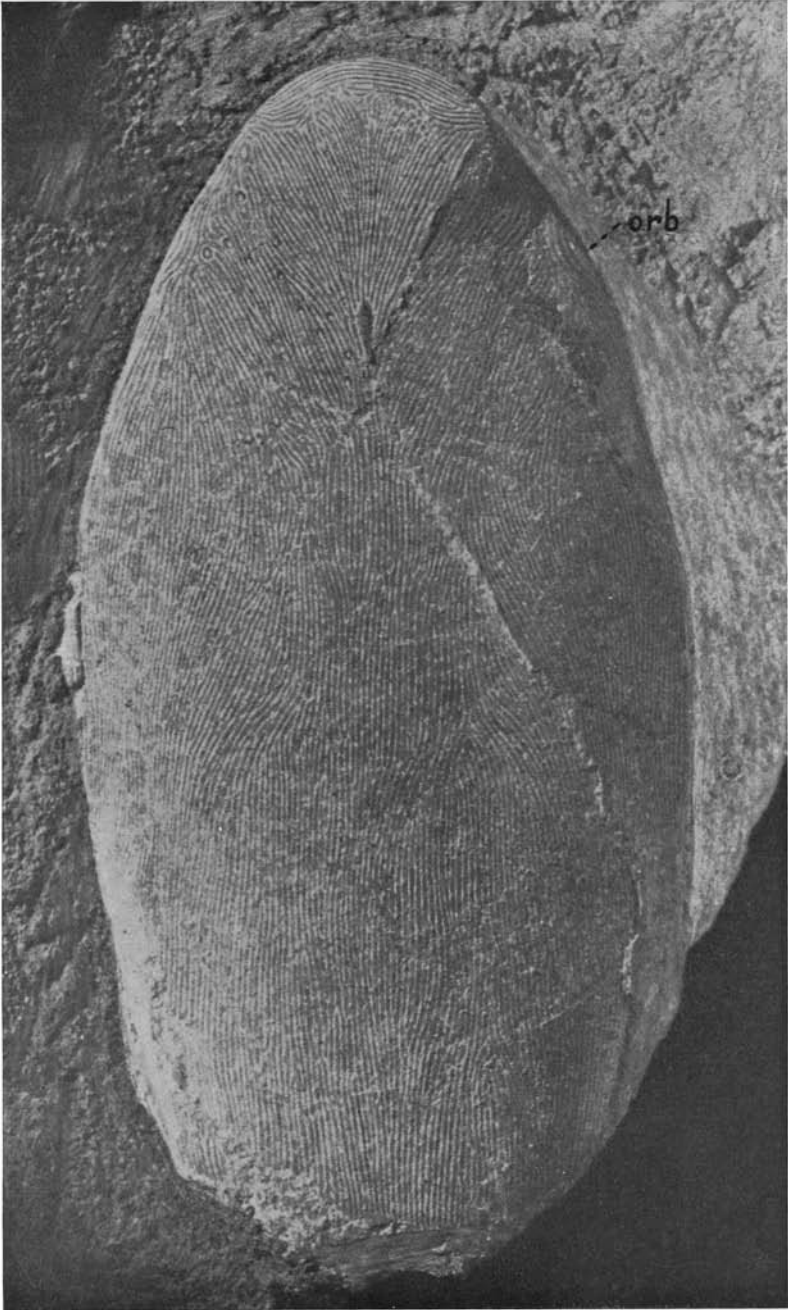


PLATE XXIII.

*Poraspis rostrata* nov. gen. & sp.

Complete dorsal shield,  $\times 3$ . The holotype. Horizon A, lower part of Ben Nevis Group, Red Bay Series. Ben Nevis, Red Bay, N. Spitsbergen. Adolf Hoel, Isachsen's Exp. 1909—10. Specimen D 124, Pal. Mus. Oslo.

Orb, Orbital notch.

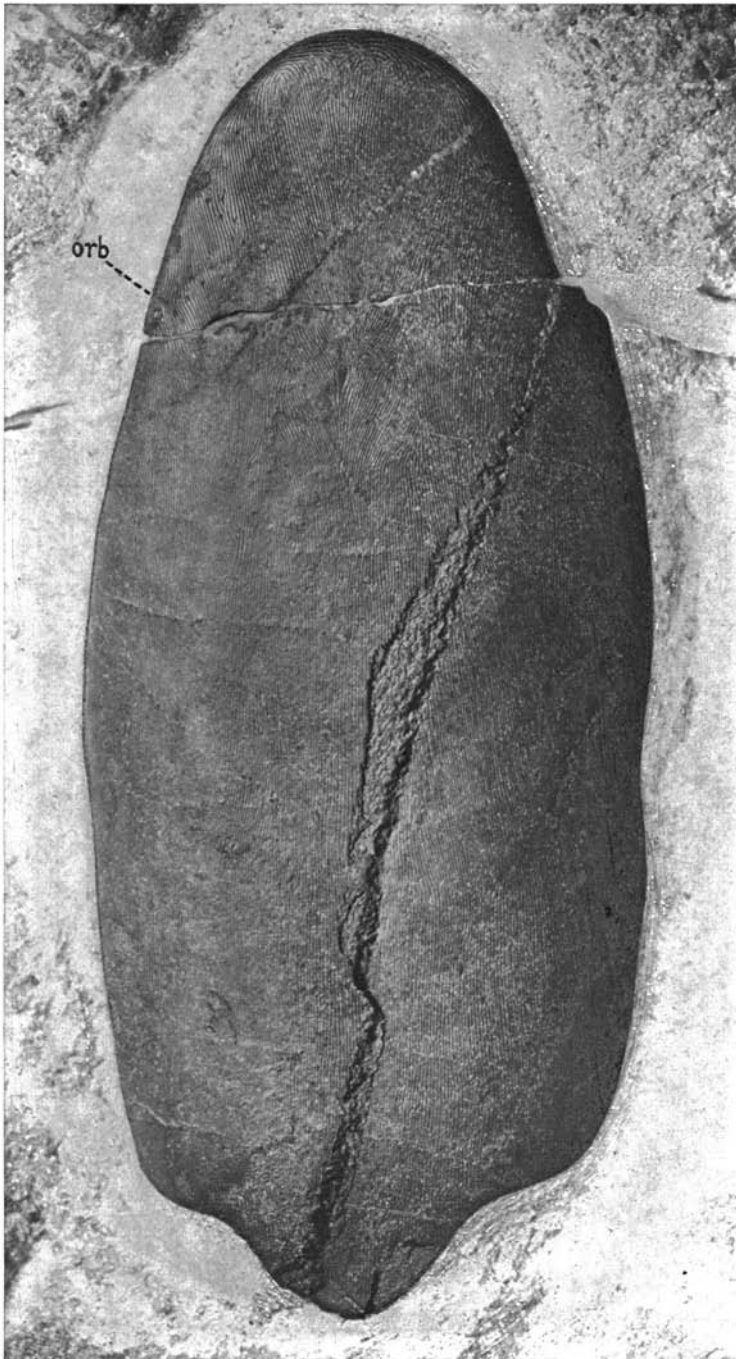


PLATE XXIV.

*Poraspis rostrata* nov. gen. & sp.

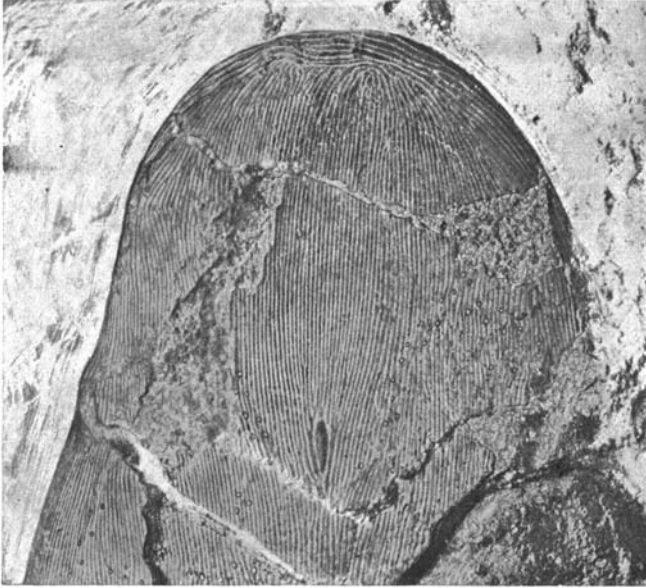
Fig. 1. Rostral part of dorsal shield,  $\times 5$ . Horizon A, lower part of Ben Nevis Group, Red Bay Series. Ben Nevis, Red Bay, N. Spitsbergen. Adolf Hoel, Isachsen's Exp. 1909—10. Specimen D 128, Pal. Mus. Oslo.

Fig. 2. Rostral part of dorsal shield,  $\times 5$ . The holotype (pl. XXIII).

The two specimens show the rostral pattern of the dentine sculpture and the pineal macula in excellent preservation.

Orb, Orbital notch.

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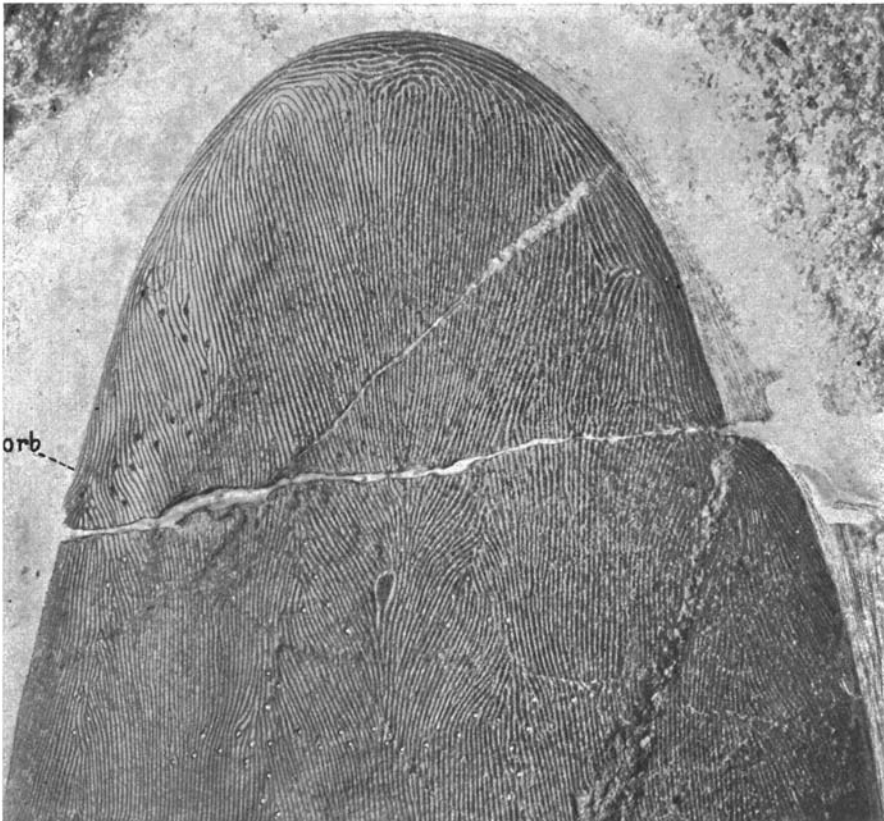


PLATE XXV.

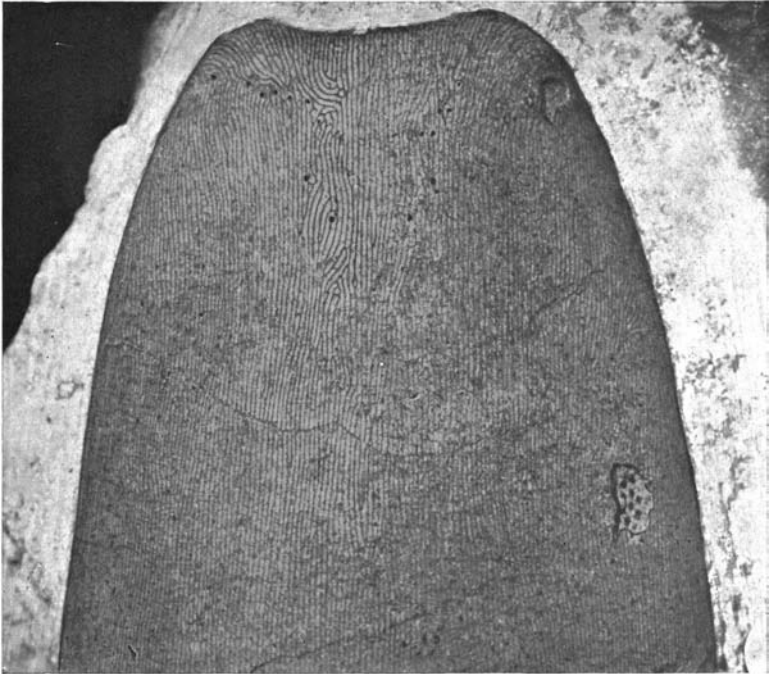
*Poraspis rostrata* nov. gen. & sp.

Fig. 1. Ventral shield,  $\times 4.5$ . Anterior part showing the fine dentine sculpture and some of the pores of the lateral line system. Horizon A, lower part of Ben Nevis Group, Red Bay Series. Ben Nevis, Red Bay, N. Spitsbergen. Adolf Hoel, Isachsen's Exp. 1909—10. Specimen D 135, Pal. Mus. Oslo.

Fig. 2. The complete ventral shield of the same specimen,  $\times 2.3$ .

Fig. 3. Same specimen in lateral aspect,  $\times 2.3$ .

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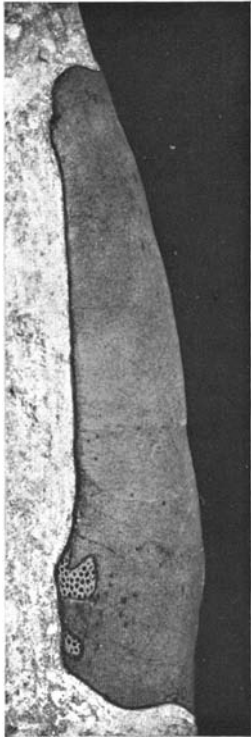


PLATE XXVI.

Fig. 1. *Poraspis polaris* nov. gen. & sp.

The maxillar brim, seen from the ventral side,  $\times 8$ . On the right the preorbital process with the notch for the nostril. Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 60, Pal. Mus. Oslo.  
*mpl*, maxillar brim. *n*, notch for the nostril. *orb*, orbital notch.

Fig. 2. *Poraspis cylindrica* nov. gen. & sp.

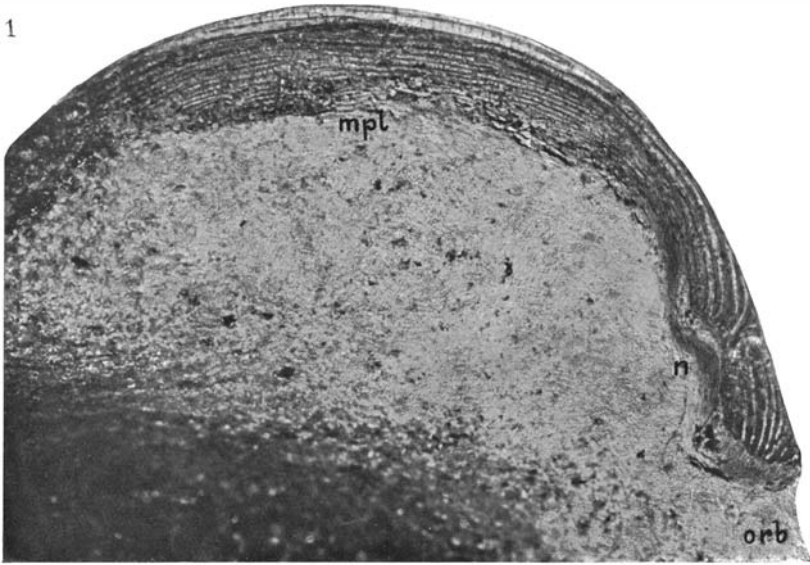
Dorsal shield,  $\times 2$ . The holotype. The plastical form well preserved. Good casts of the internal impressions. Benneviaspis Horizon, upper part of Ben Nevis Group, Red Bay Series. Ben Nevis, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 205, Pal. Mus. Oslo.

Fig. 3. *Homalaspis* sp.

Very small ventral shield,  $\times 8$ . Lower part of Ben Nevis Group, Red Bay Series. In débris below the S. Plateau, Ben Nevis, N. Spitsbergen. G. Watnelie, Isachsen's Exp. 1909--10. Specimen D 207, Pal. Mus. Oslo.



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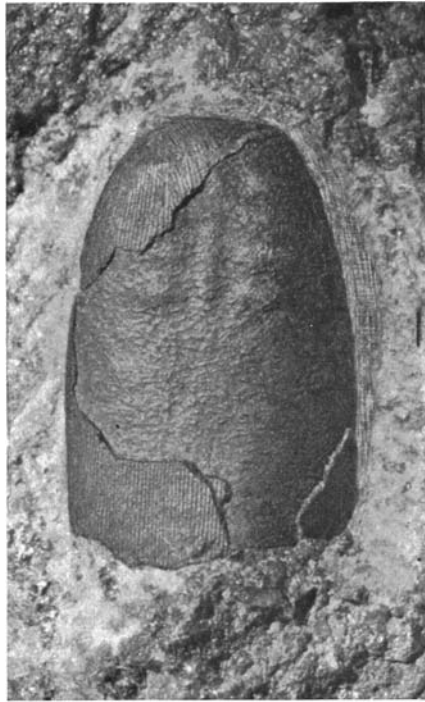


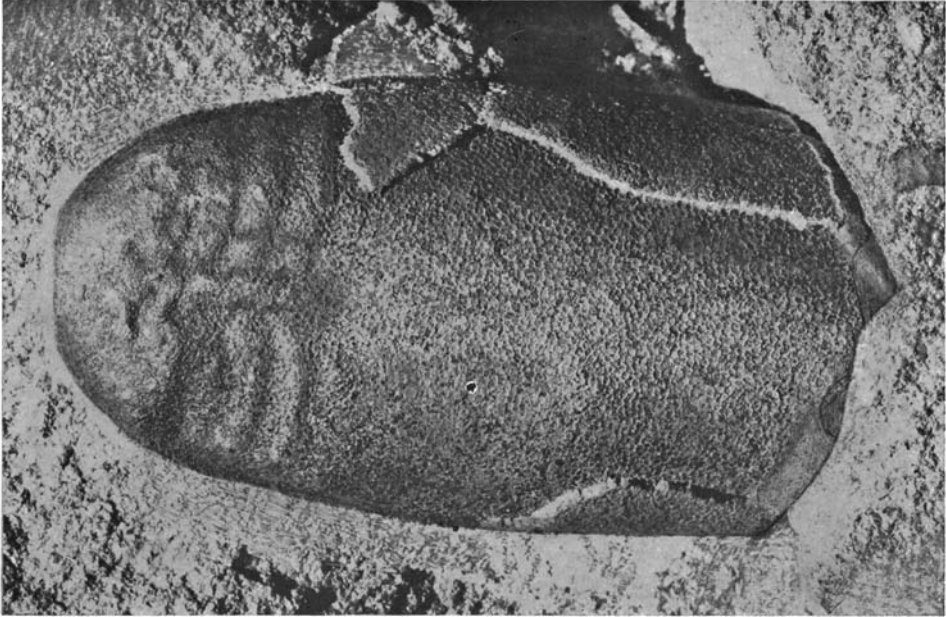
PLATE XXVII.

Fig. 1. *Poraspis* sp. Possibly *P. elongata*, forma lata.

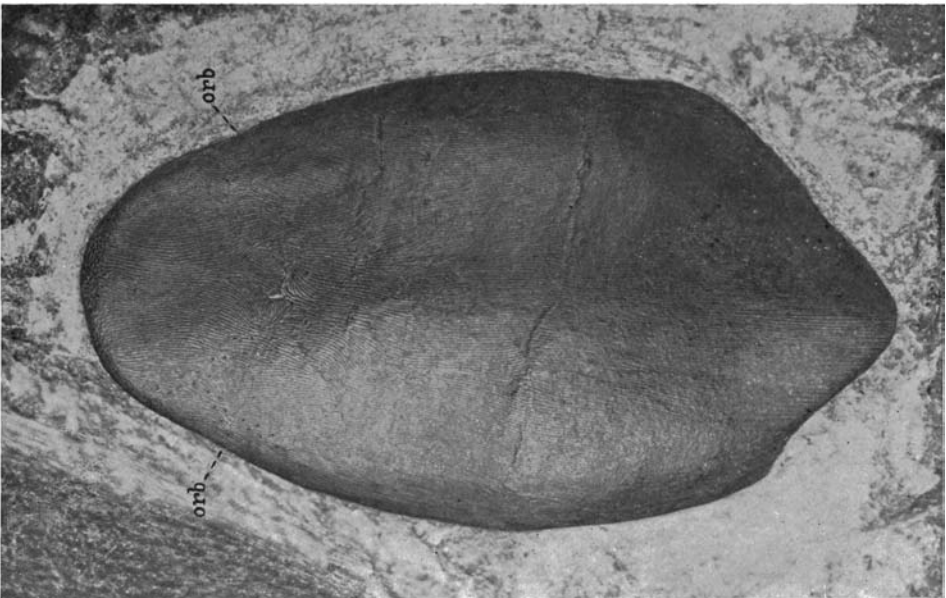
Dorsal shield in fine preservation,  $\times 3$ . Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 84, Pal. Mus. Oslo.

Fig. 2. *Poraspis cylindrica* nov. gen. & sp.

Ventral shield, natural cast,  $\times 3$ . Of special interest are the fine casts of internal impressions. In débris, probably upper part of Ben Nevis Group, Red Bay Series. Ben Nevis, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 1798, Pal. Mus. Oslo.



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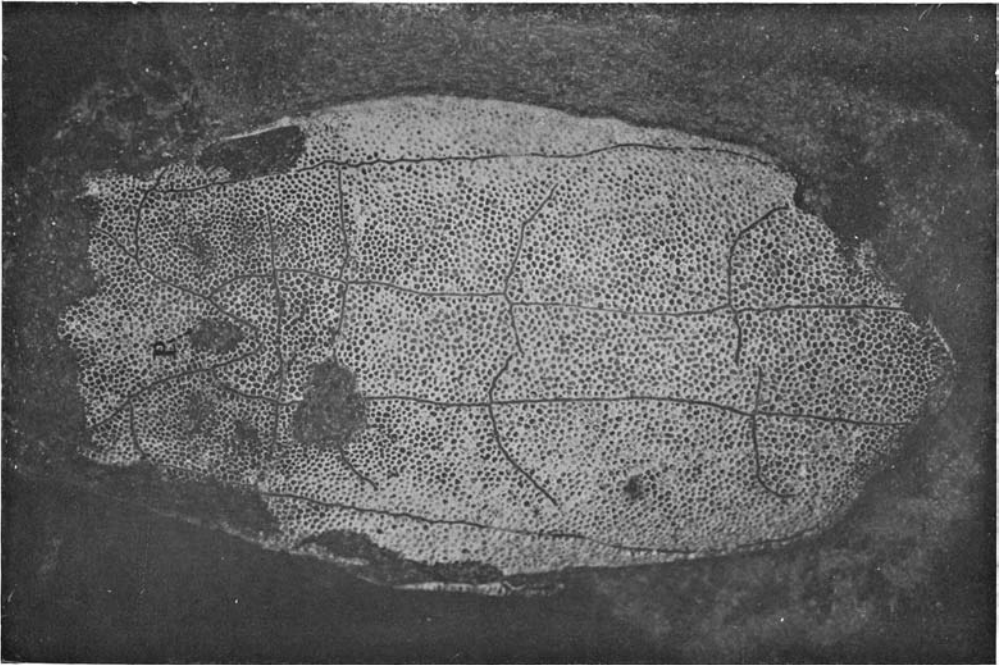
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PLATE XXVIII.

*Poraspis magna* nov. gen. & sp.

Fig. 1. Dorsal shield,  $\times 2$ . The holotype. Complete specimen, dermal skeleton missing in the posterior part. Upper part of Ben Nevis Group, Red Bay Series. Second moraine, Ben Nevis, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 203, Pal. Mus. Oslo.

Fig. 2. Dorsal shield, the most anterior part wanting. Preparation by grinding to show the canals of the lateral line system. Upper part of Ben Nevis Group, Red Bay Series. Andrée moraine, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 200, Pal. Mus. Oslo.  
*orb*, orbital notch. *P*, pineal impression.



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PLATE XXIX.

Fig. 1. *Poraspis cylindrica* n. sp.

Dorsal shield,  $\times 1.5$ . Incomplete specimen with the dermal skeleton preserved only in the most anterior part. Horizon L, upper part of Ben Nevis Group, Red Bay Series. Ben Nevis, Red Bay, N. Spitsbergen. Adolf Hoel, Hoel & Staxrud's Exp. 1912. Specimen D 140, Pal. Mus. Oslo.

Fig. 2. *Poraspis magna* n. sp.

Dorsal shield,  $\times 1.5$ . Somewhat incomplete and eroded specimen, showing a little of the lateral line system. Horizon U, uppermost part of Ben Nevis Group, Red Bay Series, Ben Nevis, Red Bay, N. Spitsbergen. Adolf Hoel, Hoel & Staxrud's Exp. 1912. Specimen D 138 Pal. Mus. Oslo.

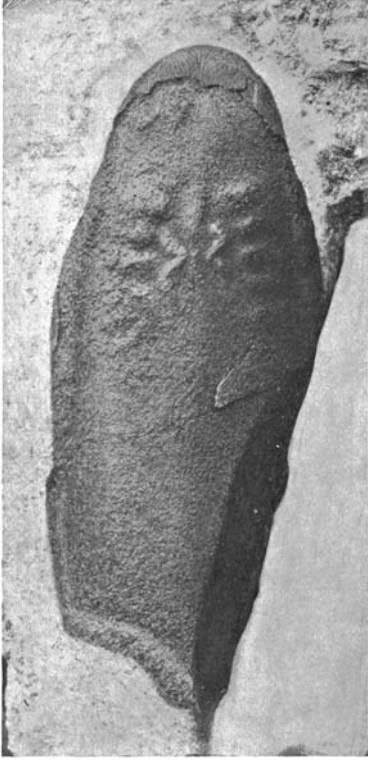
Fig. 3. *Poraspis* sp.

Ventral shield, natural cast,  $\times 1.5$ . Red Bay Series. Mt Pteraspis (50 m), Liefde Bay, N. Spitsbergen. Adolf Hoel, Hoel & Staxrud's Exp. 1912. Specimen D 278, Pal. Mus. Oslo.

Fig. 4. *Poraspis magna* n. sp.

Ventral shield,  $\times 2.5$ . Incomplete specimen, internal side strongly eroded showing a little of the lateral line system. Upper part of Ben Nevis Group, Red Bay Series. In débris, Ben Nevis 620 m, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1925. Specimen D 139, Pal. Mus. Oslo.

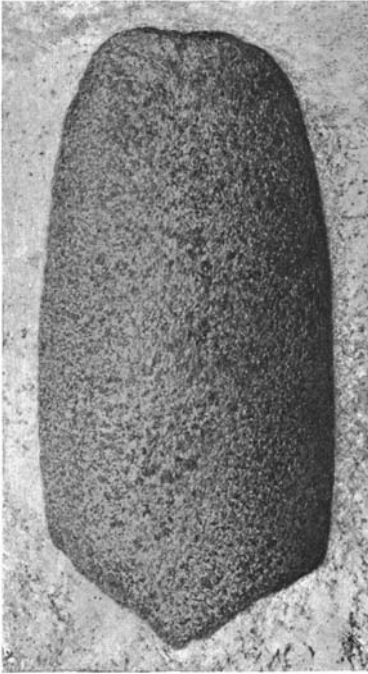
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PLATE XXX.

*Homalaspis nitidus* nov. gen. & sp.

Fig. 1. Ventral shield with branchial plate in fine preservation,  $\times 5$ . Also one of the lateral plates (*a*) from the ventral side behind the oral plates and a lateral scale (*b*) is preserved. Horizon L, upper part of Ben Nevis Group, Red Bay Series. Ben Nevis, Red Bay, N. Spitsbergen. Adolf Hoel, Isachsen's Exp. 1909—10. Specimen D 148, Pal. Mus. Oslo.

Fig. 2. Dorsal shield,  $\times 5$ . The holotype. A little lateral view of this fine and complete specimen. Horizon A, lowermost part of Ben Nevis Group, Red Bay Series. Ben Nevis, Red Bay, N. Spitsbergen. Adolf Hoel, Isachsen's Exp. 1909—10. Specimen D 156, Pal. Mus. Oslo.  
*orb*, orbital notch.

Fig. 3. Dorsal shield,  $\times 5$ . A little incomplete natural cast, showing splendidly the casts of the internal impressions. Horizon A, lowermost part of Ben Nevis Group, Red Bay Series. Ben Nevis, Red Bay, N. Spitsbergen. Adolf Hoel, Isachsen's Exp. 1909—10. Specimen D 175, Pal. Mus. Oslo.



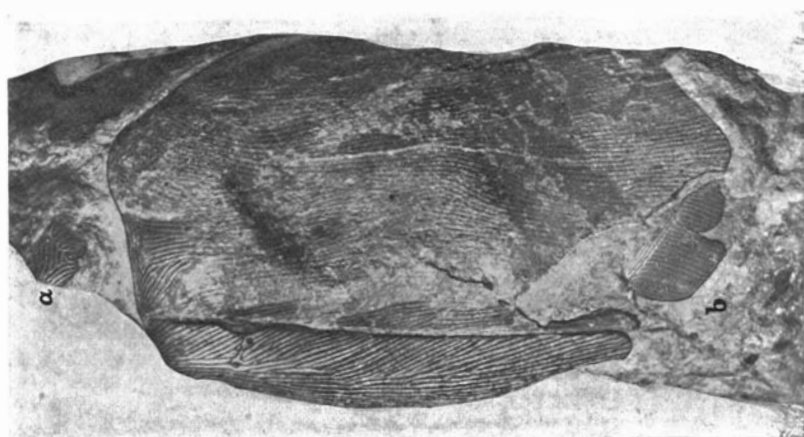
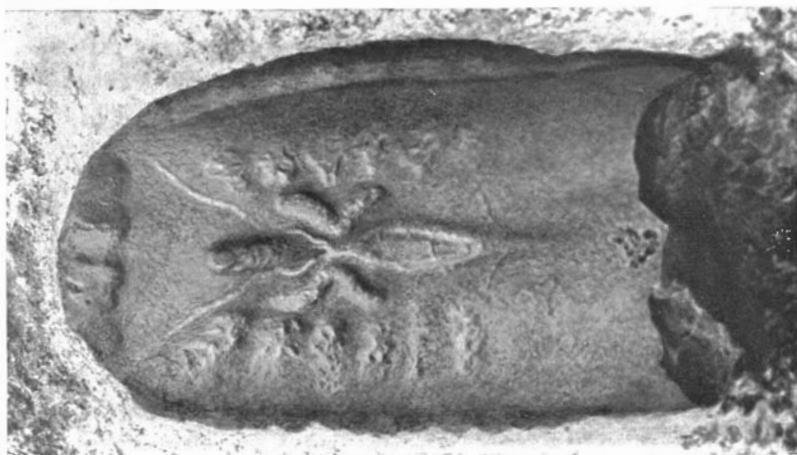


PLATE XXXI.

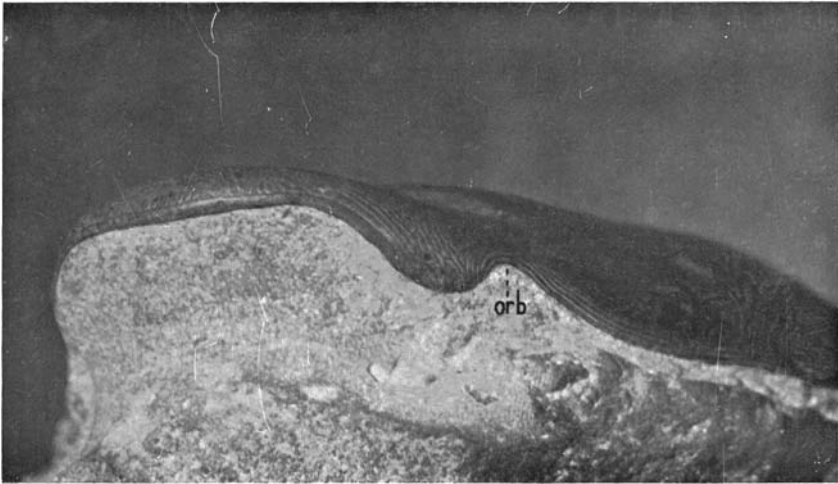
Fig. 1. *Poraspis polaris* nov. gen. & sp.

Lateral frontal view,  $\times 5$ , showing the orbital notch, the praeorbital process and the anterior margin. Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 665, Pal. Mus. Oslo.

Fig. 2. *Homalaspis nitidus* nov. gen. & sp.

Rostral part of dorsal shield, showing the pattern of the dentine ridges,  $\times 8$ . Horizon A, lower part of Ben Nevis Group, Red Bay Series. Ben Nevis, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 183, Pal. Mus. Oslo.

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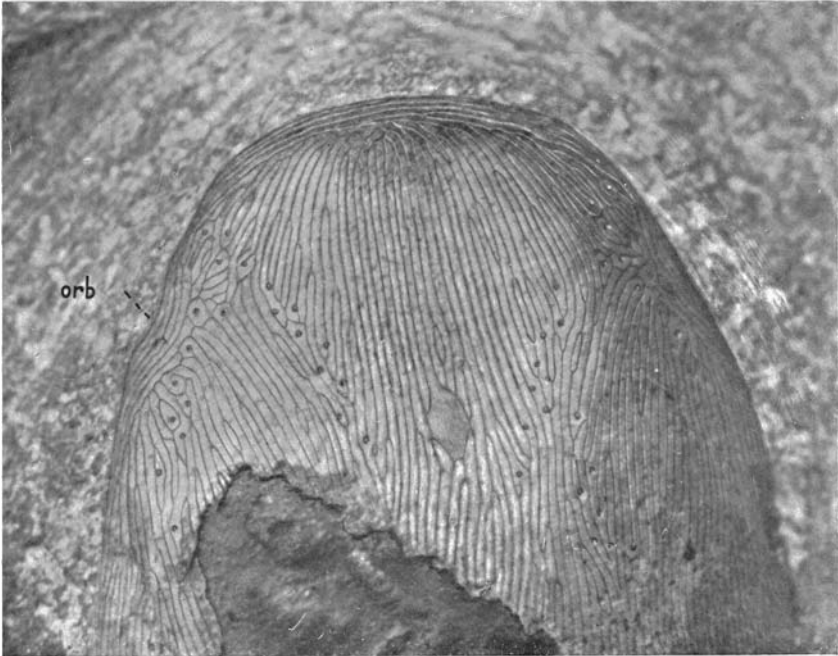


PLATE XXXII.

Fig. 1. *Homaspis nitidus* nov. gen. & sp.

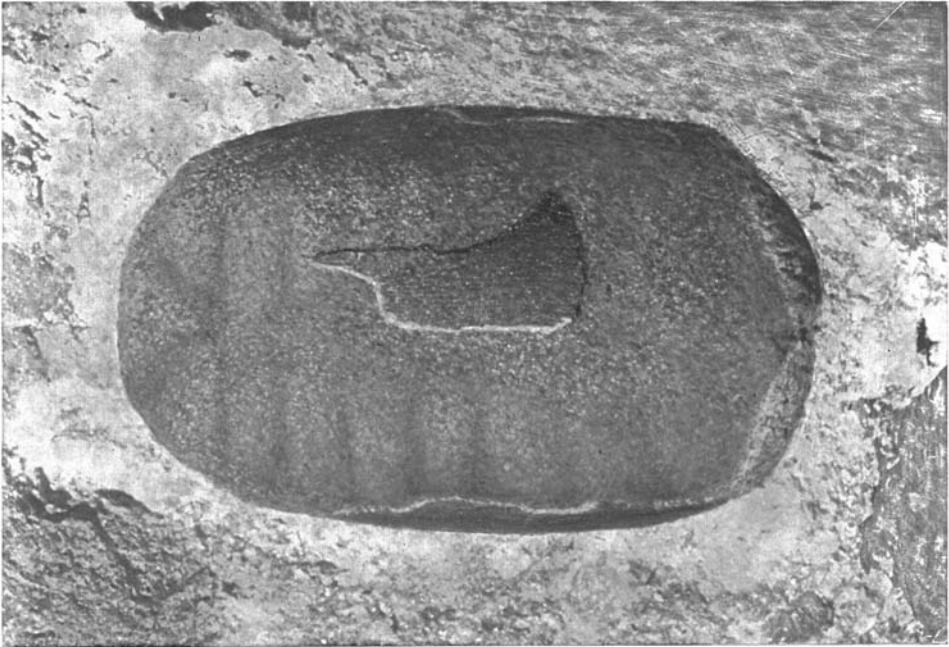
Ventral shield,  $\times 5$ . Complete specimen almost without dermal skeleton, showing faint casts of the internal impressions. Ben Nevis Group, Red Bay Series. SE-side of Mt Sigurd (200 m), N. Spitsbergen. Adolf Hoel, Hoel & Staxrud's Exp. 1912. Specimen D 176, Pal. Mus. Oslo.

Fig. 2. *Poraspis polaris* nov. gen. & sp.

Left part of dorsal shield,  $\times 5$ , with finely preserved dentine sculpture. Polaris Horizon, Frænkelryggen Group, Red Bay Series. Frænkelryggen, Red Bay, N. Spitsbergen. Th. Vogt's Exp. 1928. Specimen D 28, Pal. Mus. Oslo.



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PLATE XXXIII.

Fig. 1. *Homaspis nitidus* (KIÆR). Lateral plate Ca.  $\times$  20.

The same specimen as in Pl. XXX, 1 (D 148 Pal. Mus., Oslo.)

Fig. 2. *Poraspis* sp.

A large median-dorsal scale (?). Ca.  $\times$  6.

Horizon A, Ben Nevis Group, Red Bay, N. Spitsbergen. Specimen D 645 Pal. Mus., Oslo.

Fig. 3. *Poraspis* sp.

A large median-dorsal scale (?). Ca.  $\times$  6.

Horizon L. Ben Nevis Group, Red Bay, N. Spitsbergen. Specimen D 2064 Pal. Mus., Oslo.

Fig. 4 to 6. *Poraspis* sp.

Three different branchial plates. Ca.  $\times$  5.

Fig. 4. Left plate. Polaris Horizon. Frænkelryggen Group, Red Bay, N. Spitsbergen. Specimen D 599. Pal. Mus., Oslo.

Fig. 5. Left plate. Polaris Horizon. Frænkelryggen Group, Red Bay, N. Spitsbergen. Specimen D 1273, Pal. Mus., Oslo.

Fig. 6. Right plate. Primaeva Horizon. Frænkelryggen Group, Red Bay. N. Spitsbergen. Specimen D 1193. Pal. Mus., Oslo.

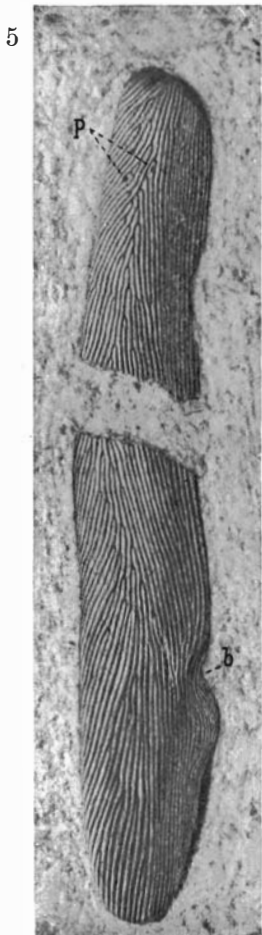
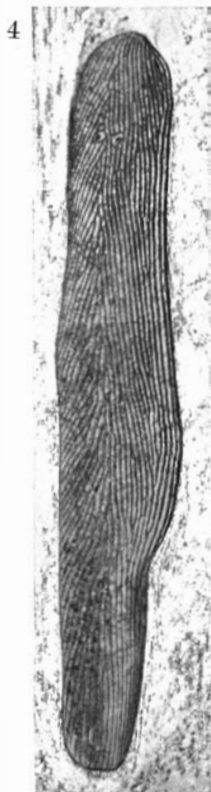
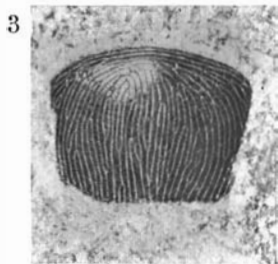
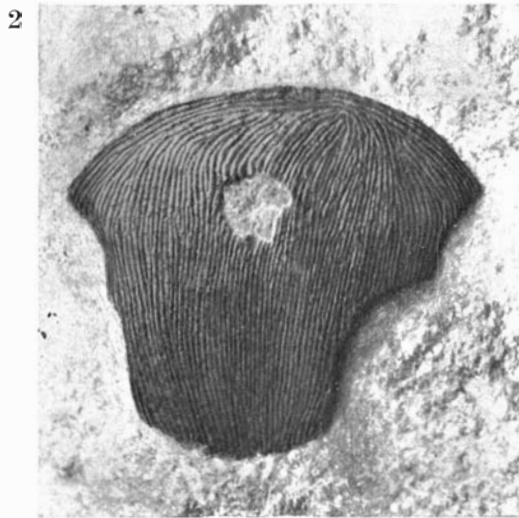
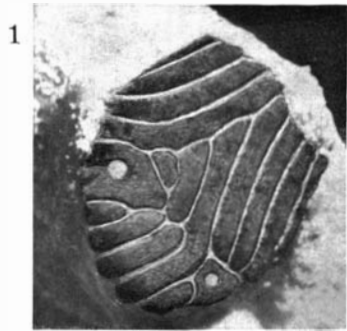


PLATE XXXIV.

Pineal macula in *Poraspis* and *Homaspis*. Ca.  $\times 10$ .

Fig. 1--5. Different variations in *Poraspis polaris* (Kiær). All specimens from Frænkelryggen Group, Red Bay, N. Spitsbergen.

Fig. 1. From Primaeva Horizon. Specimen D 198 Pal. Mus., Oslo.

Fig. 2--5 from Polaris Horizon. Specimens D 665 (Holotyp), D 208, D 204 a. Pal. Mus., Oslo.

Fig. 6. *Homaspis nitidus* (Kiær) Horizon A. Ben Nevis Group, Red Bay, N. Spitsbergen. Specimen D 156. Pal. Mus., Oslo.



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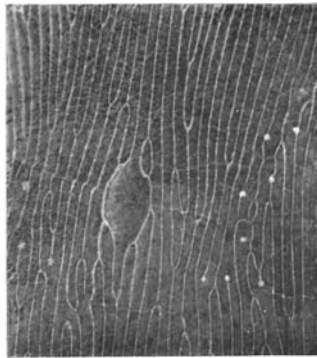


PLATE XXXV.

Fig. 1—3. *Poraspis polaris* (KIÆR).

Cross-sections of dorsal shields. Ca.  $\times 50$ . Frænkelyggen group, Red Bay, N. Spitsbergen.

Fig. 1. Cross-section in pineal region. Polaris Horizon.

Fig. 2. Cross-section, showing the dentine tubes and intercostal grooves very clearly. Primaeva Horizon.

Fig. 3. Cross-section showing details in the structure of the lateral line canals. Basal layer strongly corroded. Polaris Horizon.

Fig. 4. *Poraspis brevis* n. sp.

Longitudinal section of dorsal shield immediately in front of pineal impression. Primaeva Horizon. Frænkelyggen Group, Red Bay, N. Spitsbergen.

*bl* = basal layer. *cl* = cancellous layer. *drl* = dentine and reticular layers. *lc* = lateral line canal. *pc* = pulpa canals. *P* = pineal impression.

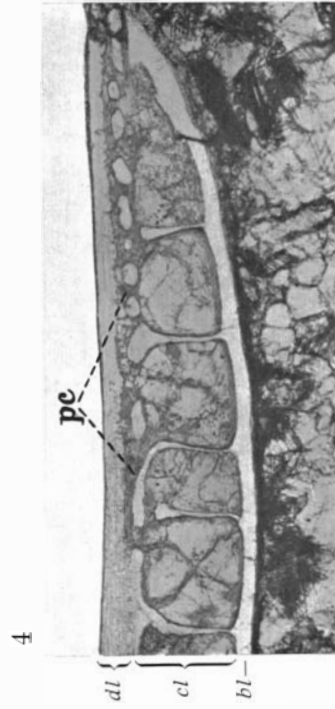
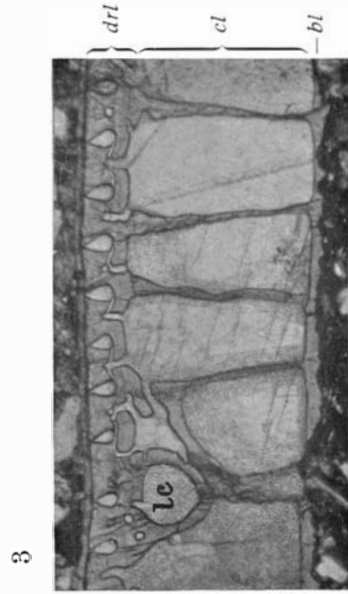
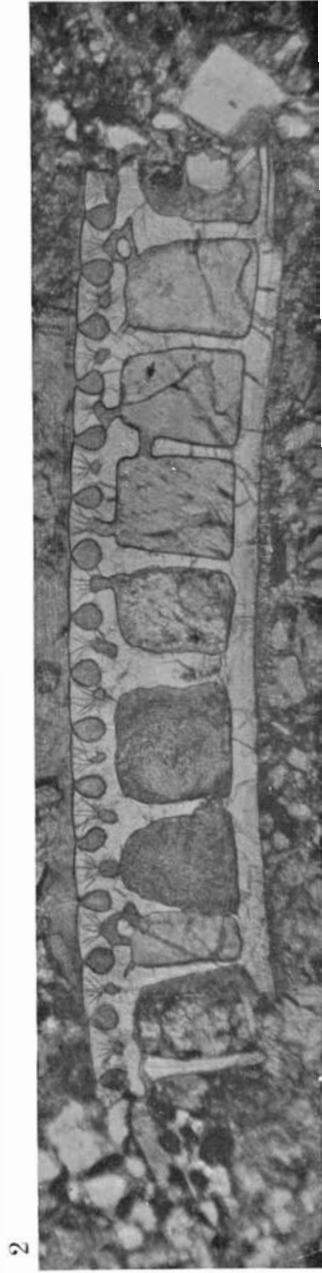


PLATE XXXVI.

*Poraspis polaris* Kiær.

Sections through the dorsal and ventral shields. Ca.  $\times$  50. Polaris Horizon. Frænkelryggen Group, Red Bay, N. Spitsbergen.

Fig. 1. Cross-section of the ventral shield, median part.

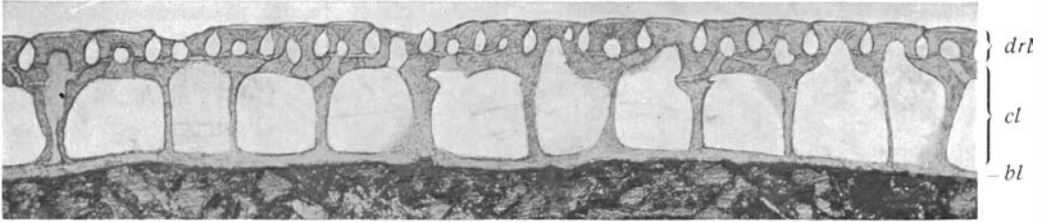
Fig. 2. Cross-section of the ventral shield along one of the branchial impressions. The skeleton is very thin. Compare fig. 1.

Fig. 3. Longitudinal section through the anterior-median part of the ventral shield, showing the oral articular area (*oaa*).

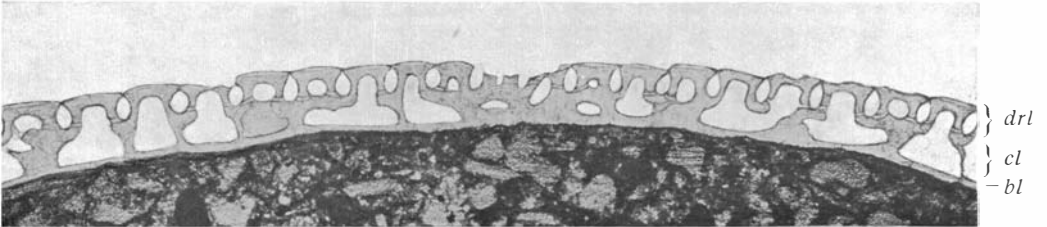
Fig. 4—5. Cross-sections through the right and left margins of the dorsal shield in the branchial region, showing the intern marginal dentine ribs.

*bl* = basal layer. *cl* = cancellous layer. *drl* = dentine and reticular layers. *imr* - intern marginal dentine ribs. *oaa* - oral articular area.

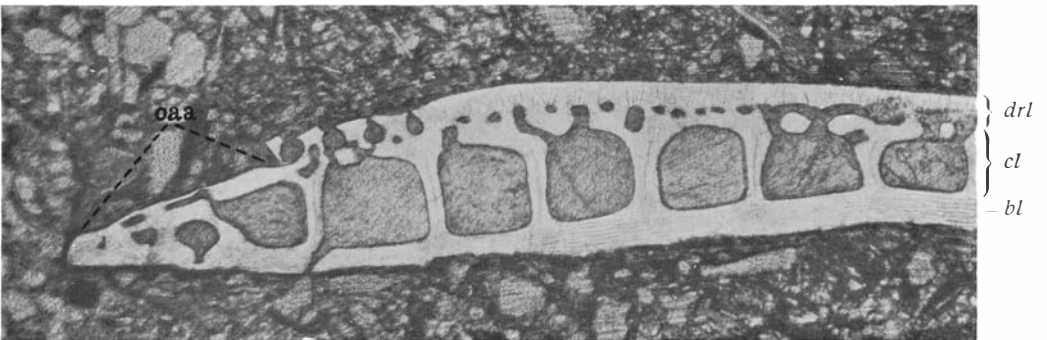
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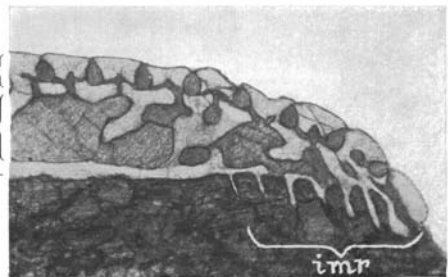


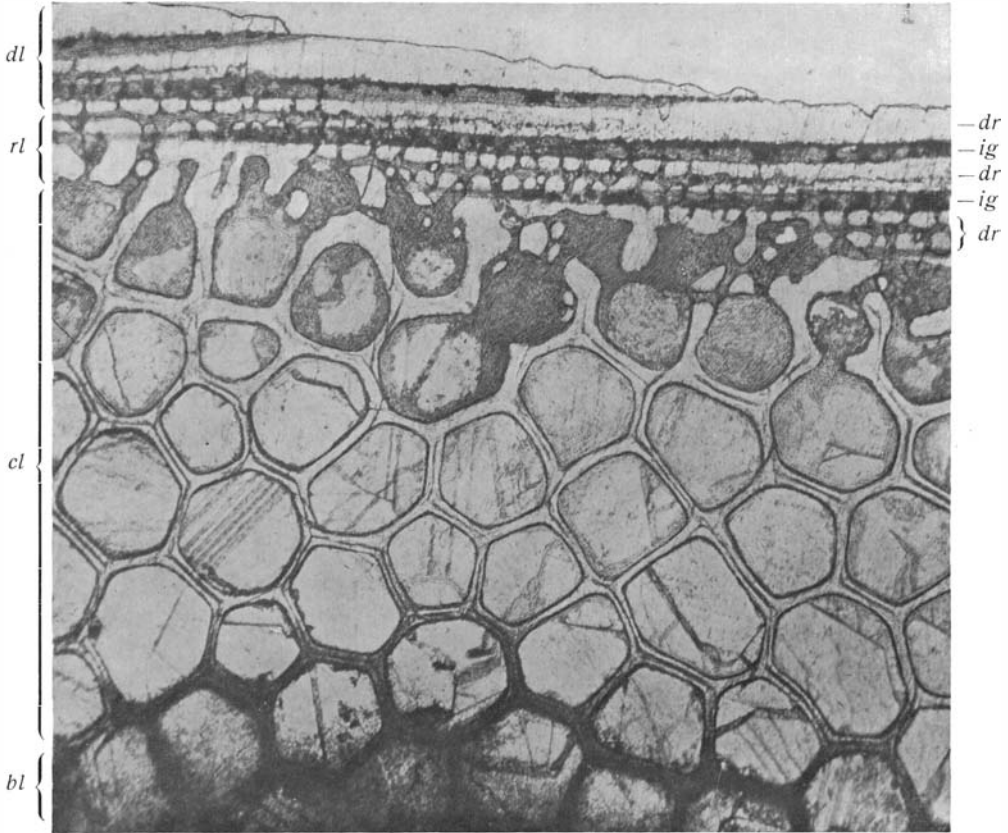
PLATE XXXVII.

*Poraspis polaris* Kiær.

Oblique sections through the dorsal shield. Ca.  $\times 50$ . Polaris Horizon.  
Frænkelryggen Group, Red Bay, N. Spitsbergen.

*bl* = basal layer. *cl* = cancellous layer, *dl* = dentine layer. *dr* = dentine ridges. *ig* = intercostal grooves. *lc* = lateral line canal. *po* = pore of lateral line canals. *rl* = reticular layer.

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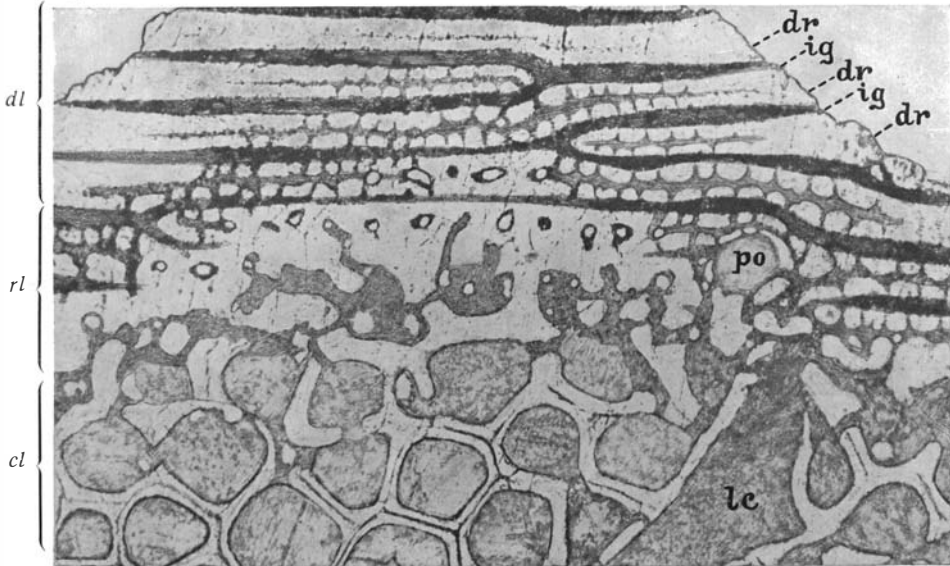


PLATE XXXVIII.

Longitudinal sections through the maxillar brim in:

Fig. 1. *Poraspis polaris* Kiær. Polaris Horizon.

Frænkelryggen Group, Red Bay, N. Spitsbergen. The inner part of the brim is partly destroyed. Ca.  $\times 50$ .

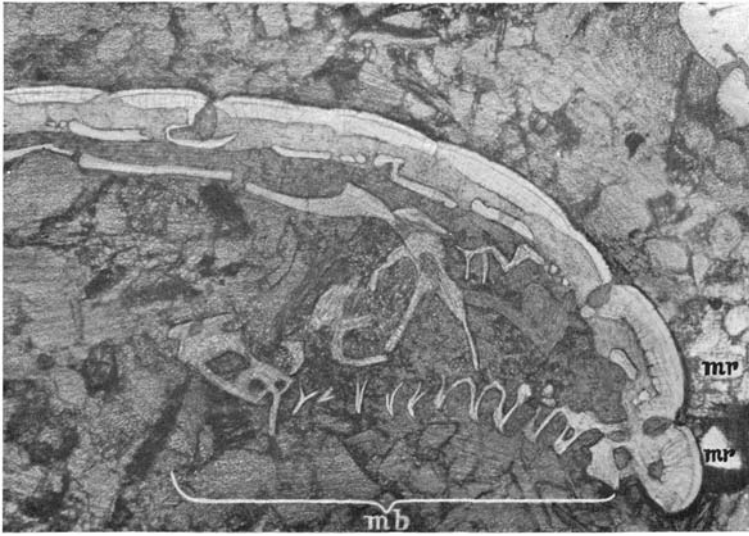
Fig. 2. *Poraspis magna* n. sp.

Upper part of Ben Nevis. Red Bay, N. Spitsbergen. Ca.  $\times 50$ .

*mb* = maxillar brim. *mr* = maxillar ridges.



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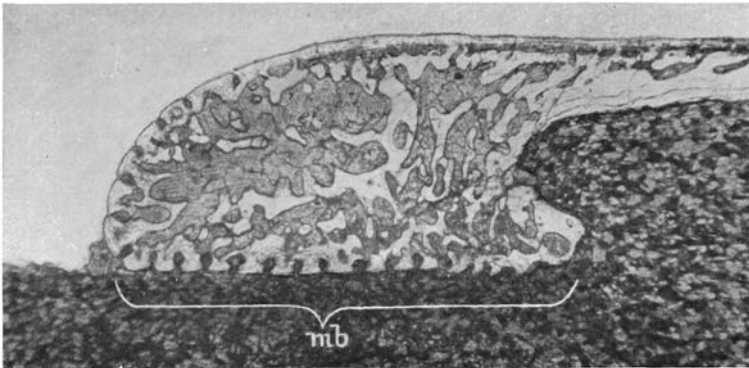


PLATE XXXIX.

*Poraspis rostrata* n. sp.

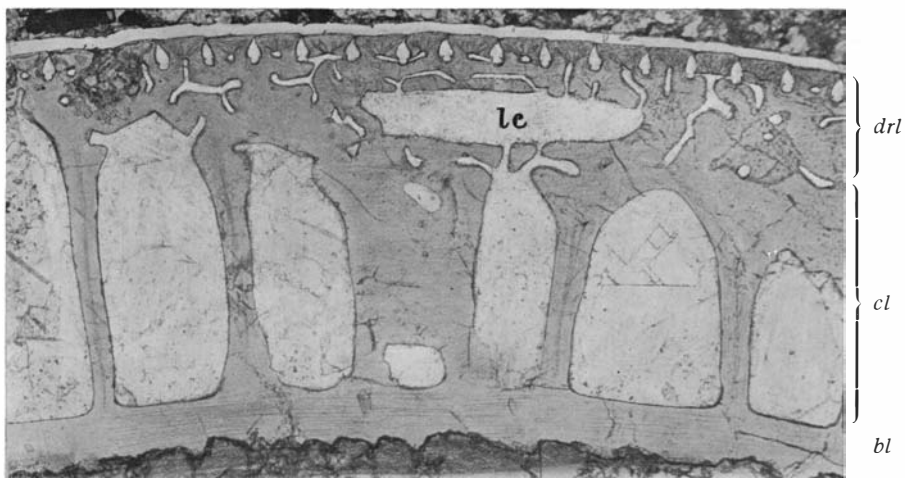
Cross-sections through the post-branchial part of the dorsal shield.  
Horizon A. Ben Nevis Group. Red Bay, N. Spitsbergen. Ca.  $\times 50$ .

Fig. 1—2. Cross-section through the median part of the shield, showing the strong development of the reticular layer, especially around the lateral line canals.

Fig. 3. Cross-section through the margin of the post-branchial lateral lobe showing the strongly thickened margin.

*bl* = basal layer. *cl* = cancellous layer. *drl* = dentine and reticular layers. *lc* = lateral line canals in oblique section.

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PLATE XL.

*Homaspis nitidus* (Kiær) Horizon A.

Ben Nevis Group, Red Bay, N. Spitsbergen.

Fig. 1. Cross-section through the dorsal shield in the pineal region.  
Ca.  $\times$  10.

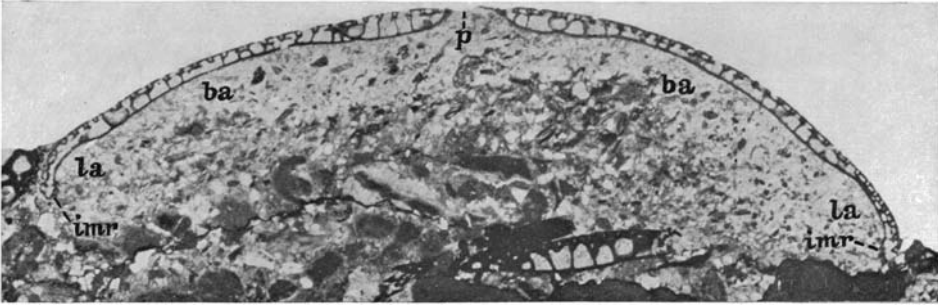
Fig. 2. Cross-section through the ventral shield in the anterior part.  
Ca.  $\times$  10.

Fig. 3. Cross-section through the anterior part of the ventral shield, showing the thin part of the skeleton under one of the branchial impressions. Ca.  $\times$  50.

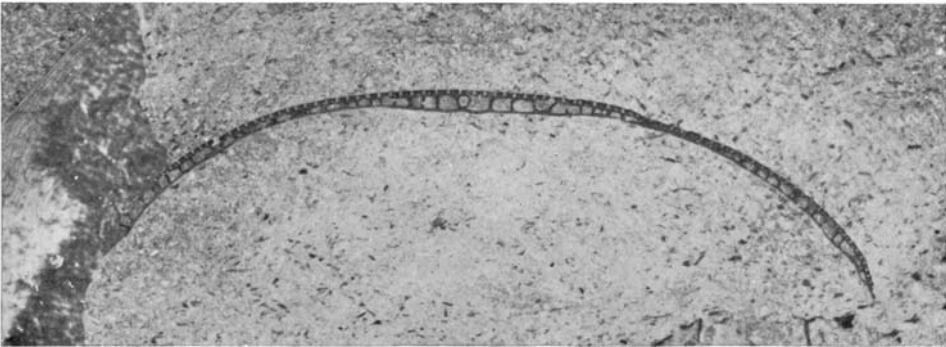
Fig. 4. Cross-section through the anterior part of the ventral shield, showing the normal thickness of the skeleton, between two branchial impressions. Ca.  $\times$  50.

*ba* = branchial impressons. *bl* = basal layer. *cl* = cancellous layer. *drl* = dentine and reticular layers. *la* = lateral area. *lc* = lateral line canals, *imr* = intern marginal ribs. *p* = impression for the pineal organ.

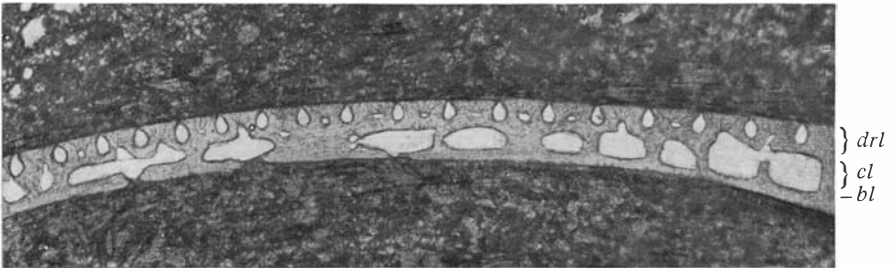
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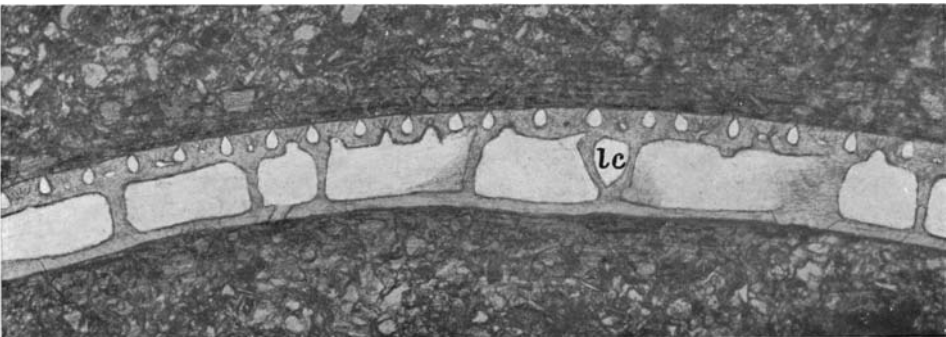
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